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Revision of the Australian Sphaerodoridae (Annelida) including the description of four new species

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Abstract

A revision of the complete sphaerodorid (Sphaerodoridae, Annelida) collections housed in the three major Australian museums (The Australian Museum, Museum and Art Gallery of the Northern Territory and Museum Victoria) has been performed. Specimens of three of the four species described to date from Australian waters, *Ephesiella australiensis*, *Sphaerodoropsis exmouthensis* and *Sphaerodoropsis fauchaldi*, have been re-encountered, resulting in changes to their previously reported distribution range. Four additional species are herein described as new: *Sphaerephesia hutchingsae* n. sp., *Sphaerodoropsis longofalcigera* n. sp., *Sphaerodoropsis megatuberculata* n. sp. and *Sphaerodoropsis wilsoni* n. sp. Moreover, *Sphaerodoropsis multipapillata heteropapillata* is elevated to the rank of species. A formal description of other specimens, most likely belonging to undescribed species, is not possible due to insufficient material, but information about some of their morphological features is provided. Descriptions, iconography, geographical and ecological information of all species part of this revision is provided together with a key for identification to all Australian species. An evaluation of some of the traditional generic taxonomic features is made, considering the variation observed within the Australian species.

Key words: sphaerodorids, new records, taxonomy, identification key

Resumen

Se ha llevado a cabo una revisión de las colecciones completas de esferodóridos (Sphaerodoridae, Annelida) de las tres mayores instituciones australianas (The Australian Museum, Museum and Art Gallery of the Northern Territory and Museum Victoria). Se han encontrado ejemplares de tres de las cuatro especies descritas hasta ahora en aguas australianas, *Ephesiella australiensis*, *Sphaerodoropsis exmouthensis* y *Sphaerodoropsis fauchaldi*, resultando en cambios su el rango de distribución conocido. Otras cuatro especies adicionales se describen aquí como nuevas: *Sphaerephesia hutchingsae* n. sp., *Sphaerodoropsis longofalcigera* n. sp., *Sphaerodoropsis megatuberculata* n. sp. y *Sphaerodoropsis wilsoni* n. sp. Además, *Sphaerodoropsis multipapillata heteropapillata* se eleva a rango de especie. Se redesciben *Ephesiella australiensis*, *Sphaerodoropsis exmouthensis* y *Sphaerodoropsis fauchaldi*. La descripción formal de otros ejemplares, que probablemente pertenecen a especies no descritas, no ha sido posible debido al escaso material disponible, pero se ha incluido información de algunas de sus características morfológicas. Se incluyen descripciones detalladas, iconografía, y datos de distribución y ecología de todas las especies identificadas como parte de la presente revisión, junto con una clave de identificación de todas las especies australianas. Se evalúan algunos de los caracteres tradicionalmente empleados en la clasificación, considerando la variación observada en las especies australianas.

Palabras clave: esferodóridos, nuevas citas, taxonomía, clave de identificación

Introduction

Sphaerodorids are scarcely known in Australian waters. Members of this family are generally small and not abundant and only four genera and seven species had been reported from Australia until very recently. Five of these species were originally described from Australian waters: *Ephesiella australiensis* Hartmann-Schröder, 1982,

Sphaerodoropsis fauchaldi Hartmann-Schröder, 1979, *Sphaerodoropsis exmouthensis* Hartmann-Schröder, 1981, *Sphaerodoropsis multipapillata heteropapillata* Hartmann-Schröder, 1987 and *Sphaerodoropsis spissum* (Benham, 1921), the latter from Macquarie Island. Additionally, *Sphaerodoropsis auranticus* Capa and Rouse, 2015 and *Sphaerodoropsis plurituberculata* Capa and Rouse, 2015 have been just described from Lizard Island. Two other species reported from Australia were described from other bio-regions: *Sphaerodoropsis parva* Ehlers, 1913, originally described from Antarctica, and *Sphaerodoropsis bisphaeroserialis* Hartmann-Schröder, 1974, originally described from South Africa (Augener 1927; Hartmann-Schröder 1985).

Sphaerodoridae are also scarcely known in other areas of the central Indo-Pacific and only nine additional species have been described or reported from this biogeographical region: *Clavodorum bengalorum* Fauchald, 1974, from India, *Clavodorum andamanense* Bakken, 2002 and *Ephesiella phuketensis* Bakken, 2002, from Thailand, *Ephesiella gallardi* Fauchald, 1974 and *Sphaerodoropsis vietnamense* Fauchald, 1974, from Vietnam, *Sphaerodoropsis malayana* Augener, 1933, from Indonesia and *Sphaerodoropsis arctowskyensis* Hartmann-Schröder and Rosenfeldt, 1988, *Sphaerodoropsis parva* (Ehlers, 1913) and *Sphaerodoropsis solis* Reuscher and Fiege, 2011, from the Challenger Plateau.

Members of Sphaerodoridae are characterised by presence of spherical tubercles over their surface (Fauchald & Rouse 1997; Pleijel & Dahlgren 1998). They also have the epithelium protected by a thick and rugose cuticle, segments poorly delineated, small and short prostomial appendages, uniramous parapodia and simple or compound chaetae. There are around 110 nominal species described so far, grouped in 10 genera (Capa *et al.* 2015). The family is partially being reviewed and the monophyly and relationships of some genera assessed (Capa *et al.* in press).

The aim of the present study is the revision of material collected along the Australian coasts, both in shallow water and in shelf and slope zones during the last almost 50 years, which have remained unrevised in the three main Australian Museums, and in other institutions outside the country. The purpose is to provide a baseline of the current knowledge of the diversity of Sphaerodoridae in Australian waters, which seems to be underestimated (Wilson 2000) and the known distribution range of these species. Diagnosis and description of studied species are provided, with detailed illustrations showing their main diagnostic features. A key to the Australian sphaerodorids and distribution maps for the species, with the current data available are also included.

Material and methods

Around one hundred and fifty specimens from The Australian Museum (AM), Sydney; Museum Victoria (NMV), Melbourne; and Museum and Art Gallery of the Northern Territory (NTM), Darwin, were borrowed and examined at the Norwegian University of Science and Technology, NTNU University Museum, Trondheim. Australian specimens housed in the Zoologisches Museum (ZMH), Hamburg, mainly collected and identified by Gesa Hartmann-Schröder were studied in place. Additional material, mainly types of other species, has been examined. This material belongs to the ZMH, the Smithsonian Institution, National Museum of Natural History (NMNH), Washington and the Natural History Museum of Los Angeles County, LACM-AHF), Los Angeles, Muséum National d'Histoire Naturelle (MNHN), Paris; and Museo Nacional de Ciencias Naturales (MNCN), Madrid. Most of the material in the collections were fixed in formalin and preserved in 70–80% ethanol as usual for this type of collections. Some more recent collected specimens were both fixed and preserved in 96–100%. Specimens were studied under dissecting and compound microscopes. Methylene-blue staining was used to highlight glandular areas and papillae by immersing selected specimens in 70–80% ethanol with some dissolved crystals of the compound for several minutes. Micrographs were taken with a Dino-Lite digital microscope (AnMo Electronics Corporation, Taiwan) attached to the microscopes or with a Leica DFC 420 camera attached to a Leica MZ 16A stereo microscope and a Leica 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 parapodia were mounted on a microscopic slide with glycerine.

Scanning electron micrographs were taken on specimens after dehydrating them in a series of 80, 90 and 100% ethanol and series of mixtures of absolute ethanol and Hexamethyldisilazane (HMDS) with the following ratios 2:1, 1:1, 1:2, and then into pure HMDS. The prepared samples were mounted on holders, sputter-coated with gold

(10 nm thickness). The micromorphology and topography were determined using a Philips FEI INSPECT (Hillsboro, Oregon, USA) scanning electron microscope (SEM) at the Museo Nacional Ciencias Naturales (Madrid, Spain) and a JEOL-JSM-6480 SEM at the Cellular and Molecular Imaging Core Facility (CMIC) of the Faculty of Medicine of the Norwegian University of Science and Technology (NTNU). The samples were observed with the Back Scattering Electron Detector (BSED) with a resolution at high vacuum of 4.0 nm at 30kV. The accelerating voltage was 30 kV and working distance of 10 mm to the detector.

Descriptions of new species are based on a combination of observations in stereo and compound microscopes of the attributes showed in the holotype but references to figures are given to the specimens used for micrographs and SEM. Variation of paratypes and/or additional material is given. In re-descriptions, the variation observed among the specimens examined is provided without distinction of the holotype and rest of specimens examined unless specified. The material examined is cited from Western Australian localities, clockwise, around Australia. Distribution maps based on examined specimens from collection sites given in "material examined" for each species, are presented as a discussion of the sphaerodorids' distribution around Australia (see Discussion and Fig. 15).

Abbreviations used on the figures: 1st parapodium of first chaetiger; al, acicular lobe; ap, antenniform papillae; co, copulatory organ; eg, egg; la, lateral antenna; ma, median antenna; mc, macrotubercle; mi, microtubercle; mo, mouth; nu, nuchal organ; pa, palp; ph, pharynx; tc, tentacular cirrus; vc, ventral cirrus.

Abbreviations used on the text, tables and figure legends: AM, The Australian Museum, Sydney; btw, between; ch, chaetiger; LACM-AHF, Natural History Museum of Los Angeles County, Los Angeles; MNCN, Museo Nacional de Ciencias Naturales, Madrid; MNHN, Muséum National d'Histoire Naturelle, Paris; NMNH, National Museum of Natural History, Washington; NMV, Museum Victoria, Melbourne; NSW, New South Wales; NTM, Museum and Art Gallery of the Northern Territory; NT, Northern Territory; NTNU, Norwegian University of Science and Technology, Trondheim; QLD, Queensland; SA, South Australia; SEM, scanning electron microscopy; TAS, Tasmania; VIC, Victoria; WA, Western Australia; ZMH, Zoologisches Museum Hamburg, Hamburg.

Key to Australian Sphaerodoridae

1. Body ellipsoid, generally with less than 30 chaetigers. Dorsum with four or more longitudinal rows of large tubercles (macrotubercles) 2
- Body elongate, generally with more than 30 chaetigers. Dorsum with two longitudinal rows of macrotubercles (with terminal papillae), one pair per segment, and two additional longitudinal rows of small tubercles consisting of collar and terminal papillae (microtubercles) *Ephesiella australiensis* Hartmann-Schröder, 1981
2. Four longitudinal rows of dorsal macrotubercles 3
- More than four longitudinal rows of dorsal macrotubercles 6
3. At least some dorsal macrotubercles with terminal papillae, or macrotubercles pear-shaped 4
- Macrotubercles spherical and smooth. Terminal papillae absent 5
4. Chaetae with long blades (more than 10 times longer than maximum width) *Sphaerephesia hutchingsae* n. sp.
- Chaetae with shorter blades (2–5 times longer than maximum width) *Sphaerephesia* sp.
5. Chaetae with long blades (more than 10 times longer than maximum width, but at least some reaching 25 times its width) *Sphaerodoropsis longofalcigera* n. sp.
- Chaetae with medium length blades (5–7 times as long as their maximum width) *Sphaerodoropsis exmouthensis* Hartmann-Schröder, 1981
- Chaetae with short blades (2–3 times as long a wide) *Sphaerodoropsis wilsoni* n. sp.
6. Dorsal macrotubercles aligned transversally in two rows per segment 7
- Dorsal tubercles aligned in more than two more or less defined transversal rows per segment. *Sphaerodoropsis heteropapillata* (Hartmann-Schröder, 1987) new rank
7. Dorsal macrotubercles hemispherical (and wider than long), arranged in alternating transversal double rows of 6 + 7 macrotubercles per chaetiger, in mid-body, no additional dorsal papillae *Sphaerodoropsis* sp.
- Dorsal macrotubercles spherical (and as long as wide), arranged in transversal double rows of 8–12+10–14 per chaetiger, in mid-body. One additional dorsal papillae next to each parapodium *Sphaerodoropsis fauchaldi* Hartmann-Schröder, 1979
- Dorsal macrotubercles ellipsoid or cylindrical (and longer than wide), arranged in transversal double rows of 8+9 per segment. Additional dorsal papillae arranged in three transversal rows per chaetiger *Sphaerodoropsis megatuberculata* n. sp.

Table 1. *Sphaerodoropsis* species with four longitudinal rows of macrotubercles (Group 1 according to Borowski 1994) and chaetae with long blades (>10 times longer than wide). Information is based on original descriptions, re-descriptions (e.g. Kudenov 1994; Aguado & Rouse 2006; Böggermann 2009) and examination of type material. Personal observations have prevailed over information provided in descriptions in case of inconsistencies. The length of blades considers all observed variation within the specimen. The number of parapodial papillae refers to mid-body chaetigers.

	Type locality	shape of macrotubercles	length of blades/width	parapodial papillae	transverse rows dorsal papillae
<i>S. anae</i> Aguado and Rouse, 2006	Pacific Antarctic Ridge, 2216 m	spherical and pear-shaped	8–10	>10	4
<i>S. artabrensis</i> Moreira and Parapar, 2007	Galicia, Spain, 209 m	spherical to pear-shaped	7–10	3–4	~4
<i>S. biserialis</i> (Berkeley and Berkeley, 1944)	Dease Strait, W Canadian Artic, 82 m	pear-shaped	4–10	~10	4
<i>S. corrugata</i> Hartman and Fauchald, 1971	New England, USA, 400 m	spherical to pear-shaped	10–15	1–3	scattered
<i>S. discolis</i> Borowski, 1994	Peru Basin, 4100 m	pear-shaped	10–15	3–8	~4
<i>S. elegans</i> Hartman and Fauchald, 1971	Ceara, Brazil, 3730 m	pear-shaped	10–15	1–3	absent
<i>S. furca</i> Fauchald, 1974	Trujillo, Peru, 1317 m	spherical to pear-shaped	10–12	4–5	?1
<i>S. laureci</i> Desbruyères, 1980	Bay of Biscay, 2325 m	hemispherical*	~7	>10	4
<i>S. longianalpapilla</i> Böggermann, 2009**	Guinea Basin, 5048 m	pear-shaped	15–20	~10	~4
<i>S. longipalpa</i> Hartman and Fauchald, 1971	Bermuda, 1700 m	spherical	10–20	~7	4
<i>S. longofalcigera</i> n. sp.	Geraldton, Australia, 409 m	hemispherical	10–25	1	4
<i>S. longopapillata</i> Desbruyères, 1980	Bay of Biscay, 4150 m	spherical	6–18	>10	~4
<i>S. parva</i> (Ehlers, 1913)	Wilhelm II Coast, Antarctica	spherical	~7	?	?1
<i>S. philipi</i> (Fauvel, 1911)	Kara Sea, 220 m	pear-shaped	~10	>10	>2
<i>S. protuberanca</i> Böggermann, 2009	Angola Basin, 5048 m	hemispherical	10–12	2	none
<i>S. sibuetae</i> Desbruyères, 1980	Bay of Biscay	hemispherical	~7	>10	4
<i>S. triplicata</i> Fauchald, 1974	Natal, South Africa, 715 m	hemispherical	10–15	10	4
<i>S. vittori</i> Kudenov, 1987	Florida, USA, 121 m	pear-shaped	~10	20	~4

* The described invaginations in macrotubercles are herein considered an artefact. Not observable in preserved holotype anymore.

** The holotype of *S. longianalpapilla* does not match the description of the species, unlike the paratypes.

Taxonomic account

Genus *Ephesiella* Chamberlin, 1919

Type species. *Sphaerodorum abyssorum* Hansen, 1878.

Diagnosis. Body long and slender. Two longitudinal rows of macrotubercles over dorsum, one pair per segment. Macrotubercles sessile, with terminal papillae. Two longitudinal rows of microtubercles, one pair per segment, running parallel between macrotubercles. Additionally, papillae arranged in 4–5 transversal rows on dorsum and ventrum. Head appendages short, spherical or digitiform. Parapodia from chaetiger 2 with compound chaetae; hooks absent or present.

Ephesiella australiensis Hartmann-Schröder, 1982

Figs 1A–C, 2, 3, 4A–B, 5A–D

Ephesiella australiensis Hartmann-Schröder, 1982: 80–81, Figs 84–87.

Material examined. Holotype: Cervantes, Western Australia, Australia. ZMH P.16773, sandy beach between *Posidonia*, 24 Oct 1975. **Paratype:** (1 spec.) same details. **Additional material. Western Australia:** AM W.42699 (1 spec.), North West Shelf, 19° 28' S, 118° 55' E, 39 m, 26 Apr 1983; AM W.42700 (1 spec.), 2 km west of Angel Island, Dampier Archipelago, 20° 29' 46" S, 116° 47' 29" E, 10 m, 04 Aug 2000, dead coral; AM W.42701 (2 specs, one for SEM), Angel Island, Dampier Archipelago, 20° 27' 41" S, 116° 47' 31" E, 14 m, 05 Aug 2000, dead coral; AM W.42702 (2 specs, one for SEM), south west Enderby Island, 20° 37' 18" S, 116° 27' 23" E, 14 m, 08 Aug 2000, dead coral; AM W.42703 (2 specs), north west end Legendre Island, 20° 21' 13" S, 116° 50' 26" E, 21 m, 30 Jul 2000, dead coral; AM W.42704 (4 specs), 1 km north east of Delambre Island, Dampier Archipelago, 20° 25' 43" S, 117° 05' 07" E, 14 m, 07 Aug 2000; NMV F.162479 (1 spec.), off Pelsart Island, near Geraldton, 29° 00' 10" S, 113° 46' 26" E, 409 m, 01 Aug 2005. **Northern Territory:** NTM W.10209 (1 spec.), Darwin Harbour, 12° 29' 3" S, 130° 50' 10" E, 7m, 1993; NTM W.15191 (1 spec.), Darwin Harbour, 12° 23' 15" S, 130° 49' 32" E, 1994; NTM W.15197 (1 spec.), Darwin Harbour, 12° 28' 10" S, 130° 46' 15" E, 5 m, 1994; NTM W.20663 (1 spec. for SEM), Arafura Sea, 18° 22' 30" S, 133° 41' 48" E, 187 m, 2005; NTM W.24312 (1 spec.), Joseph Bonaparte Gulf, NT, Australia, 12° 20' 56" S, 129° 58' 40" E, 44 m, 2009; **Queensland:** AM W.202140 (2 specs), near mouth of Althaus Creek, Halifax Bay, north of Townsville, 19° 10' S, 146° 37' E, Jul 1977; AM W.42693 (1 spec. for SEM); **New South Wales:** AM W.28133 (1 spec.), east of Wollongong, 34° 28' S, 151° 02' E, 100 m, 28 Mar 1994, in *Globigerina*; AM W.42688 (1 spec. for SEM), Cape Three Points, south-east of Third Point, 33° 31' 55" S, 151° 24' 58" E, 30 m, 06 May 2007, sand from around large boulders; AM W.42711 (1 spec.), Bass Point, 34° 36' S, 150° 54' E, 65 m, 25 Jun 1990; AM W.42712 (1 spec.), same details; AM W.42728 (3 specs), east of Malabar, 33° 58' 41" S, 151° 18' E, 81.4 m, 23 Aug 1995. **Victoria:** NMV F.132625 (1 spec.), 43 km SE of Port Albert, Eastern Bass Strait, 38° 53' 42" S, 147° 06' 30" E, 58 m, 18 Nov 1981; NMV F.132637 (1 spec.), 63 km E of North Point, Flinders Island Eastern Bass Strait, 39° 44' 48" S, 148° 40' 36" E, 124 m, 14 Nov 1981; NMV F.132642 (1 spec. for SEM), 50 km SW of Warrnambool, Western Bass Strait, 38° 49' 30" S, 142° 35' 24" E, 89 m, 21 Nov 1981.

Diagnosis. Microtubercles absent or present on first chaetigers. Palps and lateral antennae digitiform, median antenna spherical. Tentacular cirri ellipsoid or inconspicuous. Eyes not observed. Parapodia with 4–6 parapodial papillae; compound or semi-compound chaetae with blades 1.5–2.5 times as long as maximum width on mid-body chaetigers; hooks absent or present on first chaetiger.

Re-description.

Measurements and general morphology. Holotype 1.4 mm long, 0.4 mm wide, with 18 chaetigers. Body elongated, sub-quadrangular in section, with slightly convex dorsum. Anterior end bluntly rounded, slightly narrowing along posterior segments. Segmentation inconspicuous, tegument with transverse wrinkles. Preserved specimen lacking pigmentation.

Head. Prostomium with five short appendages, including a pair of digitiform palps in ventral-most position, a

pair of lateral antennae, similar in shape and size to palps, and a median antenna, shorter (one third) than lateral antennae and resembling a large semi-spherical papilla (Figs 1A–B, 2A–B, 3A, G). Two rounded small papillae between palps, two between median and lateral antennae and two between lateral antennae and mouth (Figs 1A, 2B). A pair of tentacular cirri similar in shape and size to lateral antennae and palps and several scattered papillae similar to prostomial (Fig. 2B).

