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Sabellariidae from Lizard Island, Great Barrier Reef, including a new species of *Lygdamis* and notes on external morphology of the median organ

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Abstract

We document herein the occurrence of three species of Sabellariidae at Lizard Island, Great Barrier Reef, including a new *Lygdamis* species. *Sabellaria lungalla*, described from Northern Territory, is reported for Queensland for the first time. The genus *Gesaia*, represented by a planktonic larva collected in shallow waters of the Archipelago, is a new record for Australia. *Lygdamis nasutus* n. sp. is characterised by one of the most conspicuous median organ described in the family (cylindrical, distally pigmented and is provided with a flattened, teardrop corona), its paleae morphology (with straight paleae, outer ones with asymmetrical pointed tips and subtle thecal sculpture and inner paleae with blunt tips and smooth surface), three lateral lobes on chaetiger 2, abdominal chaetigers with two type of neurochaetae, and notopodial uncini with 1–4 longitudinal rows of teeth. Comparison of the external morphology of the median organ and median ridge of several species has been undertaken. Even though its function remains uncertain, the median organ morphology seems species specific and may provide relevant information about the evolutionary history and adaptations of sabellariids.

Key words: Australia, median ridge, *Sabellaria lungalla*, *Gesaia* larva, *Lygdamis nasutus* n. sp.

Resumen

En este estudio se documenta la presencia de tres especies de Sabellariidae en Lizard Island (Gran Barrera de Coral), incluida una nueva especie de *Lygdamis*. *Sabellaria lungalla*, descrita en el Territorio Norte, constituye un nuevo registro para Queensland. El género *Gesaia*, representado por una larva planctónica colectada en las aguas someras del archipiélago, se cita en Australia por primera vez. *Lygdamis nasutus* n. sp., que se caracteriza por uno de los órganos medios más conspicuos descritos en la familia (cilíndrico, pigmentado distalmente, y provisto de una corona plana y con forma de lágrima), la morfología de las paleas, (rectas, las externas con puntas asimétricas y ligera escultura tecal y las paleas internas con punta roma y superficie lisa), tres lóbulos laterales en el setígero 2, sedas abdominales con dos tipos de neurosedas, y uncinos notopodiales con filas longitudinales provistas de 1–4 dientes. Se ha comparado la morfológica externa del órgano medio y cresta media en distintas especies. A pesar de que la función de este órgano sigue siendo desconocida, concluimos que la morfología de este órgano medio parece específica de cada especie y puede proporcionar información relevante acerca de la historia de la evolución y las adaptaciones en sabeláridos.

Palabras clave: Australia, cresta media, *Sabellaria lungalla*, larva de *Gesaia*, *Lygdamis nasutus* n. sp.

Introduction

Sabellariids (Sabellariidae Johnston, 1865) are a highly specialised group of tube-dwelling marine annelids characterised by a well-developed anterior operculum provided with rows of paleae that can seal the entrance of the tube when the animal withdraws into it, providing protection from desiccation, silt deposition, and predators. Some

species are gregarious and their cemented tubes form reef-like structures of hundreds to millions of individuals that can extend over several kilometres along the coast (e.g., Achari 1974; Kirtley 1974; Caline *et al.* 1988, 1992; McCarthy *et al.* 2008; Barrios *et al.* 2009; Faroni-Perez 2014).

Sabellariids have been reported from all oceans and major seas. Most of them live in intertidal or shallow depths, but there are some genera, and species, restricted to the continental shelf or the deep sea. There are currently 132 nominal species belonging to 12 genera (Capa & Hutchings 2014; Dos Santos *et al.* 2014). A recent revision of the family in Australia reported eleven species belonging to five genera, eight of them described as new (Hutchings *et al.* 2012). However, records for the Great Barrier Reef or the continental margin of Queensland are scarce and limited only to their northern and southern most margins and, in most cases, represented by solitary species or small clusters of individuals (Hutchings *et al.* 2012).

In addition to their conspicuous and characteristic operculum, several sabellariid species bear a median organ, an unpaired prostomial appendage, apparently unique among polychaetes. It has been described at the dorsal junction of the opercular lobes when these are not completely fused (Kirtley 1994) or at the base of the operculum, in the anterior midline, in species with fused lobes (Lechapt & Kirtley 1996). Besides the morphological variability of median organs and their conspicuous development in some species, little is known about their external and internal morphology and their function. They have been described, in most cases superficially, in only about one-third of the sabellariids described to date. The median organ has been attributed to sensory function and potentially useful for systematic and phylogenetic studies (Kirtley 1994), but further studies are needed to confirm this.

In the present paper we report two sabellariid species, at their benthic stage, found at Lizard Island, Great Barrier Reef, including the description of a new species of *Lygdamis* and a new record of *Sabellaria lungalla* (Hutchings *et al.* 2012) in Queensland. Moreover, we report and describe a planktonic larva of an unidentified species of *Gesaia* Kirtley, 1994 as the first record of the genus in Australia. Since the new species of *Lygdamis* shows one of the most conspicuous median organs ever described for a sabellariid, we have made a comparative analysis of external morphology in this and other sabellariids.

Material and methods

Specimens were collected at Lizard Island by scuba diving, or a plankton tow, sorted in the field and either fixed in formalin and preserved in 70–80% ethanol or fixed in absolute ethanol. Australian Museum and Northern Territory Museum material of other Australian species was examined for comparison of the median organ. Specimens were studied under dissecting and compound microscopes. Photographs of live specimens were taken in the lab with a Canon 5d Mark II camera with a Canon MP-E 1-5x Macro f2.8 or a Canon 100 mm f2.8L II USM Macro lenses. Photographs of preserved specimens were taken with a Leica DFC 420 camera attached to a Leica MZ 16A light microscope and a DM 6000B compound microscopes (Leica Microsystems, Wetzlar, Germany). Stacks of multi-focus shots were merged into a single photograph to improve resolution with Leica Application Suite v3.7 software (Leica Microsystems, Wetzlar, Germany). Some specimens were stained with methylene blue to improve the contrast of structures for photography. Some parapodia were mounted on a microscopic slide with glycerine. Scanning electron micrographs (SEM) were taken of specimens using a JEOL-JSM-6480 at the Cellular and Molecular Imaging Core Facility (CMIC) of the Faculty of Medicine of the Norwegian University of Sciences and Technology (NTNU) or at the Australian Museum (AM) using a Zeiss EVO LS15 SEM. Data referring to the holotype are given in the species description, with the variation observed among paratypes provided in parenthesis. Details of collecting sites made during the Lizard Island Polychaete Workshop are referred to only by their registration number (prefix AM W.) and Collection Event Code (prefix MI QLD). For a list detailing complete collection information as well as maps showing the collection sites, refer to Ribas & Hutchings (2015, *Zootaxa* 4019).

List of abbreviations used in the text and figures: bo, building organ; br, branchia; chn1, chaetae neuropodium segment 1; cn1, cirrus neuropodia segment 1; dc = dorsal cirrus; es, eyespots; ip, inner paleae; li, lips; m, mouth; mo, median organ; mr, median ridge; nh, nuchal hook; op, outer paleae; opa, opercular papillae; pa, palp; rtf, row of tentacular filaments. Number of specimens under each registration number is one unless otherwise specified.

Taxonomic account

Genus *Gesaia* Kirtley, 1994

Gesaia Kirtley, 1994: 166.

Type-species. *Phalacrostemma elegans* Hartman & Fauchald, 1971: 152 (not Fauvel 1911).

Remarks. This planktonic larva is provided with four parathoracic segments, simple (unbranched) feeding tentacles, nuchal hooks (with strongly bent sharp tips), and without limbations, operculum completely divided in two lobes, features that are characteristic for *Gesaia* species (Kirtley 1994; Capa *et al.* 2012; Capa & Hutchings 2015). The paleae morphology, with straight and cylindrical outer and inner paleae, and paleae arrangement, with outer paleae forming a semicircle and the inner paleae in an almost straight line between opercular lobes, is also most similar to benthic stages of members of this genus. However, the thecal ornamentation of the paleae, indicated to be the most important morphological trait for *Gesaia* species discrimination (Kirtley 1994: 166–167) observed in the larva described herein differs from other *Gesaia* species.

Gesaia sp.

(Fig. 1)

Material examined. AM W.47551, Queensland, Osprey Island, 14°40'S, 145°26'E, 6–15 m, plankton tow, 7 Oct 1979, larva on SEM stub.

Description. *Colour pattern.* Preserved specimen lacking pigmentation.

Body. Larva almost spherical in shape, 650 µm long and 550 µm maximum width excluding chaetae and paleae; with four clearly demarcated segments corresponding to the parathoracic region (chaetigers 3–6).

Operculum. Operculum completely divided into two free short lobes with distal ends nearly perpendicular to longitudinal body axis (Fig. 1A–C). Outer row with 8–10 paleae on each lobe. Outer paleae circular in cross section at base, tapering distally (Fig. 1A–C); shaft ornamented for most of its length with thecae as compact rings with smoothly parallel edges (Fig. 1E). Inner row of paleae with 6–8 paleae on each lobe (Fig. 1A–C), with stout bases (thicker than outer paleae) and either ellipsoid or circular cross section at base (Fig. 1B, G), distally tapering, hollowed, with truncated tip (Fig. 1F); smooth for about half of their length, and distally ornamented with thecae as compact rings with irregular edges proximally, becoming parallel towards the tip (Fig. 1F). Opercular papillae not developed or not observed. One pair of stout nuchal hooks, strongly recurved; margins smooth without limbations (Fig. 1G). Tentacular filaments small, forming a cluster partially covered by paleae and not clearly arranged in rows (Fig. 1A, B). Two wide and short palps at dorsal junction of opercular lobes, with ciliation on its surface particularly, long and dense at the base (Fig. 1D, E). Median organ between palps, with dense ciliation along its dorsal edge (Fig. 1D, F).

