New records and descriptions of recent Australian brachiopods (Terebratulida, Dallinidae and Aulocothyropsidae; and Rhynchonellida, Frieleiidae)

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Abstract

The recent brachiopod fauna of Australia remains poorly understood with several species lacking up-to-date descriptions, and with many unidentified or misidentified specimens in museum collections. A large collection of brachiopods housed at the Tasmanian Museum and Art Gallery was recently examined to allow the re-description of two Australian endemic Dallinid brachiopods, *Jaffaia jaffaensis* and *Campages furcifera*, and identify new species and species occurrences. Furthermore, the large number of specimens allowed ecological aspects to be explored. As a result, the morphology and variation of *C. furcifera* and *J. jaffaensis* were clarified and expanded, a new deep-sea Dallinid species, *Dallina tasmaniaensis,* sp. nov. was described, the first occurrence of this genus from Australia, and the deep-sea Aulocothyropsid species *Fallax neocaledonensis* and Rhynchonellid *Neorhynchia strebeli* were also recorded from Australia for the first time. *Jaffaia* was revealed to be far more alike *Nipponithyris* than previously appreciated. The morphometric relationships of the three Dallinid species were found to differ significantly, with the attachment substrata and epibiota particularly prominent and diverse for *J. jaffaensis* and *C. furcifera*. This research facilitates the improved identification of Australian brachiopods, significantly increases understanding of variation within local species, and highlights the underappreciated biodiversity of deep-sea brachiopods in Australian waters.

Introduction

Brachiopods or 'lamp shells' (Phylum Brachiopoda Duméril, 1805) are an ancient group of filter-feeding benthic marine invertebrates that are united by having dorso-ventral valves (shells), and a complex filter feeding organ, the lophophore. While the shell often creates superficial similarity to bivalve molluscs, they group closer to other lophophore bearing phyla (Phoronida and Bryozoa) and differ fundamentally in shell structure and overall morphology.

Australia hosts a large diversity of Brachiopod species, but systematic work on these species has been lacking. Following initial work in the 1800s, specialists in the early decades of the 20th century, notably Friedrich J.W. Blochmann (1858–1931) and Charles Hedley (1862–1926) made considerable headway and described much of the species known (Blochmann, 1910, 1914; Hedley 1904, 1905, 1911). Throughout the latter half of the 20th century the only prominent Australian brachiopod specialist was Joyce R. Richardson (1925–2019), who through the 1970s–90s, described and re-described further Australian species and contributed much to our understanding their ecology (*e.g.*, Richardson 1979, 1987, 1997). Recently, some taxonomic interest has resumed on Australian micromorphic brachiopods (Lüter *et al.* 2003; Hiller *et al.* 2008; Hoffmann *et al.* 2009; Robinson 2017; Robinson 2021).

The total number of Australian brachiopod species (excluding the Australian Antarctic Territories or 'AAT') is difficult to pin down. Richardson (1997) listed 23 species, but excluded *Terebratulina radula* Hedley, 1904 without clear reason, adding this species as well as *Thecidellina insolita* Hoffmann *et al.,* 2009, *Ospreyella depressa* Lüter *et al.*, 2003, and three *Novocrania* species (redescribed by Robinson 2017), *N. turbinata* (Poli, 1795)*, N. lecointei* (Joubin, 1901) and *N. huttoni* (Thomson, 1916), results in 29 species. To this must be added the *Lingula* taxa of northern Australia, which comprises four species according to Emig (1979) and Emig & Hammond (1981), *L. anatina* Lamarck, 1801, *L. rostrum* (Shaw, 1797), *L. adamsi* Dall, 1873, and *L. tumidula* Reeve, 1841, thus giving a total of 33 species. Much work is still to be done on many Australian species from both a taxonomic and ecological viewpoint, and the identification of local species is often challenging due to the lack of up-to-date descriptions.