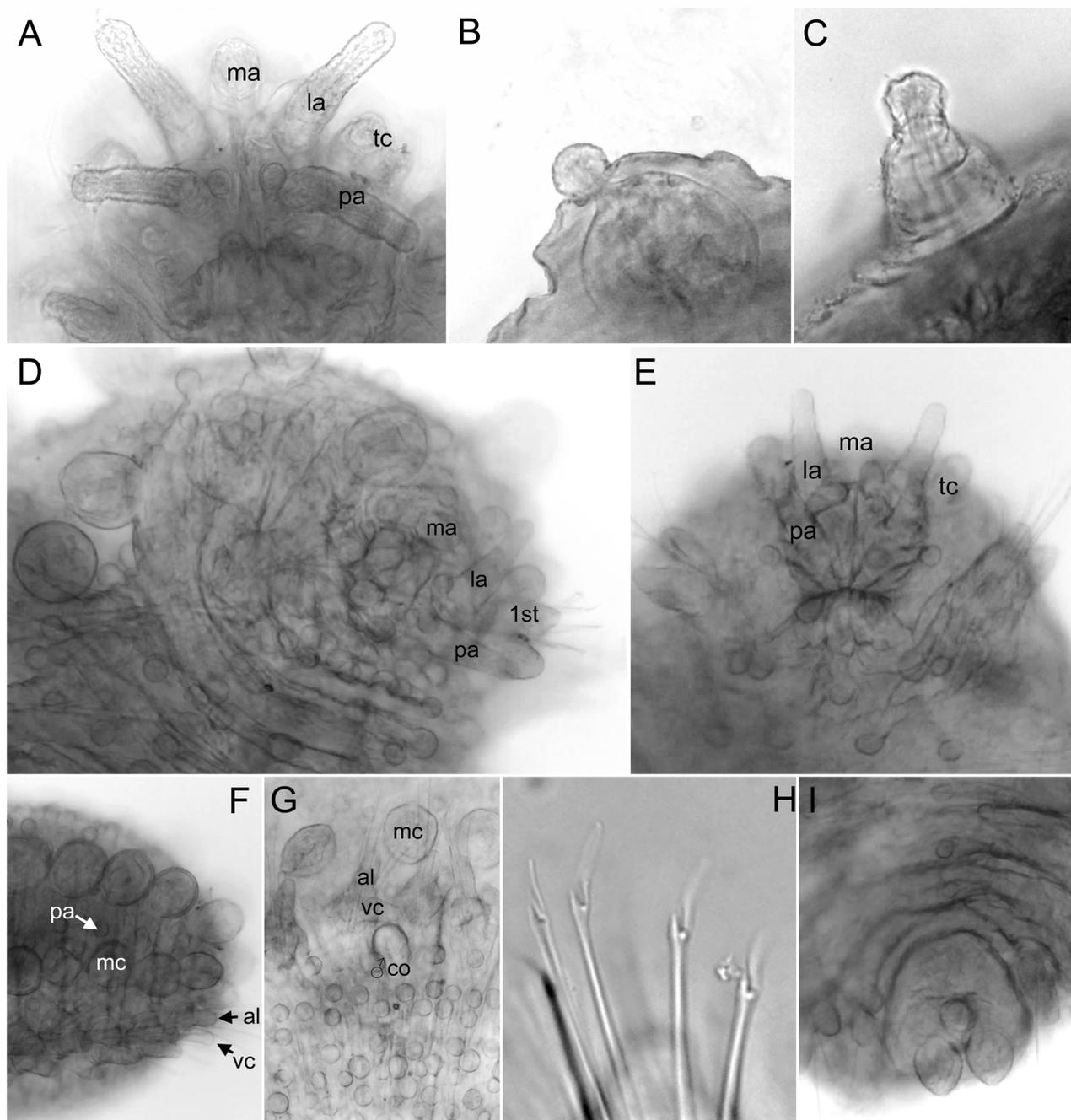


FIGURE 1. Light micrographs. A–C. *Ephesiella australiensis*, holotype ZMH P.16773. A. Anterior end, frontal view, showing head appendages and papillae. B. Mid-body macrotubercle, side view. C. Mid-body microtubercle, side view. D–I. *Sphaerodoropsis exmouthensis*, D, F–H, holotype ZMH P.16493, E, I, paratypes ZMH P.16494. D. Anterior end, lateral view, showing head appendages and papillae. E. Same, frontal view. F. Anterior chaetigers, side view, showing dorsal tubercles and parapodia. G. Chaetigers 6 and 7, side view, with digitiform copulatory organ ventral to ventral cirrus chaetiger 6. H. Chaetal fascicle, mid-chaetiger. I. Posterior chaetigers and pygidium, ventral view. Abbreviations: al, acicular lobe; co, copulatory organ; la, lateral antenna; ma, median antenna; mc, macrotubercle; pa, palp; tc, tentacular cirrus; vc, ventral cirrus; 1st, parapodium first chaetiger.

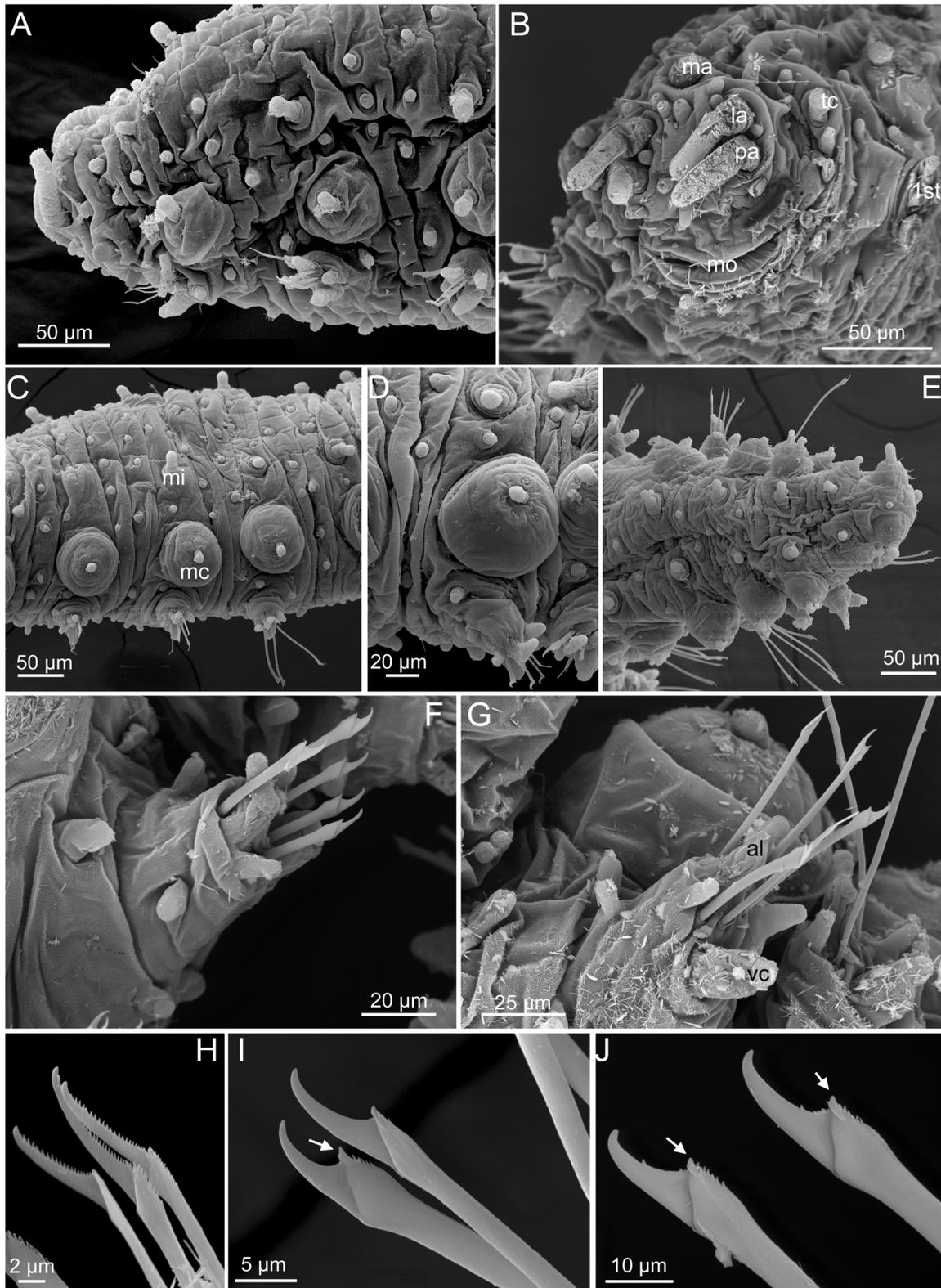


FIGURE 2. *Ephesiella australiensis* from Western Australia, AM W.42701 and W.42702. scanning electron micrographs. A. Anterior end, lateral view. B. Same, frontal view, showing head appendages and papillae. C. Mid-body chaetigers, showing dorsal tubercles, three transverse rows of dorsal papillae per segment and parapodia. D. Detail of dorsal tubercles and parapodial papillae, mid-chaetiger. E. Posterior chaetigers and pygidium, dorsal view. F. Mid-body parapodium, dorsal view, showing shape and arrangement of parapodial papillae and chaetae. G. Mid-body chaetiger, antero-ventral view. H. Chaetae chaetiger 1. I. Chaetae posterior chaetiger, with conspicuous distal tooth on shaft (arrow). J. Same, different individual. Abbreviations: al, acicular lobe; la, lateral antenna; ma, median antenna; mc, macrotubercle; mi, microtubercle; pa, palp; tc, tentacular cirrus; vc, ventral cirrus; 1st, parapodium first chaetiger.

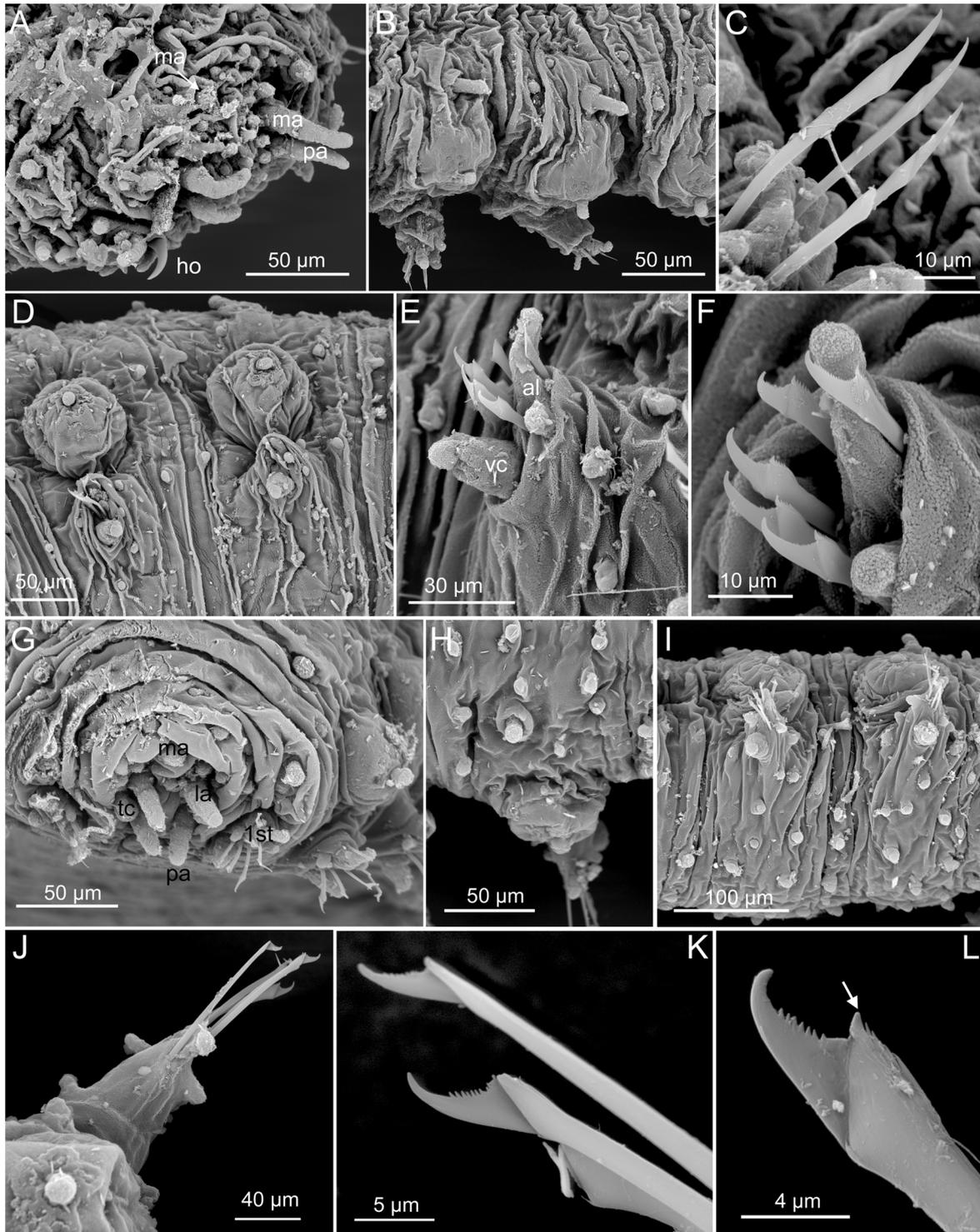


FIGURE 3. *Ephesiella australiensis* from several localities, scanning electron micrographs. A–C: Arafura Sea, NTM W.20663, D–F: Queensland, AM W.42693, G–L: New South Wales AM W.42688. Anterior end, showing head appendages and hooks on first chaetiger. B. Mid-body chaetigers, lateral view, showing microtubercles, macrotubercles and parapodial papillae. C. Chaetae mid-body segments. D. Posterior chaetigers, showing macrotubercles and parapodia. E. Mid-body parapodium, anterior view. F. Detail of chaetae mid-body parapodia. G. Anterior end, frontal view, showing a partially retracted prostomium and head appendages; hooks absent on first chaetiger. H. Posterior parapodia showing dorsal macrotubercles, microtubercles and papillae. I. Mid-body region, ventral view. J. Mid-body parapodium, dorsal view. K. Posterior chaetae. L. Detail posterior chaeta, with conspicuous distal tooth on shaft (arrow). Abbreviations: al, acicular lobe; la, lateral antenna; ma, median antenna; pa, palp; tc, tentacular cirrus; vc, ventral cirrus; 1st, parapodium first chaetiger.

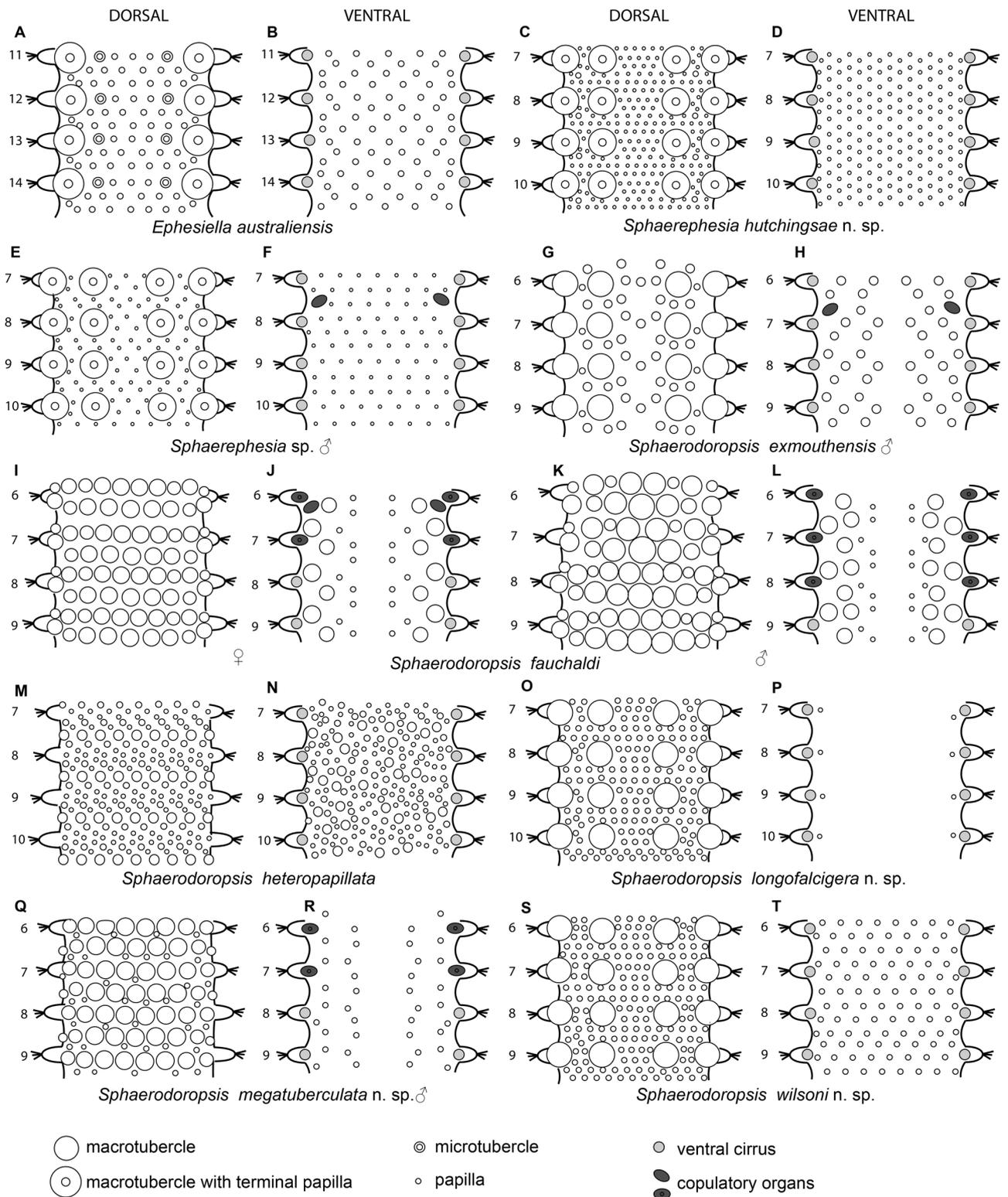


FIGURE 4. Schematic illustrations of the type and arrangement of tubercles on the dorsal and ventral surface of mid-body chaetigers. The number at the left side of the drawing refer to the chaetiger number. A, C, E, G, I, K, M, O, Q, S: dorsal view. B, D, F, H, J, L, N, P, R, T: ventral view.

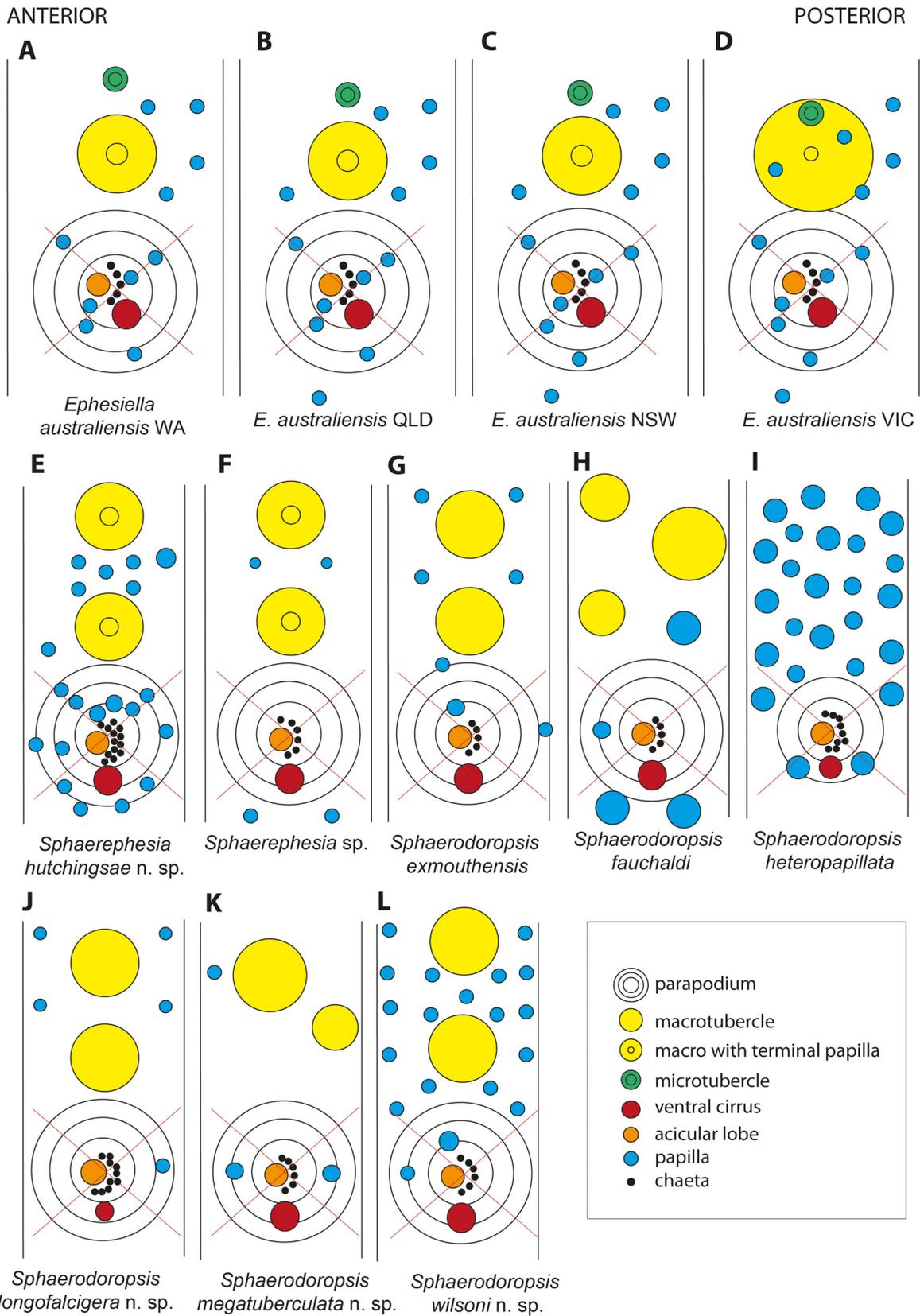


FIGURE 5. Schematic illustrations of the type and arrangement of parapodial and nearby structures and papillae. In all cases anterior faces left, posterior right, dorsal the top and ventral the bottom. The red cross centred in the middle of the parapodia divides each of the four hypothetical parapodial surfaces, and the concentric circles (larger at base, smaller at tip) indicate the parapodial volume..

Tubercles. First chaetiger with two dorsal macrotubercles; microtubercles absent (Figs 2A, 3G). Following chaetigers each with two dorsal macrotubercles arranged in two dorso-lateral longitudinal rows, and two microtubercles forming two longitudinal rows between the macrotubercles (Figs 2C, 4A). Macrotubercles sessile and spherical, each provided with a digitiform terminal papilla (Figs 1A, 2A, C, D, 3B, D); with groups of pores around terminal papilla (Fig. 2D). All macrotubercles similar in shape and size, slightly increasing in size to chaetiger 4 and decreasing in posterior chaetigers. Microtubercles with digitiform terminal papillae shorter (Fig. 1C), or longer (Figs 2A, C, E, 3B, H) than collar. Spherical papillae over dorsum, arranged in three transversal rows per chaetiger, with around 15–20 papillae on each mid-body chaetigers, including 2–3 papillae between macrotubercles and parapodia (Figs 2C, 4A). Ventral surface with spherical papillae, arranged in four more or less regular transversal rows, with a total of 20–25 per segment, in mid-body; numbers decreasing towards posterior end (Figs 3I, 4B). Body epithelium with ellipsoid granules (e.g. Fig. 3F).