Thorax. Chaetigers 1 and 2, and corresponding features not yet defined.

Parathorax. Four chaetigers with two types of notochaetae arranged transversely; four large, lanceolate chaetae, slightly concave and with frayed tips (Fig. 1H–I) interspersed with four small and straight capillaries (Fig. 1H–I). Incipient conical branchiae present dorsally on notopodia (Fig. 1H). Parathoracic neurochaetae not formed.

Abdomen and cauda. Abdominal chaetigers not observed. Cauda not yet developed (Fig. 1A–C).

Remarks. The larva studied seems it is at an advanced stage of metamorphosis, after comparison with those from other sabellariids (e.g., Dales 1952; Eckelbarger 1977). Provisional chaetae typical of early larval stages have already disappeared, and the opercular lobes are already well defined and provided with primary paleae. The opercular spines or hooks that appear in advanced larval stage and remain in the adults (e.g., Bhaud 1975a, b; Mauro 1975; Eckelbarger 1977; Wilson 1977; Bhaud & Fernández-Álamo 2001) are present. Nevertheless, paleae have still not rotated to the dorsal position, and the mouth or building organ are not yet differentiated as observed in ready to settle larvae.

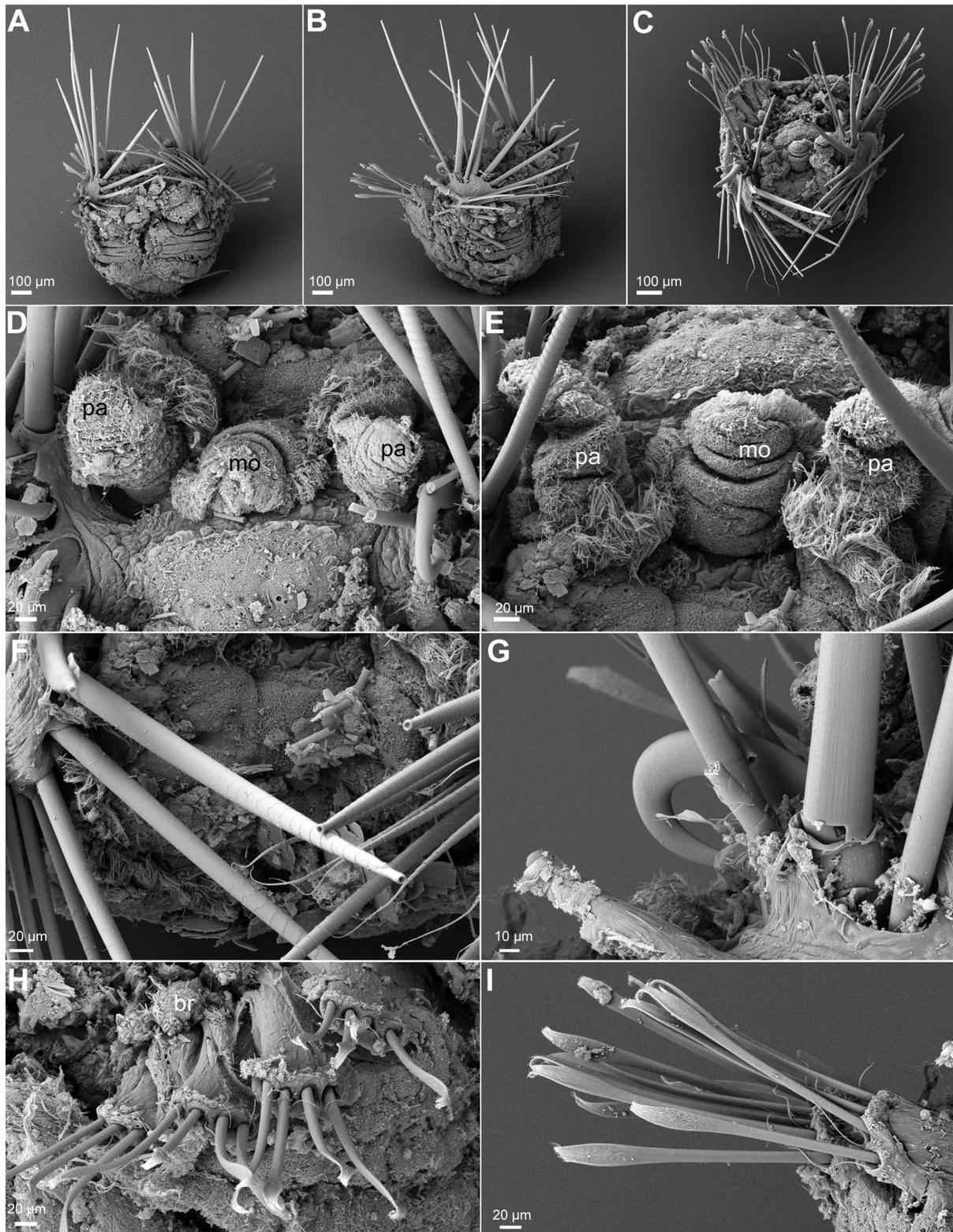


FIGURE 1. *Gesaia* sp. SEM images of larva, AM W.47551. A. Dorsal view; B. Dorsolateral view; C. Antero-ventral view; D. Detail of anterior regions showing median organ and palps, dorsal view; E. Same, ventral view; F. Inner row of paleae; G. Nuchal hooks and shafts of paleae from inner row; H. Parathoracic chaetigers, lateral view; I. Notochaetae of parathoracic chaetiger. Abbreviations: br = branchia, mo = median organ, pa = palp.

This *Gesaia* larva bears a conspicuous organ between the palps, similar to the structure referred to as the dorsal hump in *Idanthyrus* Kinberg, 1867, *Sabellaria* Lamarck, 1818 and *Phragmatopoma* Mörch, 1863 species (Dales 1952; Eckelbarger 1977; Bhaud & Fernández-Álamo 2001). This ‘dorsal hump’ apparently disappears before settlement in species that either lack median organ in the adult stages or it is poorly developed. The position and morphology of the structure herein described show some signs of being an early form of the median organ observed in the benthic stages of other members of the family.

The *Gesaia* larva described herein bear ornamented paleae with thecae as compact perpendicular rings in both outer and inner opercular rows, different to any other described species from the genus. Some congeners bear poorly expressed thecal margins or smooth outer paleae (*Gesaia lanai* Kirtley, 1994 and *G. ryani* Kirtley, 1994) and only a few species (e.g., *G. elegans* (Fauvel, 1911), *G. fauchaldi* Kirtley, 1994, and *G. fossae* Kirtley, 1994) are known to have ornamented thecae, but these form rings with irregular edges or oblique and with spikes (Kirtley 1994), not in regular parallel rings like the Australian larva. The inner paleae described herein have stout bases, similarly to *Gesaia hessi* Kirtley, 1994 and *G. ryani*. In addition, several circular holes were observed on the surface of inner paleae in *G. hessi*, possibly attributed to endobiotic activity (Kirtley 1994), whereas in the described *Gesaia* larva a unique hollow was observed at the tip. It is well known that sabellariids replace their opercular paleae in later larval stages, and these can differ from the primary larval paleae (e.g., Eckelbarger 1977; Wilson 1977; Lezzi *et al.* 2015). Therefore, is not clear if the paleae morphology described herein would have remained after settlement and description of a new species based on larvae paleae morphology is avoided.

The paleae show some similarities to those present in members of *Phalacrostemma*. Nevertheless, members of these two genera are distinguished, among other features, by the number and shape of the nuchal hooks, with multiple pairs and well-developed limbation in *Phalacrostemma* that is absent in *Gesaia* species, and the arrangement of outer paleae is a spiral in most *Phalacrostemma* species, while they are arranged in semicircles in members of *Gesaia* (Kirtley 1994; Hutchings *et al.* 2012; Capa & Hutchings 2014).

This is the first report of *Gesaia* in Australia, and also the first record of a typically deep-water sabellariid in surface water plankton samples. Members of *Gesaia* have been reported from all major oceans and from depths ranging from 770 to 5790 m (Kirtley 1994), but the eight species described to date have each been reported only once or a few times from nearby localities, leading workers to assume that species were allopatric and narrowly distributed. Undoubtedly, the potential for dispersal over long distances is greater when larvae reach shallower waters, due to low speed currents in deep water (Kelly *et al.* 1982; Shanks 1986; Bouchet & Waren 1994; Arellano *et al.* 2014; Pochelon *et al.* 2014). This suggests a larval ability to survive under a range of physical factors encountered if migrating vertically from the deep to the euphotic zone (e.g., including a broad variation in temperature and pressure). However, before the ability of larvae of *Gesaia* to disperse long distances can be accepted, substantial investigations on energy content in the oocytes, the velocity of larvae when they migrate upwards and their planktonic larval duration are needed. Interpreting the biogeographic patterns of *Gesaia* remains a major challenge, and the potential for larval dispersal is important in understanding the spatially fragmented radiation of species distribution in the major oceans.

Distribution. Only known from off Lizard Island, close to shore, collected in a plankton tow in 6–15 m water depth.

Genus *Lygdamis* Kinberg, 1867

Lygdamis.—Kirtley 1994: 116; Capa *et al.* 2012: 261–263; Hutchings *et al.* 2012: 21.

Type-species. *Lygdamis indicus* Kinberg, 1867.