The collections of the Tasmanian Museum and Art Gallery (and other Australian repositories) house unsorted or unidentified brachiopods with many attributable to the family Dallinidae Beecher, 1893. The only members of this family currently recognized from Australian waters are the endemic *Jaffaia jaffaensis* (Blochmann, 1910) and *Campages furcifera* Hedley, 1905, which lack descriptions with modern standards, and are poorly understood in terms of morphometric variations and ecology. Dallinid collections additionally contain specimens possibly attributable to several new species or genera not known from Australian waters.

This study aims to describe the Dallinid brachiopods from southern Australia and assess any new species or species records, and further aims to assess morphometric relationships, substrata, and epibiota of these taxa.

Methods

Brachiopod specimens at the Tasmanian Museum and Art Gallery (TMAG) were collected by the Commonwealth Scientific and Industrial Research Organisation (CSIRO) RV *Southern Surveyor* (SS) over 1993–2007, supplemented by material collected by CSIRO RV *Investigator* (IN), CSIRO RV *Soela* (SO), Japanese fisheries RV *Umitaka Maru* (UM), and the private motorsailer *Rambler* of Robert de Little. Collection used dredge, epibenthic sled, or beam trawl equipment. These specimens were collected around south-eastern Australia, from the Great Australian Bight, southern and eastern Tasmania, and the eastern and north-eastern Bass Strait (see **Fig. 1 A**). Comparison of important type material, and other specimens, was made from collections at the following institutions: Australian Museum (AM), Sydney, Australia; Museum für Naturkunde, Berlin, Germany (former Zoologisches Museum der Humboldt-Universität zu Berlin, ZMB); and Tohoku University Museum (TUM), Sendai, Japan. Macro photography and measurements were provided by these institutions, in part due to the difficulties imposed by the COVID pandemic and very fragile nature of specimens.

Specimens were either dry or were wet specimens that had been fixed in formalin before long term storage in 75% ethanol. For all specimens the length (L), width (W), and thickness (T) of the valves were recorded with callipers (per **Fig. 1 B, C**). The width as a percentage of length was calculated (W%L), as was the thickness as a percentage of length (T%L). Note was taken of attachment substrata and epibiota.

To illustrate the brachidium (brachial loop), it was sometimes necessary to free it of lophophore tissue. This required immersion of the specimen in a 10% dilution of domestic bleach (sodium hypochlorite) for 20–30 minutes (per Brunton & Curry 1979), before soaking in water to remove bleach, and drying. Illustration was accomplished by *Camera Lucida* (Leica MZ16 fitted with drawing tube). Structures are labelled per standard brachiopod terminology (see Brunton & Curry 1979 and Richardson 1997; as well as **Fig. 1 B–E** and below abbreviations). Anterior (end-on) aspects are illustrated with ventral valve lowermost, and several aspects are generally given of internal structures to better capture the 3D form and detail.

In the Taxonomy section (following Discussion), Dallinidae species are covered first in alphabetical order as they were the focus of research, they are followed by families uncovered during comparison of Dallinid material, the related family Aulocothyropsidae, followed by the unrelated Frieleiidae. Typically, Rhynchonellide brachiopods (such as Frieleiidae) are described before Terebratulide brachiopods (Dallinidae and Aulocothyropsidae), and this is reflected in the listing of higher taxonomy at the start of the below taxonomy section, but descriptions herein prioritize Dallinids.

General abbreviations: NE—northeast, RV—research vessel, SD—standard deviation; SE—southeast, Stn—station.

Figure abbreviations: AB—ascending branch of brachidium, AC—anterior commissure, Ad—adductor muscle, AEd—Anterior edge of valve, BR—beak ridge, CP—cardinal process, Cr—crura, CrP—crural process, DB—descending branch of brachidium, DL—dental lamellae (or plates), DP—deltidial plates, Fo—foramen, Go—gonad, Gr—groove, HT—hinge tooth (teeth), IHP—inner hinge plate, ISR—inner socket ridge, LCB—lateral connecting band of brachidium, MS—median septum, My—myophore, MP—medial process of symphytium, OHP—outer hinge plate, OSR—outer socket ridge, Pe—pedicle, Ri—ridge, Se—septalium (fused IHP's), So—socket, Sy—symphytium (fused DP's), TB—transverse band of brachidium.

