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Dallithyris and *Liothyrella* from southeastern Australia with description of a new species of *Liothyrella* (Brachiopoda: Terebratulidae)

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Abstract

Brachiopod material attributed to *Dallithyris fulva* (Blochmann, 1906) from the collections of the Tasmanian Museum and Art Gallery was assessed relative to type material, permitting an updated description of the species to be prepared, and for the morphometric variation in the species to be better understood. Specimens confused with *D. fulva* were found to be attributable to a new species in the related genus *Liothyrella*, the first confirmation of this genus from southern Australia. The new species, described as *L. southernsurveyori* **sp. nov.**, is restricted to waters off southern, eastern and western Tasmania, and is particularly abundant on seamounts between 512–1650 m depth.

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Introduction

Recent efforts have highlighted the diversity of brachiopods off southeastern Australia (Richardson 1997, Verhoeff 2023a, 2023b), increasing the number of known genera and species from the region, and providing redescrptions to enable better identifications in future. The members of Family Terebratulidae Gray, 1840 from Australian waters have received little taxonomic attention despite being well represented in the collections of Australian museums.

Two genera within Terebratulidae have been reported from either Australian waters or the Australian Antarctic Territories. *Liothyrella* Thomson, 1916 (subfamily Tere-

bratulinae Gray, 1840) is well known from the Australian Antarctic Territories (AAT) (Foster 1974) and also occurs off New Zealand (Thomson 1918, Foster 1989), but hasn't been recorded from the waters around Australia. The subfamily Dallithyridinae Katz & Popov, 1974 is represented off southern and southeastern Australia by the species *Dallithyris fulva* (Blochmann, 1906), which has been recorded widely from southeastern Australia (Richardson 1997, Zezina 2010). Four other species in the genus have been recorded from the Pacific and Indian Oceans (*D. dubia* Cooper, 1981 from the southern Indian Ocean; *D. murrayi* Muir-Wood, 1959 from the central Indian Ocean; *D. pacifica* Bitner, 2006 from Fiji, western Pacific; and *D. tahitiensis* Bitner, 2014 from French

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Polynesia, central Pacific). The closely related genera *Stenosarina* Cooper, 1977 and *Kanakythyris* Laurin, 1997 have been reported from areas adjacent to eastern Australia (New Caledonia and the Norfolk Ridges, and the Indian Ocean) (Laurin 1997, Bitner 2009, 2015).

Examination of a large collection of putative *Dallithyris* material housed in the Tasmanian Museum and Art Gallery (TMAG) collections, revealed the presence of two intermixed species (the family being excluded from Verhoeff's 2023a coverage for this reason). Herein a re-description is provided for *Dallithyris fulva*, using type material, and description is provided for a new species attributed to genus *Liothyrella*.

Methods

All brachiopod material examined at the Tasmanian Museum and Art Gallery (TMAG) was collected by the Commonwealth Scientific and Industrial Research Organisation (CSIRO) or fisheries vessels. Material was collected during nine research voyages by the CSIRO over 1987–2018 using the FRV *Soela* (SO), RV *Southern Surveyor* (SS), and RV *Investigator* (IN); these surveys used epibenthic sled or beam trawl gear. CSIRO surveys comprised: SO198704 (Jun 1987), SS199305 (Jul–Aug 1993), SS199405 (Aug–Sept 1994), SS199701 (Jan–Feb 1997), SS199903 (July–Aug 1999), SS200001 (Apr–May 2000), SS200702 (Mar–Apr 2007), IN2017_E02 (Mar–Apr 2017), and IN2018_V06 (Nov–Dec, 2018). Small collections of additional brachiopod material were obtained by fisheries vessel FV *Derwent Hunter* (1979), FRV *Challenger* (chartered by the Tasmanian Fisheries Development Authority (TFDA) or Tasmanian Sea Fisheries Division from 1981–1985 for trawl surveys around southeastern Australia*), and lastly by the Japanese fisheries research vessel RV *Umitaka Maru* which sampled off Tasmania in Jan 1968. Specimen collection localities are depicted on **Figure 1 A**.

*The only specimen relevant herein collected by FRV *Challenger* (31.iii.1982, off SE Tasmania at 1000 m according to the original label) is difficult to locate in trawl records, the date is conspicuously absent from the otherwise complete listings of *Challenger* trawls by Ford & Lyle (1992) (gap between 04.iii.1982–20.iv.1982, over *Challenger* cruises CR036–CR040). However Wilson (May 1982) in a footnote notes that the *Challenger* "early last month" (end-Mar/start-April) "...took more orange roughly in 960 metres off the Hippolites, just near Eaglehawk Neck, on the south-east coast of Tasmania.", consistent with the label information.

Material collected prior to 1999 on CSIRO voyages was formalin fixed at sea (5% seawater formalin) and transferred to ethanol, material from 1999 onwards seems to have been ethanol fixed only.

Measurement data was collected from 126 individuals across 44 specimen lots; in material examined sections, for a given registered lot the number of individuals is

given in square brackets (e.g., "E21032 [$\times 2$]"). Overall terminology, abbreviations and indices follow that used by Verhoeff (2023a), with the basic units of valve length (L), width (W), and thickness (T), along with beak length (BkL) depicted (**Fig. 1 B, C**). Indices are introduced to describe the cardinalia and loop: loop width index defined as the crura width (CrW) as percentage of the loop width (LpW) (see **Fig. 1 D**), loop length index defined as the loop length (Lp L) as percentage of the length from the base of the cardinal process to the anterior edge of the loop (Lp-CP L) (**Fig. 1 D**). The outer hinge plate (OHP) internal angle (at which plates diverge) is also assessed (**Fig. 1 D**).

Measurements and statistical testing: Statistical tests to compare each index between the two species used Student's *t*-test (two tailed, two sample unequal variance).

General abbreviations: BMNH—British Museum (Natural History) London, CSIRO—Commonwealth Scientific and Industrial Research Organisation, NE—northeast, RV—research vessel, SD—standard deviation; SE—southeast, Stn—station, TFDA—Tasmanian Fisheries Development Authority, ZMB—Museum für Naturkunde Berlin.

Morphological and Figure abbreviations: AC—anterior commissure, Ad—adductor muscle, Bk—beak, BR—beak ridge, CP—cardinal process, Cr—crura, CrP—crural process, DB—descending branch of brachidium, DP—deltidial plates, Fo—foramen, Gr—groove, HT—hinge tooth (teeth), ISR—inner socket ridge, LC—lateral commissure, MS—median septum, My—myophore, OHP—outer hinge plate, OSR—outer socket ridge, Pe—pedicle, Ri—ridge, So—socket, Sy—symphytium (fused DP's), TB—transverse band of brachidium.

Results

Valve length (L), width (W), and thickness (T) averages and ranges were calculated, along with the ratios of W%L, T%L, and T%W per methods, with standard deviations also calculated (see **Table 1**).

Indices (W%L, T%L, and T%W) were compared between *Dallithyris fulva* and *Liothyrella southernsurveyori* sp. nov. Graphing valve width vs. valve length revealed that the two species showed proportional increase in width that conformed well to linear relationships with similar gradients (similar rate of width increase), though *L. southernsurveyori* sp. nov. had proportionally greater valve width and thickness across the entire length range (see **Fig. 2 A, B**).

The T%W ratio separated the species, with the rate of thickness increase outpacing width when compared to length (i.e., linear relationships had increased gradients), and *D. fulva* had proportionally greater thickness overall (excepting some very large and thickened *L. southernsurveyori* sp. nov. specimens) (see **Fig. 2 C**).

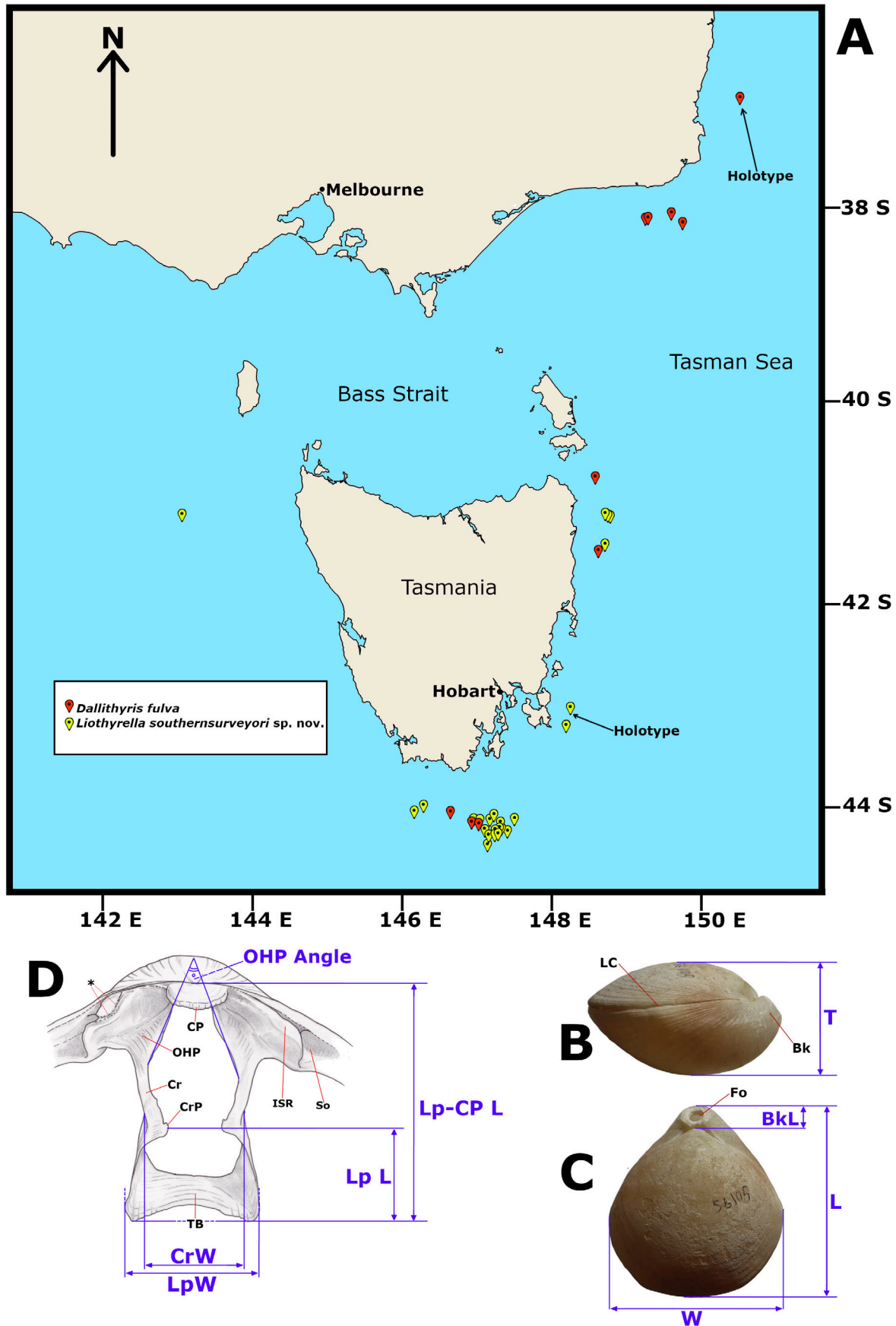


Figure 1. **A**) Locations for specimens examined in this research (species markers coloured per key, with holotype material marked). **B, C**) lateral and dorsal aspects respectively, illustrating standard valve length, width, and thickness measurements, along with beak length. **D**) Loop and cardinalia dimensions and angles. Abbreviations per Methods.