Remarks. *Lygdamis nasutus* n. sp. and most congeneric species bear considerably larger opercular papillae (1–4 pairs) on the dorsal margins of the opercular lobes than other sabellariid genera (Bhaud 1975b; Kirtley 1994; Hutchings *et al.* 2012; present study). This could be a generic attribute that has so far been overlooked.

Lygdamis nasutus n. sp. (Figs 2–7)

Type material. Holotype: AM W.47372, Lizard Island, North Point, off Mermaid Cove, 14°39'S, 145°27'E, coral rubble, 20 m. Paratypes: AM W.44467, MI QLD 2424, partially mounted on a SEM stub; AM W.47750, MI QLD 2435.



FIGURE 2. *Lygdamis nasutus* n. sp., paratype, AM W.47750, live. A. Whole specimen, dorsal view, arrowheads point to notopodial cirri; B. Anterior end, lateral view, with median organ protruding from operculum (arrow); C. Anterior end, dorsal view; D. Operculum, frontal view; E. Posterior abdominal chaetigers and cauda, ventral view. Photos by A. Semenov.

Comparative material examined. Holotype of *Lygdamis giardi* (McIntosh, 1885) BMNH 1885.12.1.6, New South Wales, off Port Jackson, 33°51'S, 151°22'E, 64 m, 3 Jun 1874.

Description. *Colour pattern.* Live specimens with bright pigmentation pattern on epithelium of operculum, consisting of white opercular lobes with 3–4 orange transverse bands on outer and inner side of opercular lobes (Fig. 2A–D) and 7–9 short brown and white transversal bands on ventral side of lobes, flanking the tentacular filaments (Fig. 2B). Median organ deep orange at base, becoming paler towards tip, dark ring around the tip with a white pigmented flattened top. Base of opercular lobes, around insertion of median organ, strongly pigmented in black. First two chaetigers with white pigment. Rest of body unpigmented except for red-brown branchiae (Fig. 2A, E). Preserved specimens lack white pigmentation (including the top of the median organ, distally dark on preserved specimens, Figs 3D–F, 4A–C) but retain the colour bands on operculum described above, now dark brown instead of bright orange (Figs 3A–E).



FIGURE 3. A–D. *Lygdamis nasutus* n. sp., holotype, AM W.47372, preserved. A. Operculum, thoracic and parathoracic chaetigers, lateral view; arrowheads point to notopodial cirri; B. Anterior end, ventral view; C. Same, dorsal view; D. Same, but with exposed well-developed median organ. E–F Paratype AM W.44467. E. Detail of median organ, dorsal view; F. Cross section of paratypes, showing half of the operculum with whole median organ. Abbreviations: br = branchia, bo = building organ, cn1 = cirrus neuropodia segment 1, chn1 = chaetae neuropodium segment 1, dc = dorsal cirrus, es = eyespots, ip = inner paleae, li = lips, m = mouth, mo = median organ, nh = nuchal hook, op = outer paleae, opa = opercular papillae, pa = palp, rtf = row of tentacular filaments, tf = tentacular filaments. Small arrow indicates conical dorsal cirrus. Photo: A–D—E. Wong.

Body. Holotype incomplete but well preserved, 39 chaetigers (32–43), 32 mm long (30–43 mm), and 4 mm maximum width excluding parapodia (6–8 mm); posterior abdominal chaetigers and cauda missing.

Operculum. Operculum completely divided into two free long lobes (Fig. 2D) with distal ends oblique (Figs 2B, 3A, B). Two rows of golden paleae, outer row with 19 (18–19) pairs of paleae, cylindrical at base and flattened, with curved tips, and some fine thecal sculpture (Figs 5A, B, 6A–C); inner row with 7 (7–8) pairs of paleae, cylindrical shafts with blunt tips and smooth surface (Figs 5C, 6D, E). Opercular papillae, 10 pairs (10–12), peripheral to outer paleae of each lobe, conical, similar in size except for the 2–3 pairs closer to nuchal spines larger than the rest (Figs 2B, 3A–B, D, F, 6A). One pair of brown nuchal spines on each side (Figs 2A, C–D,

3C–D), stout, strongly recurved without sharp limbations on concave margin (Fig. 6A). Tentacular filaments compound, arranged in 11 rows (11–12) (Figs 2B, 3B). Median ridge inconspicuous. Well-developed median organ, arising abruptly from the base of opercular lobes, near edge of upper lip; slightly shorter than lobes. Median organ cylindrical, with a planar, teardrop coronal shape when viewed head on. A row of eyespots along both sides of its stalk (Figs 3E–F, 4A–C), and tufts of cilia on its surface, more densely arranged on coronal distal end (Fig. 4D–G). Pair of grooved, ringed palps, half the length of opercular lobes (Fig. 3A–B).

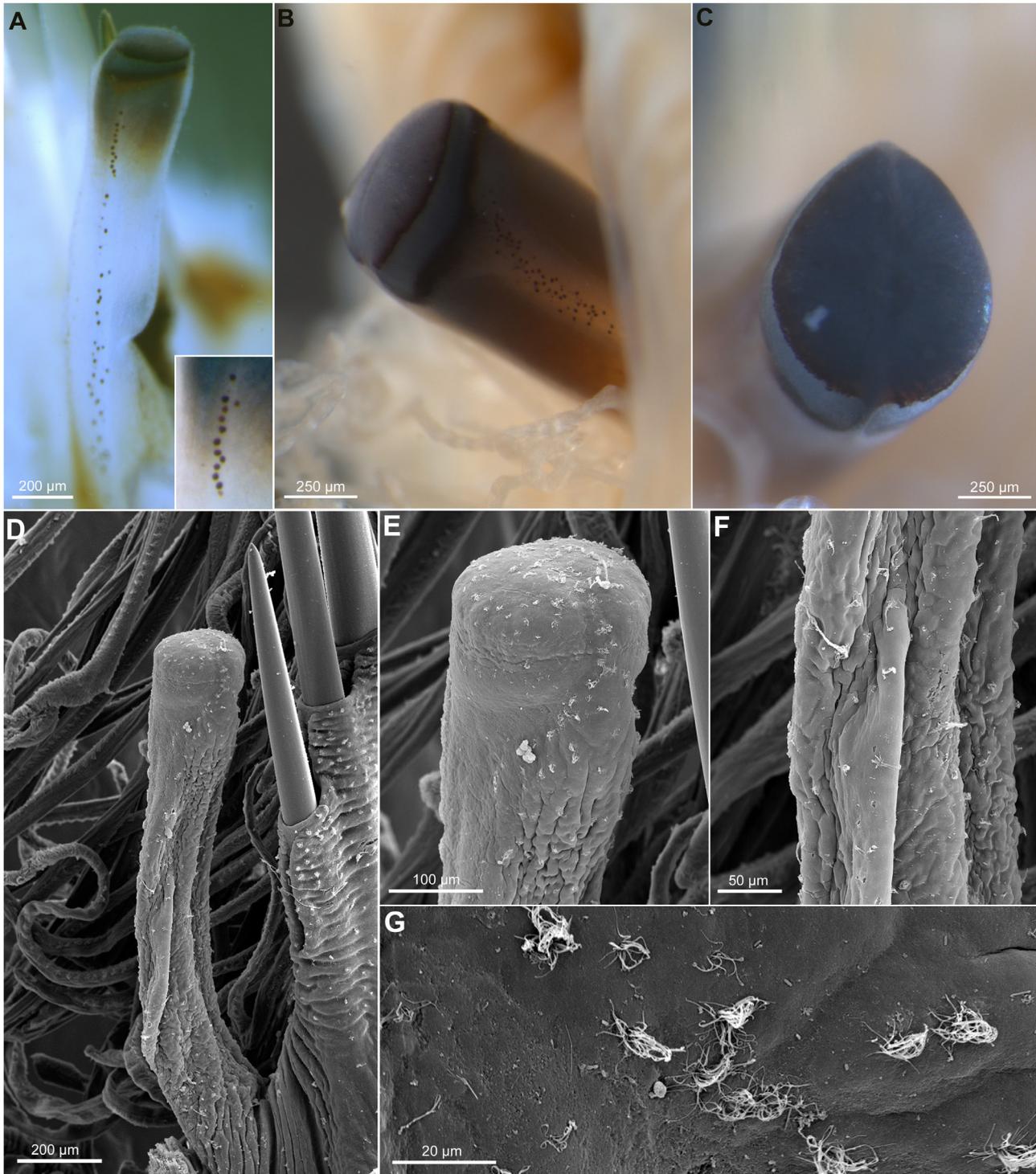


FIGURE 4. Median organ, *Lygdamis nasutus* n. sp., paratypes, AM W.44467. A. Lateral view with a close up of the eyespots along its length; B. Details of the distal tip, showing the flat corona; C. Distal end, showing teardrop coronal shape frontal view. D–G. SEM images, AM W.47750. D. Complete median organ, lateral view; E. Distal end, lateral view; F. Detail of the base of median organ with a few sparsely distributed ciliary tufts; G. Close up of ciliary tufts.