Results

Comparisons of indices: Across the three Dallinid species examined herein, W%L and T%L indices were visualized graphically and fitted with linear regression equations to compare how the width and thickness of specimens changed relative to overall valve length (linear relationships given in **Fig. 2 A, B**).

C. furcifera, *D. tasmaniaensis,* sp. nov., and *J. jaffaensis* all displayed proportional increase in width and thickness relative to length (thus conforming well to linear relationships), at least over the size ranges available. Though *C. furcifera*, especially with valve width, was somewhat more variable and had the poorest fit to a linear model.

As indicated visually by the linear relationships, the clustering of the three species were well separated by either W%L or T%L indices. Separation was analysed by One-way ANOVA with Tukey's post-hoc testing (statistical results listed in **Table 1.**), given that *Neorhynchia strebeli* were found in association with *D. tasmaniaensis,* sp. nov., they were also included in this comparison. There was strong evidence that W%L and T%L differed between species (ANOVA, F-values = 307.1 (degrees of freedom 3,114) & 157.8 (degrees of freedom 3,110) respectively, p values < 0.0001). Regarding W%L indices, relative to *C. furcifera*, *J. jaffaensis*, *D. tasmaniaensis*, and *Neorhynchia* were all proportionally greater in width with statistical significance (Tukey's test values < 0.001). But all other W%L comparisons were non-significant. T%L showed more widespread significant differences, with all comparisons between the four species being statistically significant, though *C. furcifera* and *D. tasmaniaensis,* sp. nov. were closest in T%L indices (Tukey's test value 0.015, vs. all other T%L comparisons having values <0.001).

Size-frequency histograms were also constructed for the three Dallinid species to gain insight into population structure (**Fig. 2 C**). *C. furcifera* and *J. jaffaensis* were approximately left-skewed, while *D. tasmaniaensis,* sp. nov. was less clearly skewed (and had the fewest specimens).

Discussion

The Brachiopod family Dallinidae contains 21 recognized species in four genera, *Dallina* within the subfamily Dallininae Beecher, 1895, and *Nipponithyris* Yabe & Hatai, 1934, *Campages* Hedley, 1905, and *Jaffaia* Thomson, 1927 within the subfamily Nipponithyridinae Hatai, 1938 (Emig *et al.*, 2021; Emig 2022). *Dallina tasmaniaensis,* sp. nov. is the first new member of Dallinidae recorded from Australia waters in over 110 years. The species presumably went unnoticed due to its deep-sea distribution, collected at considerably greater depth than other Australian members of Dallinidae, 1157–1712 m, *vs.* 48–439 m for *C. furcifera* and 67–550 m for *J. jaffaensis* (herein and Richardson 1997), the species likely being allopatric with other Dallinids along the south-eastern Australian slope.

When comparing *D. tasmaniaensis,* sp. nov. to other extant members of its genus, two problematic species of *Dallina* were recognized that have escaped notice in widely used databases of marine species. WoRMS (2022a) lists *D. simosensis* Hatai, 1940 as an extant species, but from the description it is clearly a fossil taxon from the Pliocene (thus not listed by BrachNet as an extant member of *Dallina*, Emig 2022) and should not be listed on databases of recent (non-fossil) species. *D. profundis* Konzhukova, 1957 was described from a single empty shell collected on the northern slope of the Sea of Okhotsk basin at 1076 m depth (Konzhukova, 1957). When Zezina (1985) examined the specimen (in 1969 at the Zoological Institute of the Academy of Sciences of the USSR), she found it to be badly broken but attributable to *Glaciarcula spitzbergensis* (Davidson, 1952) (family Laqueidae Thomson, 1927) which has a northern circumpolar distribution (Zezina 2010). Therefore, *D. profundis* is a synonym of *G. spitzbergensis.*