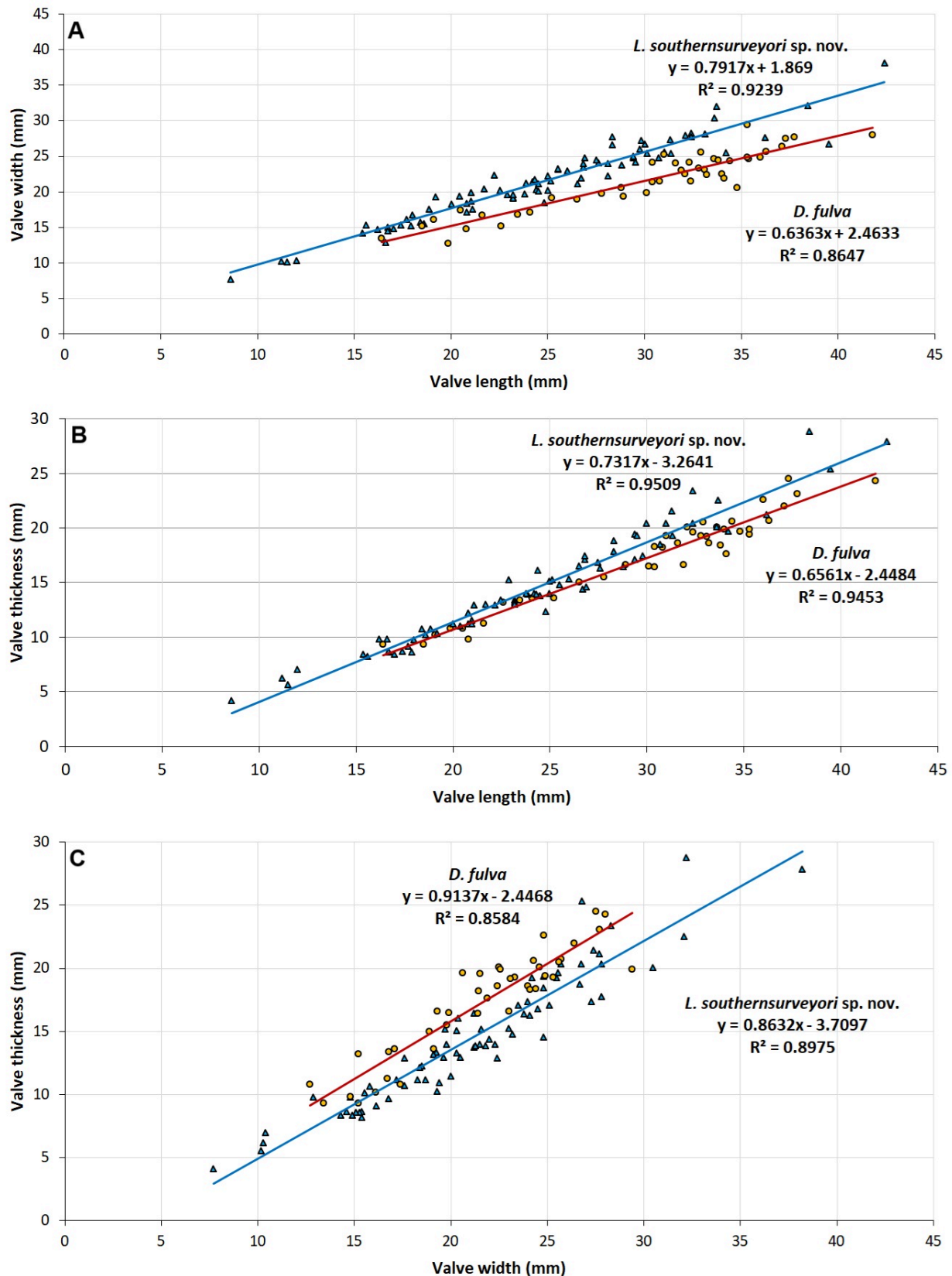


Figure 2. Morphometric comparisons of *Dallithyris fulva* (orange points) and *Liothyrella southernsurveyori* sp. nov. (blue triangles) based on TMAG material. **A)** relationships of valve width relative to valve thickness (*L. southernsurveyori* sp. nov., n = 81; *D. fulva*, n = 44). **B)** relationships of valve thickness relative to valve length (*L. southernsurveyori* sp. nov., n = 73; *D. fulva*, n = 41). **C)** relationships of valve thickness relative to valve width (*L. southernsurveyori* sp. nov., n = 73; *D. fulva*, n = 41). Linear regression equations with R² (coefficient of determination) values are added above and below respective datasets.

	<i>Dallithyris fulva</i>	<i>Liothyrella southernsurveyori</i> sp. nov.
L Average (Range)	30.14 mm (16.4–41.8 mm)	24.75 mm (8.6–42.4 mm)
W Average (Range)	21.64 mm (12.7–29.4 mm)	21.46 mm (7.7–38.2 mm)
T Average (Range)	17.23 mm (9.3–24.5 mm)	14.51 mm (4.2–28.8 mm)
W%L Average (Range)	72.23% (59.20–84.88%)	87.26% (67.85–100.90%)
STDEV W%L	5.74	5.77
T%L Average (Range)	57.03% (47.12–65.68%)	58.67 (48.05–75.00%)
STDEV T%L	3.79	5.62
T%W Average (Range)	79.45% (61.18–95.39%)	67.46% (53.25–94.78%)
STDEV T%W	8.30	8.58

Table 1. Measurement and index comparisons between TMAG *Dallithyris fulva* and *Liothyrella southernsurveyori* sp. nov. specimens. Measurements and indices are depicted as averages and as ranges (in parentheses), with standard deviations presented for indices.

Statistical comparison of the W%L, T%W, and T%L ratios between the two species, using Student's *t*-test, indicated that the species differed in W%L and T%W with statistical significance ($P < 0.0001$), but not T%L ($P = 0.07$).

Discussion

The present work adds an additional species and genus to the Australian brachiopod fauna. Both *Dallithyris fulva* and *Liothyrella southernsurveyori* sp. nov. are endemic to southern and southeastern Australia, a region that seems to have a relatively high biodiversity for brachiopods and a relatively high level of brachiopod endemism (see species and distributions in Richardson 1987, 1997, Verhoeff 2023a, 2023b). This is the first confirmation of genus *Liothyrella* from the Australian EEZ (Emig 2025's *Brachiopoda in the Antarctic Benthos [Atlas]* maps an occurrence of "*Liothyrella uva*" from southeastern Australia, but this seems to be the mistaken inclusion of the type specimen of *Dallithyris fulva*, which was originally recorded by Davidson 1880 as *Terebratula* (now *Liothyrella*) *uva*).

Re-describing *Dallithyris fulva*, including its type specimen, was primarily done to help better define the species and its intraspecific variation, this was important given that the species seemed to be both rather variable, and was apparently intermixed with a superficially similar unidentified terebratulid brachiopod (confounding accurate identifications). This unidentified terebratulid was identified as a new species of *Liothyrella* (*L. southernsurveyori* sp. nov.). With a better definition, and description of variability, *D. fulva* can be more fully compared to other representatives of *Dallithyris*, revealing it to be probably the largest species in the genus at 42 mm long, and to be rather distinct from most other *Dallithyris* given its relatively elongate form. As was found with other southeastern Australian brachiopods (per Verhoeff 2023a, 2023b), *D. fulva* was far more variable than previously appreciated in its overall indices, commissure form, and brachidium structure (creating some overlap in morphology with similar species). The regression equations of W%L, T%L, and T%W indices were also found to be a viable way of separating *D.*

fulva from the superficially similar *L. southernsurveyori* sp. nov.

It is hoped that enabling more accurate identification of Australian brachiopods will pave the way for the necessary study of their molecular biology, life cycle, and food-web interactions (which have been rather neglected).

Around southeastern Australia *Dallithyris fulva* seems to form part of a highly diverse shallow shelf to upper slope fauna (most records occurring between 130–610 m depth) attaching to hard substrates (along with *Campages furcifera* Hedley, 1905 (48–439 m), *Jaffaia jaffaensis* (Blochmann, 1910) (67–550 m), *Magellania flavescens* (Lamarck, 1819) (0–300 m), *Argyrotheca australis* (Blochmann, 1910), *Cancellothyris hedleyi* (Finlay, 1927) (2–440), and *Novocrania huttoni* (Thomson, 1916) (640 m, single specimen east of Flinders Is)) (see Richardson 1997, Robinson 2017, Verhoeff 2023a); this fauna is relatively distinct from a shallow shelf to upper slope fauna that is free-living on sands/gravels (e.g., *Anakinetica cumingi* (Davidson, 1852) (22–3155 m), *Parakinetica stewartii* Richardson, 1987 (77–115 m), *Pirothyris vercoi* (Blochmann, 1910) (22–300 m), and *Basiliolella colurnus* (Hedley, 1905) (150–300 m)) (Richardson 1987, 1997, Verhoeff 2023b).

The species *L. southernsurveyori* sp. nov. occurs much deeper (mostly 512–1650 m), and on the many seamounts around southern Tasmania it seems to be one of the more abundant species within a distinctly deeper occurring fauna along with *Dallina tasmaniaensis* Verhoeff, 2023a (1157–1712 m), *Neorhynchia strebeli* (Dall, 1908) (1157–1712 m), and possibly *Abyssothyris wyvillei* (Davidson, 1878) (1426–5000 m), with these species attaching to the hard rock and coral substrates that the seamounts provide (Richardson 1997, Verhoeff 2023a). The rough separation of these brachiopod faunal assemblages off southeastern Australia, into groups favouring different substrates and bathymetric ranges, may partially explain the high species diversity in the region.

The genus *Liothyrella* contains five accepted species (WoRMS 2025), *L. uva* (Broderip, 1833) from around Antarctica, and several species at widely dispersed temperate-sub-Antarctic locations: *L. delsolari* Cooper, 1982 from the eastern Pacific off Peru, *L. moseleyi* (Davidson, 1878) from Iles Crozet (SW Indian Ocean) (Foster 1974), *L. neozelanica* Thomson, 1918 from New Zealand (Foster 1989), and *L. winteri* (Blochmann, 1906) from southern Indian Ocean (St. Paul and Kerguelen islands); and to this *L. southernsurveyori* sp. nov. is added from far south-eastern Australia.

The species *Liothyrella neozelanica* is particularly interesting given its close geographic proximity to the Australian species (see comparison in following taxonomy section remarks), and the presence of *Liothyrella* (generally an Antarctic and sub-Antarctic genus) off southern Tasmania and New Zealand (similar latitude ~38–48° S) may indicate similarities between the Antarctic/sub-Antarctic brachiopod fauna with that of far southern Australia (at least Tasmania) and New Zealand. New Zealand shares several sub-Antarctic brachiopod species with Macquarie Island, an Australian Antarctic Territory south of Tasmania (latitude 54–54° S). Macquarie Island's recorded articulate brachiopods are *Gyrothyris mawsoni* Thomson, 1918, *Aerothyris macquariensis* (Thomson, 1918) (Foster 1974, Dawson 1988), and *Magellania joubini* Blochmann, 1906 (Foster 1989), with the former two very abundant at shallow depths (< 200 m) and shared with waters around New Zealand, and the last is shared with Antarctic waters (Dawson 1988, Foster 1989). These species have yet to turn up in southern Australian material, but intriguingly NIWA (National Institute of Water and Atmospheric Research, New Zealand) collections hold several *Liothyrella* sp. specimens from off Macquarie Island (identified J. Robinson), which may show a similarity to either the Tasmanian, New Zealand or Antarctic species assuming they are correctly identified.

The genetic relationships between *Liothyrella* from Tasmania, New Zealand, Kerguelen, Macquarie Island, and other sub-Antarctic and temperate locations, relative to the much larger population of circum-Antarctic *L. uva* (Broderip, 1833), may prove rather interesting.

Looking at the distribution, and apparent diversity of the *Liothyrella* species across the isolated sub-Antarctic and temperate populations, it may be hypothesized that *Liothyrella* originated in the Antarctic and has spread north to the various sub-Antarctic/temperate locations, perhaps using Macquarie island as a 'stepping stone' to found the New Zealand and Australian species. The extensive distribution of *Liothyrella* around Antarctica, and the high variability of the species there (resulting in authors describing a dozen or so now synonymized species and subspecies, now all *L. uva* (Foster 1974, Emig 2025)) may support this hypothesis.