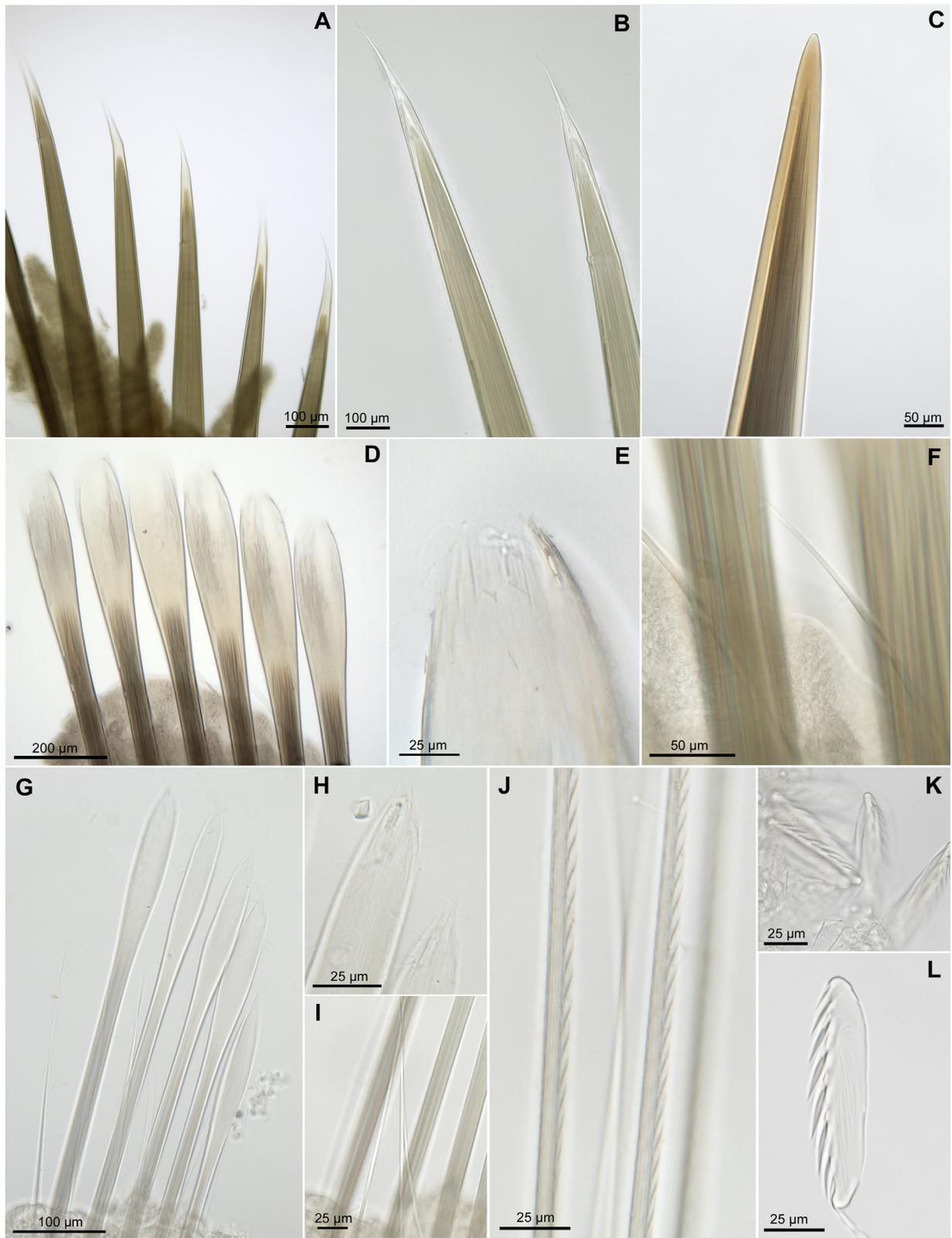


FIGURE 5. Chaetae, *Lygdamis nasutus* n. sp., paratypes. A. Outer paleae; B. Detail of tips of outer paleae; C. Inner paleae, distal end; D. Notopodium, parathoracic chaetiger; E. Detail of tips of lanceolate parathoracic notopodial chaeta; F. Parathoracic notopodial simple capillaries, interspersed with lanceolate chaetae; G. Neuropodium, parathoracic chaetiger; H. Detail of tips of lanceolate parathoracic neuropodial chaetae; I. Parathoracic neuropodial simple capillaries, interspersed with lanceolate chaetae; J. Abdominal notochaetae (two types); K. Neuropodial abdominal uncini; L. Detail of abdominal uncinus, side view.

Thorax. Chaetiger 1 with lobe-shaped neuropodia and elongated cirrus (Figs 2B, 3A–B); capillary chaetae with fibres forming distal hood (Fig. 6F). Chaetiger 2 with three pairs of elongated triangular-shaped lateral lobes, connecting branchiae to neuropodia (Figs 2A–B, 3A); capillary chaetae similar to those in chaetiger 1. About 15 pairs of branchiae present from segment 2 (Fig. 2A).

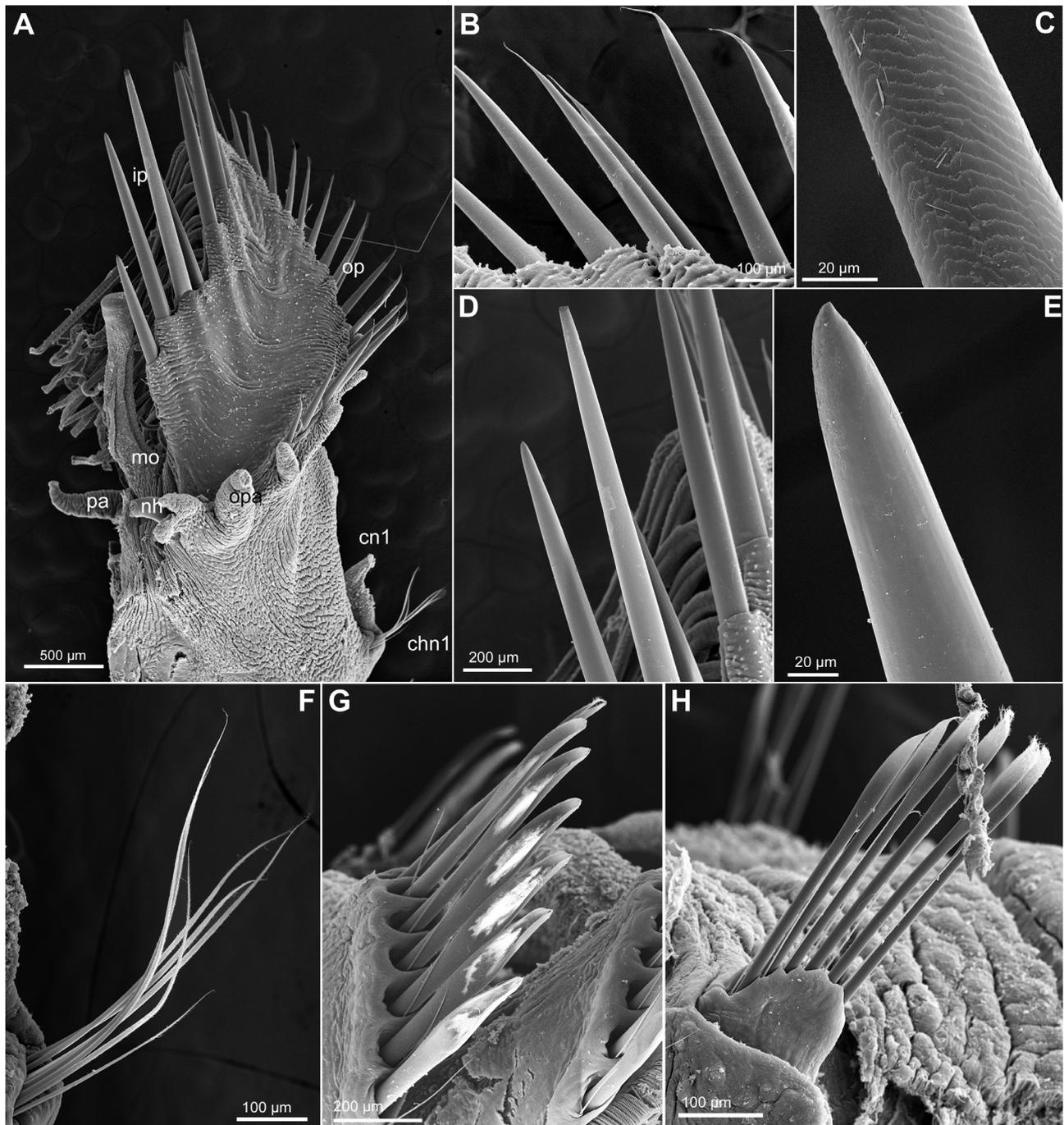


FIGURE 6. Chaetae, *Lygdamis nasutus* n. sp., paratypes, SEM images, AM W.44467. A. Operculum, lateral view; B. Outer paleae; C. Thecal sculpture, outer paleae; D. Inner paleae; E. Close up of distal end, inner paleae; F. First thoracic neuropodial chaetae; G. Parathoracic notopodia; H. Parathoracic neuropodium. Abbreviations: cn1 = cirrus neuropodia segment 1, chn1 = chaetae neuropodium segment 1, ip = inner paleae, mo = median organ, nh = nuchal hook, op = outer paleae, opa = opercular papillae, pa = palp.

Parathorax. Chaetiger 3–6, with notopodia bearing small, conical dorsal cirrus (Figs 2A–B, 3A, C). Two types of notochaetae arranged transversely, six lanceolate (6–7), distally concave, with frayed twisted tips (Figs 2B,

5D–E, 6G), and interspersed with minute capillaries (6–7) (Figs 5F, 6G). Neuropodia with large, rounded lobes directed anteriorly (Figs 2B, 3A); two alternating transverse rows of 6 (5–6) chaetae, lanceolate with frayed tips (Figs 5G–H, 6H), and thin capillaries (Figs 5I, 6H).