This study increases the known maximum size for both *C. furcifera* and *J. jaffaensis*, and better-defines intraspecific variability within these taxa. Notably, the overall outline (shape) and anterior commissure folding were found to be considerably more variable than previously appreciated. Richardson (1997) noted 17 mm as the maximum length of *J. jaffaensis*, but herein 27 specimens exceeded this size (five reaching approximately 23 mm long), the maximum size of 23.4 mm long increasing the known maximum by 1.4×. As for *C. furcifera*, Cooper (1970) noted a specimen with a length of 31.0 mm, while Richardson (1997) recognized *C. furcifera* as reaching 25 mm long, close to the holotype length of 24 mm. The largest specimen examined herein with a length of 33.7 mm was thus 1.1× the length of the previous longest known specimen.

Thomson (1927) erected the genus *Jaffaia* to accommodate *J. jaffaensis*, separating it from *Campages* and *Dallina* on the basis of its differing cardinalia form and commissure folding. The trabecular adult loop form is also distinct from these genera (typically diploform and

teloform in *Campages* and *Dallina* respectively). The cardinal process of *Jaffaia* is distinct from the poorly developed (lacking anterior support) or absent state seen in *Dallina* and *Campages* but is not unlike that seen in *Nipponithyris* (also Dallinidae), such as *N. nipponensis* Yabe & Hatai, 1934 and *N. lauensis* Bitner, 2008, which also share a sulcate anterior commissure, proportionally large and thick based hinge teeth, and a trabecular loop (Yabe & Hatai, 1934b, fig 2, 3; Bitner 2008, fig 17). Overall, *Jaffaia* and *Nipponithyris* may be more closely related than either are to *Campages* and *Dallina* and are possibly synonymous (with *Jaffaia* being the senior synonym over *Nipponithyris*), but until a thorough review is undertaken of all *Nipponithyris* species relative to *Jaffaia*, no genus level changes are proposed.

Regions adjacent to Australia are inhabited by multiple other Dallinids including *C. mariae* (Adams, 1860) from New Caledonia and the Norfolk Ridges (Bitner 2009, 2010, 2015), *C. ovalis* Bitner, 2008 from Fiji Islands, *C. asthenia* (Dall, 1920) from Borneo and possibly Bali, north of Australia (Cooper 1970; Zezina 1981), *Nipponithyris afra* Cooper, 1973 from New Caledonia (Laurin 1997), and *N. lauensis* Bitner, 2008 from the Fiji Islands. At least some of these, as well as a wide variety of other families and genera recorded in the south-west Pacific, are likely to occur in Australian waters, and will probably be encountered as more deep-sea material is critically examined. This was demonstrated herein by the discovery of Australian examples of *Dallina, Fallax,* and *Neorhynchia*, with the three occurrences bringing the total number of Australian brachiopod taxa (excluding the AAT) to 36. Even though not Dallinids, the surprise discovery of *Fallax neocaledonensis* of the related family Aulocothyropsidae, and *Neorhynchia strebeli* within a different brachiopod order, resulted in their brief description herein as both finds represent considerable range extensions for these species.

Linear relationship of W or T with L (*i.e.*, relatively constant W%L and T%L indices with increasing total length) were observed for all three Dallinid species observed herein and were found to be a good means of separating the taxa both graphically and by statistical testing. Specifically, W%L was suitable at separating *Campages* from *Dallina* and *Jaffaia* (but not the latter two from each other), whereas T%L was better at separating all three species, as well as the sympatric *Neorhynchia* that may be confused for small individuals of *Dallina* (given its triangular form). However, the three local Dallinid species were all in distinct genera, and it remains to be seen if such relationships separate species reliably within these genera. This further implies that these species grow in a proportional manner without greatly altering their shape as they grow, with the caveat that the smallest individuals were not available. Population structure was also briefly analysed with size-frequency histograms. Resulting distributions were approximately normal, and for *C. furcifera* and *J. jaffaensis* were left-skewed (less clear for *D. tasmaniaensis,* sp. nov.) with juvenile specimens rare or lacking and larger specimens increasingly common. This pattern has been observed in the brachiopods *Liothyrella neozelanica* Thomson, 1918 and *Magellania fragilis* (Smith, 1907) from New Zealand and Antarctica respectively, and may be indicative of poor sampling of smaller specimens (due to equipment used), sporadic recruitment events, low mortality vs. growth rate, or size dependent mortality (smaller individuals more likely to die) (Baird *et al.* 2013; Brey *et al.* 1995). Future study will need to assess the seasonality, age, and growth rate of these taxa.