Alternatively these *Liothyrella* populations (at least across Antarctica, southern Australia, and New Zealand) may be the remnants of a larger Gondwanan fauna that has been separated. By the late Cretaceous – early-Cenozoic (Tertiary), Antarctica, Australia and New Zealand were closely associated, with New Zealand separating off first (late Cretaceous–Palaeocene), and Australia and Antarctica separating later (late-Palaeocene, ~53 million years ago, the gap opening west–east and progressively widening into the Eocene, ~30 million years ago) (Veevers & McElhinny 1976, Craig 2002). Cenozoic fossil *Liothyrella* have been recorded from New Zealand (Eocene–Miocene), Australia (Paleocene–Eocene), and the Antarctic Peninsula (Eocene), indicating that an original Gondwanan *Liothyrella* fauna was separated as Gondwana broke up and the basins of the Tasman Sea and Southern Ocean formed (Craig 2001, 2002). Therefore, it may be hypothesized that the extant species of *Liothyrella* off New Zealand and southern Australia have evolved from these long separated populations (rather than extinction of the cenozoic Australian and New Zealand species, followed by re-colonizing from Antarctica more recently).

These two hypotheses could be tested genetically if sufficient tissue samples can be collected across the different *Liothyrella* populations (similar to what was recently done with Southern Ocean and Antarctic octopods (Strugnell et al. 2008)). Molecular work has already shown the New Zealand species *L. neozelanica* to be distinct from *L. uva* (Bitner & Cohen 2015), but it remains to be seen if the other sub-Antarctic and temperate species are similarly distinct.

Taxonomy

Phylum **BRACHIOPODA** Dumeril, 1805

Sub-Phylum **Rhynchonelliformea** Williams, Carlson, Brunton, Holmer & Popov, 1996

Class **Rhynchonellata** Williams, Carlson, Brunton, Holmer & Popov, 1996

Order **Terebratulida** Waagen, 1883

Sub-Order **Terebratulidina** Waagen, 1883

Super-family **Terebratuloidea** Gray, 1840

Family **Terebratulidae** Gray, 1840

Subfamily Dallithyridinae Katz & Popov, 1974

Type genus: *Dallithyris* Muir-Wood, 1959

Diagnosis: Medium to large, smooth, strongly biconvex or ventri-biconvex; symphytium partially visible; pedicle collar short, teeth very small; crural bases broad, blunt; loop small, narrow; transverse band broad, with strong median fold. (Lee & Smirnova 2006, p. 2061)

Description: Per diagnosis.

Genus *Dallithyris* Muir-Wood, 1959

Type species: *Dallithyris murrayi* Muir-Wood, 1959 (by original diagnosis).

Diagnosis: Medium to large, subtrigonal to subpentagonal; ventribiconvex, anterior commissure rectimarginate to broadly uniplicate; beak suberect, short, labiate; foramen large, submesothyrid to mesothyridid; symphytium short; cardinal process a small semiellipse; outer hinge plates broadly triangular, crural bases poorly defined; loop narrow (width similar to width across crural bases, loop without pronounced anterior expansion in width), relatively short (transverse band only slightly longer than width), variable. (modified from Lee & Smirnova 2006, p. 2061).

Description: Per diagnosis.

Remarks: Cooper (1983, pp. 256–257) created the genus *Epacrosina*, comprising *Liothyryna fulva* Blochmann, 1906 as the type species as well as *Tichosina elongata* Cooper, 1977. This genus was diagnosed as follows: “Elongate oval, rectimarginate terebratulaceans with broad-banded, anteriorly narrowed loop with outer hinge plates attached to the dorsal side of the crural bases”. Genus *Epacrosina* was still recognized by Richardson (1997) for the Australian species, but was synonymized by the Treatise (Vol. 5, 2006, p. 2061), as it wasn't differentiated strongly from *Dallithyris* at a genus level (subjective synonym).

Dallithyris and *Stenosarina* are rather clearly distinguished from *Kanakythyris* given the latter genus' strongly biconvex form (vs. ventribiconvex), unisulcate anterior commissure (vs. rectimarginate–broadly uniplicate), and incurved beak (vs. sub-erect). *Dallithyris* and *Stenosarina* are closer morphologically, *Stenosarina* are generally elongate triangular, and have narrower and more tapering outer hinge plates compared to *Dallithyris* and crural bases elevated along inner hinge plate margins. The loop of *Stenosarina* is narrower compared to *Dallithyris*, and distinctly longer in the antero-posterior axis (length from crural processes to anteriormost edge of loop far exceeding distance from crural processes to base of cardinal process).

The above diagnosis for genus *Dallithyris* has only been slightly modified from the Treatise (Lee & Smirnova 2006, p. 2061), adding that the beak can be mesothyridid, and defining the width and length of the loop.

Dallithyris fulva (Blochmann, 1906)

Figs. 3–5; Table 2

Synonymy

Terebratula uva: as illustrated by Davidson 1880 (Plate 2, fig. 3, 4)

Liothyryna fulva Blochmann (original combination), 1906, Blochmann 1908 (fig. 22 a,b, fig. 26)

Terebratula (Liothyryna) fulva: Blochmann 1913

Liothyrella fulva: Thomson 1918

Gryphus fulva: Thomson 1927

Epacrosina fulva: Cooper 1983, Richardson 1997 (fig. 19.10a,b)

Dallithyris (Epacrosina) fulva: Zezina 2010

Type specimen at the Natural History Museum, London (**BMNH ZB 1314**).

Diagnosis: *Dallithyris* of large size (up to 42 mm long), generally elongate oval to subpentagonal in outline, with widest point ~midway along valve length, with lateral commissure flat or curved dorsally, and with anterior commissure directed ventrally and flat medially (rectimarginate). Outer hinge plates broad-triangular (OHP angle 23–27°), loop variable, crura poorly-differentiated from hinge plates, narrow (loop width index 84%–93%) and elongate (loop length index 40%–48%), with weak to strong median fold. Beak suberect and with foramen large.

Description

Overall valve form: Maximum valve length 41.8 mm (average 30.1 mm, SD 6.1, smallest observed length 16.4 mm), exceeding maximum length 40 mm reported by Richardson (1997); longer than wide, W%L averaging 72.2% (SD 5.7%, range 59.2%–84.9%), and relatively thick, T%L averaging 57.0% (SD 3.8%, range 47.1%–65.7%).

Overall outline (viewed dorso-ventrally) elongate ovoid to sub-pentagonal with widest point approximately midway along length (e.g., **Fig. 3 A, B** holotype; longer specimens **Fig. 4 D, G, J, M**; shorter specimens **Fig. 4 A, P**), juvenile specimens more rounded (**Fig. 4 S, V**). In lateral profile valves ventri-biconvex, i.e., with the ventral valve slightly deeper than dorsal valve. Lateral commissure variable, gently to moderately arched (convex) towards dorsal valve medially (lateral commissure more strongly convex, see **Fig. 4 B, E, Q**; or more weakly convex, see **Fig. 4 H, K, N, T**; as well as for holotype **Fig. 3 E**). Anteriorly the lateral commissure descends ventrally where it meets the flat, rectimarginate, anterior commissure (see anterior profile in **Fig. 4 C, F, I, L, O, R**; holotype **Fig. 3 D**), in juvenile specimens the anterior commissure is an arc with a subtle ventral deflection (**Fig. 4 U, W**).

Valves punctate, thicker on larger specimens, growth striae clearly visible on most specimens (especially larger and older specimens), with very faint and fine radial marks present (not developed as distinct radial ribs/costae). Colouration white to yellowish-brown.

Dorsal (brachial) valve: Cardinal process, produced as a small half-circle shaped plate folded anteriorly from the umbo, and having a rough-surfaced muscle attachment patch (myophore) on the posterior face (see **Fig. 5 A–G**).

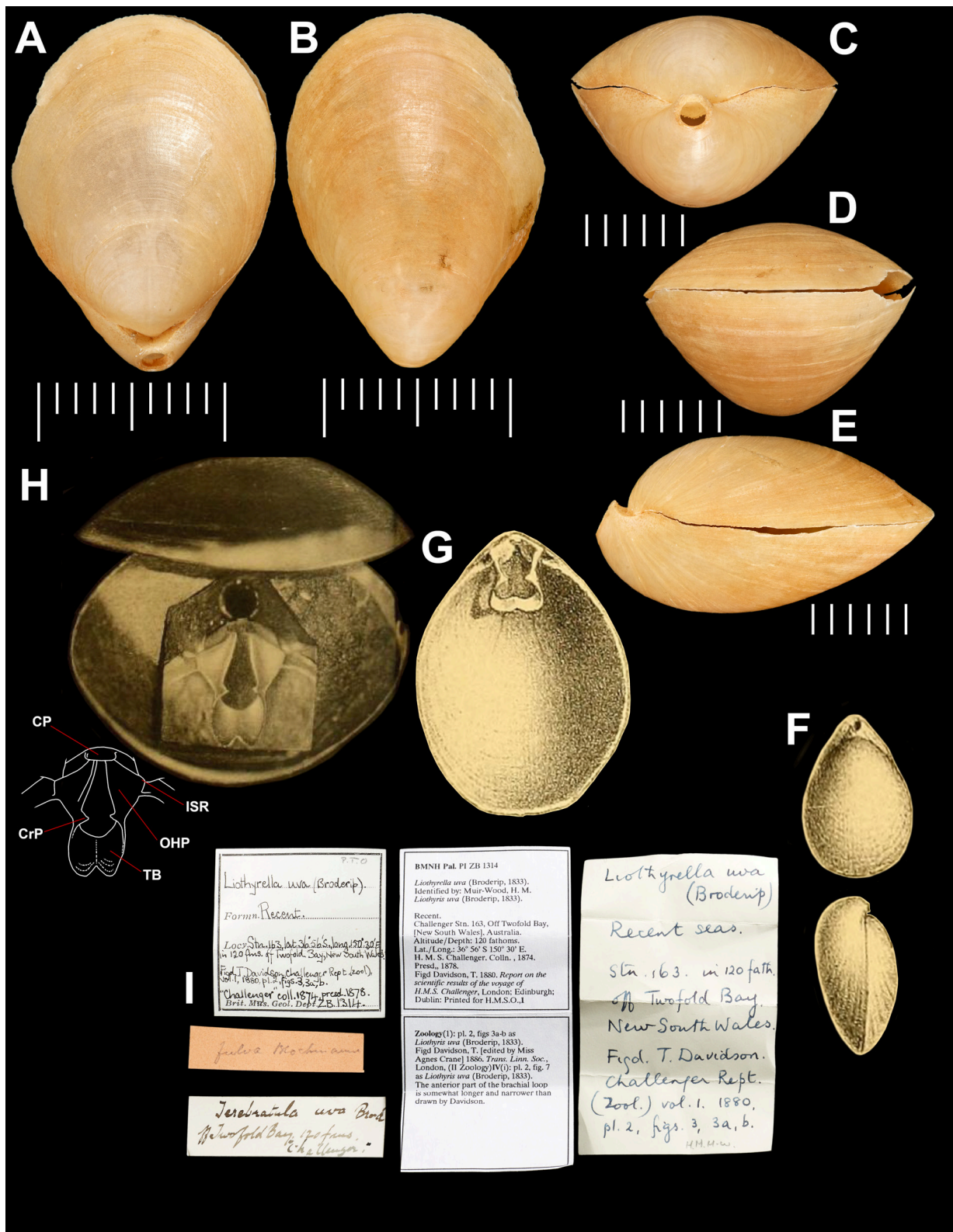


Figure 3. *Dallithyris fulva* Holotype (BMNH ZB 1314). **A, B**) Dorsal and ventral aspects respectively. **C**) Posterior aspect. **D**) Anterior aspect (ventral valve lowermost). **E**) Lateral aspect. **F**) Dorsal and lateral aspects as illustrated by Davidson (1880: Plate II, fig 3a). **G**) Interior of dorsal valve with loop as drawn/reconstructed by Davidson (1880: Plate II, fig 3b), Davidson never disarticulated the valves of this specimen with the illustration being a reconstruction (with some inaccuracies in the loop and cardinal area). **H**) Loop photography of holotype by Blochmann (1908: fig 26), inset at lower-left depicts loop as a line illustration; compare the rather different loop form relative to 'G'. **I**) various labels stored with the holotype specimen. Photography (**A–E**) provided by Zoë Hughes, Natural History Museum London (used with permission). Abbreviations per Methods (* denotes damage), scale bars: in mm marks (provided with photography).