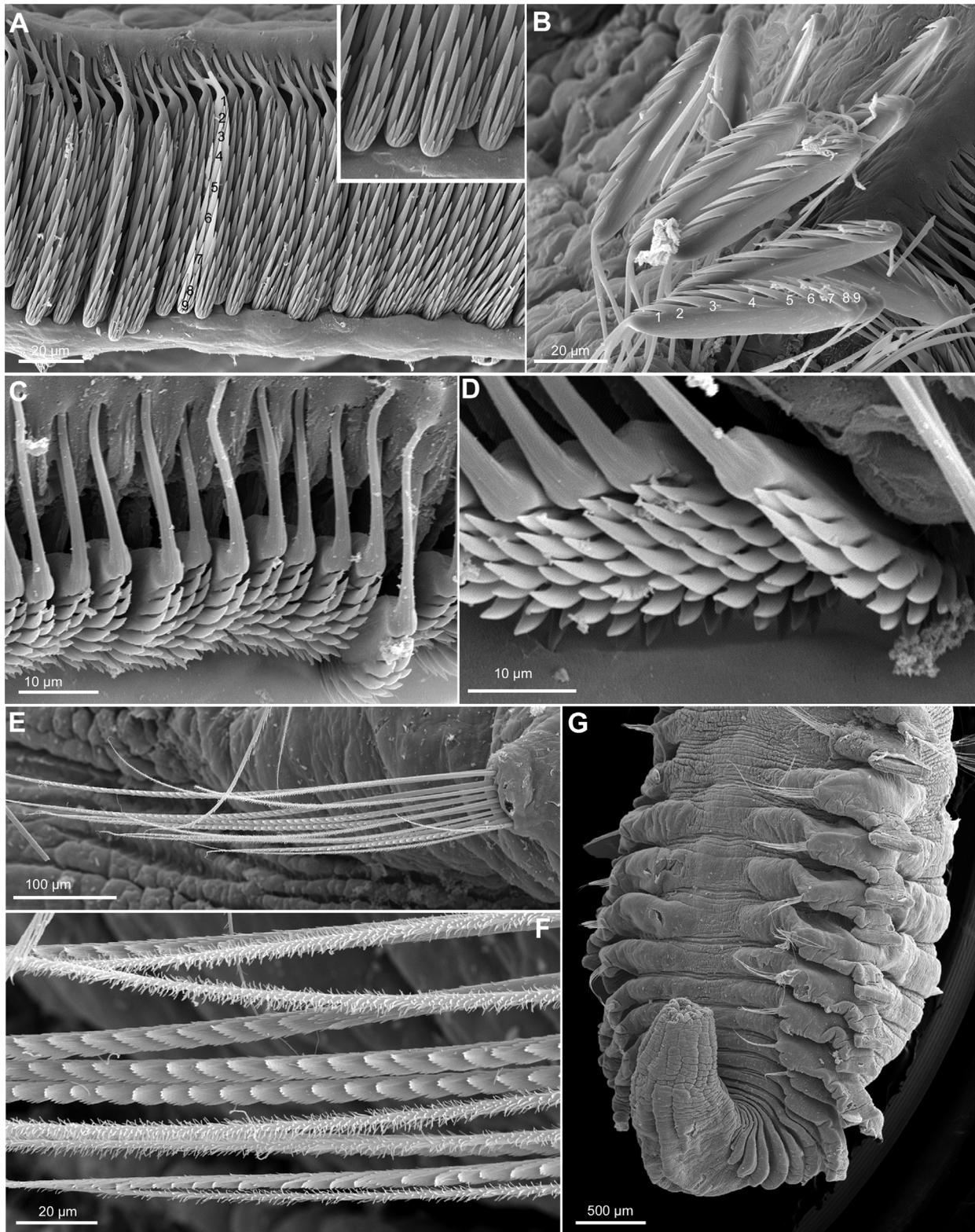


FIGURE 7. Chaetae, *Lygdamis nasutus* n. sp., paratypes, SEM images, AM W.44467. A. Anterior abdominal uncini with number of rows of teeth provided in one uncinus, close up of distal dentition; B. Detached uncini, with number of rows of teeth provided in one uncinus; C. Posterior abdominal uncini; D. Detail of posterior abdominal uncini; E. Abdominal notopodium; F. Detail of the two types of abdominal notochaetae; G. Posterior abdominal chaetiger and cauda.

Abdomen. Abdominal notopodia lobe-like, each with a transverse row of uncini decreasing in number posteriorly. Uncini of anterior abdominal chaetigers with 8–9 transverse rows of teeth with characteristic arrangement: single basal tooth, median 5–6 rows with two teeth each (not aligned but alternating), and distal 2–3 rows with 3–4 teeth each (Figs 5K–L, 7A–B). Uncini of posterior chaetigers with two rows of seven teeth each, thicker than those of anterior uncini (Fig. 7C–D). Abdominal neuropodia with capillaries, arranged in two longitudinal rows; dorsal row with slightly larger chaetae, ornamented with irregular thecal laminar extensions and ventral row with thinner and with fibres forming distal hood (Figs 5J, 7E–F). Last 5–7 abdominal chaetigers thinner and compacted (Figs 2E, 7G), not bearing chaetae or uncini. Branchiae diminishing in size posteriorly, present to chaetiger 14 (12–18), and absent in posterior-most abdominal chaetigers.

Cauda. Cauda smooth, about the length of ten posterior abdomen segments, with no signs of segmentation but some longitudinal ridges (Figs 2E, 7G).

Gut. Straight tube running from mouth to anus, with a broadened structure or ‘proventriculus’ between the last parathoracic segment and the first abdominal. Not obvious in preserved specimens.

Remarks. *Lygdamis nasutus* n. sp. is distinguished from its congeners by a unique combination of features: well-developed cylindrical median organ distally pigmented, with a flattened, teardrop corona, outer paleae (18–19 pairs) with asymmetrical pointed tips and subtle thecal sculpture, inner paleae (7–8 pairs) with blunt tips and smooth surface, three elongated and pointed lateral lobes on chaetiger 2, and abdominal chaetigers with two types of neurochaetae and notopodial uncini with three or four distal teeth.

The three species of *Lygdamis* previously reported in Australia are characterised by a small or medium size, conical and unpigmented median organ. In contrast, the new species bears a conspicuous, well-developed, cylindrical and strongly pigmented median organ. *Lygdamis nasutus* n. sp. is provided with rows of eyespots along both sides of the median organ, whereas *L. augeneri* Kirtley, 1994 and *L. giardi* (McIntosh, 1885), two of the species previously reported from Australia, bear eyes on the median ridge, not the median organ (free distal end) (Hutchings *et al.* 2012: Figs 8A, B), and in the third one, *L. wambiri* Hutchings *et al.*, 2012, eyespots seem absent both on the median organ and median ridge. Moreover, *L. augeneri* and *L. giardi* bear symmetrical outer paleae, unlike the new species. Other differences between the Australian species of *Lygdamis* can be found in Table 1.

There are several attributes that are outstanding in *L. nasutus* n. sp., but seem not to have been noticed and described in other congeners. A comprehensive revision of these features in *Lygdamis* species and other sabellariids may provide informative characters for taxonomic purposes and phylogenetic reconstruction. These are:

- 1) The new species has small and conical cirri on the distal dorsal margin of parathoracic notopodia (Figs 2B, 3A). These structures have also been described in other *Lygdamis* species (i.e., *L. indicus* Kinberg, 1867 *sensu* Kirtley, 1994, *L. splendidus* Lechapt & Kirtley, 1998, and *L. japonicus* Nishi & Kirtley, 1999) but have often not been reported in the literature.
- 2) *Lygdamis nasutus* n. sp. bears chaetae of two different morphologies on abdominal neuropodia (Figs 5J, 7E, F), similar to those described in *L. curvatus* (Johansson, 1922) and also *Bathysabellaria spinifera* Lechapt & Kirtley, 1996. Remaining *Lygdamis* species have been described with a single type of abdominal neurochaetae (i.e., the other Australian species), but it is probable that in other species this feature has been overlooked.
- 3) Posterior abdominal chaetigers in *L. nasutus* n. sp. specimens examined lack uncini in their notopodial tori. Since new abdominal segments are added between the abdomen and the cauda during development (Eckelbarger 1975), it is possible that uncini are formed after the addition of chaetigers, but it could also be a species specific feature.
- 4) Abdominal uncini are generally described as having two longitudinal rows of teeth (Lana & Gruet 1989; Lechapt & Gruet 1993; Kirtley 1994). However, variations to this typical pattern have been found after reviewing the literature, suggesting it has not always been studied in detail. For instance, *Lygdamis indicus* Kinberg, 1867, *L. giardi*, *L. wirtzi* and *L. nasutus* n. sp. have up to three or four longitudinal rows of teeth at the distal end of the uncini. Moreover, *Lygdamis japonicus* Nishi & Kirtley, 1999, *L. augeneri* and the new species present a single tooth proximally. This structural variation in uncini has not always been formally described but is clearly visible in species illustrations (e.g., Uebelacker 1984; Nishi & Kirtley 1999; Nishi & Núñez 1999; Hutchings *et al.* 2012). Other sabellariids, for example *Phalacrostemma maloga*, have been described as having uncini with three rows of teeth (Hutchings *et al.* 2012). Moreover, *Lygdamis nasutus* n. sp. shows a large variation range in the morphology of uncini along the abdominal chaetigers, a character not often commented in the literature. The structural complexity in morphology of uncini is due to the develop-

ment and linked to differences in chaetoblasts and chaetogenesis (O'Clair & Cloney 1974; Bartolomaeus 1995, 2002; Hausen 2005) and is considered a diagnostic feature among other polychaete families (e.g., Bartolomaeus 1995, 2002; Garraffoni & Lana 2004; Hausen 2005; ten Hove & Kupriyanova 2009; Capa *et al.* 2011). Since the variability of uncinial morphology seems to be greater than previously documented among sabellariids, further detailed revisions are required to reveal the morphological traits among species not previously analysed.