Parapodia. Parapodia sub-conical, increasing in size towards chaetiger 3, around 1–2 times longer than wide; acicular lobe projecting distally anterior to chaetae, resembling other parapodial papillae or slightly longer, ventral cirri bottle-shaped projecting as long as acicular lobe (Figs 2A, C–D, F–G, 3B, E–F, I–J). Anterior parapodia with four hemispherical papillae: one anterior, one antero-ventral, one anterior dorsal and one posterior, in addition to the acicular lobe. Mid-body parapodia with six semi-spherical papillae, all similar in size, in addition to the acicular lobe: one anterior dorsal, one anterior, near the acicular lobe, one anterior ventral, two postero-dorsal (one of them distal) (Figs 2F–G, 3E, J, 5A–D).

Chaetae. First chaetiger apparently with hooks absent. Compound or semi-compound chaetae in all chaetigers, arranged in a curved transverse row around acicular lobe and numbering 4–6 per fascicle (Figs 2F, G, 3E, F). First and second chaetigers with well serrated long blades, 5–6 times longer than wide (Fig. 2H). Chaetae from chaetiger 3 with shafts widened distally, a larger distal tooth and fine spinulation; blades twice as long as wide, recurved and with smooth or few serration of the inner edges, with dorso-ventral gradation in the width and length (Fig. 2I–J, 3C, K–L).

Pygidium. Pygidium terminal, with mid-ventral digitiform anal cirrus and a pair of dorsal anal cirri, similar in shape but slightly smaller than macrotubercles (Fig. 2E).

Internal features. Eyes or muscular pharynx not observed.

Reproductive features. Gametes or ‘copulatory organs’ not observed on either type or additional material. Some gravid females (e.g. NMV F.132637) are completely filled with discoid eggs, 250 µm of diameter.

Variation. The holo- and the paratype are the smallest individuals reported. Other preserved specimens range between 2.2 and 22 mm long, 0.2 and 1.8 mm wide and had between 30 and 64 chaetigers. The relative length of the prostomial antennae is constant among specimens, palps and lateral antennae are similar in shape and size, and larger than median antenna. Some specimens have small or even inconspicuous tentacular cirri while these are digitiform and clearly visible in others. Differences in the absence/presence of microtubercles on the first chaetiger have been observed even within type material (the paratype bears microtubercles on first chaetiger). Chaetae also showed variation among the material examined. Some specimens from Northern Territory bear hooks on first chaetiger (Fig. 3A) and most specimens, regardless their origins, bear semi-compound chaetae with joined shaft and blade although recognisable (e.g. Fig. 3C, F, L). Diversity in the relative length/width of the blades was also observed within (Fig. 2H–J) and among specimens (being the Northern Territory specimens the one presenting longer blades, Fig. 3C). Moreover, a few specimens collected from Victoria, show enlarged macrotubercles with embedded microtubercles and some papillae, what is interpreted as an artefact due to swollen macrotubercles (Fig. 5D). The number (4–6) and arrangement of parapodial papillae show little variation among specimens (Fig. 5A–D).

Remarks. This species was originally described based on the combination of the following features: absence of eyes, absence of hooks on first chaetiger, median antenna shorter than lateral, 4–5 parapodial papillae and compound chaetae with blades 1.5–2 times as long as maximum width (Hartmann-Schröder 1981). The specimens collected along the Australian coast mostly fit on this description but present slight variation on other morphological traits, as indicated above, not congruent with particular geographical patterns. It is therefore difficult, at this stage, to determine if there are more than one *Ephesiella* species present in Australia, despite the large geographical range and environmental diversity reported here for the species. The genus *Ephesiella* is a homogenous group of sphaerodorids currently with 15 species described and reported from around the world. The species boundaries and their diagnostic features need reassessment considering intraspecific variability which is not often taken into account (Desbruyères 1980; Hartmann-Schröder 1981). For the time being, all the specimens

collected in Australia have been considered as a single entity but this hypothesis should be tested, desirably with molecular data.

Type locality. Cervantes, Western Australia (Fig. 15).

Distribution. Western Australia, Northern Territory, Queensland, New South Wales and Victoria (Hartmann-Schröder 1981; Wilson & Bakken 2003; Capa & Rouse 2015; Fig. 15).

Habitat. Sand, sea-grass beds, dead coral, 10–400 m depth.

Genus *Sphaerephesia* Fauchald, 1972

Type species. *Sphaerephesia longisetis* Fauchald, 1972

Diagnosis: Body mainly short and ovoid, some species slender. Four longitudinal rows of macrotubercles. Macrotubercles sessile with short terminal papillae. Microtubercles absent. Papillae over body surface and parapodia. Head appendages short, spherical or digitiform. Parapodia with compound chaetae; hooks absent.

Sphaerephesia hutchingsae n. sp.

Figs 4C–D, 5E, 6

Material examined. Holotype: East of Malabar, Sydney, New South Wales, Australia, AM W.42748, 33° 58' 43" S, 151° 18' E, 82 m, 22 Aug 1995. **Paratypes:** east of Malabar, Sydney, New South Wales, AM W.42717 (1 spec.), 33° 58' 41" S, 151° 17' 51" E, 80.1m, 17 Oct 1995; AM W.42719 (1 spec.), 33° 58' 36" S, 151° 17' 54" E, 80.1m, 15 Nov 1995; AM W.42721 (1 spec.), 33° 58' 43" S, 151° 18' 00" E, 82.3 m, 23 Jul 1996; AM W.42730 (1 spec.), 33° 58' 43" S, 151° 17' 54" E, 81.5 m, 23 Jul 1996; AM W.42731 (2 specs), 33° 58' 41" S, 151° 17' 54" E, 80.7 m, 19 Sep 1995; AM W.42749 (1 spec.), 33° 58' 43" S, 151° 17' 54" E, 81.7 m, 22 Aug 1995; AM W.42751 (1 spec.), 33° 58' 43" S, 151° 17' 48" E, 80.9 m, 19 Jun 1996; AM W.42752 (2 specs), 33° 58' 43" S, 151° 17' 54" E, 81.6 m, 19 Jun 1996; AM W.42758 (1 spec.), 33° 58' 46" S, 151° 17' 57" E, 81.8 m, 23 Jul 1996. **Additional material. New South Wales:** AM W.42705 (1 spec.), Bass Point, 34° 36' S, 150° 54' E, 45 m, 01 Feb 1990; AM W.42707 (1, spec.), Cape Banks, 34° 00' S, 151° 16' E, 65 m, 03 Jan 1991; AM W.42708, (1 spec.), same collection details; AM W.42709 (1 spec.), same collection details; AM W.42710 (1 spec. bad conditions), same collection details; AM W.42713 (1 spec.), south-east of Bate Bay, 34° 04' 36" S, 151° 13' E, 46 m, 15 Jan 1990; AM W.42715 (2 specs), off Providential Head, Wattamolla, 34° 08' S, 151° 08' 30" E, 65 m, 29 Oct 1990; AM W.42716 (1 spec.), Bass Point, 34° 36' S, 150° 54' E, 35 m, 29 Oct 1990; AM W.42718 (1 spec.), east of Malabar, 33° 58' 41" S, 151° 18' 00" E, 81.7 m, 21 Dec 1995; AM W.42722 (1 spec.), east of Malabar, 33° 58' 46" S, 151° 18' E, 81.1 m, 26 Feb 1996; AM W.42723 (1 spec.), east of Malabar, 33° 58' 36" S, 151° 17' 48" E, 81.2 m, 08 Dec 1995; AM W.42724 (1 spec.), east of Malabar, 33° 58' 43" S, 151° 17' 51" E, 79.5 m, 17 Apr 1996; AM W.42725 (1 spec.), east of Malabar, 33° 58' 41" S, 151° 18' 00" E, 81.6 m, 17 Oct 1995; AM W.42726 (2 specs), east of Malabar, 4 km south of ocean outfall, 34° 00' 30" S, 151° 16' 45" E, 82.5 m, 20 Jun 1996; AM W.42727 (2 specs), east of Malabar, 33° 58' 36" S, 151° 18' E, 81.2 m, 21 Sep 1995; AM W.42728 (2 specs), east of Malabar, 33° 58' 41" S, 151° 18' E, 81.4 m, 23 Aug 1995; AM W.42729 (1 spec. bad conditions), east of Malabar, 33° 58' 36" S, 151° 17' 48" E, 80.1 m, 17 Oct 1995; AM W.42732 (1 spec.), east of Malabar, 33° 58' 41" S, 151° 17' 54" E, 80.9 m, 19 Jun 1996; AM W.42733 (2 specs), east of Malabar, Sydney, 33° 58' 43" S, 151° 17' 57" E, 81.9 m, 23 Aug 1995; AM W.42734 (2 specs, one used for SEM), east of Malabar, 33° 58' 41" S, 151° 18' E, 81.6 m, 17 Jan 1996; AM W.42736 (1 spec.), east of Malabar, 33° 58' 38" S, 151° 18' E, 82.1 m, 23 Aug 1995; AM W.42737 (1 spec.), east of Malabar, 33° 58' 46" S, 151° 17' 51" E, 80.3 m, 19 Sep 1995; AM W.42738 (1 spec.), east of Malabar, Sydney, 33° 58' 43" S, 151° 17' 54" E, 79.5 m, 17 Jan 1996; AM W.42739 (1 spec.), east of Malabar, 33° 58' 36" S, 151° 17' 57" E, 81.5 m, 20 Feb 1996; AM W.42740 (1 spec.), east of Malabar, 33° 58' 38" S, 151° 17' 54" E, 81.5 m, 19 Jun 1996; AM W.42747 (1 spec.), east of Malabar, 33° 58' 38" S, 151° 17' 54" E, 8.7 m, 17 Oct 1995; AM W.42753 (1 spec. for SEM), east of Malabar, 33° 58' 36" S, 151° 17' 54" E, 81.6 m, 19 Dec 1995; AM W.42754 (1 spec.), east of Malabar, 33° 58' 38" S, 151° 18' 00" E, 81.6 m, 17 Oct 1995; AM W.42755 (1 spec.), east of Malabar, 33° 58' 36" S, 151° 17' 51" E, 82.4 m, 17 Oct 1995; AM W.42756 (1 spec.), east of Malabar, 33° 58' 41" S, 151° 18' 00" E, 81.2 m, 19 Jun 1996; AM W.42757 (1 spec.), east of Malabar, 33° 58' 41" S, 151° 17' 48" E, 79.7 m, 15 Nov 1995. **Victoria:** NMV F.132843 (2 specs), Central Bass Strait, 100 km SSE of Cape Liptrap, 39° 45' 54" S, 145° 33' 30" E, 74 m, 13 Nov 1981; NMV F.132864 (5 specs), Central Bass Strait, 66 km S of Rodondo Island, 39° 49' 30" S, 146° 18' 30" E, 82 m, 13 Nov 1981; NMV F.132869 (5 specs), Central Bass Strait, 26 km SE of Aireys Inlet, 38° 39' 48" S, 144° 18' 12" E, 79 m, 19 Nov 1981; NMV F.63833 (1 spec.), Eastern Bass Strait, 7.3 km SSW of Cape

Conran, 37° 52' 39" S, 148° 42' 09" E, 49 m, 04 Jun 1991; NMV F.69678 (2 specs), Eastern Bass Strait, 15.3 km of eastern edge of Lake Tyers, 37° 53' 13" S, 148° 15' 14" E, 43 m, Feb 1991; NMV F.69679 (2 specs), Eastern Bass Strait, 20.2 km of Pt Ricardo, 37° 52' 25" S, 148° 25' 03" E, 46 m, 26 Sep 1990.

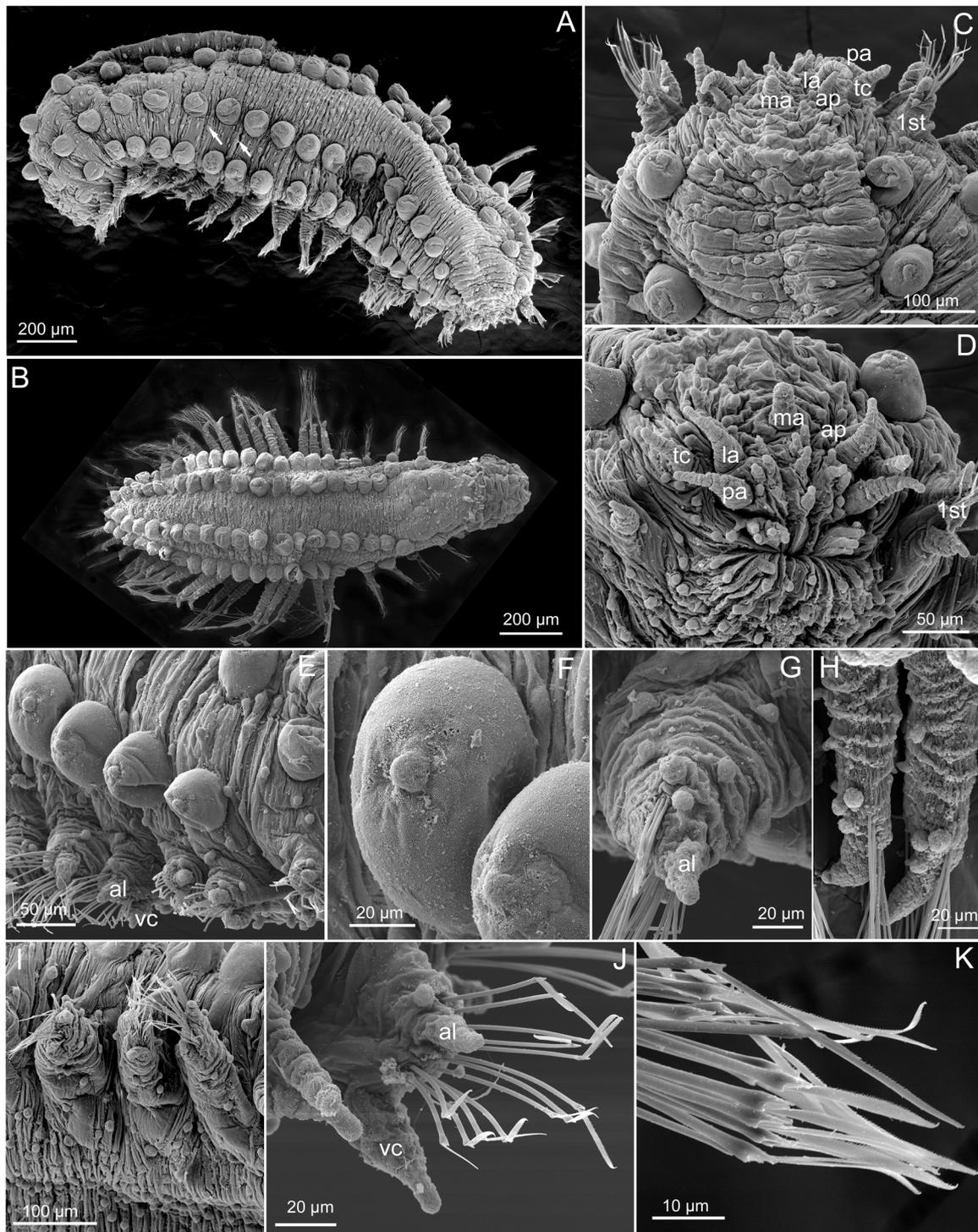


FIGURE 6. *Sphaerephesia hutchingsae* n. sp., AM W.42753 and AM W. 42734, scanning electron micrographs. A. Whole specimen, dorsal view, head on right end. External segmentation is evident (arrows). B. Whole specimen, dorsal view, with everted pharynx. C. Anterior end, dorsal view, showing head appendages and arrangement of tubercles and papillae on anterior chaetigers. D. Same, frontal view. E. First five chaetigers, lateral view, showing parapodia and lateral macrotubercles. F. Detail of macrotubercle chaetiger 5, with distal papilla. G. Mid-body parapodium, right side is anterior surface. H. Posterior parapodia, dorsal view. I. Mid-body parapodia and ventral body surface. J. First parapodium, anterior view. K. Chaetal fascicle, mid-body chaetiger. Abbreviations: al, acicular lobe; ap, antenniform papillae; la, lateral antenna; ma, median antenna; pa, palp; tc, tentacular cirrus; vc, ventral cirrus; 1st, parapodium first chaetiger.

Comparative material: *Sphaerephesia fauchaldi* Kudenov, 1987, holotype NMNH 102785; *Sphaerephesia longisetis* Fauchald, 1972, holotype AHF POLY 0964; *Sphaerephesia regularis* Böggemann, 2009, holotype ZMH P25498, paratypes ZMH P25497 (4 specs), ZMH P25499 (4 specs); *Sphaerephesia similisetis* Fauchald, 1972, paratype AHF POLY 0967 (2 specs).

Diagnosis. Body slightly flattened dorso-ventrally (wider than high), with four longitudinal rows of sessile, pear-shaped macrotubercles with small spherical terminal papillae (often not conspicuous) and 4–5 transversal rows of small spherical papillae per segment. Distance between dorsal-most macrotubercles exceeds distance between those and lateral ones. Parapodia with ventral cirri as long as acicular lobe and 14–16 rounded and small papillae, sometimes a distal one, on dorsal surface slightly larger. Parapodia with 14–20 compound chaetae, with thin shafts and blades 10–12 times as long as wide.

Description. *Measurements and general morphology.* Gravid female, 2 mm long, 0.5 mm wide; 20 chaetigers. Body ellipsoid, slightly flattened dorso-ventrally (wider than high). Dorsum convex, slightly sub-trapezoidal, and ventrum flattened (Fig. 6A–B). Tegument with transverse wrinkles and segmentation only slightly discernible in some segments (Fig. 6A). Preserved specimen lacking pigmentation.

Head. Anterior end bluntly rounded (Fig. 6A, C). Prostomium with seven longer appendages, including a pair of palps, in ventral-most position near the mouth, sub-conical and wrinkled; a pair of lateral antennae, similar in shape and size to palps; a median antenna, shorter (two thirds) than lateral antennae and with a rounded distal end; and a pair of antenniform papillae behind lateral antennae, slightly shorter than lateral antennae (Fig. 6C–D). Around 20 digitiform smaller papillae are confined by prostomial appendages and the mouth in frontal view (Fig. 6D). A pair of tentacular cirri similar in shape and size to lateral antennae and palps and several scattered papillae similar to prostomial.

Tubercles. First chaetiger with two macrotubercles, sessile, pear-shaped or provided with an incipient rounded terminal papillae (Fig. 6A–D). Rest of chaetigers with four macrotubercles each arranged in four longitudinal rows along dorsum (Figs 4C, 6A–B). Distance between mid-rows is larger than between these and lateral rows of macrotubercles (Figs 4C, 6A–B). Shape and size of all macrotubercles similar, slightly increasing in size in first four chaetigers (Fig. 6A, E) and also slightly reducing in size in posterior chaetigers towards pygidium. Macrotubercles with pores arranged mainly in three groups around terminal papilla (Fig. 6F). Spherical papillae present over dorsum, arranged in five transversal rows per segment (Fig. 6A), around 25 papillae present between mid-macrotubercles and 8–10 between these and the lateral ones in mid-segments, one of them, larger than the others (Fig. 4C). One to three papillae between lateral macrotubercles and parapodia. Ventral surface with small spherical papillae, arranged in 5–6 transversal rows, with a total of around 30 papillae per segment, in mid-body; numbers decreasing towards posterior end (Figs 4D, 6I). Body epithelium with ellipsoid granules (e.g. Fig. 6F).

Parapodia. Parapodia sub-conical, increasing in size towards chaetiger 5 and around 1–2 times longer than wide, wrinkled (Fig. 6G–J). Acicular lobe projecting distally anterior to chaetae (Fig. 6G–J). Ventral cirri sub-conical–pear-shaped as long as acicular lobe (Fig. 6I, J). Mid-body parapodia with around 12–13 small spherical papillae, all similar in size: 4–5 on dorsal surface, two distal ones larger, 2–3 on anterior surface, 3–4 on ventral surface and 1–2 on posterior surface (Figs 5E, 6G–I).

Chaetae. Compound chaetae present in all chaetigers, arranged in a curved transverse row around acicular lobe and numbering 14–20 per fascicle in mid-body chaetigers (Figs 5E, 6I–K). Shaft with slightly widened distal end with delicate, almost inconspicuous spinulation (Fig. 6K). Blades similar in length along fascicles (10–12 times longer than maximum width), only slightly longer than those from mid-fascicle, with fine and short spinulation along superior edge and a distal recurved tip (Fig. 6J–K).

Pygidium. Pygidium terminal, with mid-ventral digitiform anal cirrus and a pair of dorsal anal cirri, similar in shape to macrotubercles but slightly smaller.

Internal features. Eyes not observed in any specimen. Muscular pharynx runs along chaetigers 1–4.

Reproductive features. Holotype and a few of the additional specimens examined are gravid females carrying large discoid eggs, 200 µm in diameter that occupy most of the body coelom, from the anterior to the posterior segments (e.g. AM W.42708, AM W.42715, AM W.42748), other specimens seem to be filled with sperm. However, ‘copulatory organs’ are not obvious in either females or males.

Variation. Paratypes and additional material examined measure 1–2 mm long and 0.3–0.5 mm wide (without parapodia), with 13–23 segments, in all cases body is about 3–4 times longer than wide. Variation of relative size of head appendages is quite stable and median antenna is the shorter appendage, but in some individuals the antenniform papillae are not distinct. Relative size of parapodia varies with and between specimens from 1–3 times longer than wide. Parapodial papillae are often difficult to count under light microscopy but numbers are constant, only in some specimens the three larger distal dorsal papillae have been spotted (Fig. 5E). Relative length of blades of falcigers is variable within parapodia but the range is fixed between specimens (10–12 times longer than

maximum width). Muscular pharynx runs from chaetigers 1 to 4–5. In specimens immersed in blue methylene, only the four longitudinal rows of macrotubercles stained deep blue.