Attachment substrates of Australian Dallinids were recorded herein, though for most specimens the attachment substrate was absent or the fragment attached to the pedicle was too small to be identified. *J. jaffaensis* was attached to a variety of small fragments from bryozoans, coral, and mollusc shells. Contrastingly, Dunstan *et al.* (2012) reported that *J. jaffaensis* off southern Tasmania was associated with 'intermediate values of mud', but they comment that the species was however known to be associated with coral-matrix. *C. furcifera* was attached to coral fragments, but often also to the calcified tubes of polychaete worms (Serpulidae?), the fragments often being large, similar to the length of the valves. Richardson (1979) reported *C. furcifera* (201 m depth, northeast of Flinders Island) were attached to shell fragments, and collected from 'coarse shell sand', whereas Hedley (1905) recorded that the type specimen of *C. furcifera* was attached to a stone (no longer attached to the Holotype). It is possible that both *J. jaffaensis* and *C. furcifera* occur in environments with coarse shell/rock fragments (rather than fine sands or rocky substrates), attaching to either shell/bryozoan fragments, or serpulid tubes and rocks imbedded in such substrates.

Taxonomy

Phylum **BRACHIOPODA** Duméril, 1805

Class **RHYNCHONELLATA** Williams *et al.,* 1996

Order **RHYNCHONELLIDA** Kruhn, 1949

- Family **FRIELEIIDAE** Cooper, 1959
- Genus *Neorhynchia* Thomson, 1915

Order **TEREBRATULIDA** Waagen, 1883

SubOrder **TEREBRATELLIDINA** Muir-Wood, 1955

- Family **DALLINIDAE** Beecher, 1893
- Genera *Campages* Hedley, 1905, *Dallina* Beecher, 1893, and *Jaffaia* Thomson, 1927
- Family **AULACOTHYROPSIDAE** Dagys, 1972
- Genus *Fallax* Atkins, 1960
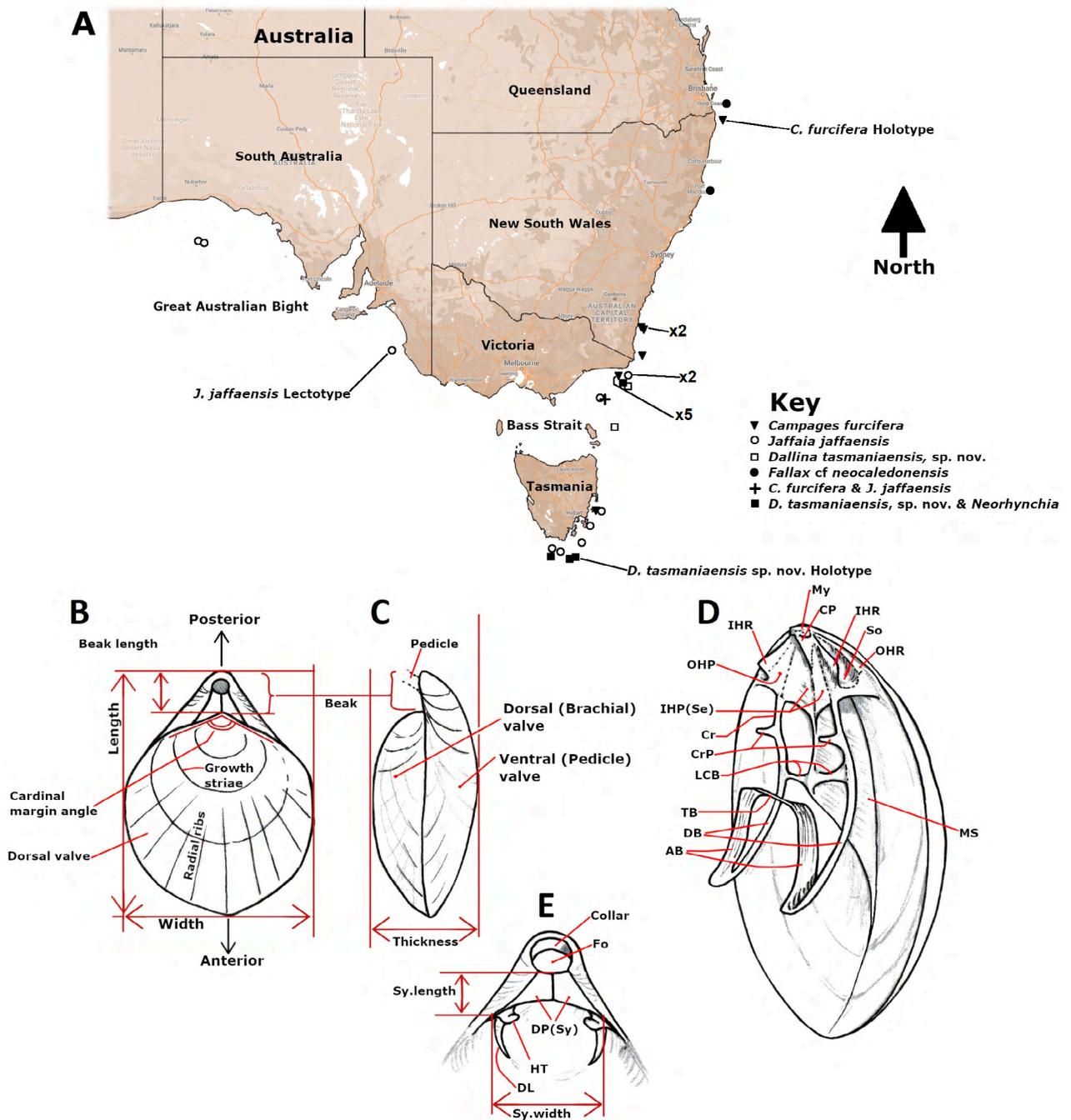
Fig. 1. A) Locations of Australian brachiopod material examined. Each marker represents a station, with some stations collecting two different species (per key). Type specimen locations are marked. Map generated with *Google My Maps* and subsequently modified. **B–E)** Schematic diagrams of morphology and measurements, with dorsal (**B**) and lateral (**C**) aspects, interior of dorsal valve (**D**), and close-up of ventral valve interior (**E**).

Genus *Campages* Hedley, 1905

Type species: *Campages furcifera* Hedley, 1905 (by original designation); accepted Type species *Terebratella mariae* Adams, 1860.