- 5) The presence of an abdominal expansion of the gut often referred to the 'proventriculus' (e.g., Kirtley 1994) has been observed in *Lygdamis nasutus* n. sp. and other *Lygdamis* species, but not as conspicuous as found in other Sabellariidae (e.g., Hutchings *et al.* 2012: Fig 14C). Since this organ is involved in the food processing, its morphology and development may be related to some functional traits (i.e., feeding preferences or digestion).
- 6) The median organ described for this species resemble that described for *L. ehlersi* (Caullery, 1913), *L. rayrobertsi* Kirtley, 1994, and *Lygdamis wirtzi* Nishi & Núñez, 1999. In these species, the median organ is well-developed, arising from the dorsal sagittal suture between opercular lobes and is cylindrical with a planar coronal shape. In at least *L. wirtzi*, this organ is provided with eyespots on both sides, but these have not been described in the other two species (Kirtley 1994; Nishi & Núñez 1999; Dos Santos *et al.* 2014). The new species differs from *L. ehlersi* in the relative size of the median organ, which is thinner in the former species (Kirtley 1994). *Lygdamis rayrobertsi* is distinguished from *L. nasutus* n. sp. in the morphology of the outer paleae, with more pointed tips in the former. The most similar species is *L. wirtzi* and both species also share the opercular colour pattern, with a white stalk and dark distal end, and a similar morphology of the parathoracic lanceolate notochaetae with concave blades. Differences between *L. nasutus* n. sp. and *L. wirtzi* include the shape of the outer paleae with a thinner and acute tip in the new species and the number of eyespots on the median organ (*L. wirtzi* bears only two at the base and *L. nasutus* n. sp. has numerous ones along both sides of the organ) (Nishi & Núñez 1999). *Lygdamis wirtzi* seems to be a larger species (three times the size of *L. nasutus* n. sp.) also bearing a larger number of paleae than the new species. Even though *L. wirtzi* was described as presenting over 100 pairs of tentacular filaments, these are clustered in around 13 oblique compound rows (Nishi & Núñez 1999: Fig. 3), a similar number to that found in *L. nasutus* n. sp.

TABLE 1. Comparison of morphological traits in *Lygdamis* species reported from Australia

| | <i>Lygdamis augeneri</i> | <i>Lygdamis giardi</i> | <i>Lygdamis wambiri</i> | <i>Lygdamis nasutus</i> n. sp. |
|--------------------------------|---|---|--|---|
| Colour pattern | colourless* | some pigmentation on operculum in some specimens | colourless* | as described above |
| Length (mm; excl. cauda) | 15–20 | 12–43 | 14 | 30–43 |
| Max width (mm) | 2–3 | 2–5 | 2 | 6–8 |
| Number of outer paleae (pairs) | 42–44 | 16–20 | 27–29 | 18–19 |
| Morphology of outer paleae | flattened shafts, distally tapering, with nearly symmetrical abruptly pointed tips and smooth surface | flattened shafts, distally tapering, with nearly symmetrical abruptly pointed tips and smooth surface | flattened shafts, margins symmetrical, progressively tapering to acute tip with small distal denticles | flattened shafts, margins asymmetrical, progressively tapering to acute tip with fine chaetal sculpture |
| Number of inner paleae (pairs) | 30–36 | 10–14 | 12–16 | 7–8 |
| Morphology of inner paleae | cylindrical, distally tapering, smooth surface | cylindrical, distally tapering, smooth surface | cylindrical, distally tapering, smooth surface | cylindrical, distally tapering, smooth |

.....continue on next page

TABLE 1. (Continued)

| | <i>Lygdamis augeneri</i> | <i>Lygdamis giardi</i> | <i>Lygdamis wambiri</i> | <i>Lygdamis nasutus</i> n. sp. |
|-----------------------------|---|--|--|---|
| Opercular papillae (pairs) | 12 | 8–12 | 18 | 10–12 |
| Nuchal spines (pairs) | 1 | 1 | 1 | 1 |
| Morphology of nuchal spines | strongly recurved, margins smooth, without limbation | strongly recurved, margins smooth, without limbation | strongly recurved, margins smooth, without limbation | strongly recurved, margins smooth, without limbation |
| Tentacular filaments (rows) | 15–19 | 15–19 | 15–30 | 12–19 |
| Median ridge | present | present, short, not reaching the distal margin of operculum | present, as a basal continuation of MO | present, as a basal continuation of MO, reaching the distal margin of operculum |
| Median organ | present? | small, conical; at junction of lobes of opercular stalk, as a continuation of median ridge | small, conical; at junction of lobes of opercular stalk, as a continuation of median ridge | large, cylindrical, with planar teardrop-shape corona; at junction of lobes of opercular stalk. |
| Eyespots | present along sides of median ridge | present on either side of median ridge | absent | present along either sides of median organ |
| Segment 2 (lateral lobes)** | 3 elongate triangular lateral lobes (short) | 3 elongate triangular lateral lobes (short) | 3 elongate triangular lateral lobes (long) | 3 elongate triangular lateral lobes (long) |
| Branchiae (pairs) | 8 | 9–10 | 12 | 15 |
| Segments 3–6 (notochaetae) | 6 lanceolate chaetae, and 6 capillaries in between | 7–8 lanceolate chaetae and 7–8 capillaries in between | 8 lanceolate chaetae and fine capillaries in between | 6–7 lanceolate chaetae and 6–7 capillaries in between |
| Segments 3–6 (neurochaetae) | 4 lanceolate chaetae and 4 fine capillaries with thin flattened blades with short narrow thecae, in between | 5–6 lanceolate chaetae and 5 fine capillaries with compact thecae in between | 5 lanceolate chaetae and fine capillaries in between | 5 lanceolate chaetae and fine capillaries in between |
| Uncinal rows of teeth | 1–3 rows from proximal to distal end | 2 rows of teeth after a first proximal single tooth | ?2 | 2–3 rows from proximal to distal end on anterior chaetigers, 2 in posterior uncini |
| Number of teeth/row | 6–8 | 7–9 | 8 | 7 |

.....continue on next page

TABLE 1. (Continued)

| | <i>Lygdamis augeneri</i> | <i>Lygdamis giardi</i> | <i>Lygdamis wambiri</i> | <i>Lygdamis nasutus</i> n. sp. |
|----------------------|---|---|---|---|
| Abdominal neuropodia | one type of capillaries, ornamented with irregular fibres ('pilose type') | one type of capillaries, ornamented with irregular fibres ('pilose type') | one type of capillaries, ornamented with irregular fibres ('pilose type') | dorsal row ornamented with irregular thecal laminar extensions; ventral row with irregular fibres ('pilose type') |

* Pigmentation may be related to methods of preservation and subsequent storage.

** Short or long is just a relative comparison between the species dealt with herein (based on Hutchings *et al.* 2012).

Etymology. This species is named *nasutus* (big-nosed and sensory, in Latin) in reference to the well-developed median organ, considered to have a sensory function.

Habitat. This solitary species was collected at 5–12 m, from coral rubble.

Type locality. Mermaid Cove, Lizard Island, Great Barrier Reef.

Distribution. Only known from Lizard Island. Specimens were collected twice (in 1995 and 2013), in spite of extensive collecting for polychaetes over the last 40 years at Lizard, indicating this species is rare. The type locality is an easily accessible site which has been dived at many times by Pat Hutchings since Lizard Island Research Station was established in 1973.

Genus *Sabellaria* Lamarck, 1812

Sabellaria Lamarck, 1812: 96.—Kirtley 1994: 45–46; Nishi *et al.* 2010: 7; Capa *et al.* 2012: 268–269.

Type-species. *Sabella alveolata* Linnaeus, 1767.

Sabellaria lungalla Hutchings, Capa & Peart, 2012

Sabellaria lungalla Hutchings *et al.* 2012: 44–46.

Material examined. AM W.47552, MI QLD 2194, Lizard Island, Watson's Bay, 14°39'41"S, 145°22'27"E, in amongst *Halimeda* on coral rubble, 4.6 m, 28 Aug 2010.

Comparative material examined. Holotype of *Sabellaria lungalla* Hutchings, Capa & Peart, 2012, NTM W16893, Northern Territory, McArthur River, 15°23'S, 136°30'E, 17 Mar 1993. Paratypes: NTM W16896, Drimmie Arm, Melville Bay, Gove, 12°14'S, 136°42'E; NTM W10043, Darwin Harbour, 12°29'31"S, 130°50'10"E, 7 m, 14 Jul 1993.

Remarks. The single well preserved specimen collected lacked pigmentation at the base of the opercular lobes (unlike the types). The morphological traits observed in the specimen mostly match the description of the species (Hutchings *et al.* 2012). The median ridge, pigmented at its proximal end, is thin and elongated, with a free terminal portion, the median organ, extending to base of the paleae. *Sabellaria lungalla* is characterised by the morphology of the paleae, bearing outer paleae with serrated distal margin, a midline plume, a single type of middle paleae, geniculate and with smooth pointed tips, and asymmetrical inner paleae with short blunt tips, two pairs of nuchal spines and one pair of lateral lobes on segment 2. The specimen from Lizard Island reported herein bears middle paleae with notable longer distal tips than those described previously (Hutchings *et al.* 2012), similar to the intraspecific variation observed in other congeners (Lezzi *et al.* 2015). This new record expands its known distribution range within tropical Australia.

Habitat. Intertidal in sheltered bays from intertidal to 15 m, often associated with *Halimeda* beds.

Distribution. Tropical Australia (Northern Territory, north Western Australia and northern Queensland).