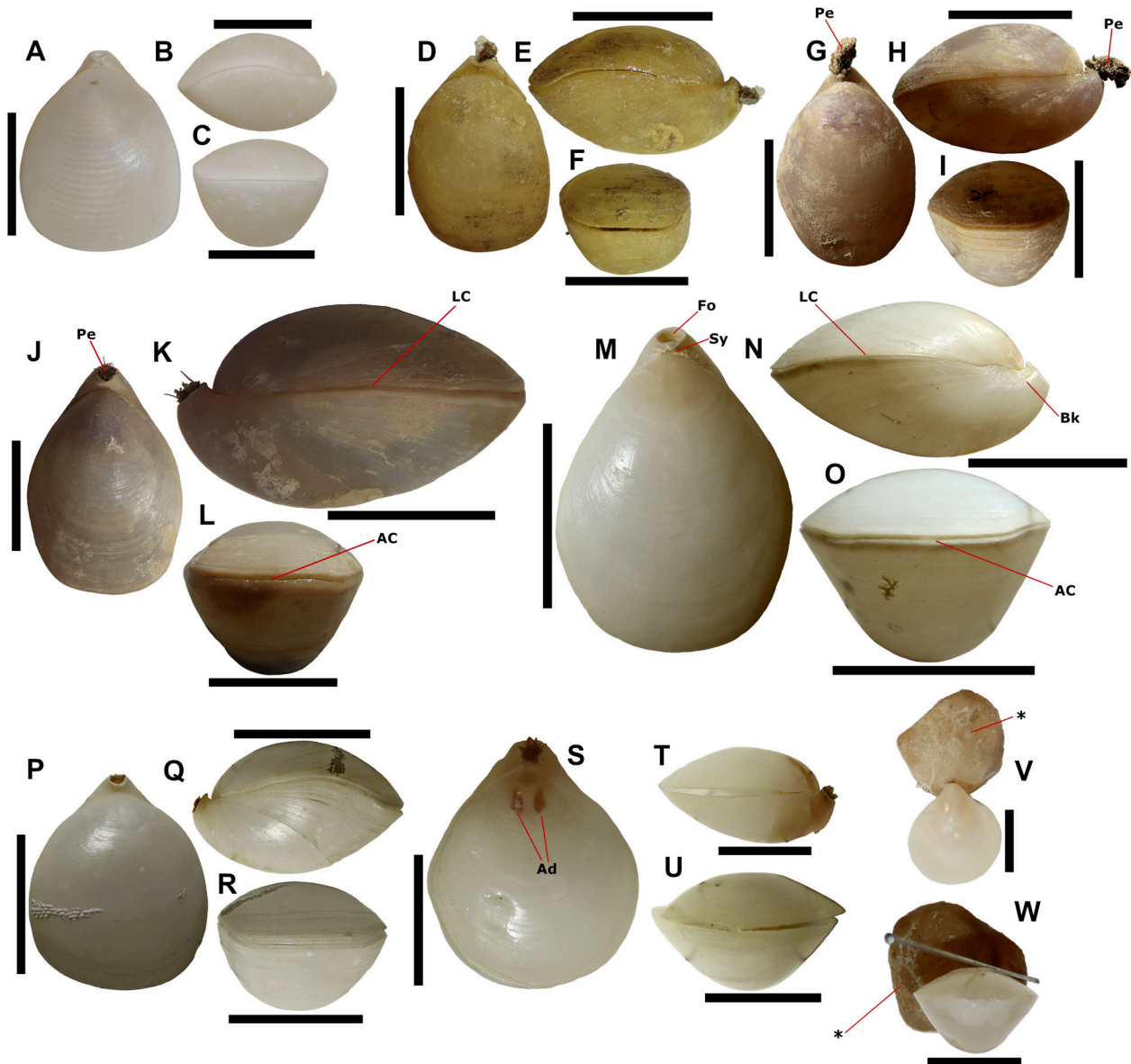


Figure 4. *Dallithyrus fulva* TMAG material, external valve morphology. **A–C**) Dorsal, lateral, and anterior aspects (E58680, L = 32.9 mm, W = 25.6 mm). **D–F**) same aspects for E22114 (L = 30.8, W = 21.5 mm). **G–I**) specimen E21980 (L = 34.4 mm, W = 24.3 mm). **J–L**) specimen E22129 (L = 41.8 mm, W = 28.0 mm). **M–O**) specimen E22129 (L = 35.3, W = 24.9, loop illustrated in **Fig. 5**). **P–R**) Specimen E22131 (L = 31.0 mm, W = 25.3 mm). **S–U**) Juvenile specimen E21980 (L = 19.1 mm, W = 16.1 mm). **V, W**) ventral and anterior aspects of juvenile attached to *Basiliolella* valve (L = 16.4 mm, W = 13.4 mm). Abbreviations per Methods (* denotes dead *Basiliolella* valve, **V, W**), scale bars: 20.0 mm (**A–R**), 10.0 mm (**S–W**).

Hinge sockets well defined; inner socket ridges plate-like, each ridge higher in its posterior half and deflected over the socket. Outer hinge plates triangular, broad (**Fig. 5 A, C, G**) but narrower on juveniles (**Fig. 5 E**), slightly concave, inner edges of hinge plates diverging from each other at $\sim 23\text{--}27^\circ$, each attaching along the 'upper' (ventrally directed) edge of the crural base. Inner hinge plates absent. Crura bases poorly differentiated from anterior end of hinge plates (more visible in semi-lateral profile, **Fig. 5 B, D, F**). Crural processes very short, blunt, directed ventro-medially.

Loop simple, form variable and changing with ontogeny (see **Fig. 5 A–G**). Loop length index, from crural processes to anterior-most edge, relative to whole loop and cardinalia length, 40%–48% (i.e., loop anterior to crural processes slightly shorter than distance back to the crural process); Loop width index, width across crura bases relative to width across loop, $\sim 84\text{--}93\%$ (loop only slightly wider than width across the crura).

Descending branches ribbon-like, continuous with transverse band, weakly converging (loop becoming narrower) towards anterior end; transverse band with a ventrally directed median fold variably developed, form-

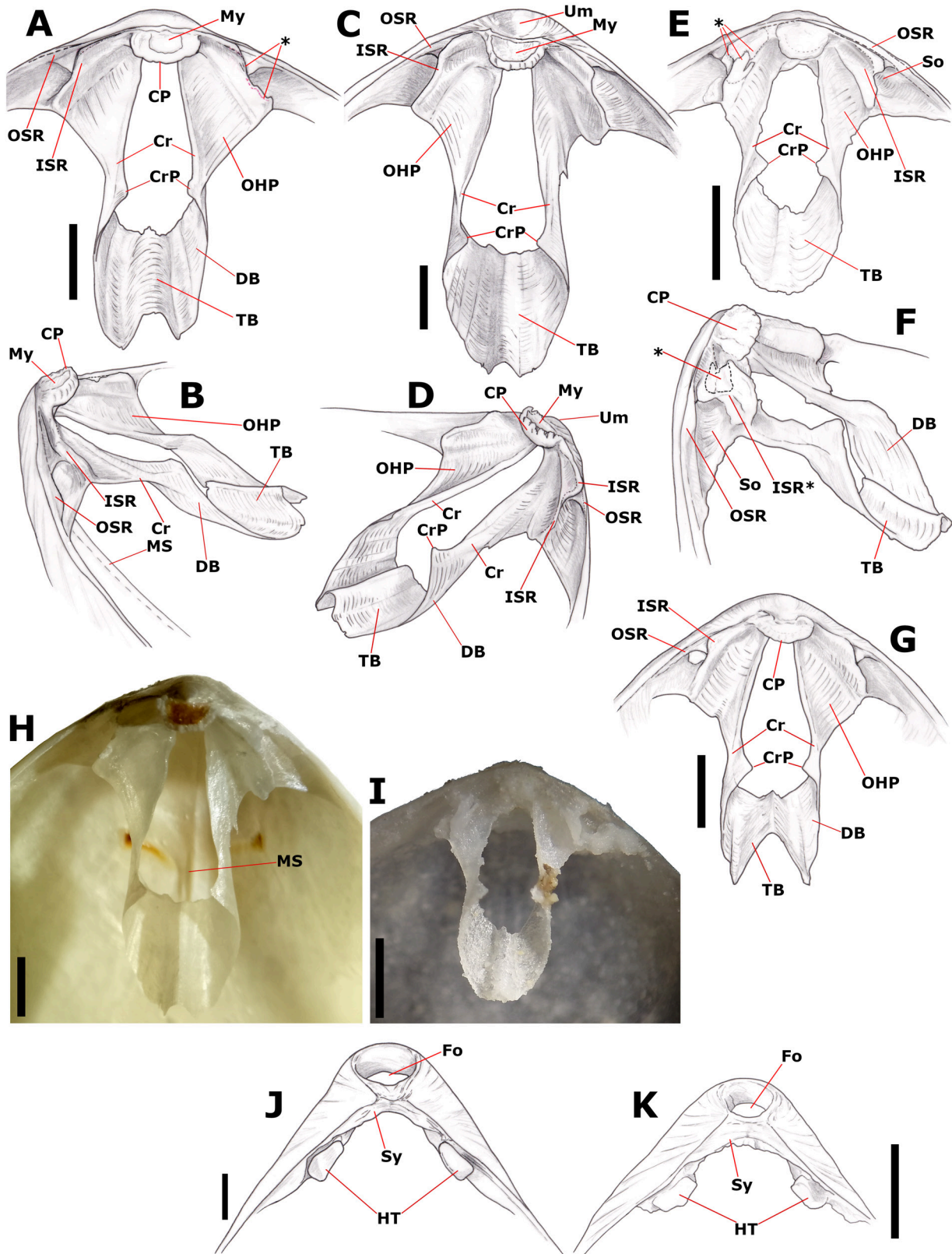


Figure 5. *Dallithyris fulva* TMAG material, internal valve structures. **A, B**) Cardinalia and brachial loop ventral and semi-lateral aspects (E24312; L = 31.0 mm). **C-F**) Same for larger specimen (**C, D**; E22129, L = 35.3 mm), and for a smaller specimen (**E, F**; E58674, L = 20.8 mm). **G**) Ventral aspect of cardinalia and brachial loop for specimen with more strongly angled loop (E22128, L = 28.8 mm). **H, I**) photographs of cardinalia and loop (**H**, same specimen as **C & D**; **I**, same specimen as **E & F**). **J, K**) beak and delthirium detail for a larger and smaller specimen respectively (**J**, same specimen as **C & D**; **K**, same specimen as **E & F**). Abbreviations per Methods (* denotes damage), scale bars: 2.0 mm.