Diagnosis: Small to medium sized, valves biconvex, elongate oval to subtriangular in outline; lateral commissure straight or curved towards dorsal valve, anterior commissure rectimarginate to intraplicate. Beak short, suberect to erect; beak ridges not developed; deltidial plates conjunct as narrow symphytium, exposed; foramen large, permesothyridid to mesothyridid; hinge teeth small, dental plates absent; pedicle collar very short. Cardinalia lamellar with lightly excavate inner and outer hinge plates separated by poorly- to well-developed crural bases, inner hinge plates a V-shaped septalium supported by median septum, inner socket ridges lightly inclined; cardinal process a small plate folded (and not supported) anteriorly (and bearing an oval myophore facing posteriorly); median septum extend-
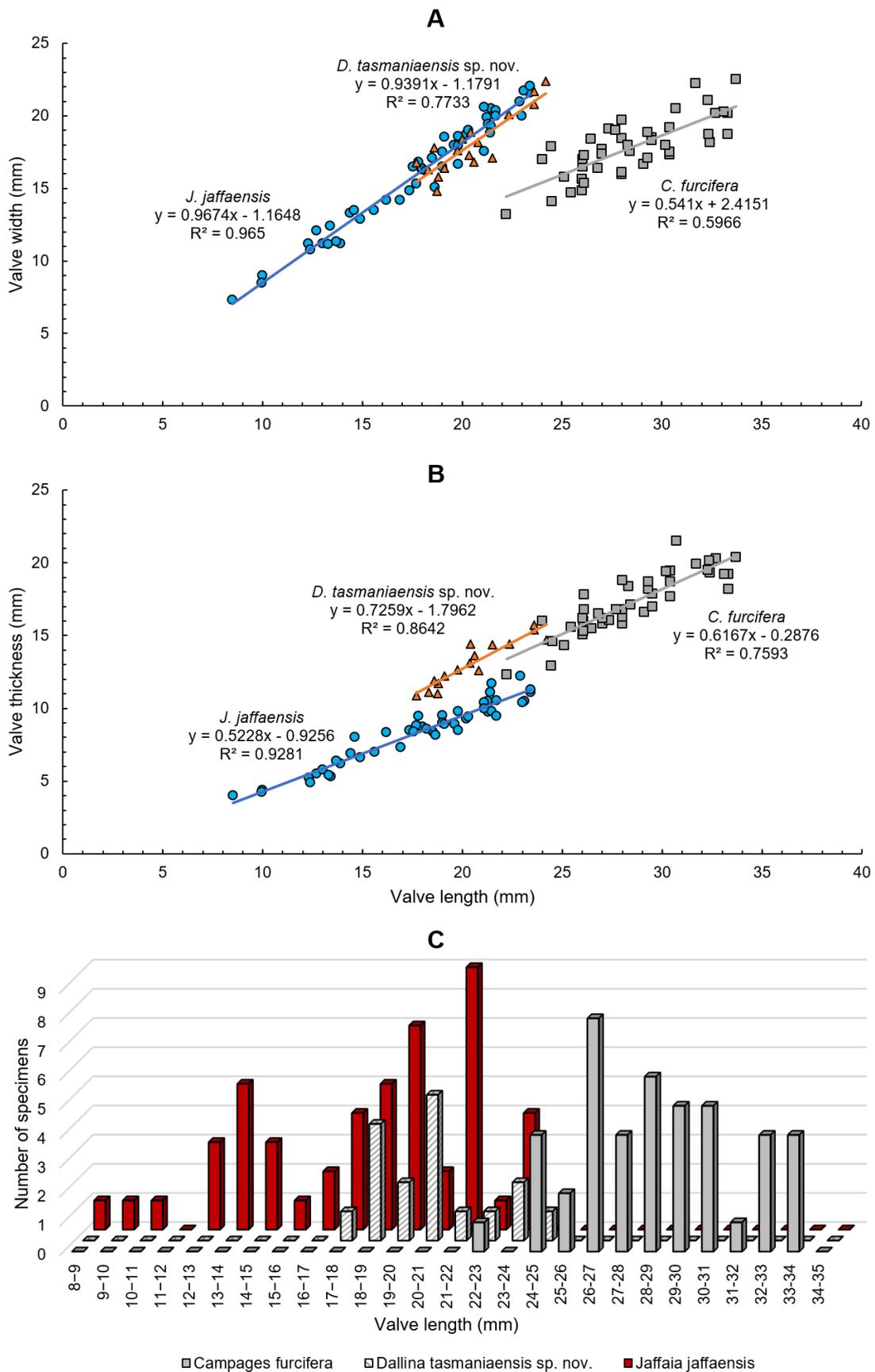
Fig. 2. A, **B**) Scatterplots to compare relationships between valve width (**A**) and thickness (**B**) relative to length for *C. furcifera* (grey boxes), *D. tasmaniaensis,* sp. nov. (orange triangles), and *J. jaffaensis* (blue circles), using material examined herein (including type material). Linear relationships are fitted with equations displayed. **C**) histograms of the same specimens, displaying the frequency distribution of overall valve lengths, specimens are grouped into 1 mm bins and are coloured per the key below.