Comparison of external morphology of the median organ and median ridge in other Sabellariids

Comparative analysis of the external morphological traits among previous sabellariids from Australia, and *Phragmatopoma caudata* Mörch, 1863 from Brazil can be found in Table 2. Morphological traits considered relevant for the median organ and median ridge comparison between different taxa and their corresponding state characters observed are:

1. Median ridge: a) not observed; b) present.

The median ridge is a longitudinal crest running along the ventral surface of the base of the operculum, from the dorsal edge of the upper lip (Figs 8, 9). In species with fused or partially fused opercular lobes, the median ridge is located on the ventral side of the operculum and in species with separated lobes, in between these (Figs 8, 9).

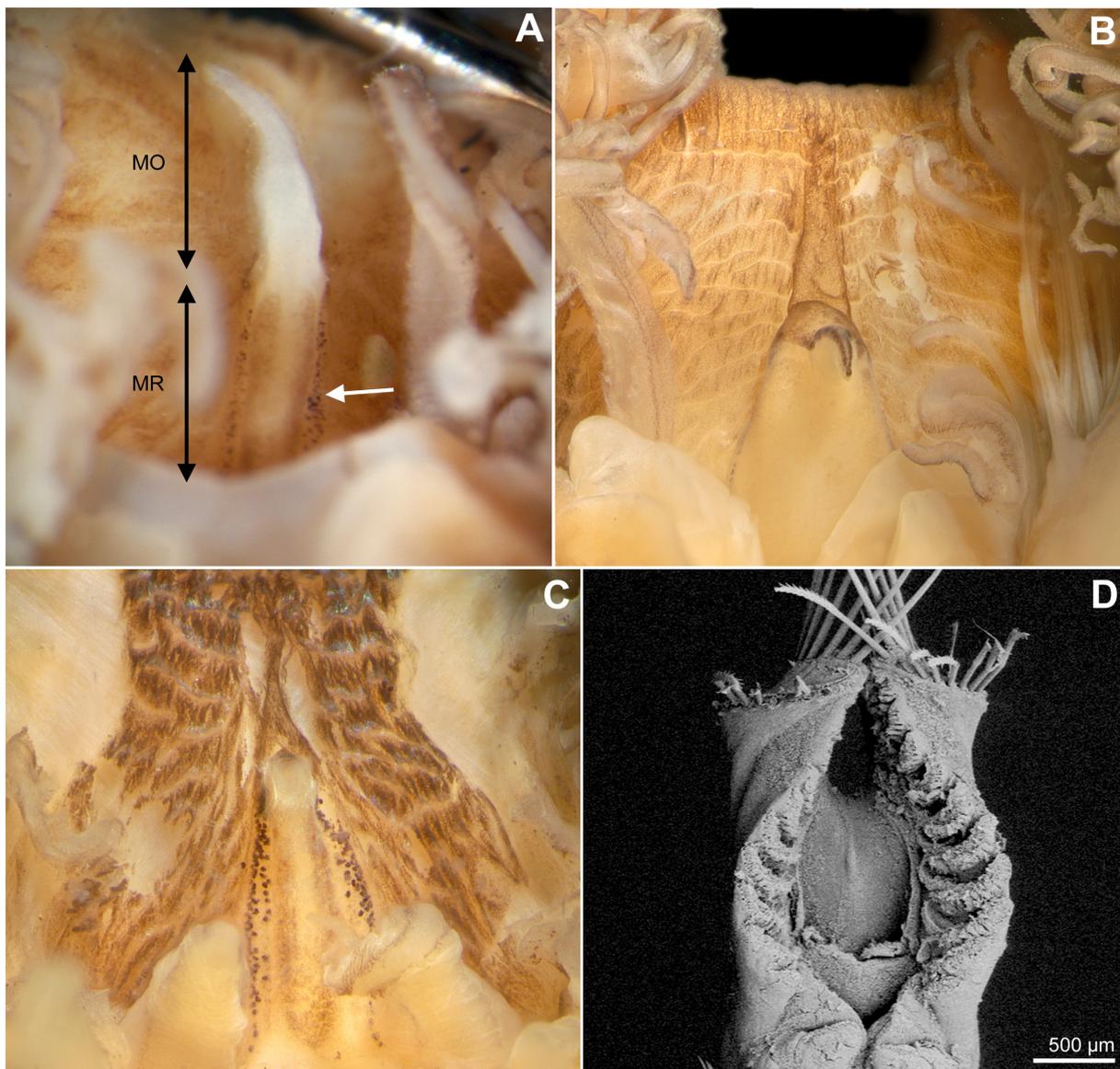


FIGURE 8. Median organ and ridge diversity in Australian *Idanthysus*. A. *Idanthysus australiensis*, AM W.201770, with conical median organ (MO), eyespots (white arrow) along median ridge (MR); B. *Idanthysus* sp. cf. *I. australiensis* AM W.29153, with flattened, triangular median organ; eyespots absent along median ridge; C. *Idanthysus* sp. cf. *I. australiensis*, AM W.29125 with flattened, triangular median organ, eyespots present along median ridge; D. *Idanthysus willora*, scanning electron micrograph, with inconspicuous median organ.

On its proximal end, the median ridge is generally wider, almost triangular in shape (Figs 8A–C, 9B); and thinner distal end may be detached from the operculum forming a lobe that it is known as the median organ. The median ridge is generally covered by the tentacular filaments (in fixed material) a reason why it may have been overlooked in most species descriptions. It varies in shape and size between species. In *Idanthysus australiensis* (Haswell, 1883) (types), *Lygdamis augeneri*, *L. giardi* and *Phalacrostemma maloga* Hutchings *et al.*, 2012, it is well-developed (e.g., Fig. 9A–C), and in other species such as *Phragmatopoma caudata* Mörch, 1863 it is reduced (Fig. 10A, B) or even inconspicuous, as in *Tetereus terribilis* Hutchings *et al.*, 2012 (Fig. 9D) and *Lygdamis nasutus* n. sp. (Table 2).

2. Median organ: a) absent; b) present.

The median organ is a free lobe, extension of the median ridge. It has been reported as absent in members of the genera *Gunnarea* Johannson, 1927 *Mariansabellaria* Kirtley, 1994, *Neosabellaria* Kirtley, 1994 and *Paraidanthysus* Kirtley, 1994, *Phragmatopoma* (Fig. 10A–B) and some species of *Sabellaria* and present in the rest of sabellariids (e.g., Kirtley 1994; Capa *et al.* 2012; Capa & Hutchings 2014). However, we now interpret it as absent in *Idanthysus willora* (contrary to Hutchings *et al.* 2012, Fig. 8D).

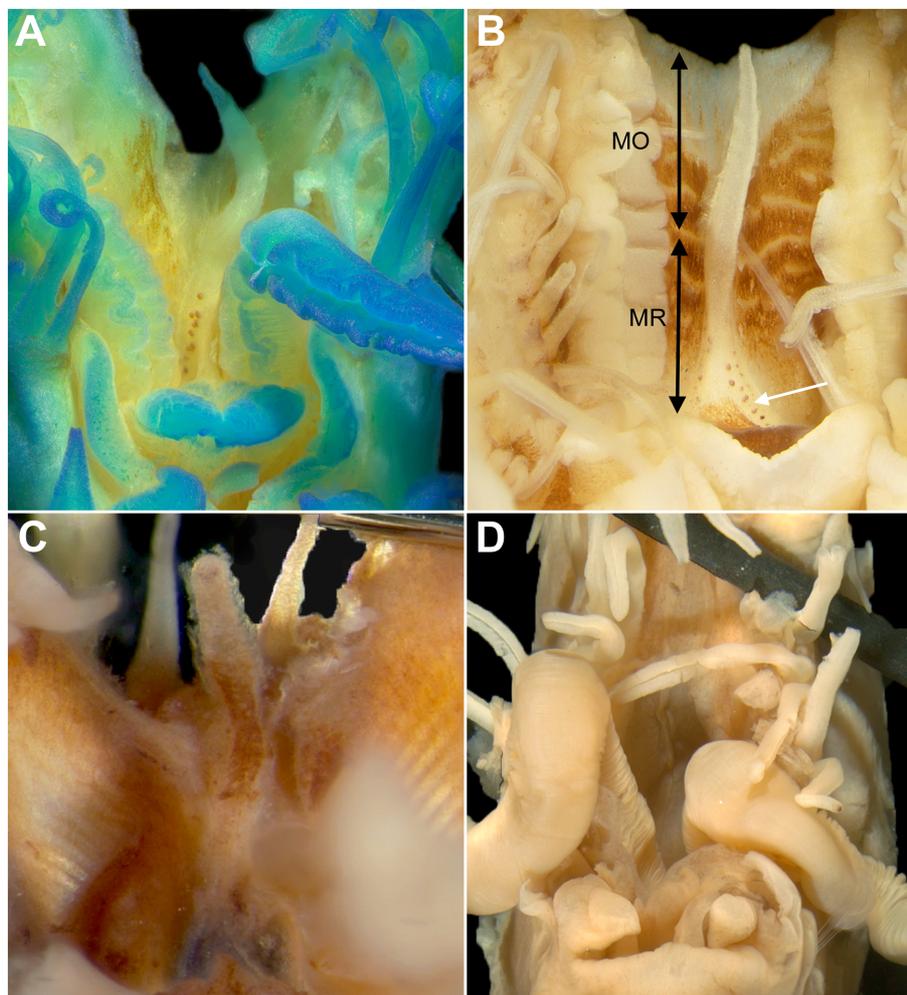


FIGURE 9. Median organ and ridge diversity in other Australian sabellariids. A. *Lygdamis augeneri*, AM W.27564, stained with methylene blue, with conical median organ, eyespots along median ridge; B. *Lygdamis giardi*, AM W.7958, with conical median organ (MO) and eyespots (white arrow) along median ridge (MR); C. *Phalacrostemma maloga*, AM W.27567, with a cylindrical and rounded distal end median organ as a prolongation of the median ridge; D. *Tetereus terribilis*, AM W.4994, lacking median organ, median ridge inconspicuous.