Specimen	L	W	T	W%L	T%L	T%W	Notes
E21979	23.45	16.8	13.4	71.64	57.14	79.76	
	26.5	18.9	15.0	71.32	56.60	79.37	
	22.6	15.2	13.2	67.26	58.41	86.84	
E21980	34.4	24.3	20.6	70.64	59.88	84.77	Fig. 4 G–I
	19.1	16.1	10.2	84.29	53.40	63.35	Fig. 4 S–U
E21981	37.3	27.5	24.5	73.73	65.68	89.09	
	28.9	19.3	16.6	66.78	57.44	86.01	Attached to dead <i>Basiliolella</i> .
	32.1	22.5	20.1	70.09	62.62	89.33	
E21987	35.4	24.6	NA	69.49	NA	NA	Dry (ventral valve broken)
E22114A	37.75	27.7	23.1	73.38	61.19	83.39	Dry
	31.6	24.0	18.6	75.95	58.86	77.50	Dry
	30.8	21.45	18.2	69.64	59.09	84.85	Dry; Fig. 4 D–F
	21.6	16.7	11.25	77.31	52.08	67.37	Dry
E22127	33.6	24.6	20.1	73.21	59.82	81.71	
	34.8	20.6	19.65	59.20	56.47	95.39	
	34.0	22.55	19.9	66.32	58.53	88.25	
	30.1	19.9	16.5	66.11	54.82	82.91	Attached to dead <i>Basiliolella</i> .
	33.8	24.4	18.4	72.19	54.44	75.41	
E22128	33.2	22.4	18.6	67.47	56.02	83.04	
	24.1	17.1	13.6	70.95	56.43	79.53	
	33.1	23.1	19.2	69.79	58.01	83.12	
	32.8	23.3	19.3	71.04	58.84	82.83	
	19.85	12.7	10.8	63.98	54.41	85.04	
	28.8	20.6	NA	71.53	NA	NA	Fig. 5 G (In glass vial in main jar)
E22129	41.8	28.0	24.3	66.99	58.13	86.79	Largest specimen of species; Fig. 4 J–L
	34.1	21.9	17.6	64.22	51.61	80.37	
	35.3	24.9	19.4	70.54	54.96	77.91	Fig. 4 M–O; Fig. 5 C, D, H, J
	31.9	23.0	16.6	72.10	52.04	72.17	
	30.4	21.4	16.4	70.39	53.95	76.64	
	36.0	24.8	22.6	68.89	62.78	91.13	Attached to dead <i>Basiliolella</i> .
E24312	31.0	25.3	19.3	81.61	62.26	76.28	Bleach prepped (in separated jar); Fig. 4 P–R; Fig. 5 A, B (separated from E22131)
E22166	32.4	21.5	19.6	66.36	60.49	91.16	Attached to Bryozoan fragment.
	36.3	25.7	20.7	70.80	57.02	80.54	Attached to Bryozoan fragment.
	27.8	19.8	15.5	71.22	55.76	78.28	Attached to dead <i>Basiliolella</i>
	16.4	13.4	9.3	81.71	56.71	69.40	Attached to dead <i>Basiliolella</i> ; Fig. 4 V, W
E33755	37.1	26.4	22.0	71.16	59.30	83.33	
E58674	35.3	29.4	19.9	83.29	56.37	67.69	
	30.4	24.1	18.3	79.28	60.20	75.93	
	25.2	19.1	13.6	75.79	53.97	71.20	
	20.5	17.4	10.8	84.88	52.68	62.07	
	18.5	15.2	9.3	82.16	50.27	61.18	
	20.8	14.8	9.8	71.15	47.12	66.22	Fig. 5 E, F, I, K
	32.3	24.1	NA	74.61	NA	NA	
E58680	32.9	25.6	20.52	77.81	62.37	80.16	Dry; Fig. 4 A–C

Table 2. *Dallithyris fulva* measurements, indices, and notes.

ing a weak–strong indent on the anterior edge of the band (juvenile with fold weaker, see **Fig. 5 E, F**; moderately developed fold in some older specimens, see **Fig. 5 C, D**; some with strongly developed fold, see **Fig. 5 A, B, G**). The overall length of the brachidium is relatively short, the anterior-most edge of the loop reaching ~29%–35% dorsal valve length. Median septum reduced to little more than a faint ridge running along the valve

floor from the cardinal area anteriorly to ~33% dorsal valve length (visible in **Fig. 5 B, H**).

Ventral (pedicle) valve: Beak small (beak length ~8.6%–10.2% overall valve length), suberect. Foramen generally transapical or somewhat subapical, moderately large (foramen diameter ~7%–8% overall valve length), mesothyridid, though beak ridges are poorly defined. Pedicle collar short, reduced to a ring lining

inside of foramen opening. Deltidial plates largely covered by dorsal valve umbo, fused (*i.e.*, as a symphytium) with no trace of medial seam, symphytium very short in antero-posterior axis and tapering along lateral edges towards hinge teeth. Hinge teeth small, ~rectangular, attached to a slight thickening along the valve wall, dental plates absent. Symphytium and hinge teeth illustrated in **Fig. 5 J, K** (also illustrated for holotype **Fig. 3 A**).

Soft tissue: Pedicle very short (not extending beyond beak) and with fibrous attachment end (e.g., **Fig. 4 D, E, J, K**). Lophophore plectolophous.

Attachment substrata and epibiota: Majority of specimens lacked epibiota, with a small number having some encrusting bryozoan and serpulid tubes. Attachment substrates comprised small rocks, dead *Basiliolella columnus* valves (five specimens) or chunks of bryozoan colony (two specimens).

Specimens examined.

Holotype. BMNH ZB 1314, off Twofold Bay, New South Wales, 36°56'S, 150°30'E, 120 fathoms (219 m), HMS *Challenger*, Stn. 163, 04.iv. 1874.

Other material examined.

E21979, 40.84°S, 148.59°E, 130 m, RV *Umitaka Maru*, UM 68.16 (dredge), 08.i.1968; **E21980B**, 38.196–1892°S, 149.2672–2843°E, 210–220 m, RV *Southern Surveyor*, SS199405 Stn. 083 (epibenthic sled), 29.viii.1994; **E21981**, 38°11.6'S, 149°16.9'E, 230–240 m, RV *Southern Surveyor*, SS199305 Stn. 173 (epibenthic sled), 06.viii.1993; **E21987**, east of St Patricks Head (eastern Tasmania), 41.57°S, 148.63°E, 2000 fathoms (610 m), coll. T. Jenkins, ix.1969; **E22114A** (**×5 D. fulva**; **×2 split out as *Liothyrella n. sp.***), 38.2383–2563°S, 149.7353–7376°E, 522–608 m, RV *Southern Surveyor*, SS200001 Stn. 196 (epibenthic sled), 23.iv.2000; **E22127**, 38°11.8'S, 149°16.3'E, 212–240 m, RV *Southern Surveyor*, SS199305 Stn. 115 (epibenthic sled), 31.vii.1993; **E22128** & **E33755**, 38°11.6'S, 149°15.6'E, 190–240 m, RV *Southern Surveyor*, SS199305 Stn. 191 (epibenthic sled), 08.viii.1993; **E22129** & **E32782**, 38°11.5'S, 149°15.6'E, 202–246 m, RV *Southern Surveyor*, SS199305 Stn. 181 (epibenthic sled), 07.viii.1993; **E24312**, 44.2117°S, 147.0450–0517°E, 1084 m, RV *Southern Surveyor*, SS199701 Stn. 052 (epibenthic sled), 29.i.1997; **E22166**, 38°10.0'S, 149°35.8'E, 266–263 m, RV *Southern Surveyor*, SS199305 Stn. 203 (epibenthic sled), 09.viii.1993; **E32781**, 38°11.7'S, 149°16.0'E, 215 m, RV *Southern Surveyor*, SS199305 Stn. 180 (epibenthic sled), 07.viii.1993; **E58674**, 44.0953–1002°S, 146.6827–6657°E, 568 m, RV *Investigator*, IN2018_V06 Stn. 105 (4m beam trawl), 08.xii.2018; **E58680**, 44.1967–1980°S, 146.9710–9603°E, 980–1111 m, RV *Investigator*, IN2018_V06 Stn. 132 (4m beam trawl), 10.xii.2018.

Distribution: Richardson (1997) records the species from the eastern and southern coasts of Australia over a 73–640 m bathymetric range, while Zezina (2010)

records a more restricted bathymetric range of 73–274 m, though it is unclear if these sources are confusing this species with *Liothyrella southernsurveyori* sp. nov. Material examined herein was collected from off southern New South Wales, northeastern Bass Strait, eastern and southern Tasmania (**Fig. 1 A**), with the majority from a bathymetric range of 130–610 m, though two specimen lots were from 980–1111 m (E24312, E58680).

Remarks

Davidson (1880, pp. 31–32) recorded two dead shells of "*Terebratula uva*" collected by the Challenger Expedition, one from Australia (Twofold Bay, 36°55'S, 150°30'E, 120 fathoms, station 163 on the 4th April 1874), and a second from off Buenos Ayres (Atlantic). The specimen from off Australia is now registered as BMNH ZB 1314, and Blochmann (1908, fig 22a,b, & fig 26) provided illustrations of this single original Australian specimen as *Dallithyrus fulva* and noted it as such (thus retroactively making it the holotype by monotypy). Blochmann (1906) only very briefly described the species (but referred to the specimen illustrated by Davidson (1880)).

The holotype was only very briefly described by Davidson (1880) "*Shell ovate, longer than wide, white, or of a very light salmon colour. Dorsal valve uniformly convex, rather less deep than the opposite one, rounded in front. Ventral valve convex. Beak moderately produced and truncated by a circular foramen, separated from the hinge-line by a deltidium. Surface smooth, marked by a few concentric lines of growth. Loop short, simple. Shell finely punctated. Length 25, width 17, depth 15 mm.*"

Davidson's illustrations (Plate II, fig 3a,b) are roughly consistent in shell outline with the present holotype, but the loop is not; Davidson drew the loop as short but with the transverse band being distinctly widened anteriorly, and being relatively thin (see **Fig. 3 G**). Blochmann (1908, fig 26) photographed the loop from the same specimen, with it being very different in the width and length of the transverse band, as is shown in **Fig. 3 H** (reproduced from Blochmann), the loop is relatively long antero-posteriorly compared with Davidson's drawing, tapers in width anteriorly (being narrower than the crura anteriorly), and has a relatively strong medial fold. Davidson also drew the outer hinge plates as being very poorly developed, with the crura directly attaching to the inner socket ridge, while Blochmann's illustration reveal these plates to be well-developed and triangular. Overall the loop on the holotype strongly resembles that of TMAG material (compare **Fig. 3 H** to **Fig. 5 A–G**), indicating that Davidson made an error in illustrating the loop, indeed a note with the holotype remarks "*The anterior part of the brachial loop is somewhat longer and narrower than drawn by Davidson*" (**Fig. 3 I**).

The form of the shell in anterior and lateral profile is also consistent between holotype and TMAG material, especially the anterior aspect with the relatively deep

ventral valve compared to the dorsal, and the anterior commissure being flat and slightly deflected ventrally.

Blochmann (1913) described and illustrated two new specimens collected in 1910 by Mr W.L. May off the east coast of Tasmania (3 miles east of Schouten Island, 73 m depth), these specimens (now ZMB Bra 587 & 588) seem comparable with the type specimen and material examined herein. Later authors (Helmcke 1939, Cooper 1983) erroneously designated these Blochmann (1913) specimens as types (or lectotypes).

Dallithyrus murrayi, the type species of the genus is known from the Indian Ocean at the Maldive Islands and Saya de Malha Bank (Muir-Wood 1959, Zezina 2010), and has recently been recorded from northwestern Australia (Bitner 2025). The species is similar to *D. fulva* in having a dorsally convex lateral commissure (though this varies in *D. fulva*), but differs in being proportionally wider (sub-pentagonal or triangular in outline with widest point towards the anterior end (see Bitner 2025, fig 2f,i)) rather than the elongate shape of *D. fulva*, and also differs in having the anterior commissure being widely uniplicate, forming a distinctly dorsally directed arc (with a groove/sulcus on the ventral valve) (see Bitner 2025, fig 2h,k), opposite the ventrally directed anterior commissure seen in *D. fulva*.