Remarks. *Sphaerephesia* is a genus with eight nominal species (Alalykina 2015). Five of them, *Sphaerephesia similisetis* Fauchald, 1972, *S. longisetis* Fauchald, 1972, *S. chilensis* Fauchald, 1974, *S. fauchaldi* Kudenov, 1987 and *S. regularis* Böggemann, 2009, have been described with four rows of macrotubercles with a terminal rounded papilla, several additional papillae on dorsal surface, and falcigers with long blades, features also found in *Sphaerephesia hutchingsae* n. sp. *Sphaerephesia regularis* is distinguished from the new species in the different general body shape, cylindrical and slender instead of oval, wide and flattened dorso-ventrally. Moreover, the rows of macrotubercles are very close to each other, almost in contact, unlike in the rest of species (Böggemann 2009). The other taxa are mainly distinguished by the number of parapodial papillae. *Sphaerephesia chilensis* has one or two parapodial papillae, *S. fauchaldi* has eight, *S. longisetis* around 15 and *S. similisetis* around 20–25 (Fauchald 1972, 1974; Kudenov 1987a), although these numbers were erroneously interpreted for *S. longisetis* and *S. similisetis* in recent publications (original descriptions in Fauchald 1972 versus Magalhães *et al.* 2011 or Alalykina 2015). The latter two are the most similar to *S. hutchingsae* n. sp. with around 15 parapodial papillae. *Sphaerephesia longisetis*, *S. similisetis* and the new species share the number and arrangement of dorsal papillae (in five more or less clear transverse rows), the presence of a prominent acicular lobe and a ventral cirrus similar in shape and size, and little variation of blade length on each chaetal fascicle (Fauchald 1972). *Sphaerephesia similisetis* and *S. longisetis* were described lacking antenniform papillae (Fauchald 1972), but these have been observed in types of the former, a feature shared by *S. hutchingsae* n. sp. Other differences between *S. longisetis* and *S. hutchingsae* n. sp. include the extremely long characteristic chaetae and the presence of microtubercles of *S. longisetis* being absent in the Australian species. Microtubercles have, however, not been observed on the holotype of *S. longisetis* after direct examination, and all the small tubercles were spherical and had no distinct collar or terminal papillae. Differences between *S. similisetis* and *S. hutchingsae* n. sp. also rely in the number of parapodial papillae.

The terminal papillae on macrotubercles are often not conspicuous and well delineated in some species of *Sphaerephesia* and these tubercles show a pear-shaped outline. This is the case for at least *S. mamalaensis* (Magalhães *et al.*, 2011), *S. regularis* and *S. similisetis* (Magalhães *et al.* 2011; Böggemann 2009; pers. obs.). There are also some specimens currently considered as *Sphaerodoropsis*, such as *S. philippi* Fauvel, 1911, *S. biserialis* Berkeley & Berkeley, 1944, *S. anae* Aguado and Rouse, 2006 and *S. protuberanca* Böggemann, 2009 that have four longitudinal rows of macrotubercles with similar morphology (provided with a terminal papillae or at least being pear-shaped) and could in fact be related to the former ones. Since the presence of macrotubercles with terminal papillae has been considered the main features to distinguish between *Sphaerephesia* and *Sphaerodoropsis*, a deep revision of members of these two groups and a reassessment of the systematic value of this feature is needed.

Etymology. This species is dedicated to Pat Hutchings for her contribution to polychaete taxonomy for several decades, her continuous support and friendship.

Distribution. Specimens have been found south of Sydney (New South Wales) and in Eastern and Central Bass Strait (Victoria) (Fig. 15).

Ecology. The species has only been found in samples with fine sediments (muddy sand), 43–83 m depth.

Sphaerephesia sp.

Figs 4 E–F, 5F, 7

Material examined. East of Malabar, Sydney, New South Wales, Australia, AM W.42720 (1 spec.), 1 km south of ocean outfall, 33° 59' 00" S, 151° 17' 33" E, 79.4m, 20 Jun 1996.

Comparative material. *Sphaerephesia mamalaensis* Magalhães *et al.*, 2011, holotype, NMNH 1154142; paratypes, NMNH 1154143.

Diagnosis. Body strongly flattened dorso-ventrally, with four longitudinal rows of sessile, macrotubercles, pear-shaped or with distal short papilla, and minute spherical papillae arranged in four transversal rows per segment. Distance between dorsal macrotubercles exceeding distance between those and lateral ones. Parapodia with ventral cirri as long as acicular lobe and apparently lacking papillae. Six to eight chaetae per parapodium, with shaft distally enlarged and blades 1–3 times as long as wide. Male ‘copulatory organs’ present as an elongated conical papilla between ventral cirri of chaetigers 7 and 8.

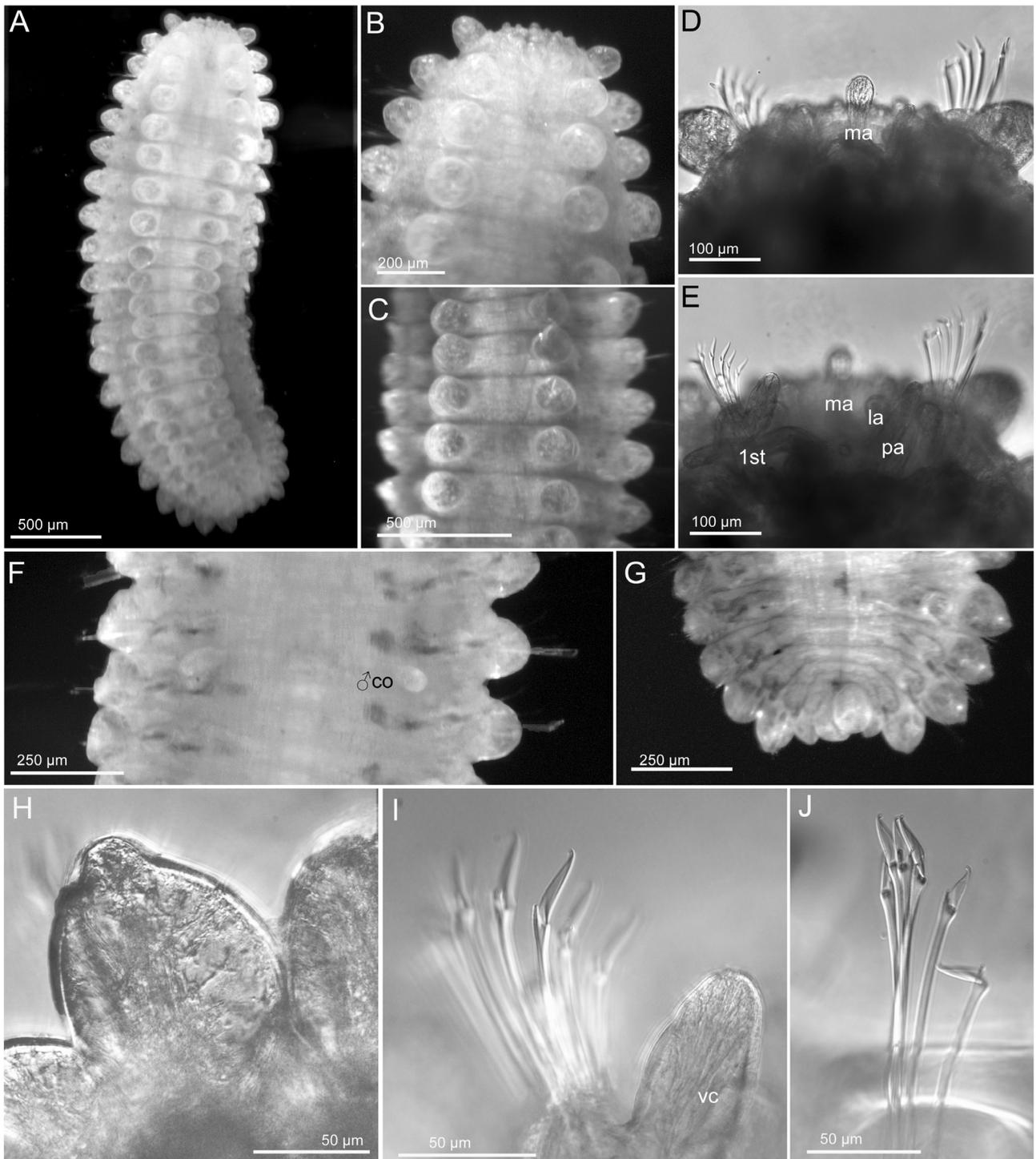


FIGURE 7. *Sphaerephesia* sp. AM W.42720, light micrographs, F, G, stained with methylene blue. A. Whole specimen, dorsal view; head on top. B. Anterior end, dorsal view. C. Mid-body regions, dorsal view. D. Anterior end, ventral view, showing head and first chaetiger. E. Same, image focused on ventral prostomial appendages. F. Mid-body chaetigers, ventral view, with copulatory organ between chaetiger 7 and 8. G. Posterior chaetigers and pygidium, ventral view. H. Lateral macrotubercle, with terminal papillae, dorsal view. I. Anterior parapodium, ventral view. J. Mid-body chaetal fascicle. Abbreviations: co, copulatory organ; la, lateral antenna; ma, median antenna; pa, palp; 1st, parapodium first chaetiger.

Table 2. Description and position of the structures referred to as copulatory organs in the literature and the present study. These structures are provided, in all cases, with obvious pores. Unless stated, as in the case of the inflated ventral cirri, these structures are present in addition to the normal ventral cirri present in other parapodia. Abbreviations: ch, chaetiger; btw, between.

Species	♀ copulatory organ	Position	♂ copulatory organ	Position	Source
<i>Sphaerephesia</i> sp.	not observed	-	conical papilla	btw ch 7 & 8	present study
<i>Sphaerodoridium campanulata</i> Böggemann, 2009	not observed	-	inflated ventral cirrus	ch 6	Böggemann 2009
<i>S. guerritai</i> Moreira and Parapar 2015	oval tubercle	btw ch 9 & 10	not observed		Moreira & Parapar 2015
<i>Sphaerodoropsis arctowskyensis</i> Hartmann-Schröder and Rosenfeldt, 1988	oval tubercle	ch 6	inflated ventral cirrus	ch 6	Moreira <i>et al.</i> 2004
<i>S. bisphaeroserialis</i> Hartmann-Schröder, 1974	oval tubercle	ch 6	inflated ventral cirrus	ch 6	Moreira <i>et al.</i> 2004
<i>S. exmouthensis</i> Hartmann-Schröder, 1981	not observed	-	conical papilla	btw ch 6 & 7	present study
<i>S. fauchaldi</i> Hartmann-Schröder, 1979	oval tubercle + inflated ventral cirri	ch 6 + 4-7	inflated ventral cirrus	Ch 5-8	present study
<i>S. garcialvareci</i> Moreira <i>et al.</i> , 2004	oval tubercle + inflated cirri	ch 6 + 4-7	inflated ventral cirrus	ch 6	Moreira <i>et al.</i> 2004
<i>S. gudmunduri</i> Moreira and Parapar, 2012	oval tubercle	btw ch 7 & 8	conical papilla	btw ch 7 & 8	Moreira & Parapar 2012
<i>S. halldori</i> Moreira and Parapar, 2012	oval tubercle + inflated ventral cirri	ch 6 + 4-7	conical papilla	btw ch 7 & 8	Moreira & Parapar 2012
<i>S. macrotubercula</i> Böggemann, 2009	not observed	-	inflated ventral cirrus	ch 6	Böggemann 2009
<i>S. megatuberculata</i> n. sp.	oval tubercle	btw ch 5 & 6	inflated ventral cirrus	chaetigers 4-7	present study
<i>S. plurituberculata</i> Capa and Rouse, 2015	oval tubercle	ch 6	inflated ventral cirrus	ch 6	Capa & Rouse 2015
<i>S. rosehipiformis</i> Böggemann, 2009	not observed	-	inflated ventral cirrus	ch 6	Böggemann 2009
<i>S. solis</i> Reuscher and Fiege, 2011	oval tubercle	ch 6	inflated ventral cirri	ch6	Reuscher & Fiege 2011
<i>S. translucida</i> Böggemann, 2009	not observed	-	inflated ventral cirrus	ch 4-6	Böggemann 2009

Description. *Measurements and general morphology.* Male, 3.2 mm long, 1 mm wide, 20 chaetigers. Body ellipsoid (Fig. 7A), strongly flattened dorsoventrally. Dorsum slightly sub-trapezoidal, flattened ventrum. Segmentation conspicuous (Fig. 7A). Preserved specimen lacking pigmentation. Anterior end bluntly rounded (Fig. 7A–B, D–E).

Head. Prostomium with five digitiform appendages (Fig. 7D–E), including a pair of palps, in ventral most position; a pair of lateral antenna, similar in shape and size to palps; and a median antenna, shorter (two thirds) than lateral antennae and with a rounded distal end. Antenniform papillae not observed (Fig. 7D–E). A pair of tentacular cirri similar in shape and size to lateral antennae and palps. Head with several rounded and hemispherical papillae, difficult to count due to retraction of prostomium (Fig. 7B, D–E).

Tubercles. First chaetiger with two macrotubercles, sessile, pear-shaped. Rest of chaetigers with four macrotubercles each, arranged in four longitudinal rows along dorsum, similar in shape to first ones but larger (Fig. 7A–C), or with short terminal papillae (Fig. 7G–H). Distance between mid-rows is larger than between these and lateral macrotubercles (Figs 4E, 7A–C). Additional minute hemispherical papillae are present over dorsum, arranged in four transversal rows per segment (Fig. 4E). Ventral surface with small spherical papillae, arranged in 3–4 transversal rows (Fig. 4F).

Parapodia. Parapodia sub-conical, as long as wide, wrinkled. Acicular lobe oval, projecting distally. Ventral cirri oval, slightly longer than acicular lobe in anterior segments and similar in length in the rest. Mid-body parapodia without papillae; two or three small spherical papillae located ventral to parapodial base, not considered herein parapodial (Fig. 5F). Dorsal surface of parapodia not clearly visible due to proximity and large size of macrotubercles.

Chaetae. Compound chaetae present in all chaetigers, arranged in a curved transverse row around acicular lobe and numbering 6–8 per fascicle (Figs 5F, 7D–E, I–J). Shaft with slight widened distal end with delicate almost inconspicuous spinulation (under compound microscope). Blades ranging between 2–4 times longer than wide, those from mid-fascicle longer, with fine and short spinulation along superior edge and a distal recurved tip (Fig. 7I, J).

Pygidium. Pygidium terminal, with mid-ventral spherical anal cirrus and a pair of dorsal anal cirri, similar in shape to macrotubercles but slightly smaller (Fig. 7G).

Internal features. Muscular pharynx not visible through body wall. Eyes not seen.

Reproductive features. Male ‘copulatory organs’ present as an elongated conical papilla between ventral cirri of chaetiger 7 and 8 (Figs 4F, 7F).

Remarks. Of the eight currently accepted species of *Sphaerephesia*, only *S. mamalaensis* has four longitudinal rows of macrotubercles and chaetae with short blades (less than five times longer than wide). *Sphaerephesia mamalaensis* shares several diagnostic features with the Australian specimen: median antenna is slightly shorter than lateral, macrotubercles are not clearly papillated but more pear shaped, there are 3–4 transversal rows of papillae per segment on both dorsal and ventral surfaces, chaetae have blades 2–4 times longer than wide showing intra-fascicle variation (Magalhães *et al.* 2011; per. obs.). The specimen herein described differs from *S. mamalaensis* in the conspicuous delineation of segments, the absence of parapodial papillae and the different shape of the pygidial ventral cirrus, spherical (generally digitiform), but this could be an artefact of this specimen. This specimen could belong to an undescribed species, but features such as the shape of the pygidial cirrus and the absence of parapodial papillae should be confirmed with more specimens.

Distribution. Sydney, New South Wales (Fig. 15).

Habitat. Sand, 80 m depth.

Genus *Sphaerodoropsis* Hartman and Fauchald, 1971

Type species. *Sphaerodorum sphaerulifer* Moore, 1909.

Diagnosis. Body generally short and ovoid, some forms slender. Four or more longitudinal rows of macrotubercles, in one or several transversal rows per segment. Macrotubercles sessile and smooth, without terminal papillae. Microtubercles absent. Papillae over body surface and parapodia. Head appendages short, spherical or digitiform. Parapodia with compound chaetae; hooks absent.

***Sphaerodoropsis exmouthensis* Hartmann-Schröder, 1981**

Figs 1D–I, 4G–H, 5G, 8

Sphaerodoropsis exmouthensis Hartmann-Schröder, 1981: 44, Figs 94–99; 1984: 31; 1986: 51.

Material examined. **Holotype** ZMH P.16493: Western Australia, Exmouth, Tantabiggly Creek, in sand on the reef plateau, 11 Oct. 1975. **Paratype** MZH P.16494 (1 spec.) same sample. **Additional material.** ZMH P.16995 (1 spec. for SEM), Drummonds core, Geraldton, Western Australia, Australia; in fine sand with seagrass, 22 Oct 1975.

Diagnosis. Ellipsoid body with strongly convex dorsum. Four longitudinal rows of sessile and spherical (sometimes pear-shaped) dorsal macrotubercles and three transversal rows (total up to 11) of dorsal spherical papillae per segment. Distance between dorsal-most macrotubercles exceeding distance between those and lateral ones. Parapodia with long digitiform acicular lobe, shorter ventral cirrus and a single rounded papilla on anterior distal end. Four or five chaetae per parapodium, with thin shafts slightly enlarged distally and lacking spinulation, and short blades (5–7 times longer than wide), serrated and with smooth distal end. Males with ‘copulatory organ’ as conical papillae ventral to ventral cirri between chaetiger 6 and 7.

Re-description. *Measurements and general morphology.* Male, body ellipsoid, measuring 1.3 mm long and 0.42 mm wide, with 19 chaetigers. Tegument with transverse wrinkles, segmentation inconspicuous. Dorsum convex and ventrum flattened. Preserved specimen lacking pigmentation.

Head. Anterior end bluntly rounded. Prostomium with five longer appendages, including a pair of digitiform palps, in ventral-most position; a pair of lateral antennae similar in size and shape to palps; and a median antenna, ellipsoid, about one half of the size of lateral antennae (Figs 1D–E, 8A–B). Antenniform papillae absent (Figs 1D–E, 8A–B). Up to 10 spherical papillae confined by prostomial appendages and the mouth (Figs 1D–E, 8A–B). A pair of tentacular cirri similar in shape and size to median antenna and palps and several scattered papillae similar to prostomial (Fig. 8A–B).

Tubercles. First chaetiger with two macrotubercles, slightly smaller than following, spherical and sessile (Figs 1D, 8A). Rest of chaetigers with four macrotubercles each, arranged in four longitudinal rows along dorsum (Figs 1F, 4G, 8A). Distance between mid-dorsal rows is similar or slightly larger than between these and lateral macrotubercles (Figs 1A, 4G). Lateral macrotubercles are slightly smaller than dorsal (Figs 1F, 8A). Spherical papillae are present over dorsum, arranged in three transversal rows per segment (Figs 4G, 8A). Around 6–8 papillae between mid-macrotubercles and around 2–3 between these and the lateral ones in mid-segments, papillae closer to macrotubercles slightly larger than the rest (Figs 4G, 8A, D). None to two papillae between lateral macrotubercles and parapodia (Fig. 8D). Ventral surface with spherical papillae, arranged in 2–3 transversal rows, with a total of 9–13 papillae in mid-body segments; numbers decreasing towards posterior end (Figs 1G, 4H), with a group of three near the base of parapodia and a midline group of 5–7 papillae, being the anterior larger. Body epithelium with ellipsoid granules.

Parapodia. Parapodia sub-conical, about 1–2 times longer than wide. First chaetiger with a long (as long as parapodia), digitiform acicular lobe projecting distally; ventral cirri shorter and wider (Fig. 8D), parapodial papillae absent. Second and following chaetigers similar or with longer acicular lobes, and one dorso-anterior spherical papillae (Figs 5G, 8C).

Chaetae. Compound chaetae present in all chaetigers, arranged in a curved transverse row around acicular lobe, numbering 3–5 per fascicle (Figs 5G, 8C–D). Shaft with slightly widened distal end and delicate, almost inconspicuous, spinulation. Blades similar in length along fascicles (5–7 times longer than maximum width), with fine and short spinulation along superior edge and a distal recurved tip (Figs 1H, 8E–G).

Pygidium. Pygidium terminal, with distal dorsal spherical papillae, a mid-ventral digitiform anal cirrus and a pair of pear-shaped dorsal anal cirri, slightly larger than macrotubercles (Figs 1I, 8H).

Internal features. Eyes not observed, muscular pharynx inconspicuous.

Reproductive features. Holotype, male, with ‘copulatory organs’ as conical papillae ventral to ventral cirri between chaetiger 6 and 7 (Figs 1G, 5H). Females have not been examined herein but there is a record of a gravid female with 13 chaetigers (Hartmann-Schröder 1981).

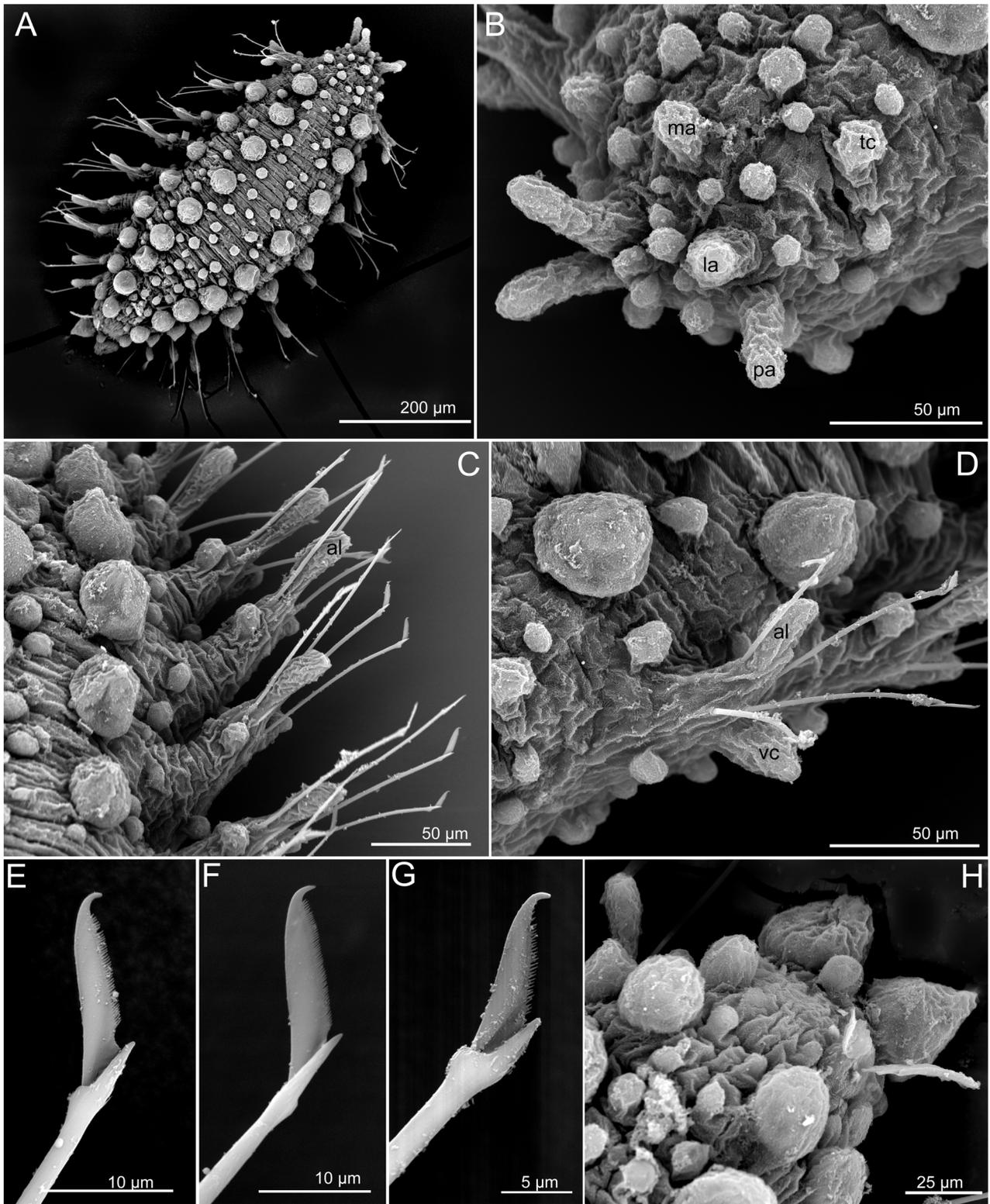


FIGURE 8. *Sphaerodoropsis exmouthensis*, ZMH P.16995, scanning electron micrographs. A. Whole specimen, dorsal view; anterior end on top. B. Detail of anterior end and head appendages. C. Mid-body parapodia and row of lateral macrotubercles, anterior view. D. Parapodium first chaetigers, anterior view. E. Chaeta mid-body chaetigers. F. Same. G. Chaeta posterior chaetiger. H. Posterior chaetiger and pygidium. Abbreviations: al, acicular lobe; la, lateral antenna; ma, median antenna; pa, palp; tc, tentacular cirrus; vc, ventral cirrus.