TABLE 2. Characters and characters states related to the fusion of opercular lobes, median ridge and median organ on a selected group of sabellariids from Australia except *Phragmatopoma caudata*, from Brazil. Abbreviations: MR = median ridge, MO = median organ, n/a = not applicable.

| Species | Opercular lobes | MR | MO | MO shape | MO distal end | MO pigmentation | Eyespots |
|---|-----------------|---------------|---------|----------------|-----------------------|-----------------|------------|
| <i>Idamthysus australiensis</i> Haswell, 1883 (AM W.7087; W.26857, W.201770, W.26926) | separated | present | present | conical | tapering | absent | present MR |
| <i>Idamthysus</i> cf. <i>australiensis</i> (AM W.29125) | separated | present | present | triangular | tapering | absent | present MR |
| <i>Idamthysus</i> cf. <i>australiensis</i> (AM W.29153) | separated | present | present | triangular | tapering | absent | absent |
| <i>Idamthysus willora</i> Hutchings <i>et al.</i> , 2012 | separated | present | absent | conical | tapering | absent | present MR |
| <i>Lygdamis augeneri</i> Kirtley, 1994 | separated | present | present | conical | tapering | absent | present MR |
| <i>Lygdamis giardi</i> McIntosh, 1885 | separated | present | present | conical | tapering | absent | present MR |
| <i>Lygdamis nasutus</i> n. sp. | separated | inconspicuous | present | cylindrical | teardrop-shape corona | present | present MO |
| <i>Phalacrostemma maloga</i> Hutchings <i>et al.</i> , 2012 | separated | reduced | present | cylindrical | rounded | absent | absent |
| <i>Phragmatopoma caudata</i> Mörch, 1863 | fused | reduced | absent | n/a | n/a | n/a | absent |
| <i>Sabellaria kooraltha</i> Hutchings <i>et al.</i> , 2012 | separated | present | present | conical | tapering | absent | present MR |
| <i>Sabellaria lungalla</i> Hutchings <i>et al.</i> , 2012 | separated | present | present | conical (tiny) | tapering | absent | present MR |
| <i>Sabellaria pyramis</i> Hutchings <i>et al.</i> , 2012 | separated | present | present | conical (tiny) | tapering | absent | present MR |
| <i>Tetres terribilis</i> Hutchings <i>et al.</i> , 2012 | fused at base | inconspicuous | absent | n/a | n/a | n/a | absent |

3. Shape of the median organ: a) conical; b) cylindrical; c) triangular.

The shape of the median organ has been proposed to have significant diagnostic importance, although this can be altered after fixation and preservation (Kirtley 1994). Some general shape groups have herein been made trying to minimize the effect of these potential artificial transformations. Most sabellariids examined present a conical median organ with a broader rounded bases tapering progressively to the distal end (*Idanthyrus australiensis sensu stricto*, *Lygdamis giardi*, *Sabellaria lungalla* and *S. pyramis*, e.g., Figs 8A, 9B). In the two species of *Sabellaria*, the median organ is reduced (not shown). Some specimens identified as *Idanthyrus australiensis* (Hutchings *et al.* 2012) present flattened and triangular median organs (Fig. 8B) with margins sometimes rolled inwards (Fig. 8C), instead of the typical conical structure observed in the types and other specimens from near the type locality, indicating they may actually belong to different species (Hutchings *et al.* in prep). Cylindrical median organ is present in *Phalacrostemma maloga* (Fig. 9C), but this is not as large and prominent as in some *Lygdamis* species (Caullery 1913; Kirtley 1994; Nishi & Núñez 1999), including *L. nasutus* n. sp. (Fig. 2A–D, 3D–F, 4A–E). Additional median organ shapes have been found in *Sabellaria* sp. from Brazil not included in the present study (e.g., trilobed, L. F. P. pers. obs.)

4. Median organ distal end: a) teardrop-shape corona; b) rounded/tapering.

Only four species of *Lygdamis*: *L. rayrobertsi*, *L. ehlersi*, *L. nasutus* n. sp., and *L. wirtzi* (Caullery 1913; Kirtley 1994; Nishi & Núñez 1999; Dos Santos *et al.* 2014) have median organs with a planar distal end with a teardrop-shape corona (e.g., Fig. 4A–E). The rest of the species with conical, cylindrical or triangular median organs have a tapering or rounded distal end (Table 2).

5. Median organ pigmentation: a) absent, b) present.

The pigmentation pattern of the median organ has been considered to provide important taxonomic information, especially for members of *Lygdamis* (Kirtley 1994). This feature may also show changes between live (e.g., Fig. 2A–D) and preserved material (e.g., Figs 3D–F, 4A–C) so should be used with caution. We have therefore only considered its absence or presence (Table 2), instead of utilizing detailed pigmentation patterns. In most cases, where pigmentation has been scored as absent, it seems not to have faded due to preservatives since other epithelial surfaces in the operculum still retain their pigmentation (e.g., Figs 8A–C, 9B, C).

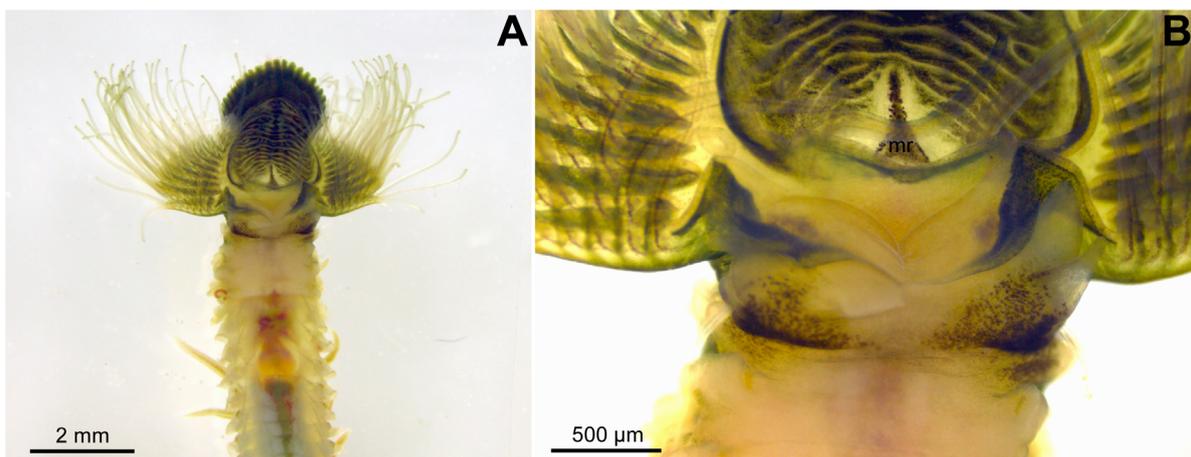


FIGURE 10. *Phragmatopoma caudata* from Brazil, live female. A. Anterior end, ventral view; B. Detail of base of operculum showing a pigmented with eyespots median ridge, and median organ absent.

6. Eyespots: a) not observed, b) present.

Eyespots form clusters or rows on both sides of the median ridge in most described cases (Figs 8A, C, 9A, B). But eyes can also be present in the median organ, either as a pair of single eyespots near the base, as in *L. wirtzi* (Nishi

& Núñez 1999) or longitudinal rows of numerous ocelli along most of the median organ's length, as in *L. nasutus* n. sp. (Fig. 4A).

Discussion and conclusions

Median organs have been reported in at least in 35 of the 132 valid sabellariids. Members of this family show a high degree of cephalization and the nuchal nerves extend forward (i.e., to anterior end of operculum) (Orrhage 1978, 1980; Brinkmann & Wanninger 2008). Sensory organs, such as the apical organ, palps, tentacles, statocysts, eyespots and nuchal organs have been documented in sabellariid larvae and adult stages (Orrhage 1978; Kirtley 1994). The suggested functions of those organs with external ciliation include chemoreception, mechanoreception, and feeding (Eckelbarger 1977, 1978; Pennington & Chia 1984; Smith & Chia 1985; Amieva & Reed 1987; Amieva *et al.* 1987; Dubois *et al.* 2005; Riisgård & Nielsen 2006).

In some species, the median organs can bear tufts of cilia (e.g., *Lygdamis nasutus* n. sp., Fig. 4D–G). Nevertheless, although the median organ is probably a sensory organ that plays a crucial role in sabellariid life history (Kirtley 1994), its function has been largely ignored to date. It is unclear whether the median organ detects chemical stimuli or other exogenous factors such as changes of pressure in the water (and therefore able to detect the presence of predators or turbulence). In the species bearing median organ eyespots, these also act as photoreceptive organs. The median organ has been described as lacking muscular tissue, being replaced by cartilage and being innervated directly from the cerebral ganglion (Tovar-Hernández & Salazar-Vallejo 2008).

A further detailed study of the external and internal morphology of the median ridge and the median organ on a variety of sabellariids (Faroni-Perez *et al.* in prep.) will hopefully shed some light on the structure, function, and variation among Sabellariidae and its potential phylogenetic implications. The data provided leave no doubt that the median organ is potentially relevant for systematic analysis, may be species-specific and may provide relevant information about the evolutionary history and adaptations of the species.

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