Dallithyrus pacifica from off Fiji (tropical western Pacific, 640–753 m depth) is smaller than *D. fulva* (maximum length 28.0 mm) and is generally wider and more sub-pentagonal in outline compared to *D. fulva* (which tends to be more elongate and ovoid), the W%L ratio of *D. pacifica* averages 85% (79%–90%) tending to be wider than most *D. fulva* (W%L averaging 72.2%), though some *D. fulva* specimens are relatively similar in overall outline and commissure form (e.g., compare **Fig. 4 A–C** to Bitner 2006, fig 2b–i) and the loop is comparable (Bitner 2006). *Dallithyrus tahitiensis*, from French Polynesia (tropical central Pacific, 340–1050 m depth), is again smaller than *D. fulva* (maximum length 29.5 mm) and also differs in being generally wider with W%L averaging 81% (76%–88%), and while the anterior commissure similarly has some ventral deflection, in *D. tahitiensis* the commissure is unisulcate (with a subtle groove on the dorsal valve antero-medially). Bitner (2014) also differentiated *D. tahitiensis* from *D. fulva* based on the former having a rounded median fold on the loop's transverse band, vs. a more angular fold in the latter, the results herein demonstrate that *D. fulva* has a somewhat more variable loop morphology than previously indicated (and so the loop median fold isn't as useful in distinguishing these species).

Subfamily Terebratulinae Gray, 1840

Type genus: *Terebratula* Mueller, 1776

Diagnosis: Anterior commissure rectimarginate, uniplicate or sulcinate; loop triangular, short to moderately long, crural processes usually anterior of midloop, may

be very long, transverse band narrow to broad, antero-lateral extremities of loop usually subangular, inner hinge plates rarely developed. (Lee & Smirnova 2006, pp. 2054–2055)

Description: Per diagnosis.

Genus *Liothyrella* Thomson, 1916

Type species: *Terebratula uva* Broderip, 1833

Diagnosis: Large to very large, elongate oval to subcircular; ventribiconvex, anterior commissure usually rectimarginate, occasionally broadly uniplicate; smooth or with faint, radial or zigzag capillae; beak usually short, suberect; foramen usually large, submesothryd, labiate; symphytium wholly or partly visible; pedicle collar short, teeth triangular, narrow; low myophragm may be present; cardinal process transverse semiellipse; outer hinge plates variable in width and length, attached near dorsal edge of crural bases; loop variable, usually widely triangular (crura and transverse bands diverging anteriorly), crural processes located near socket openings, transverse band relatively narrow, variable; spicules abundant. (Lee & Smirnova 2006, pp. 2056–2057).

Description: Per diagnosis.

Liothyrella southernsurveyori sp. nov.

Figs. 6, 7; Table 3

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Type specimen lodged at the Tasmanian Museum & Art Gallery (**TMAG E21985**).

Diagnosis: *Liothyrella* of large size (up to 42.4 mm), outline rounded sub-pentagonal, with widest point just anterior of midway along valve length, biconvex, with lateral commissure curved ventrally (weakly to strongly), and with anterior commissure forming a dorsally directed arc (without apparent sulcation). Larger specimens becoming increasingly thickened/inflated, causing commissures to become indented. Hinge plates narrow-triangular (OHP angle 44–70°), loop variable, crura distinct and free from hinge plates, converging medially, descending and transverse bands approximately triangular in shape due to bands diverging, loop wide (loop width index 65%–74%), elongate (loop length index 39%–47%), and with weak median fold. Beak erect to sub-erect, foramen sub-apical but falling within a deeply cut antero-posteriorly directed groove on thickened specimens.

Description

Overall valve form: Maximum valve length 42.4 mm (average 24.8 mm, SD 6.1, smallest observed length 8.6 mm); width equal or slightly less than valve length, W%L averaging 87.3% (SD 5.8%, range 67.9%–100.9%), valves relatively thick dorso-ventrally, T%L averaging 58.7% (SD 5.6%, range 48.1%–75.0%).

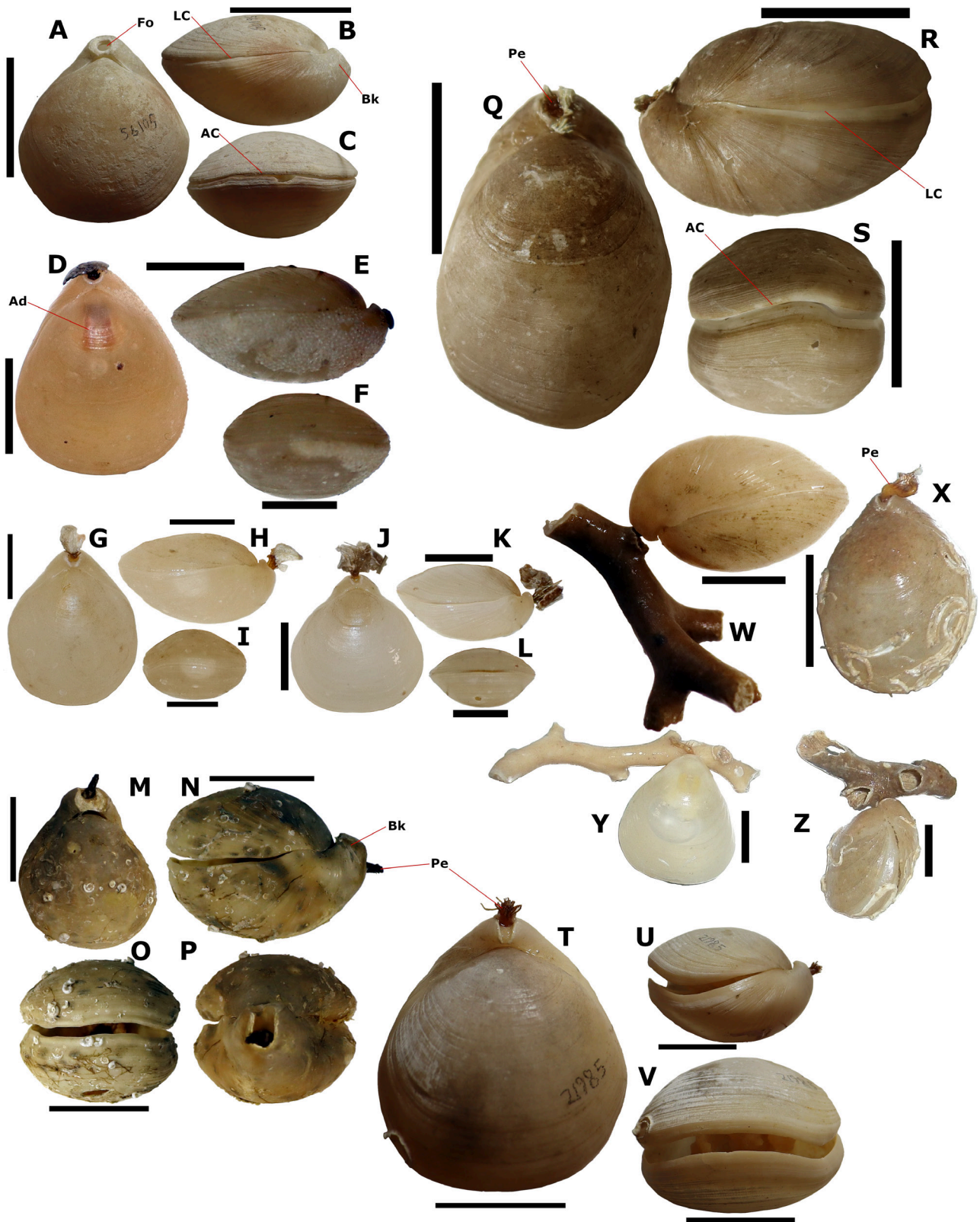


Figure 6. *Liothyrella southernsurveyori* sp. nov., external valve morphology. **A–C**) Dorsal, lateral, and anterior aspects (E56105, L = 31.4 mm, W = 25.56 mm). **D–F**) same aspects for E55893 (L = 22.2, W = 22.4 mm). **G–I**) specimen E22131 (L = 23.2 mm, W = 19.1 mm). **J–L**) specimen E22131 (L = 20.4 mm, W = 19.4 mm). **M–P**) specimen E21831 (L = 38.4, W = 32.2). **Q–S**) specimen E22130 (L = 39.5 mm, W = 27.0 mm, loop illustrated **Fig. 7**). **T–V**) holotype specimen E21985 (L = 42.4 mm, W = 38.2 mm). **W**) specimen E22133 (L = 26.5) attached to coral, lateral aspect with ventral valve uppermost. **X**) specimen from lot E22168 (L = 36.2 mm) with encrusting serpulid tubes. **Y, Z**) ventral and lateral aspects of smaller specimen attached to coral (both E22168, L = 25.2 and 22.9 mm for **Y** & **Z** respectively). Abbreviations per Methods (* denotes damage), scale bars: 20.0 mm (**A–C, M–V, X**), 10.0 mm (**D–L, W, Y, Z**).

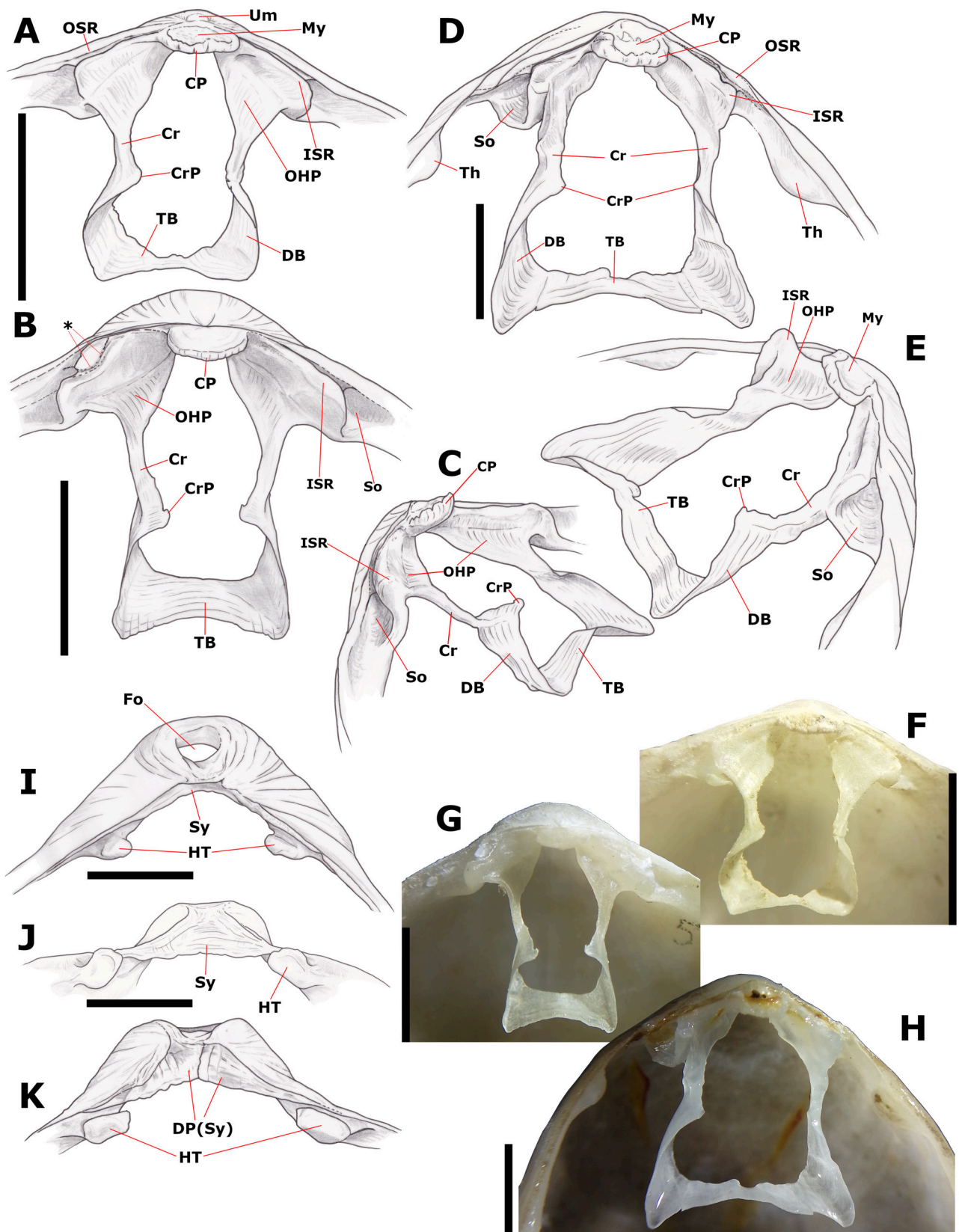


Figure 7. *Liothyrella southernsurveyori* sp. nov. **A)** cardinalia and brachial loop ventral aspect (E56113, L = 28.1 mm). **B, C)** cardinalia and brachial loop ventral and semi-lateral aspects (E56105; L = 32.8 mm); **D, E,** same for a large and thickened specimen (E22130, L = 39.5 mm). **F–H)** photographs of cardinalia and loop for the three specimens illustrated earlier (**F,** same as **A;** **G,** same as **B;** **H,** same as **D**). **I–K)** beak and delthrium detail, (**I, J**) dorsal aspect and anterior aspect respectively (E56105, same specimen as **B**), (**K**) anterior aspect of beak on a specimen with remnant seam separating deltidial plates (E56113, same specimen as **A**). Abbreviations per Methods (* denotes damage), scale bars: 5.0 mm.