Variation. Specimens measure 0.5–1.3 mm long and 0.25–0.42 mm width, in all cases body is about 4–5 times longer than wide. Paratype with eight chaetigers. Median antenna is in the three specimens examined shorter than lateral and no antenniform papillae have been observed in specimens examined. Prostomial papillae confined by antennae and mouth are less than 10. Macrotubercles are, in the specimen studied under SEM, not completely rounded and somehow pear-shaped (Fig. 8C–D). Number of epithelial papillae, including parapodial with a single papilla in all except first chaetiger, and arrangement seem to be constant. Parapodia do not exceed twice the length of the width. Number of chaetae range between 4–5 per parapodium. Length of blades shows a slight variation in number of chaetae and the relative length of blades. Examined specimens are not transparent and muscular pharynx was not conspicuous. Eyes have not been observed. ‘Copulatory organs’ only observed in holotype.

Remarks. In the original description there were some details lacking and others that have been interpreted differently herein. The palps and lateral antennae (referred to as outer and inner antennae respectively in original description) were described as being shorter and oval and digitiform to filiform but are considered here to be similar in shape and size. The arrangement of epithelial papillae both on dorsal and ventral body surface seems not random (Fig. 8A). Parapodia were described with a rounded papilla on superior margin that has here interpreted as anterior; chaetae were considered as smooth but fine dentation is observed under SEM. Pygidial macrotubercles as pear shaped (as drawn in original description, Hartmann-Schröder 1981).

Type locality. Tantabiddy Creek, Exmouth, Western Australia (Fig. 15).

Distribution. Western Australia (Exmouth and Geraldton; Fig. 15), ?South Australia (Ceduna and Kangaroo Island) (Hartmann-Schröder 1981, 1984, 1986). South Australian material needs confirmation; they could belong to *Sphaerodoropsis wilsoni* n. sp. described below.

Habitat. Sand near reef plateau or sea-grasses, shallow depths.

***Sphaerodoropsis fauchaldi* Hartmann-Schröder, 1979**

Figs 4I–L, 5H, 9, 10

Sphaerodoropsis fauchaldi Hartmann-Schröder, 1979: 122–123, Figs 238–242; 1989: 39.

Material examined. Holotype ZMH P.15486, Port Hedland, Western Australia, sand with algae and detritus, 27 Sept 1975. **Additional material. Western Australia:** AM W.42679 (1 spec.), off jetty at Green Island, Rottneest Island, 32° 01' S, 115° 30' E, intertidal, 21 Dec 1983, algal turf and sediment on reef flat. **Northern Territory:** NTM W.10209 (1 spec.), Darwin Harbour, 12° 29' 52", 130° 50' 18"E, 7 m, 14 Jul 1993, 7 m; NTM W.10205 (1 spec.), Darwin Harbour, 12° 31' 08" S, E130° 47' 05" E, 7 m, Jul 1993; NTM W.10207 (1 spec.), Darwin Harbour, 12° 34' 52" S, 130° 51' 03" E, 6 m, 13 Jul 1993; NTM W.15192 (1 spec.), Darwin Harbour, 12° 33' 45"S, 130° 52' 01" E, 3 m, 18 Mar 1994; NTM W.10204 (1 spec.), Darwin Harbour, 12° 31' 13" S, 130° 56' 02", 11 m, 16 Jul 1993. **New South Wales:** AM W.42692 (1 spec.), Red Head, 32° 03' 17" S, 152° 33' 14" E, 22 Mar 2003, 13 m, sand and rocky reef; AM W.42687 (2 specs), Surgeons Reef, North West Solitary Island, 30° 00' 27" S, 153° 16' 13" E, 11 m, 30 Apr 2005, sand and shelly sediment; AM W.42706 (1 spec.), Bass Point, 34° 36' S, 150° 54' E, 1 Feb 1991, 45 m; AM W.42690, (2 specs), S. of Baronda Head, Tathra, 36° 41' 12" S, 149° 59' 53" E, 11 m, 5 Apr 2008, *Ecklonia* holdfasts; AM W.42696 (2 spec.), NE side Little Broughton Island, north-east of Port Stephens, 32° 37' 05" S, 152° 20' 06" E, 17 m, 11 Mar 2006, alga *Ecklonia* holdfasts; AM W.42697 (1 spec.), Esmeralda Cove, Broughton Island, Port Stephens, 32° 37' 19" S, 152° 19' 10" E, 18 m, 12 Mar 2006, coarse shelly sediment; AM W.42698 (1 spec.), Esmeralda Cove, Broughton Island, Port Stephens, 32° 37' 19" S, 152° 19' 10" E, 18 m, 12 Mar 2006, bushy brown algae; AM W.42689 (1 spec.), E. of Baronda Head, Tathra, 14 m, 4 Apr 2008, among red algae and bryozoans; AM W.42685 (1 spec.), Halfway Reef, Ulladulla, 35° 21' 25" S, 150° 29' 19" E, 15 m, 3 May 1997, sponges, bryozoan and hydrozoan; AM W.42686 (2 spec.), north west end of South Solitary Island, 30° 12' 07" S, 153° 15' 59" E, 14.5 m, 1 May 2005, coarse sediment; MZH P. 20094 (3 specs), Malua Bay, Batemans Bay, 4 Jan 1976. **Victoria:** NMV F. 90824 (1 spec.), Schomberg Reef, near Peterborough 38° 36' 49" S, 142° 53' 19" E, 13 May 1998; NMV F.90825 (1 spec.), Mutton Bird Island, near Port Campbell, 38° 38' 55" S, 143° 03' 46" E; NMV F.132899, Central Bass Strait, 38° 30' 12" S, 144° 15' 00" E; NMV F.217162, 11.7 km W of Pt Ricardo, Eastern Bass Strait, 37° 49' 53" S, 148° 30' 07" E, 27 m, Feb 1991, coarse sand.

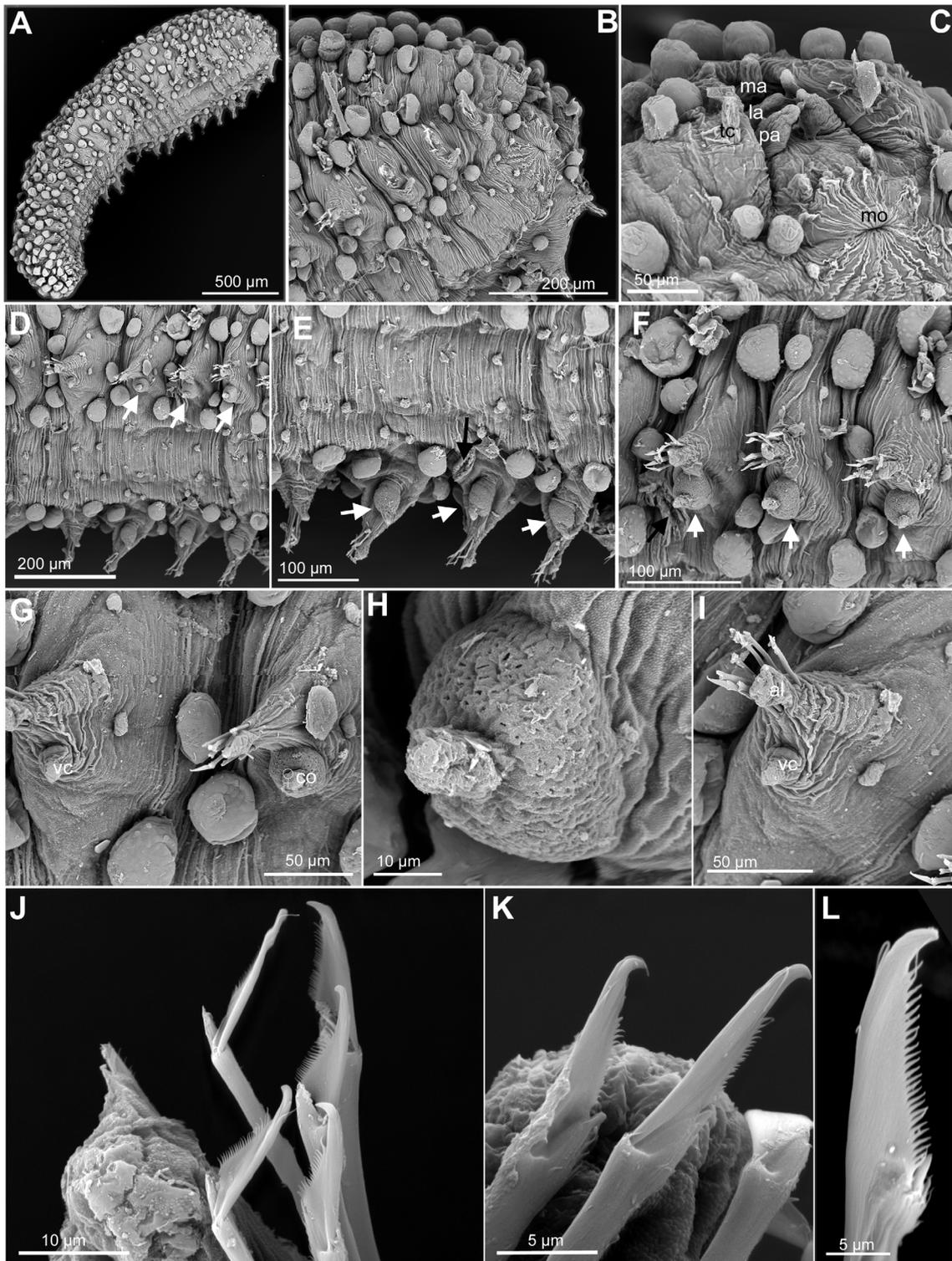


FIGURE 9. *Sphaerodoropsis fauchaldi*, NTM W.10206, scanning electron micrographs. A. Complete specimen, ventro-lateral view. B. Anterior end, ventral view. C. Detail anterior end and head appendages, ventral view. D. Chaetigers 9–5 (left to right), ventral side, with female inflated and porous ventral cirri (white arrows) in chaetigers 7–5. E. Same, opposite side, with inflated and porous ventral cirri (white arrows) in chaetigers 7–5 and oval tubercle (black arrow) on chaetiger 6. F. Parapodia, chaetigers 6–4, with ‘copulatory organs’ (arrows). G. Parapodia of chaetigers 8 (with normal ventral cirrus) and 7 (with copulatory organ), antero-lateral view. H. Detail of copulatory organ in chaetiger 6 with pores scattered on the surface. I. Parapodium chaetiger 8, anterior view. J. Chaetal fascicle, mid-body chaetiger. K. Chaetae chaetiger 5. L. Chaeta posterior chaetiger. Abbreviations: al, acicular lobe; co, copulatory organ; la, lateral antenna; ma, median antenna; pa, palp; tc, tentacular cirrus; vc, ventral cirrus.

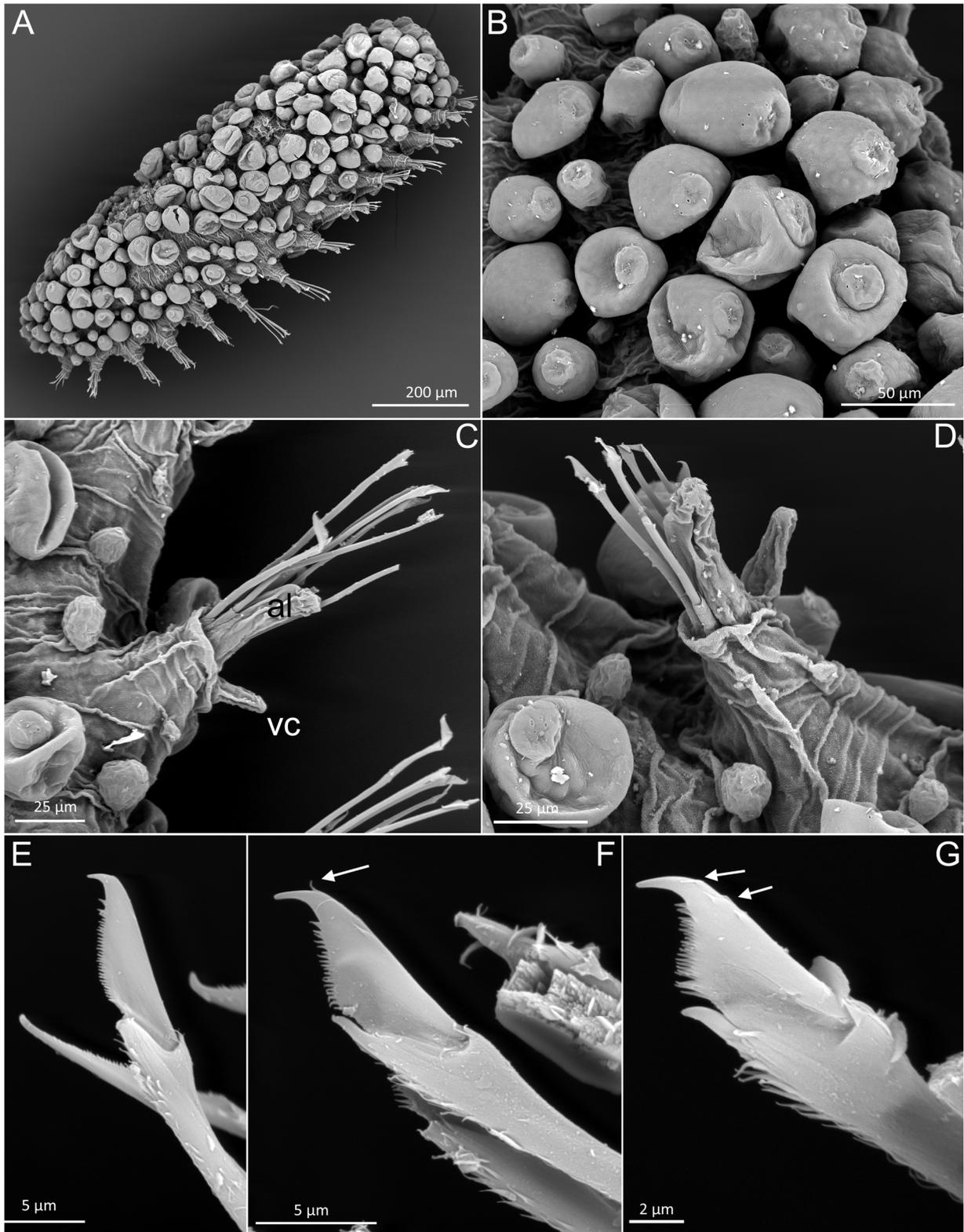


FIGURE 10. *Sphaerodoropsis fauchaldi*, NMV F.217162. A. Whole specimen, dorsal view (anterior end on top). B. Dorsal macrotubercles, posterior chaetigers. C. Parapodium mid-body, anterior view. D. Same, dorsal view. E. Compound chaeta, chaetiger 3. F. Chaetae, mid-body parapodium (arrow pointing to the distal spine in blade). G. Shorter blade, chaetae in mid-body parapodium. Abbreviations: al, acicular lobe; vc, ventral cirrus.

Diagnosis. Ellipsoid body with 10–14 longitudinal rows of spherical macrotubercles, in two transversal rows per segment, with 8–12 macrotubercles in a row between parapodia and 10–14 in posterior row. Dorsum with spherical papillae in two longitudinal rows next to parapodia. Ventrum with two longitudinal rows of large tubercles, near parapodia and four longitudinal rows of spherical papillae. One papilla on anterior surface of each parapodium. Parapodia with 5–6 chaetae per fascicle, slightly enlarged distally, blades 3–4 times as long as wide. Both females and males with porous swollen ventral cirri, in chaetigers 4–7 and 5–8, respectively; additionally, females bear with porous tubercle-like structure ventral to parapodia of chaetiger 6.

Re-description. *Measurements and general morphology.* Body ellipsoid, 0.8 mm long and 0.4 mm wide, with 16 chaetigers. Dorsum convex, ventrum flattened (Fig. 9A, C). Segmentation inconspicuous, tegument with transverse wrinkles (Fig. 9A–D). Preserved specimen lacking pigmentation.

Head. Anterior end bluntly rounded (Fig. 9A–B). Prostomium with five digitiform appendages, including a pair of short palps in a ventral position, a pair of lateral antennae and a median antenna; lateral antennae similar in size and shape to palps; median antenna, about as long as lateral antennae (Fig. 9C). Antenniform papillae not observed. A pair of tentacular cirri shorter than lateral antenna. A few scattered papillae present on the head (Fig. 9C).

Tubercles. Dorsal macrotubercles sessile and spherical. First chaetiger with two transversal rows of four and five macrotubercles each. Following chaetigers with 17 longitudinal rows of macrotubercles, arranged in double transversal rows on each segment (with 8 and 9 tubercles each), decreasing in size from dorsal-most to lateral rows (Figs 4I, 9A). Additional single spherical papilla above each parapodia (Figs 4I, 9A, D). Two large spherical macrotubercles close to the base of each parapodium, forming four longitudinal rows on ventrum (Figs 4J, 9A–B, D). Additional small spherical papillae in four longitudinal rows, leaving a gap mid-ventrally without papillae (Figs 4J, 9A, D–E). Body epithelium with irregular granules (Fig. 10D).

Parapodia. Parapodia sub-conical, about 1–2 times longer than wide. Chaetigers with digitiform acicular lobe, present from chaetiger 2, projecting longer than ventral cirrus (Fig. 9D–G, I, 10C); ventral cirri bottle-shaped (Fig. 9D, G, I). One spherical papilla on each parapodium on the anterior surface, variable in size (Figs 5H, 9G, I, 10C–D).

Chaetae. Compound chaetae present in all chaetigers, arranged in curved transverse rows posterior to acicular lobe, numbering 5–6 per fascicle (Figs 5H, 9E–F, I). Shaft with slender distal end with long spinulation on edge (Figs 9K–L, 10 E–G). Blades varying in shape and size within fascicle, ranging 2–4 times longer than maximum width, with a distal recurved tip, fine spinulation on cutting edge and 1–3 thin spines on outer distal margin (Figs 9J–L, 10E–G).

Pygidium. Pygidium sub-terminal, with a mid-ventral digitiform anal cirrus (Fig. 9A).

Internal features. Eyes not seen in holotype, but a pair observed in other specimens, in first chaetiger. Muscular pharynx not observed.

Reproductive features. Gender of holotype unknown, gametes or ‘copulatory organs’ not observed. Females with a porous tubercle-like structure ventral to parapodia of chaetiger 6 and modified ventral cirri present in chaetigers 4–7 (Fig. 9D–F), with a swollen base with pores scattered over the surface and a distal knob (Figs 4J, 9G–H). Few oblong eggs measuring 200 µm in length were observed in two specimens. Male (NMV F.132899) with modified ventral cirri present in chaetigers 5–8, with a swollen and porous base and a distal knob, similar in morphology to those found in the females (Fig. 4L), and sperm packages distributed along the coelom.

Variation. Specimens measuring 0.8–3.1 mm long and 0.1–0.6 mm wide, with 11–27 chaetigers. One preserved specimen (NTM W.10206) showed red dots of pigment over parapodia; pigmentation not conspicuous in other specimens. Prostomial appendages digitiform in relaxed specimens, blunt and wide at basis in specimens where anterior end is contracted. Macrotubercles increasing in number from first to mid-body chaetigers. Transversal rows of tubercles are indistinct in contracted specimens and macrotubercles seem arranged randomly. The number of macrotubercles in each transversal row seems to be dependent on size of specimen, small specimens with 8–10+9–12 macrotubercles (Figs 4K, 10A–B), and 10–12+12–14 in larger specimens (Figs 4I, 9A), and the size of tubercles, also seem larger in small specimens (e.g. Figs 4K, 10A). A couple of specimens showed atypical tubercles, with a distal swelling (Fig. 10B), considered herein as an artefact. The number and size of ventral tubercles and papillae show some variation and in some specimens three pairs of longitudinal rows have been observed (Fig. 4L). Number and morphology of chaetae similar in all specimens examined. Some variation in the size and morphology of chaetae was observed among specimens. Larger individuals seem to bear more slender and similar blades within and across chaetigers (e.g. Fig. 9J–L) while smaller specimens presented a wider range in

sizes of blades and included shorter and wider ones (Fig. 10G). Nevertheless, in all cases chaetae presented shafts distally provided with long spines and spines also in the distal outer edge of the blades.

Remarks. The specimens studied mostly agree with the original description (Hartmann-Schröder 1979). The original description is not accurate on details regarding prostomial appendages, variability in size and arrangement on epithelial tubercles and chaetal morphology. Nevertheless, the original description is in line with what can be confirmed here from observations in the holotype, and from additional material.

This species belongs in Group 3 (*sensu* Borowski 1994), gathering species with more than four longitudinal rows and two transversal rows of macrotubercles per segment. *Sphaerodoropsis fauchaldi* is unique among other congeners in having a larger number of longitudinal rows of macrotubercles and large tubercles on the ventral side. *Sphaerodoropsis megatuberculata* n. sp. have as many longitudinal rows of macrotubercles as observed in smaller specimens of *S. fauchaldi*, but *S. megatuberculata* n. sp. has large ellipsoid to cylindrical macrotubercles and lack the characteristic large ventral tubercles. Only two other *Sphaerodoropsis* species have conclusively been reported to have presence of macrotubercles on the ventral side, *S. malayana* Augener, 1933, *S. solis* Reuscher and Fiege, 2011, but only the latter belong to Group 3 (*S. malayana* has four longitudinal rows of macrotubercles on the dorsum). *Sphaerodoropsis solis* has up to 13 (6+7) longitudinal rows of macrotubercles while *S. fauchaldi* has up to 26 (12+14) longitudinal rows of macrotubercles. Of species currently accepted in *Sphaerodoropsis* only *S. spissum* Benham, 1921 possesses a number of macrotubercles within the range described for *S. fauchaldi*. The original description of *S. spissum* does not describe enough details to compare necessary characters, and it seems to lack the ventral macrotubercles. It has not been possible to trace type specimens of *S. spissum* (see comments on *S. spissum* below).

Originally described from the northern part of Western Australia this species was also reported from New South Wales in a later survey (Hartmann-Schröder 1989). Despite the wide geographic distribution (Fig. 15) representing different environments from the tropical north to the temperate south-east it has not been possible to observe conclusive morphological differences on specimens from Western Australia, Northern Territory, New South Wales and Victoria in this study, confirming earlier records and the observed variability in number of macrotubercles, and other morphological traits, is here considered to be related to size of specimens. Pending more available specimens of different size classes or specimens collected from more localities should reveal if the species is broadly distributed along the East Australian coastline or if the disjunct populations truly represent distinct species.

Habitat. In coarse sand, rocks or as epibionts of algae and Bryozoa; from 3 to 45 m.

Type locality. Port Hedland, Western Australia (Fig. 15).

Distribution Western Australia, Northern Territory, New South Wales and Victoria, Australia (Fig. 15).

***Sphaerodoropsis heteropapillata* Hartmann-Schröder, 1987 new rank**

Figs 4M–N, 5I, 11

Sphaerodoropsis multipapillata heteropapillata Hartmann-Schröder, 1987: 50–51, Figs 32–36.

Material examined. Holotype ZMH P.18875 Point Lonsdale, Geelong, Victoria, Australia, Abrasion terrace near lighthouse, on coralline algae, 24 Dec 1975.

Additional material. New South Wales: AM W.42683 (1 spec.), Split Solitary Island, 30° 14' S, 153° 10' 48" E, 15 m, 7 Mar 1991, mixed red algae; AM W.42686 (4 specs, 2 on SEM stubs), South Solitary Island, 30° 12' 07" S, 153° 15' 59" E, 14.5 m, 1 May 2005, coarse sediment; AM W.42684 (1 spec.), Burrill Rock, Ulladulla, 35° 23' 25" S, 150° 28' 11" E, 10 m, 1 May 1997, *Ecklonia* holdfasts. **Tasmania:** AM W.42678 (2 specs), Maquarie Island, 54° 30' S, 158° 57' E, 15 m, 19 Oct 1983, algae. **Victoria:** NMV F.90823 (2 specs), Beware reef, Cape Conran, 37° 49' 20" S, 148° 47' 23" E, 5 m, 15 Apr 1998, subtidal rocky reefs.

Comparative material. *Sphaerodoridium multipapillata* Hartmann-Schröder, 1974, holotype, ZMH P.14336.

Diagnosis. Ellipsoid body. Dorsum with more than 50 spherical sessile tubercles in two sizes in about five transversal rows per segment, in an irregular pattern. Ventrum with 50–60 spherical papillae in two sizes in 5 irregular transversal rows. Two parapodial papillae, one each on anterior and posterior surfaces. Parapodia with 6–10 chaetae per fascicle, blades as long as wide. Chaetae semi-compound, with shaft distally widened and blades short and wide (as long as broad), both provided of stout spines.

Re-description. *Measurements and general morphology.* Female with eggs. Body ellipsoid, measuring 2.8

mm long, 1.0 mm wide, with 19 chaetigers, anterior end bluntly rounded (Fig. 11B–C), slightly narrowing along posterior segments; convex dorsum (Fig. 11A) and flat ventrum (Fig. 11B). Segmentation inconspicuous (Fig. 11B–D), tegument wrinkled (Fig. 11A–B). Preserved specimen yellowish, lacking pigmentation.

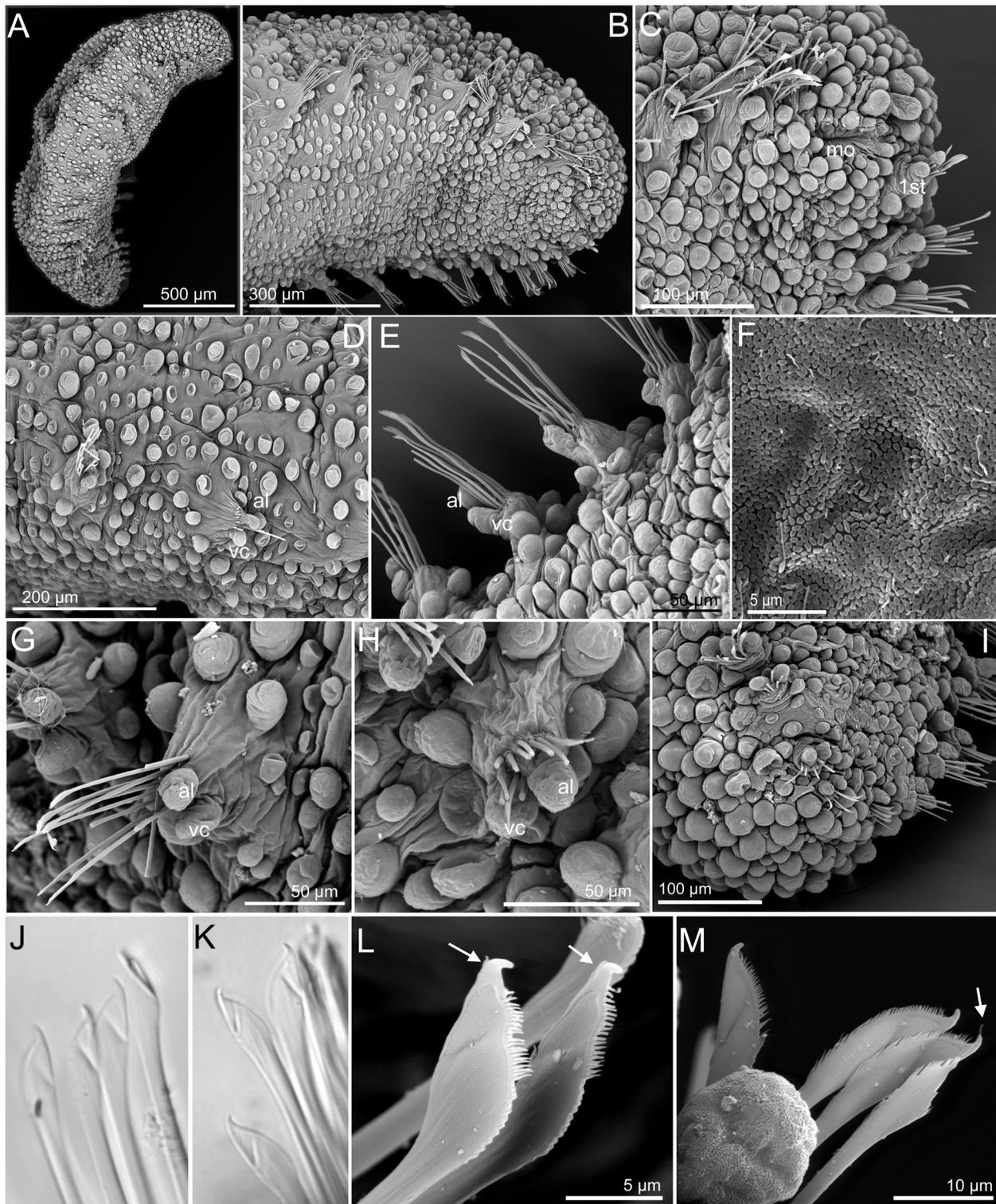


FIGURE 11. *Sphaerodoropsis heteropapillata*, AM W.42686, scanning electron micrographs. A. Complete specimen, dorso-lateral view. B. Anterior end, ventral view. C. Detail anterior chaetiger and head, ventral view. D. Parapodia in mid-body chaetigers, lateral view. E. Mid-body parapodia, ventral view. F. Detail of cuticular granules. G. Parapodium mid-body chaetiger, anterior view. H. Parapodium posterior chaetigers, lateral view. I. Posterior chaetiger and pygidium, ventro-lateral view. J, K. Light micrographs of holotype. J. Chaetal fascicle mid chaetiger. K. Chaetae posterior chaetiger. L. Semi-compound chaetae anterior chaetiger, with distal spines on blade (arrow). M. Same, following chaetiger. Abbreviations: al, acicular lobe; la, lateral antenna; ma, median antenna; pa, palp; tc, tentacular cirrus; vc, ventral cirrus; 1st, parapodium first chaetiger.

Head. Indistinguishable rounded appendages, similar to surrounding papillae (Fig. 11B–C).

Tubercles. Spherical and sessile tubercles dissimilar in size present on dorsum in 5–7 irregular transversal rows with more than 50 tubercles in each chaetiger (Figs 4M, 11A, C–D). Ventral surface with sessile and spherical papillae dissimilar in size, with 50–60 papillae per chaetiger in five irregular transversal rows, ventral papillae somewhat smaller than dorsal tubercles (Figs 4N, 11B, D). Body epithelium with microscopic oblong granules (Fig. 11F).

Parapodia. Parapodia sub-conical, increasing in size towards chaetiger 3, around 1–2 times longer than wide in mid-chaetigers (Fig. 11E, G–H), and decreasing slightly towards posterior chaetigers. Acicular lobe anterior to chaetae fascicle, ellipsoid, 2–3 times longer than wide, projecting longer than ventral cirrus (Fig. 11G–H), with pores on distal end (Fig. 11H). Ventral cirri ellipsoid (Fig. 11G–H). Parapodial papillae spherical, one at base of anterior surface (Figs 5I, 11G), and one at base of posterior surface (Figs 5I, 10H); similar throughout chaetigers.

Chaetae. Chaetal fascicles arranged in a curved transverse row behind acicular lobe, numbering 6–10 chaetae per fascicle (Figs 5I, 11E, G–H). All chaetae semi-compound (Fig. 11J–M), appearing sometimes as simple and suggesting a fusion of shaft and blades (Fig. 11L–M). Blades as long as wide (Fig. 11J–M); with an outer distal thin spine in some chaetae (Fig. 11L–M). Shaft with widened distal end with saw-toothed spinulation (Fig. 11L–M), continuing along most of blade length.

Pygidium. Pygidium terminal, with inconspicuous spherical anal cirri similar in shape as surrounding papillae (Fig. 11I).

Internal features. One pair of eyes as sickle-shaped dark brown or black spots deeply embedded below integument in chaetigers 2–3. Muscular pharynx not observed.

Reproductive features. Holotype and other two females with large eggs measuring approximately 130 µm. ‘Copulatory organs’ not observed in any specimen.

Variation. Specimens examined are all ellipsoid, ranging 1.0–2.3 mm long, 0.3–0.7 mm wide, with 14–20 chaetigers and resemble the holotype in the short and inconspicuous prostomial appendages similar in shape to surrounding papillae and the shape and size of parapodia. In the original description four parapodial papillae were reported, only two have been observed after reexamination of the holotype and in additional material. Parapodial papillae are difficult to observe, and also judgment of their position as they are placed at the base of parapodia. Definition of chaetae is ambiguous. Most chaetae are simple when observed in the scanning electron microscope, although some give the impression of being semi-compound (Fig. 11J–M), and even break at the joint between shaft and blade (Fig. 11M). In the light microscope chaetae have a clear appearance of being compound (Fig. 11J–K), as they were described in the original description (Hartmann-Schröder 1987: Fig. 36).

Remarks. *Sphaerodoropsis heteropapillata* is characterized by having relatively large dorsal tubercles of a range of sizes and by bearing semi-compound chaetae. In addition, relatively large papillae are present on the ventral side. Dorsal and ventral tubercles are arranged in irregular transversal rows being difficult to outline, especially when specimens are contracted. It was included within the informal *Sphaerodoropsis* Group 4 (*sensu* Borowski 1994) gathering species with ‘macrotubercles’ scattered in 3–4 transversal rows, together with *S. multipapillata* (Hartmann-Schröder, 1974), from Tanzania. Both species also share the similar type of wide semi-compound chaetae (Hartmann-Schröder 1974a, 1987). *Sphaerodoropsis heteropapillata* (which only the holotype had been reported to date) was originally described as a subspecies of *S. multipapillata*. The geographic distance suggests it is unlikely the two represent separated populations of the same species. There are also clear differences between the species. *Sphaerodoropsis heteropapillata* bears parapodial papillae while in *S. multipapillata* parapodia lack papillae (Hartmann-Schröder 1974a, 1987; this study). Moreover, in *S. heteropapillata* dorsal tubercles clearly have different sizes, while in *S. multipapillata* papillae are of similar size. This warrants elevation of the subspecies to rank of species.

Sphaerodoropsis heteropapillata also resembles a recently described species from Lizard Island, Great Barrier Reef, *Sphaerodoropsis plurituberculata* Capa and Rouse, 2015. Both species bear several more or less clearly longitudinal rows of spherical and sessile tubercles, variable in size, arranged in several transverse rows per segment, over dorsum and ventrum; around six semi-compound chaetae per parapodium with distally enlarged shaft and short blades, serrated, with distal long spines on the edge opposite to serration and shaft with conspicuous spinulation continuing along most of blade. Differences between these two Australian species lay in the relative length of the head appendages, number and arrangement of dorsal and ventral tubercles.

Sphaerodoropsis plurituberculata is most similar to *S. heteropapillata* because both species are covered with dissimilar dorsal tubercles, while in *S. multipapillata* these are of similar size (Hartmann-Schröder 1974a; Hartmann-Schröder 1987; Capa & Rouse 2015). Differences between *S. heteropapillata* and the new species include the length of the prostomial appendages (inconspicuous in *S. heteropapillata* and digitiform in *S. plurituberculata*, at least when not contracted); the number of ventral papillae (around 50 per segment in *S. heteropapillata* and 30 in *S. plurituberculata*); and the number of parapodial papillae (*S. heteropapillata* bears one per parapodium: one at anterior surface while *S. plurituberculata* lacks parapodial papillae) (Capa & Rouse 2015).

‘Copulatory organs’ have not been observed in *S. heteropapillata*, but in *Sphaerodoropsis plurituberculata* male copulatory organ were described as enlarged, bottle-shaped and porous ventral cirrus and females presented an oval and flat tubercle with a porous surface also ventral to parapodia of chaetiger 6, in addition to the ventral cirrus (Capa & Rouse 2015).

Type locality. Point Lonsdale, Geelong, Victoria.

Distribution. Victoria, New South Wales and the Sub-Antarctic Maquarie Island, from 0 to 15 m (Hartmann-Schröder 1987, Fig. 15).

Habitat. Coarse sediment and among algae in subtidal rocky reefs.

Sphaerodoropsis longofalcigera n. sp.

Fig. 4O–P, 5J, 12

Material examined. Holotype: NMV F.162479 off Pelsart Island, Geraldton, Western Australia, 29° 00' 06" S, 113° 46' 15" E, 409 m, 01 Aug 2005. **Paratypes:** NMV F.162484 (1 spec.), Abrolhos region, 28° 59' 15" S, 113° 45' 34" E, 388 m, 30 Jul 2005; NMV F.162483 (1 spec.), Two Rocks region, north of Perth, Western Australia, 31° 39' 25" S, 114° 58' 31" E, 403 m, 04 Aug 2005.

Comparative material. *S. anae* Aguado & Rouse, 2006, holotype, MNCN 16.01/10817; *S. artabrensis* Moreira & Parapar, 2007, holotype, MNCN 16.01/11043; *Sphaerodorum biserialis* Berkeley & Berkeley, 1944, holotype, NMNH 32867; *Sphaerodoropsis corrugata* Hartmann & Fauchald, 1971, holotype, LACM-AHF POLY 950; *S. discolis* Borowski, 1994, paratypes, ZMH P.21951, ZMH P.21952; *S. elegans* Hartmann & Fauchald, 1971, holotype, LACM-AHF POLY 954, paratypes, LACM-AHF POLY 955; *S. furca* Fauchald, 1974, holotype, LACM-AHF POLY 951; *S. laureci* Desbruyères, 1980, holotype, MNHN TYPE 1286; *S. longianalpapilla* Böggemann, 2009, paratypes, ZMH P.25538; *S. longipalpa* Hartmann & Fauchald, 1971, holotype, LACM-AHF POLY 948; *S. longisetis* Fauchald, 1972, holotype, LACM-AHF POLY 964; *S. longopapillata* Desbruyères, 1980, holotype, MNHN TYPE 1283; *S. protuberanca* Böggemann, 2009, holotype, ZMH P. 25557, paratypes, ZMH P.25556; *S. sibuetae* Desbruyères, 1980, holotype, MNHN TYPE 1284; *S. triplicata* Fauchald, 1974, holotype, LACM-AHF POLY 958, paratypes, LACM-AHF POLY 958; *S. vittori* Kudenov, 1987a, holotype, NMNH 102792; *Sphaerephesia longisetata* Fauchald, 1972, holotype, LACM-AHF POLY 964.

Diagnosis. Body cylindrical, slightly tapering posteriorly. Four longitudinal rows of sessile and hemispherical dorsal macrotubercles and four transversal rows of small spherical papillae per segment. Distance between dorsal-most macrotubercles exceeding distance between those and lateral ones. Parapodia with short and wide acicular lobe, thinner ventral cirrus and a single rounded papillae on anterior surface. Around 10 chaetae per parapodium, with thin shafts slightly enlarged distally and lacking spinulation, and blades ranging in length within fascicles (8–25 times longer than wide), finely serrated.

Description. Measurements and general morphology. Body cylindrical, measuring 1.2 mm long and 0.3 mm wide, with 14 chaetigers. Tegument with some transverse wrinkles, segmentation inconspicuous (Fig. 12A). Preserved specimen lacking pigmentation.

Head. Anterior end bluntly rounded (Fig. 12A–B). Prostomium with seven appendages, including a pair of digitiform palps, in ventral-most position; a pair of lateral antennae similar in size and shape to palps; and a rounded median antennae, about one half of the size of lateral antennae (Fig. 12B). Antenniform papillae as long as median antenna but thinner (Fig. 12B). A pair of tentacular cirri similar in shape and size to median antenna and palps (Fig. 12B). Several small and hemispherical scattered papillae cover the head.

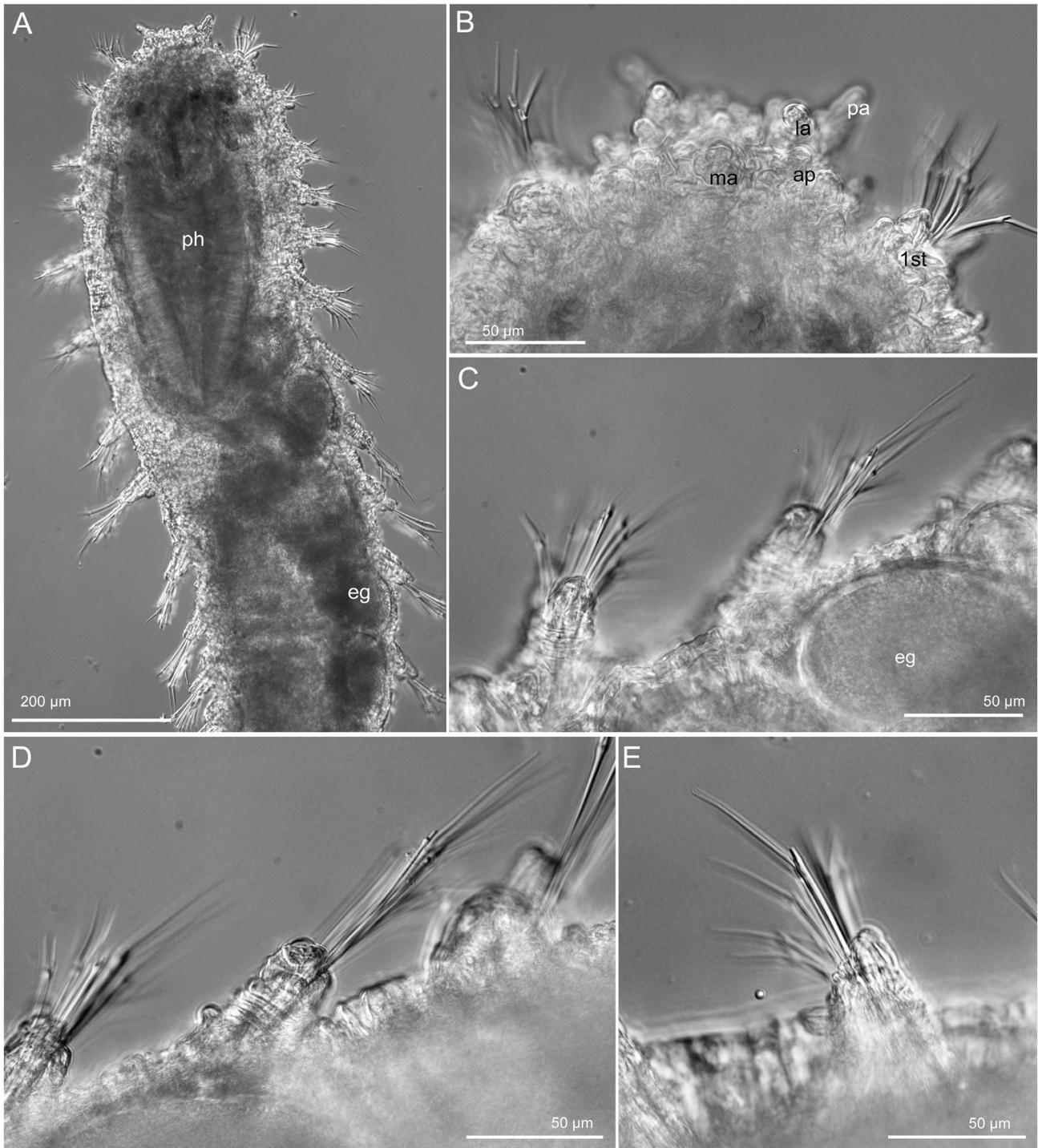


FIGURE 12. *Sphaerodoropsis longofalcigera* n. sp., holotype, NMV F.162479, light micrographs. A. Anterior end, dorsal view. B. Detail of head and first chaetiger, dorsal view. C. Parapodia chaetigers 7 and 8, dorsal view. D. Parapodial chaetigers 8 and 9, dorsal view. E. Parapodium posterior chaetiger. Abbreviations: al, acicular lobe; ap, antenniform papilla; eg, egg; la, lateral antenna; ma, median antenna; pa, palp; ph, pharynx; 1st, parapodium first chaetiger.