Specimen	L	W	T	W%L	T%L	T%W	Notes
E21032	33.1	28.2	NA	85.20	NA	NA	Both attached to coral, dorsal valves broken.
	28.1	24	NA	85.41	NA	NA	
E21040	31.3	27.4	21.5	87.54	68.69	78.47	Thickened specimen; attached to coral.
E21787	24.2	21.5	14	88.84	57.85	65.12	
E21831	38.4	32.2	28.8	83.85	75.00	89.44	Dry; thickened specimen; with encrusting serpulids. Fig. 6 M-P
E21984	24.8	18.5	12.3	74.60	49.60	66.49	
	26.7	22	14.4	82.40	53.93	65.45	
E21985	42.4	38.2	27.9	90.10	65.80	73.04	Thickened; Fig. 6 T-V
E22104	30	26.75	20.4	89.17	68.00	76.26	Thickened.
	29.4	24.8	19.4	84.35	65.99	78.23	Thickened.
	20.8	17.2	11.2	82.69	53.85	65.12	
E22110	24.5	21.2	13.8	86.53	56.33	65.09	
	25.5	23.2	14.8	90.98	58.04	63.79	
	21	20	11.5	95.24	54.76	57.50	
	17.4	15.4	8.7	88.51	50.00	56.49	
E22114B	28.8	23.8	16.4	82.64	56.94	68.91	
	17.9	15.3	8.6	85.47	48.04	56.21	
E22130	39.5	27.0	25.4	67.85	64.30	94.78	Thickened. Fig. 6 Q-S. Fig. 7 D, E, H
	29.4	25.1	17.1	85.37	58.16	68.13	Thickened.
	20	18.3	11.2	91.50	56.00	61.20	Thickened.
	30.7	24.8	18.5	80.78	60.26	74.60	
	15.6	15.4	8.2	98.72	52.56	53.25	
	16.7	15.1	8.6	90.42	51.50	56.95	
E22131A	23.2	19.25	13.4	82.97	57.76	69.61	
	23.2	19.1	13.2	82.33	56.90	69.11	
	25	20.3	15.1	81.20	60.40	74.38	
	20.4	19.4	11	95.10	53.92	56.70	
	21.7	20.5	13	94.47	59.91	63.41	Fig. 6 J-L
E22132	26.9	24.8	14.6	92.19	54.28	58.87	
E22133	26.5	21.2	16.5	80.00	62.26	77.83	Attached to coral. Fig. 6 W
	28.3	26.7	18.8	94.35	66.43	70.41	Attached to coral.
	15.4	14.3	8.4	92.86	54.55	58.74	
E22134	33.7	32.1	22.55	95.25	66.91	70.25	Thickened.
	30.1	25.5	NA	84.72	NA	NA	Dorsal valve broken.
	20.8	18.4	12.2	88.46	58.65	66.30	
	18.4	15.8	10.7	85.87	58.15	67.72	
	12	10.4	7	86.67	58.33	67.31	
	11.2	10.3	6.2	91.96	55.36	60.19	
	8.6	7.7	4.15	89.53	48.26	53.90	
E22135	22.5	20.3	13.35	90.22	59.33	65.76	
E22136	32.4	28.3	23.4	87.35	72.22	82.69	Largest specimen in lot (others not measured).
E22163	24.3	21.8	13.9	89.71	57.20	63.76	
E22165	34.2	25.55	19.7	74.71	57.60	77.10	Thickened
	29.5	24.2	19.3	82.03	65.42	79.75	Thickened
	11.5	10.2	5.6	88.70	48.70	54.90	
E22168	36.2	27.7	21.2	76.52	58.56	76.53	With encrusting serpulids. Fig. 6 X
	18.85	17.6	10.75	93.37	57.03	61.08	
	22.9	19.7	15.2	86.03	66.38	77.16	Both attached to coral (hexacorallia) & with encrusting serpulids. Fig. 6 Y, Z
	25.15	21.6	15.2	85.88	60.44	70.37	
	17	14.9	8.4	87.65	49.41	56.38	
E22171	18.6	15.55	10.2	83.60	54.84	65.59	
E55891	26	23	15.3	88.46	58.85	66.52	
	25.5	23.3	NA	91.37	NA	NA	
E55893	27.6	24.1	16.3	87.32	59.06	67.63	
	26.8	23.5	17.1	87.69	63.81	72.77	
	22.2	22.4	12.9	100.90	58.11	57.59	
	18.0	16.8	9.7	93.33	53.89	57.74	
E55894	31.0	25.7	20.4	82.90	65.81	79.38	
	21.0	18.7	11.2	89.05	53.33	59.89	
	16.7	14.6	8.7	87.43	52.10	59.59	
E56105	32.8	27.8	20.4	85.80	62.96	73.38	Fig. 7 B, C, G, I, J
	29.8	27.3	17.4	91.61	58.39	63.74	
	31.35	25.5	19.3	81.34	61.56	75.69	Dry; Fig. 6 A-C
E56110	28.3	27.8	17.8	98.23	62.90	64.03	
E56113	27.5	24.5	16.8	89.09	61.09	68.57	
	23.85	21.3	13.9	89.32	58.28	65.26	
	24.4	20.4	16.1	83.61	65.98	78.92	
	28.1	22.3	NA	79.36	NA	NA	
E58671	32.1	28.0	NA	87.23	NA	NA	Dry
	19.2	19.3	10.3	100.52	53.65	53.37	Dry
	17.7	16.15	9.15	91.24	51.69	56.66	Dry
E58679	26.8	24	17.4	89.55	64.92	72.50	
	25.0	22.3	14.0	89.20	56.00	62.78	
E58681	33.6	30.5	20.1	90.77	59.82	65.90	Dry
	23.8	19.8	14	83.19	58.82	70.71	Dry
	21.1	17.6	12.9	83.41	61.14	73.30	Dry
	16.6	12.9	9.8	77.71	59.04	75.97	Dry
	23.2	19.65	13	84.70	56.03	66.16	Dry
E58687	29.75	26.1	NA	87.73	NA	NA	Dry
E59287	24.5	20.2	NA	82.45	NA	NA	Dry
	16.2	14.8	9.8	91.36	60.49	66.22	Dry

Table 3. *Liothyrella southernsurveyori* sp. nov. measurements, indices, and notes.

Overall outline strongly rounded to sub-pentagonal (dorso-ventral aspects **Fig. 6 A, D, G, M, T**), rarely more ovoid (**Fig. 6 Q, X**), widest point slightly anterior to mid-way along length. Valves biconvex in lateral-profile (dorsal and ventral valves of similar depth). Lateral commissure gently to strongly arched towards ventral valve (ventrally convex), the ventral deflection strongest in anterior half (see lateral profile in **Fig. 6 B, E, H, K, N, R, W, U**). Anterior commissure forms a dorsally directed arc (without plication) (see anterior profile in **Fig. 6 C, F, I, L, O, S, V**). Larger specimens becoming strongly inflated/thickened, causing the commissure to be somewhat overgrown/indented, and the pedicle to become increasingly cut into the thickened beak (creating a distinct groove containing the foramen) (see **Fig. 6 M-V**).

Valves punctate, growth striae visible on most specimens (especially larger and older specimens), with very faint and fine radial marks present (not developed as distinct radial ribs/costate). Colouration white to yellowish-brown.

Dorsal (brachial) valve: Cardinalia and loop illustrated per **Figure 7 A-E**. Cardinal process, a small half-circle shaped plate folded anteriorly from the umbo, with a rough-surfaced muscle attachment patch (myophore) on the posterior face. Hinge sockets well defined; inner socket ridge large and plate-like, somewhat higher anteriorly (especially on larger specimen, **Fig. 7 E**), and angled posteriorly to partly enclose the socket.

Outer hinge plates small, very-narrow triangular (somewhat broader on smaller specimens, see **Fig. 7 A**, compared to larger specimens, see **Fig. 7 B, D**), slightly concave, inner edges of hinge plates diverging strongly from each other at ~44–70°. Inner hinge plates absent. Outer hinge plates attached along outer (lateral) edge of crura bases, crura relatively long, clearly differentiated from the hinge plates and extending anteriorly well beyond where the plates attach, converging anteriorly. Crural processes short, blunt, directed ventro-medially.

Loop simple and somewhat variable with ontogeny, the overall form being triangular, due to the descending bands diverging, divergence of descending bands seeming to become more extreme with age (see progression with specimen size across **Fig. 7 A, B, D**).

Loop length index, length of loop from crural processes to anteriormost edge, relative to whole loop and cardinalia length, ~39%–47%; Loop width index, width across crura bases relative to width across loop, ~65%–74%.

Descending branches ribbon-like, continuous with transverse band, strongly diverging towards antero-lateral corners (divergence stronger in larger specimens relative to smaller, see **Fig. 7 A, B, D**); transverse band wide but relatively narrow (in antero-posterior axis), with only a weak median fold directed ventrally (see **Fig. 7 C, E**).

Overall length of the brachidium (loop and cardinalia) relatively short, the anterior-most edge of the loop reaching ~30–35% dorsal valve length. Median septum absent.

Ventral (pedicle) valve: Beak small (beak length 10%–16% overall valve length), suberect to erect (in larger and more thickened specimens). Foramen subapical and circular in smaller specimens (e.g., **Fig. 6 A, D**), as specimens become larger and more thickened the pedicle seems to cut into the beak antero-posteriorly, creating a deep groove extending transapically (partially apparent **Fig. 6 G, Q**; well apparent **Fig. 6 M-P, T-U, X**). Foramen diameter ~5%–8% overall valve length. Mesothryridid, beak ridges poorly defined. Pedicle collar short, lining inside of foramen. Deltidial plates largely fused as a symphytium, mostly exposed on smaller specimens (e.g., **Fig. 6 A, D**), becoming more covered by dorsal valve umbo on older/thickened specimens (e.g., **Fig. 6 M, Q, T**); symphytium very short in antero-posterior axis, wide, tapering along lateral edges towards hinge teeth, with or without trace of medial seam (see **Fig. 7 I-K**). Hinge teeth small, rectangular, dental plates absent.

Soft tissue: Pedicle short (extending only a short distance beyond beak), distal end fibrous (variously depicted across **Fig. 6**). Lophophore plectolophous.

Attachment substrata and epibiota: Majority of specimens lacked epibiota, some with encrusting bryozoan and serpulid tubes (see **Fig. 6 M-P, X**). Multiple specimens were attached to large broken-off pieces of deep-sea coral (hexacorals) (see **Fig. 6 W, Y, Z**), all others had no attachment substrate.

Specimens examined.

Holotype.

E21985, off SE Tasmania, off (~east of) the Hippolites, ~43.1°S, 148.2–3°E, 960–1000 m, FV *Challenger*, CR036–CR040 (station unknown) (coll. P.J. Last, TFDA), 31.iii.1982. [station data relatively uncertain, see methods]

Paratypes.