Tubercles. First chaetiger with two macrotubercles, slightly smaller than following, hemispherical. Rest of chaetigers with four macrotubercles each, similar in shape and size, arranged in four longitudinal rows along dorsum; distance between mid-dorsal rows slightly larger than between these and lateral macrotubercles (Fig. 4O). Spherical papillae are present over dorsum, arranged in four transversal rows per segment, total number difficult to assess. Ventral surface with spherical papillae, at least one ventral to each parapodium, but total number not possible to ascertain (Fig. 4P).

Parapodia. Parapodia sub-conical, about 2–3 times longer than wide (Fig. 12C–E), with a wide and short acicular lobe and ventral cirri similar in length, but thinner; ventral cirri decrease length towards posterior chaetigers. One spherical parapodial papilla on anterior surface of parapodia (Figs 5J, 12D).

Chaetae. Compound chaetae present in all chaetigers, arranged in a curved transverse row around acicular lobe, numbering around 10 per fascicle (Figs 5J, 12B–E). Shaft narrow with slightly widened distal end and inconspicuous spinulation (under compound microscope). Blades, thin and straight, of a wide range of lengths within same fascicle, ranging from eight to more than 25 times longer than wide (Fig. 12C–E). Longer blades in mid fascicle, and shorter in dorsal and ventral positions.

Pygidium. Pygidium terminal, with distal dorsal pear-shaped papillae and mid-ventral digitiform anal cirrus, slightly larger than posterior macrotubercles.

Internal features. Eyes not observed. Muscular pharynx occupying chaetigers 2–7 (Fig. 12A).

Reproductive features. Holotype, female with about 10 eggs measuring 150 µm, occupying the coelom, behind the muscular pharynx. Enlarged ventral cirri on chaetigers 4 and 5, may indicate the presence of ‘copulatory organs’, but this should be confirmed.

Variation. The three examined specimens are small, measuring between 0.8 and 1.2 mm long, 0.1 and 0.3 mm wide, and having around 14 chaetigers, gametes have only been observed in the holotype. Shape and relative size of head appendages similar in all specimens, but in one paratype antenniform papillae not conspicuous. No specimens were observed under SEM therefore the number and arrangement of the small epithelial papillae has not been possible to ascertain, but all specimens seem to bear dorsal papillae arranged in four transversal rows and at least one ventral papilla, near the base of parapodia, as described for holotype. The most obvious feature in this species is the maximum length of blades, reaching in all specimens up to 25 times its width.

Remarks. *Sphaerodoropsis longofalcigera* n. sp. bears dorsal macrotubercles arranged in four longitudinal rows, in a single transversal row per segment, and therefore resembles other species in the artificial Group 1, proposed by Borowski (1994). Most of these species have falcigers with long blades (e.g. Aguado & Rouse 2006). But they are particularly long and thin in *S. corrugata* Hartman & Fauchald, 1971, *S. discolis* Borowski, 1994, *S. elegans* Hartman & Fauchald, 1971, *S. longianalpapilla* Böggemann, 2009, *S. longipalpa* Hartman & Fauchald, 1971, *S. triplicata* Fauchald, 1974, together with the new species since they are up to 15 times longer than wide or longer (Table 1). The new species is the one with longest blades reaching in some chaetigers up to 25 times the length of the maximum width. The new species resembles *Sphaerephesia longiseta* Fauchald, 1972 in this attribute, the sphaerodorid with longest falcigers described to date measuring 20–30 times their maximum width. Nevertheless *S. longiseta* is characterised, as its congeners, by the presence of terminal papilla on macrotubercles (conspicuous in lateral rows in the holotype of this species). *Sphaerodoropsis longofalcigera* n. sp. shares with *S. laureci* Desbruyères, 1980, *S. protuberanca*, *S. sibuetae* Desbruyères, 1980 and *S. triplicata* the shape of dorsal macrotubercles, being hemispherical (not always described as such in original descriptions), while they are spherical or pear-shaped in the other species. Of these species, only *S. protuberanca* has similarly low number of parapodial papilla, more numerous in the other species (Fauchald 1974; Desbruyères 1980).

After the revision of type material some attributes not referred to in original descriptions have been compared here (Table 1). Several inconsistencies in the interpretation of some morphological traits with respect to the original descriptions have also been encountered, including shape of macrotubercles and number of parapodial papillae (Table 1), and other characters that will be dealt with in a further study (e.g. none of the specimens examined presented postchaetal lobes, unlike indicated in some descriptions (Fauchald 1974; Böggemann 2009).

Etymology. The name of the species is attributed to the long blade falcigers.

Distribution. Central Western Australia.

Habitat. Sediments around 400 m depth.

Sphaerodoropsis megatuberculata n. sp.

Fig. 4Q–R, 5K, 13

Sphaerodoropsis sp. MoV632 Wilson & Bakken 2003 (in part).

Material examined. Holotype: NMV F.69689, 15.5 km SW of Pt Ricardo, Eastern Bass Strait, 37° 53' 08" S, 148° 28' 56" E, 45 m, Feb 1991, medium sand. **Paratypes:** NMV F.69687 (1 spec. for SEM), 15.5 km SW of Pt Ricardo,

Eastern Bass Strait, 37° 53' 08" S, 148° 28' 56" E, 45 m, Feb 1991, medium sand; NMV F.69688 (1 spec.), 15.5 km SW of Pt Ricardo, Eastern Bass Strait, 37° 53' 08" S, 148° 28' 56" E, 45 m, 4 Jun 1991, medium sand; NMV F.69686 (1 spec. for SEM), 15.5 km SW of Pt Ricardo, Eastern Bass Strait, 37° 53' 08" S, 148° 28' 56" E, 45 m, 4 Jun 1991, medium sand; NMV F.63844 (1 spec.), 15.5 km SW of Pt Ricardo, Eastern Bass Strait, 37° 53' 10" S, 148° 28' 57" E, 45 m, 26 Sep 1990, sand-shell; NMV F.132659 (1 spec.), 14 km SW of Marlo, Eastern Bass Strait, 37° 54' 00" S, 148° 25' 07" E, 26 m, 12 Aug 1989, sand-shell; NMV F.63845 (1 spec.), 3.2 km S of Cape Conran, Eastern Bass Strait, 37° 50' 37" S, 148° 43' 28" E, 49 m, 28 Sep 1990, sand-shell; NMV F.132902 (1 spec.), 43 km SE of Port Albert, Bass Strait, 38° 53' 42" S, 147° 06' 30" E, 58 m, 18 Nov 1981.

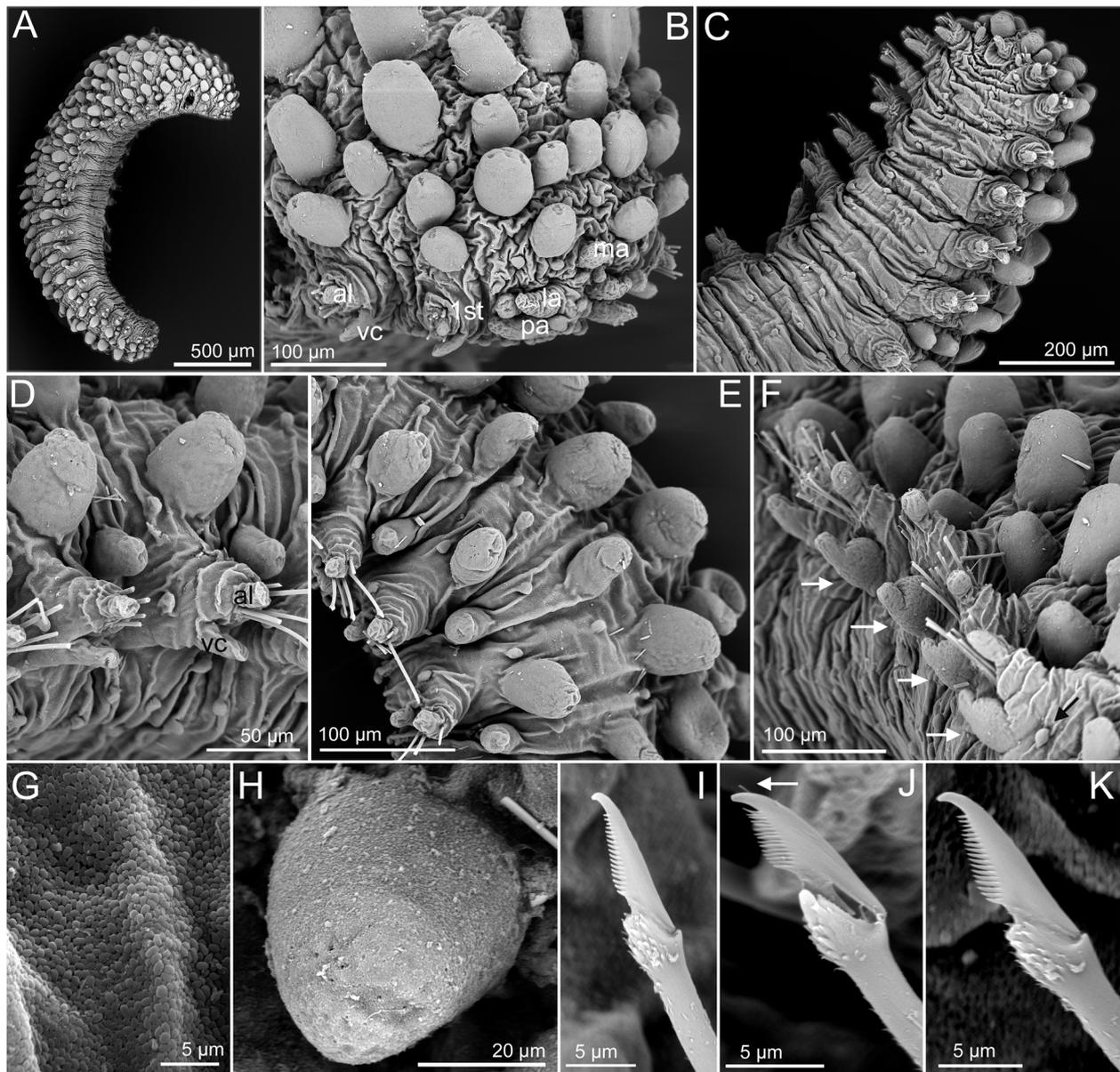


FIGURE 13. *Sphaerodoropsis megatuberculata* n. sp., NMV F.69686–7, scanning electron micrographs. A. Complete specimen lateral view. B. Anterior chaetiger and head, dorsal view. C. Posterior end, ventral view. D. Parapodia in chaetigers 6–9, anterior view. E. Mid-body chaetigers, dorso-lateral view. F. Parapodia in chaetigers 8–4 (left to right) with ‘copulatory organs’ on chaetigers 7–4 (arrows). G. Detail of ellipsoid cuticular granules. H. Detail of macrotubercle with pores scattered over the surface from posterior chaetiger. I. Compound chaeta chaetiger 4. J. Posterior chaeta, with spine on tip of blade (arrow). K. Same without distal spine. Abbreviations: al, acicular lobe; la, lateral antenna; ma, median antenna; mc, macrotubercle; pa, palp; vc, ventral cirrus; 1st, parapodium first chaetiger.

Diagnosis. Ellipsoid body with 17 longitudinal rows of large ellipsoid to cylindrical macrotubercles in two transversal rows per segment, with eight macrotubercles between parapodia and nine in posterior transversal row. Dorsum with additional spherical papillae in 2–3 transversal rows per segment; ventrum with spherical papillae in four longitudinal rows. Two parapodial papillae, one on each of anterior and posterior surfaces. Parapodia with 5–6 chaetae per fascicle, blades 2–3 times as long as wide. Females with an oval tubercle between chaetigers 5–6, males with modified ventral cirrus in chaetigers 4–7.

Description. *Measurements and general morphology.* Holotype female with ellipsoid body measuring 2.5 mm long and 0.5 mm wide, for 20 chaetigers, convex dorsum and flattened ventrum (Fig. 13A). Segmentation unremarkable, tegument with transverse wrinkles (Fig. 13C–E). Preserved specimen lacking pigmentation.

Head. Anterior end bluntly rounded. Prostomium with short appendages, including a pair of digitiform blunt lateral antennae, a pair of palps similar in shape and length to lateral antennae, median antenna half the length than lateral antennae (Fig. 13B). Tentacular cirri similar to median antenna. Antenniform papillae not observed. A few scattered spherical papillae on the head, in different sizes (Fig. 13B).

Tubercles. First chaetiger with two dorsal macrotubercles, sessile large, ellipsoid to cylindrical. Number increases towards chaetiger 5. Following chaetigers with 17 longitudinal rows of macrotubercles, arranged in double transverse rows on each segment in a zig-zag pattern (Figs 4Q, 13A–B, E), with eight macrotubercles in rows between parapodia and nine in posterior transverse rows. Macrotubercles ellipsoidal to cylindrical of different sizes (Fig. 13B, D–F), with pores mainly over the distal surface (Fig. 13H). Dorsum with additional small spherical papillae arranged in 2–3 transverse rows per segment, with 6–8 papillae per row (Figs 4Q, 13D–E). Ventral surface with spherical papillae in 4–6 (zig-zag) longitudinal rows, two rows close to parapodia and 2–4 rows in mid-body, arranged in more or less two segmental and one intersegmental transverse row, where the mid-body longitudinal rows are skewed in position compared to outer lines giving a zig-zag pattern (Figs 4R, 13C). Body epithelium with microscopic rounded granules (Fig. 13G).

Parapodia. Parapodia sub-conical, about 1–2 times longer than wide. Digitiform acicular lobe projecting anterior to chaetae, projecting beyond ventral cirri, ventral cirri slender digitiform. Two parapodial papillae, one close to base on anterior surface and one on posterior surface (Figs 5K, 13C–F).

Chaetae. Compound chaetae present in all chaetigers, arranged in a curved transverse row posterior to acicular lobe, numbering 5–7 per fascicle (Figs 5K, 13D–F). Shaft with slender distal end and strong spinulation on edge (Fig. 13I–K). Blades mostly similar in length within each fascicle and along chaetigers (2–3 times longer than maximum width), with recurved distal end and conspicuous spinulation along the proximal 3/4th length of blade (Fig. 13I–K). Some blades observed with fine distal spines on the edge opposite to serration (Fig. 13J).

Pygidium. Pygidium sub-terminal, with a mid-ventral digitiform anal cirrus (Fig. 13C).

Internal features. Eyes present in holotype, as dark brown to black spots positioned deep in integument in chaetigers 1–2. Muscular pharynx not observed.

Reproductive features. Holotype and one paratype female with ‘copulatory organs’ as oval tubercle between chaetigers 5 and 6. Males with modified ventral cirri swollen at the base, with a distal knob and surface with pores in chaetigers 4–7 (Fig. 13F). Eggs not observed.

Variation. Specimens measuring 1.5–4.5 mm long and 0.3–0.6 mm wide, for 18–23 chaetigers. Prostomial appendages barely visible in contracted specimens, in specimens relaxed appendages clearly visible and longer than shown in SEM (Fig. 13B), shape and relative length of appendages as described for holotype. Macrotubercles similar in shape in all specimens examined but in some individuals they are relatively larger than those described for holotype and observed under SEM (Fig. 13D–F). Number of macrotubercles in examined specimens agree with holotype; being six on second chaetiger, remaining chaetigers with eight between parapodia and nine in rows posterior to “parapodial row”, per segment; last chaetiger with four macrotubercles. Parapodial papilla on anterior surface of parapodia difficult to observe in stereo microscope at its position at the base of parapodia, it gives an appearance of this papilla sit on body surface in contracted specimens.

Remarks. A distinct and unique feature of *Sphaerodoropsis megatuberculata* n. sp. is the large ellipsoid to cylindrical macrotubercles, not described in any other *Sphaerodoropsis* species. This species belongs in *Sphaerodoropsis* Group 3 (*sensu* Borowski 1994), and resembles *S. solis*, but the latter has ventral ‘macrotubercles’ which are absent in *S. megatuberculata* n. sp., and has double transverse rows of six and seven macrotubercles per segment, while *S. megatuberculata* n. sp. has eight and nine. The new species also resembles *S. bisphaeroserialis*, *S. garciaalvarezi* and *S. arctowskyensis* in arrangement of macrotubercles and dorsal and ventral papillae (Moreira *et al.* 2004). With its 8+9 macrotubercles in double transverse rows per segment *S. megatuberculata* n. sp. has

higher number of macrotubercles than the group of three closely related species which all have 6+7. Further, there are differences in number and distribution of dorsal and ventral papillae between the species (Moreira *et al.* 2004). Moreira *et al.* (2004) use "microtubercles" for dorsal and "papillae" for ventral papillae, for what is termed "papillae" here. *Sphaerodoropsis megatuberculata* n. sp., *S. bisphaeroserialis*, *S. garciaalvarezi* and *S. arctowskyensis*, seem to be a group of species with close affinities (Moreira *et al.* 2004). The group also shares an austral distribution where respective species have been found in southern Australia, Sub-Antarctic and Antarctic environments.

Sexual dimorphism is observed in this species. A structure believed to be genital opening in female specimens has been observed as a disc-like tubercle immediately ventral to parapodia between chaetigers 5 and 6, being similar to what has been observed in other *Sphaerodoropsis* species (Moreira *et al.* 2004; Reuscher & Fiege 2011). In male specimens 'copulatory organs' appear as modified ventral cirri in chaetigers 4–7.

Etymology. The species is named after its characteristic enlarged and uniquely looking macrotubercles.

Type locality. 15.5 km SW of Pt Ricardo, Eastern Bass Strait (Fig. 15).

Distribution Bass Strait (Fig. 15).

Habitat. Sand, 26–58 m depth.

Sphaerodoropsis wilsoni n. sp.

Figs 4S, T, 5L, 14

Material examined. Holotype: Jervis Bay, New South Wales, Australia. NMV F. 217161, 35° 06' 04" S, 150° 44' 18" E, 22.4 m, 27 Jun 2008. **Paratypes:** NMV F.166667 (6 specs), same sample. **Additional material. New South Wales:** AM W.194299 (1 spec.), Murrays Basin, Jervis Bay, 35° 07' 30" S, 150° 45' 30" E, 17 Oct 1972, sand; AM W.42741 (1 spec.), east of Malabar, 33° 59' 11" S, 151° 17' 54" E, 83.7 m, 18 Jan 1996; AM W.42750 (2 specs), east of Malabar, 33° 58' 46" S, 151° 17' 54" E, 79.6 m, 19 Mar 1996. **Victoria:** NMV F.131344 (1 spec.), Eastern Bass Strait, 38° 32' 15" S, 146° 29' 24" E, 40 m, 11 May 1998. **South Australia:** ZMH P.18249 (1 spec. for SEM), Denial Bay, Ceduna, South Australia, Australia, 1.2 m, 30. Nov. 1975. **Western Australia:** AM W.17728 (1 spec.), Horrocks, 28° 23' S, 114° 26' E, 17 Oct 1975, sandy reef platform with calcareous algae; AM W.42676 (1 spec.), Two Peoples Bay, 2 km south-east of South Point, 34° 58' S, 118° 12' E, 10 m, 16 Dec 1983, dictyotalean algae.

Comparative material. *Sphaerodoropsis laevis* Fauchald, 1974, holotype LACM-AHF POLY 0952; paratype LACM-AHF POLY 0953; *Sphaerodoropsis martinae* Desbruyères, 1980, holotype MNHN Type 1285.

Diagnosis. Ellipsoid body with strongly convex dorsum. Four longitudinal rows of sessile and spherical dorsal macrotubercles and four transversal rows (with up to 38) of spherical papillae per segment. Distance between dorsal-most macrotubercles exceeds distance between those and lateral ones. Parapodia with digitiform acicular lobe, shorter ventral cirrus and a single rounded papilla on anterior end (often other two papillae, on anterior and posterior surfaces present). Four or six chaetae per parapodium with short blades (2–3 times longer than wide), serrated, with distal long spines; shaft with conspicuous spinulation.

Description. Measurements and general morphology. Body ellipsoid, measuring 2.3 mm long and 0.5 mm wide, with 20 chaetigers. Tegument with transverse wrinkles, segmentation inconspicuous (Fig. 14A). Dorsum convex and ventrum flattened (Fig. 14A). Preserved specimen lacking pigmentation.

Head. Anterior end bluntly rounded. Prostomium with five longer appendages, including a pair of digitiform palps, in ventral most position; a pair of lateral antennae similar in size and shape to palps; and a median antenna, about one third longer than lateral antennae (Fig. 14A–B). Antenniform papillae not observed. Around 15–20 spherical papillae are confined by prostomial appendages and the mouth (Fig. 14B). A pair of tentacular cirri similar in shape and size to lateral antenna and palps (Fig. 14B). Nuchal organ pits anterior to tentacular cirri (Fig. 14B).

Tubercles. First chaetiger with two macrotubercles spherical and sessile (Fig. 14A–B). Rest of chaetigers with four macrotubercles each, arranged in four longitudinal rows along dorsum. Distance between mid-rows is similar or slightly larger than between these and lateral macrotubercles. All macrotubercles similar in size, with distal pores arranged 4–6 groups (Fig. 14E). Spherical papillae over dorsum, arranged in four transverse rows per segment, adding 16–20 papillae between mid-macrotubercles, 6–10 between these and the lateral ones in mid-segments, and 6–8 papillae between lateral macrotubercles and parapodia (Figs 4S, 14A, C). All papillae similar in size and shape. Ventral surface with spherical papillae, arranged in three transverse rows, with around 20 papillae in mid-body segments; numbers decreasing towards posterior end (Figs 4T, 14D). Body epithelium with microscopic granules.

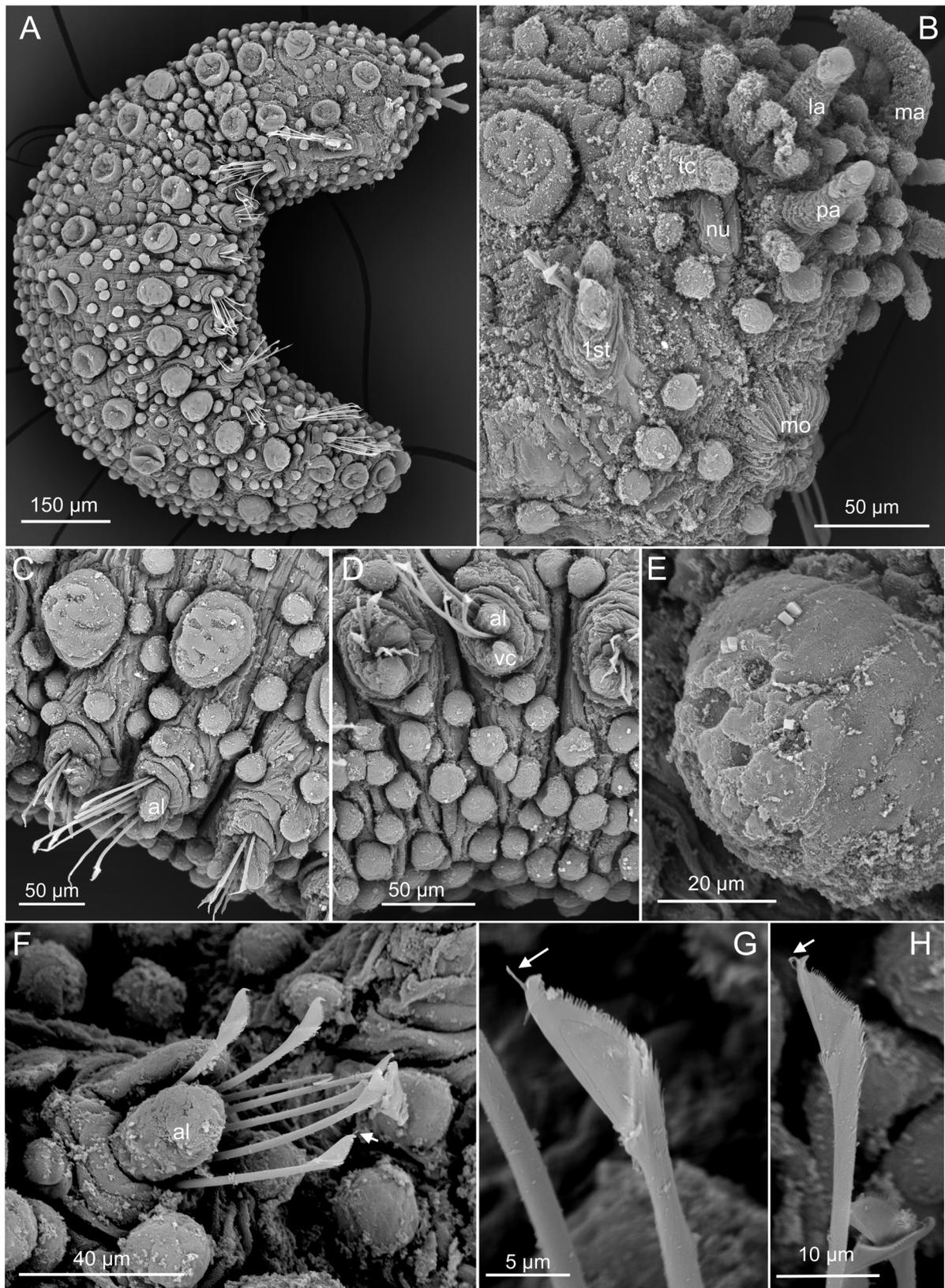


FIGURE 14. *Sphaerodoropsis wilsoni* n. sp., ZMH P.18249, scanning electron micrographs. A. Whole specimen, lateral view. B. Detail of anterior end and head appendages, lateral view. C. Mid-body chaetigers, dorsal view. D. Mid-body chaetigers, ventral view. E. Detail of lateral macrotubercle with invaginations and pores. F. Posterior parapodium and chaetal fascicle, anterior view. G. Chaetae mid-body chaetiger, with distal spine on blade (arrow). H. Chaetae posterior parapodia, with distal spine on blade (arrow). Abbreviations: al, acicular lobe; la, lateral antenna; ma, median antenna; mo, mouth; nu nuchal organ; pa, palp; tc, tentacular cirrus; vc, ventral cirrus; 1st, parapodium first chaetiger.

Parapodia. Parapodia sub-conical, about 1–2 times longer than wide. First chaetiger with digitiform acicular lobe projecting; ventral cirri similar in shape and size, parapodial papillae absent. Second and following chaetigers similar, with one anterior spherical papillae, and sometimes a dorsal papilla and/or a ventral papilla close to base of parapodia (Figs 5L, 14A, C–D, F). Acicular lobe digitiform in middle chaetigers, longer than ventral cirri (Fig. 14C, D, F).

Chaetae. Compound chaetae present in all chaetigers, arranged in a curved transverse row around acicular lobe, numbering 7–8 per fascicle (Figs 5L, 14C–D, F). Shaft with widened distal end and fine and long spinulation on edge. Blades similar in length along fascicles, wide and short (2–3 times longer than maximum width), with fine and short spinulation along superior edge and a distal recurved tip (Fig. 14F–H). One or two long and thin distal spines present behind distal tip (Fig. 14G–H). Blades showing a design on their sides with an inverted V (Fig. 14G–H).

Pygidium. Pygidium terminal, with mid-ventral anal cirrus and a pair of dorsal anal cirri, all spherical and similar in size.

Internal features. Eyes not observed on holotype, but a pair of eyes has been observed on one specimen. Muscular pharynx rounded, from first to third chaetiger.

Reproductive features. ‘Copulatory organs’ not observed in types or additional material.

Variation. Specimens measure 1.2–3mm long and 0.5–0.8mm wide, body is about 3–4 times longer than wide, with around 20 chaetigers. Macrotubercles are in all specimens spherical. Relative length of head appendages show no variation with holotype and median antenna is longer to rest of prostomial appendages, and with a distal knob. Relative length/width of parapodia and number of parapodial papillae do not vary among specimens. The dorsal papillae observed in some parapodia of the holotype, could be considered as not parapodial in some types and additional material. Methylene blue stains the ventral parapodial gland and ventral cirri of all parapodia, but not the macrotubercles. Most preserved specimens present an opaque tegument and the presence of gonads, eyes or the shape and length of the muscular pharynx could not be assessed.

Remarks. The genus *Sphaerodoropsis* is very specious but only four species have been described as having four longitudinal rows of macrotubercles (Group 1 according to Borowski 1994) and falcigers with short blades (Aguado & Rouse 2006). These are *S. exmouthensis*, re-described above; *S. laevis* Fauchald, 1974 (from Chile and Peru); *S. martinae* Desbruyères, 1980 (from the North-East Atlantic); and *S. simplex* Amoureux, Rullier and Fishelson, 1978 (from the Red Sea). *Sphaerodoropsis wilsoni* n. sp. differs from these species in the number of epithelial papillae. *Sphaerodoropsis simplex* was described without tubercles other than the macrotubercles, *S. laevis* only showed papillae around the head, and *S. exmouthensis* and *S. martinae* have only a few (less than 10 per segment), while the new species is densely covered with up to 38 papillae in mid-body segments. The new species shares some superficial morphological attributes with *S. exmouthensis* Hartmann-Schröder, 1981 (re-described above) and erroneous identifications have been found in collections. Some specimens identified as *S. exmouthensis* by Hartmann-Schröder (ZMH P.18249) belong in fact to *S. wilsoni* n. sp. Differences between these two Australian species are: the shape of macrotubercles (pear-shaped in *S. exmouthensis* and spherical in the new species), number and arrangement of epithelial papillae (scarce and different in size in *S. exmouthensis* and similar size papillae densely covering the surface in *S. wilsoni* n. sp.), and the morphology of chaetae (narrow shaft, longer blades and smooth distal end in *S. exmouthensis*, and wide shaft, short blades and distal spine in new species).

Etymology. This species is dedicated to Robin Wilson, a generous colleague and good friend, for his contribution to polychaete systematics and continuous efforts of making taxonomic information available for all of us.

Type locality. Jervis Bay, New South Wales (Fig. 15).

Distribution. Along the southern Australian coastline (New South Wales, Victoria, South Australia and Western Australia) (Fig. 15).

Ecology. Sand and algal communities, between 1–40 m depth.

Sphaerodoropsis sp.

Material examined. Western Australia: NMV F.162489 (1 spec.), Two Rocks region, 31° 41' 48" S, 114° 52' 00" E, 734 m, 5 Aug 2005.

Description. *Measurements and general morphology.* Body short and arched measuring 1.2 mm long and 0.5 mm wide, with 10 chaetigers. Dorsum convex and ventrum flattened, inconspicuous segmentation. Preserved specimen white with red fibrillar material in most macrotubercles.

Head. Retracted head, anterior appendages hard to observe in detail, but seem to consist of a median antenna, a pair of lateral antennae and a pair of palps.

Tubercles. Dorsal macrotubercles sessile and semispherical. First chaetiger with 4 macrotubercles, following chaetigers with 13 macrotubercles in double transversal rows, with six tubercles between parapodia, and seven on posterior row, macrotubercles of similar size, dorsal papillae not observed. Ventral surface with two longitudinal rows of large tubercles close to parapodia. Fibrillar material, as coiled treads, beneath the epidermis of most dorsal and ventral macrotubercles. Ventral spherical papillae in 4–6 longitudinal rows, arranged in double transversal rows per segment, and in a zig-zag pattern.

Parapodia. Parapodia wider than long. Acicular lobe only a low ridge anterior to chaetae, ventral cirri short rounded projecting beyond acicular lobe. Parapodial papillae not observed.

Chaetae. Compound chaetae present in all chaetigers in an arch posterior to acicular lobe, numbering 5–6 chaetae in each fascicle. Slender blades with recurved tip, 3–4 times longer than maximum width.

Pygidium. Pygidium with a pair of semispherical papillae, and a median rounded papilla, smaller than macrotubercles.

Reproductive features. No eggs, sperm or ‘copulatory organs’ observed.

Remarks. The single specimen is well preserved and is in good condition and seems to represent a different species than the others reported in this work. It belongs in *Sphaerodoropsis* group 3 (*sensu* Borowski 1994), and most closely resembles *S. solis* and *S. fauchaldi*, which are the *Sphaerodoropsis* species up to now described with longitudinal rows of ventral macrotubercles. The present specimen can be distinguished from *S. fauchaldi* by having a single ventral large tubercle close to the parapodia, while in *S. fauchaldi* there are two (or three) longitudinal rows on each side. It also has fewer dorsal macrotubercles, 6–7 per transversal row, compared to 12–14 (8–10) in *S. fauchaldi*. In terms of dorsal macrotubercles the present specimen is more similar to *S. solis*, but has fewer ventral papillae per segment and seems to have shorter blades of chaetae than in *S. solis*. It should, however, be noted that the present specimen is small with only 10 chaetigers and presumably not fully grown. More specimens should be found before assessing the true identity of the species, in if appropriate describe it as new.

Distribution. South Western Australia (Fig. 15).

Ecology. Sand, 734 m depth.

Sphaerodoropsis spissum (Benham, 1921)

Sphaerodorum spissum Benham, 1921: 74–77, Pl. 9, Figs 82–89.– Augener 1927: 208–210, Fig. 11.

Remarks. This species was originally described from the Sub-Antarctic Macquarie Island as a species densely covered with papillae of not exact same sizes (Benham 1921). It has been suggested that this species has longitudinal rows of macrotubercles on the ventrum (Reuscher & Fiege 2011), but this is not quite clear from the original description and illustrations. In the original description and remarks given there were obviously problems to observe necessary details, and uncertainty in observation of characters was explicitly stated (Benham 1921: 74–77). This species was reported a few years later from the head of Sydney Harbour (Augener 1927). Due to the small size of the single specimens found then (2.5 mm long), Augener had trouble observing all details and it is not unlikely that specimen belong to *S. fauchaldi* with its numerous macrotubercles distributed with no apparent pattern. It is necessary to study specimens reported as *S. spissum* to prepare a re-description in order to establish the true identity of this species. Until then, the species should not be considered to be a part of the continental Australian fauna, and should be considered known only from the original description. Nevertheless, it has not been possible to examine original or reported specimens.

Discussion

The present study reveals that both the abundance and diversity of Sphaerodoridae in Australia is larger than previously reported. The number of species described to date from continental Australia has increased from six species (Hartmann-Schröder, 1979, 1981, 1982, 1987; Capa & Rouse 2015) to 10 after the present revision. This study highlights the crucial role of natural history collections. Over 150 specimens collected since the 1970's as part of several scientific surveys and fieldtrips were available for study in the three main Australian museums, even though they had not been identified to species or described. Specimen collections are an invaluable source of data for biodiversity assessments and taxonomic revisions (e.g. Krishtalka & Humphrey 2000; Johnson *et al.* 2011; Nelson *et al.* 2013). None of the specimens examined belong to the previously reported *Sphaerodoropsis bisphaeroserialis*, *S. parva* and *S. spissum* (Augener 1927; Hartmann-Schröder 1974b, 1985), raising the question of the presence of these species in the continental Australian coastline.

The study of the Australian sphaerodorid fauna has uncovered, once more, the need of a thorough systematic revision of the family (see also Capa & Rouse 2015; Capa *et al.* in press). Some morphological attributes traditionally regarded as diagnostic for some of the sphaerodorid genera is here considered to demonstrate a continuous gradient of character states that hamper the unambiguous assignment of some of the species to a particular group. The presence of simple and/or compound chaetae, for example, is an attribute that distinguish between members of *Ephesiella*, *Ephesiopsis* Hartman & Fauchald, 1971 and *Sphaerodorum* Örsted, 1843. Several species of *Ephesiella*, including *E. australiensis* in this work, supposedly bearing only compound chaetae, are here reported to have semi-compound chaetae, and intermediate condition (e.g. Moore 1909). Similarly, members of *Sphaerodoropsis* bear typically compound chaetae (e.g. Fauchald 1974) but species such as *S. heteropapillata*, *S. multipapillata* and *S. plurituberculata* have been assigned to *Sphaerodoropsis* even if they bear semi-compound chaetae (Hartmann-Schröder 1979, 1987; Capa and Rouse 2015; present study). The wide range of shape, size and arrangement of epithelial tubercles present in the family does not correspond unequivocally to the terminology currently in use. Primary homology statements are in most of these cases lacking. There are only evidences in favor of the homology of dorsal cirri of other Phyllodocida and the 'microtubercles' found dorsal to parapodia typical of *Ephesiella*, *Ephesiopsis* and *Sphaerodorum* (Helm & Capa 2015). The term macrotubercles is used for the large protuberances, generally located on the dorsal surface, regardless if they are sessile or stalked, or if they bear a terminal papillae or not. Macrotubercles and the so called papillae seem to be only distinguished by its size, even though this may be a continuous character. For instance, the group of *Sphaerodoropsis* species gathered in the informal Group 4 *sensu* Borowski (1994) bear medium size tubercles (referred to as macrotubercles), compared to other *Sphaerodoropsis*, and arranged almost randomly but in more than two transversal rows per chaetiger. This group of species, in which *S. heteropapillata* is re-described herein and *S. plurituberculata* recently described (Capa & Rouse 2015), resemble other sphaerodorids traditionally considered as lacking macrotubercles, and described with dorsum covered by papillae, such as *Amacrodoum* Kudenov, 1987b and *Euritmia* Sardá-Borroy, 1987. In this line, the boundary between dorsal macrotubercles with a terminal papilla characteristic of *Sphaerephesia* and those described as pear-shaped in many *Sphaerodoropsis* species are not clear and several species even seem to bear the two type of tubercles (see for example Table 1).

It is suspected that further studies including molecular data will help resolving some of the issues mentioned above. Assessing the sphaerodorid evolutionary relationships is crucial for establishing the classification and evaluating the use of the morphological traits for his purpose. Molecular analyses could also reveal the species boundaries by assessing connectivity along broadly distributed species, such as *Ephesiella australiensis* or between disjunct populations like the distribution pattern described here for *Sphaerodoropsis fauchaldi*. Unfortunately, specimens appropriately fixed for molecular studies have not been available for this study.

Morphological features that seem to be species specific and may also provide some clues to resolve evolutionary relationships within Sphaerodoridae are the presence and morphology of what has been referred as 'copulatory organs' (e.g. Moreira & Parapar 2012). These structures have previously been described in species of *Sphaerodoropsis* and *Sphaerodoridium* (Moreira *et al.* 2004; Böggemann 2009; Reuscher & Fiege 2011; Moreira & Parapar 2012, 2015; Capa & Rouse 2015) but the current knowledge has increased after the present paper, including also species of *Sphaerephesia* (Table 2).

It has also been noted that spines are often present on the distal end of the chaetal blades, in the edge opposite to the typical serrated spinulation is present in several of the Australian species described herein. Revision of the

literature reveals that these spines are also present in other previously described species such as *Sphaerodoropsis garciaalvarezi* Moreira *et al.*, 2004 and in *Sphaerodorum olgae* Moreira and Parapar, 2011. These spines are only visible under SEM and further investigation could reveal if it have any systematic utility.

TABLE 3. Collecting sites for Australian sphaerodorids studied, including type locality, as shown in Fig. 15.

Species	Map	Holotype	Type locality	# samples
<i>Ephesiella australiensis</i>	A	ZMH P.16773	1	24
<i>Sphaerephesia hutchingsae</i> n. sp.	B	AM W.42748	2	44
<i>Sphaerephesia</i> sp.	B	-	-	1
<i>Sphaerodoropsis exmouthensis</i>	A	ZMH P.16493	8	3
<i>Sphaerodoropsis fauchaldi</i>	A	ZMH P.15486	4	17
<i>Sphaerodoropsis heteropapillata</i>	B	ZMH P.18875	5	5
<i>Sphaerodoropsis longofalcigera</i> n. sp.	A	NMV F.162479	6	3
<i>Sphaerodoropsis megatuberculata</i> n. sp.	B	NMV F.69689	7	7
<i>Sphaerodoropsis wilsoni</i> n. sp.	B	NMV F.217161	3	12
<i>Sphaerodoropsis</i> sp.	A	-	-	1

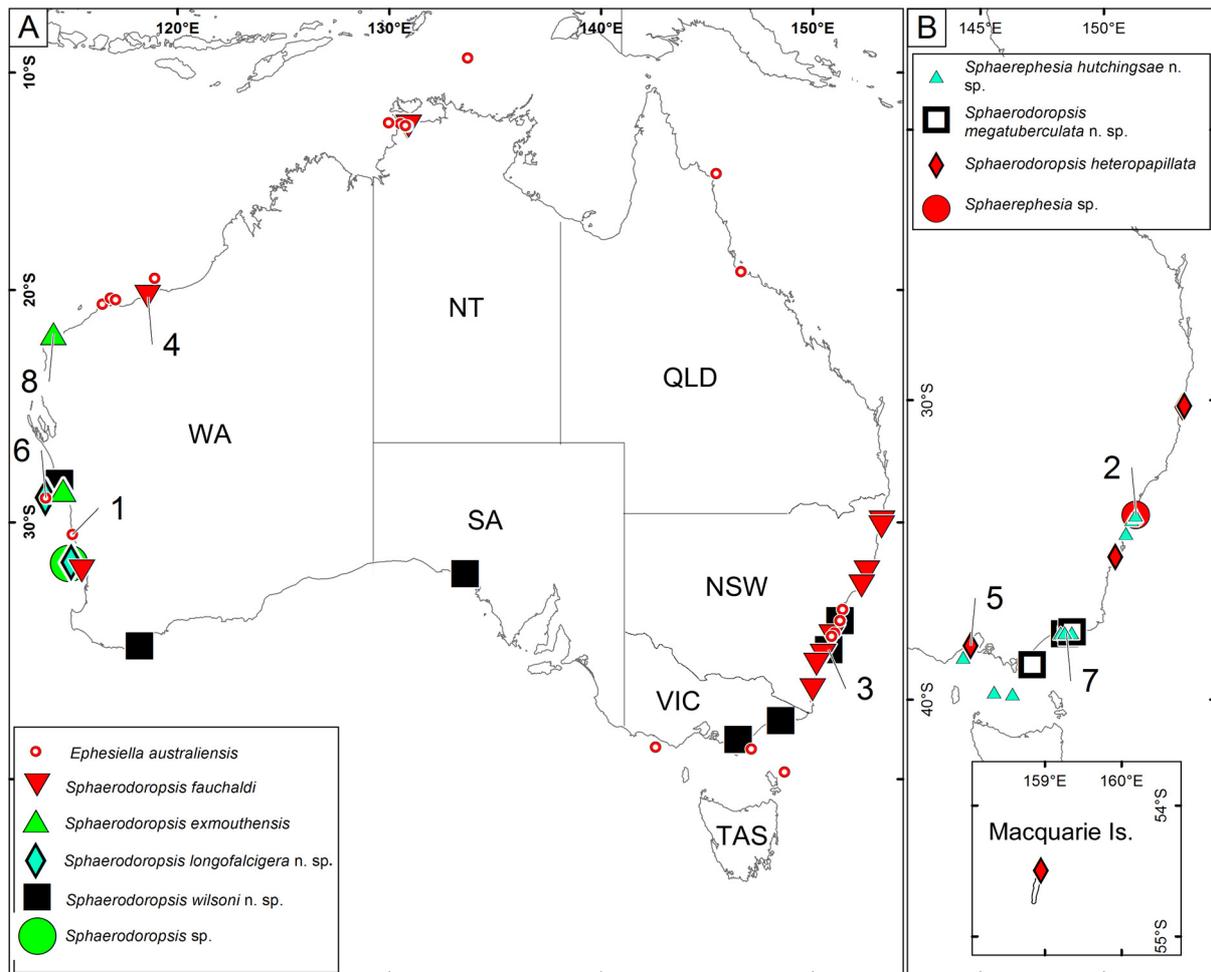


FIGURE 15. Map of Australia with collecting sites of the different species found in Australian waters (as in Table 3). A. Outline of continental Australia. B. Detail of south eastern coastline and Macquarie Island. Type locality marked by numbers and plotted according to table 3. Abbreviations: NSW, New South Wales; NT, Northern Territory; SA, South Australia; TAS, Tasmania; QLD, Queensland; WA, Western Australia.

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