E21032 [**x2**], 44.27–30°S, 147.29–23°E, 1100–1122 m, RV *Southern Surveyor*, SS199701 Stn. 015 (epibenthic sled), 23.i.1997; **E21040**, 44.40°S, 147.15–18°E, 1400–1650 m, RV *Southern Surveyor*, SS199701 Stn. 069 (epibenthic sled), 31.i.1997; **E21787**, 44.167°S, 147.515°E, RV *Investigator*, IN2017_E02 Stn. 02-014, 02.iv.2017; **E21831**, offshore from Tasman Island, 280 fathoms (512 m), FV *Derwent Hunter*, coll. Robertson, vii.1979; **E21984** [**x3**], 44.3269–3288°S, 147.1792–1790°E, 1200–1300 m, RV *Southern Surveyor*, SS200702 Stn. 013 (Sherman epibenthic sled), 01.iv.2007; **E22104** [**x8**], 44.31–30°S, 147.27–34°E, 1150–1550 m, RV *Southern Surveyor*, SS199701 Stn. 043 (epibenthic sled), 28.i.1997; **E22110** [**x4**], 44.27–24°S, 147.33–36°E, 987 m, RV *Southern Sur-*

veyor, SS199701 Stn. 036 (epibenthic sled), 27.i.1997; **E22114B** [**×2**], 38.2383–2563°S, 149.7353–7376°E, 522–608 m, RV *Southern Surveyor*, SS200001 Stn. 196 (epibenthic sled), 23.iv.2000; **E22130** [**×7**], 44.23–19°S, 147.38–29°E, 1200–1400 m, RV *Southern Surveyor*, SS199701 Stn. 059 (epibenthic sled), 30.i.1997; **E22131A** [**×4**], 44.21–22°S, 147.05°E, 750–900 m, RV *Southern Surveyor*, SS199701 Stn. 052 (epibenthic sled), 29.i.1997; **E22132**, 44.18–20°S, 147.00–146.96°E, 800 m, RV *Southern Surveyor*, SS199701 Stn. 056 (epibenthic sled), 29.i.1997; **E22133** [**×10+**], 44.24–27°S, 147.36–32°E, 1200–1450 m, RV *Southern Surveyor*, SS199701 Stn. 040 (epibenthic sled), 27.i.1997; **E22134** [**×20**], 44.22–19°S, 147.38–30°E, 1140 m, RV *Southern Surveyor*, SS199701 Stn. 058 (epibenthic sled), 30.i.1997; **E22135**, 44.21–16°S, 147.04–05°E, 640–700 m, RV *Southern Surveyor*, SS199701 Stn. 050 (epibenthic sled), 29.i.1997; **E22136** [**×20+**], 44.29–34°S, 147.30–24°E, 1073–1100 m, RV *Southern Surveyor*, SS199701 Stn. 042 (epibenthic sled), 27.i.1997; **E22163** [**×10+**], 44.19°S, 146.95–147.01°E, 620–800 m, RV *Southern Surveyor*, SS199701 Stn. 055 (epibenthic sled), 29.i.1997; **E22165** [**×5**], 44.28°S, 147.42°E, 1600 m, RV *Southern Surveyor*, SS199701 Stn. 017 (epibenthic sled), 23.i.1997; **E22168** [**×5**], off Sandy Cape, Tasmania, 41.18–25°S, 143.97°E–144.0°E, 1090–1150 m, RV *Soela*, SO198704 Stn. 016 (Engel high rise demersal trawl), 09.v.1987; **E22171**, 44.0417–0489°S, 146.3116–3071°E, 410–450 m, RV *Southern Surveyor*, SS200702 Stn. 032 (Sherman epibenthic sled), 04.iv.2007; **E55891** [**×3**], 44.1256–1334°S, 147.2479–2483°E, 800–1000 m, RV *Southern Surveyor*, SS200702 Stn. 027 (Sherman epibenthic sled), 03.iv.2007; **E55893** [**×10**], 44.3269–3288°S, 147.1792–1790°E, 1200–1300 m, RV *Southern Surveyor*, SS200702 Stn. 013 (Sherman epibenthic sled), 01.iv.2007; **E55894** [**×10**], 44.3257–3240°S, 147.1752–1776°E, 1100–1160 m, RV *Southern Surveyor*, SS200702 Stn. 016 (Sherman epibenthic sled), 02.iv.2007; **E56105** [**×3**], 41.2150–2017°S, 148.7433–7217°E, 320–340 m, RV *Southern Surveyor*, SS199903 Stn. 063 (benthic sled), 27.vii.1999; **E56110**, 41.5183–5117°S, 148.7133–7167°E, 800–900 m, RV *Southern Surveyor*, SS199903 Stn. 075 (benthic sled), 28.vii.1999; **E56113** [**×5**], 41.2133–2067°S, 148.7517–7483°E, 320–340 m, RV *Southern Surveyor*, SS199903 Stn. 062 (benthic sled), 27.vii.1999; **E58671** & **E58679**, 44.1788–1762°S, 147.1940–1972°E, 1093–1124 m, RV *Investigator*, IN2018_V06 Stn. 157 (4m beam trawl), 13.xii.2018; **E58674**, 44.0953–1002°S, 146.6827–6657°E, 568 m, RV *Investigator*, IN2018_V06 Stn. 105 (4m beam trawl), 08.xii.2018; **E58681** [**×5**], 44.2680–2723°S, 147.1100–1320°E, 1341–1348 m, RV *Investigator*, IN2018_V06 Stn. 017 (4m beam trawl), 25.xi.2018; **E58685** [**×1**, damaged dorsal valve], 44.1032–0960°S, 146.1977–1852°E, 941 m, RV *Investigator*, IN2018_V06 Stn. 094 (4m beam trawl), 07.xii.2018; **E58687**, 44.1967–1980°S, 146.9710–9603°E, 980–1111 m, RV *Investigator*, IN2018_V06 Stn. 132 (4m beam trawl),

10.xii.2018; **E59287** [**×2**], 41.2243–2227°S, 148.7595–7562°E, 793–982 m, RV *Investigator*, IN2018_V06 Stn. 178 (4m beam trawl), 16.xii.2018.

Etymology: Specific epithet “southernsurveyori” is after the former CSIRO research vessel *Southern Surveyor* (operated 1990–2013) which collected most of the material used to describe this species (and indeed most brachiopods in the collection), this research vessel and her crew contributed enormously to marine invertebrate and fish collections throughout Australia.

Distribution: Material was collected from off eastern and western Tasmania, but most material was from seamounts off southern Tasmania (**Fig. 1 A**), with the bathymetric range for the majority of material being 512–1650 m, though three specimen lots were collected somewhat shallower at 320–450 m (E22171, E56105, E56113).

Remarks:

This species marks the first record of genus *Liothyrella* from the Australian exclusive economic zone. The superficial similarity in the loop to *D. fulva* has previously caused this species to be confused with it in collections.

This species generally occurs at greater depths than *D. fulva* (though a small number of specimens overlap in bathymetric range), and it seems to have a more restricted range, being only known from the slope and seamounts around Tasmania (particularly the seamounts off southern Tasmania) where it is relatively common. Consistent with this, *Liothyrella* has not been reported further north off eastern Australia, despite large collections from that region being thoroughly investigated by Richardson (1997).

The species is differentiated from *D. fulva* given its more rounded and wider overall form (reflected in indices, see **Fig. 2**), and the dorsally arcing anterior commissure (the anterior commissure effectively arcing in the opposite direction to *D. fulva*). The approximately triangular shape of the loop, created by the diverging descending bands, and the relatively broad yet short transverse band, strongly distinguishes the genus and species from *Dallithyrus* (in *D. fulva* and other species the loop descending bands remain parallel or even converge slightly anteriorly, and the transverse band is relatively elongate in the antero-posterior axis).

Distinguishing the species from other members of *Liothyrella* is more difficult, as many species have been described in this genus which may or may not be valid. The genus contains five accepted species (WoRMS 2025), *L. uva* from around Antarctica, *L. delsolari* from the eastern Pacific off Peru, *L. moseleyi* from the Iles Crozet, *L. neozelanica* from New Zealand, and *L. winterei* from St. Paul and Kerguelen islands (Foster 1974, Cooper 1982, Foster 1989). Molecular rDNA phylogenetic work by Bitner & Cohen (2015) showed that the Antarctic *L. uva* and New Zealand *L. neozelanica* were distinct

species, but no other *Liothyrella* species have been sequenced to allow comparison.

Given the geographical proximity (compared to other *Liothyrella* species), the Australian taxon, *L. southernsurveyori* sp. nov., is most likely to be comparable to *L. neozelanica* which was described by Thomson (1918, pp. 17–19, plates XVI–XVIII) from ~40 specimens attached to a rock entangled on a fishing line from < 200 fathoms in the Cook Strait, New Zealand, the holotype measured 47 mm long. Foster (1989) illustrated ‘hypotype’ material over a greater bathymetric range from locations around New Zealand and the Chatham Rise (6–805 m). The New Zealand species is similar in size (9.6–47 mm) to the Australian taxon and its overall broad-ovate form is also similar, but the extensive thickening seen in *L. southernsurveyori* sp. nov. is absent in *L. neozelanica*, even the very large 47 mm long holotype illustrated by Thomson (1918, plate XVI, figs 36, 37) lacks the distinct thickening seen in *L. southernsurveyori* sp. nov., lacks the strongly cut-in foramen groove and has a very flat lateral commissure. No such thickening/inflated forms were otherwise described, including by Foster (1989). The bathymetric ranges also seem rather different between these species, *L. neozelanica* is very common in depths < 100 m around New Zealand, with the deepest specimen recovered from 805 m depth (Foster, 1989), and while ~8 stations yielding *L. southernsurveyori* sp. nov. were collected from 320–800 m, the majority (23 stations, or ~75%) were from depths 800–1650 m.

Further comparison between these Australian and New Zealand species is needed, Thomson (1918) described the anterior commissure of *L. neozelanica* as a flattened dorsally directed arch, similar to the Australian species, and the loop as illustrated by Thomson for *L. neozelanica* is similar to *L. southernsurveyori* sp. nov., though somewhat shorter.

Liothyrella delsolari from off Peru (tropical eastern Pacific) seems to differ from *L. southernsurveyori* sp. nov. in smaller size (L = 25.5 mm), its nearly circular outline, relatively flat and uniplicate anterior commissure, and possibly a shorter and broader loop (Cooper 1982, Foster 1989 figs 5.10–5.18). *Liothyrella moseleyi* also seems to be smaller (L = 22.1 mm), more rounded in shape, and has a rather flat anterior commissure (Foster 1974).

The more problematic comparison is *Liothyrella uva*, an abundant species found all around Antarctica, this large species is highly variable in its loop morphology, overall shape, folding and thickening of larger individuals. Foster (1974, 1989) recognized several species and subspecies which are generally recognized as synonyms (per WoRMS 2025, Emig 2025), but this shows how highly variable *L. uva* is for most aspects of its morphology. *Liothyrella uva* as presently understood is difficult to distinguish morphologically from *L. neozelanica*, *L. southernsurveyori* sp. nov., and several other *Liothyrella* species given how variable it can be. Indeed, Lee *et al.*

(2001) found that the loop variability was high and largely overlapping between *L. neozelanica* and *L. uva*, rendering loop variability of somewhat uncertain use in distinguishing *Liothyrella* species, but this requires further testing with more species.

Overall, it is not without reservation that I describe the southern Australian *Liothyrella* species as new, but the apparent morphological and bathymetric differences relative to the nearby occurring *L. neozelanica*, combined with the genetic separation of this latter species relative to the Antarctic *L. uva*, suggests the species may be distinct. Follow up molecular analyses of *Liothyrella* from a much broader range of locations across the southern hemisphere would be very insightful. Tissue samples were taken last year from several *L. southernsurveyori* sp. nov. (as well as *D. fulva*) specimens at TMAG for the CSIRO National Biodiversity DNA Library project, so hopefully sequencing will become available to answer this question in the next few years.

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