Comparison	W%L comparisons (P value)	T%L comparisons (P value)
J. jaffaensis vs. *C. furcifera*	<0.001	<0.001
J. jaffaensis vs. *D. tasmaniaensis*, sp. nov.	0.548	<0.001
C. furcifera vs. *D. tasmaniaensis*, sp. nov.	<0.001	0.0152
N. strebeli vs. *D. tasmaniaensis*, sp. nov.	0.0719	<0.001
N. strebeli vs. *C. furcifera*	<0.001	<0.001
N. strebeli vs. *J. jaffaensis*	0.290	<0.001

Table 1. Statistical significance of brachiopod comparative indices. P-values for Tukey's post-hoc tests on one-way ANOVA.

ing anteriorly approximately ½ to ⅔ dorsal valve length; crura short, subparallel or weakly diverging, crural processes large and pointed. Adult brachial loop diploform ('campagiform') to trabecular; lophophore plectolophous. (Modified from Emig 2022)

Genus description: As per diagnosis.

Campages furcifera Hedley, 1905

Fig. 3, 4; Table 2.

Type specimen lodged (by Hedley 1905) at the Australian Museum, Sydney (AM C.19824).

Diagnosis: A *Campages* with overall outline elongate sub-trigonal to sub-pentagonal, weakly to strongly intraplicate anterior commissure, rectangular plate-like and unsupported cardinal process, V-shaped septalium, diploform loop extending ½–⅔ dorsal valve length and not exceeded in length by medial septum, and with valves variously thickened and bearing relatively light and irregular growth striae.

Etymology: Not defined by Hedley (1905). Specific epithet from 'furca' (Latin noun for fork) and suffix '-fera' (Latin for bearing/carrying; feminine singular of suffix -fer), likely describing either the strong anterior folding or perhaps the distinctive brachidium.

Description

Overall valve form: Maximum valve length 33.7 mm (average 28.5 mm, SD 2.9, smallest 22.2 mm long). Valves relatively narrow, W%L averaging 62.6% (SD 4.7, range 56.2%–73.2%), and relatively thick, T%L averaging 60.6% (SD 3.6, range 52.8%–70.0%).

Overall outline (viewed dorso-ventrally) elongate sub-rectangular or sub-pentagonal, widest point approximately midway along length with anterior margin truncated. Valves biconvex from lateral profile, ventral (pedicle) valve deeper. Lateral commissure dorsally convex, gently curved towards dorsal (brachial) valve (see dorsal and lateral aspects **Fig. 3 A–C**). Anterior commissure weakly to strongly intraplicate (plicosulcate)[1], dorsal valve with small antero-medial ridge folding dorsally, flanked by shallow grooves folding ventrally and creating a shallow antero-medial groove on the ventral valve (**Fig. 3 D**). On some smaller specimens, as well as the largest and most thickened specimens, the anteri-

or commissure folding was irregular (see **Fig. 3 E, F**). Holotype specimen similar but elongate sub-triangular in overall outline, with the widest point closer to the anterior end of the valves (**Fig. 4 A–F**).

Valves punctate, increasingly thick and rough on larger specimens, the growth striae becoming low ridges. Radial ribs/costae absent. Colouration cream or yellowish-brown.

Dorsal (brachial) valve: Cardinal margin angle obtuse (~100–106°). Cardinal process small, produced as a rectangular plate folded anteriorly from the umbo, with a deep indentation anterior to the process and an oval myophore on the posterior face. Hinge sockets well defined but ridges are relatively small, socket ridges diverging at approximately 71–86° (to antero-posterior axis), relatively flat (only gently inclined ventrally). Outer hinge plates small and slightly grooved, demarcated from inner plates by fairly poorly-developed crural bases (bases narrow, outer edges somewhat continuous with inner socket ridges). Inner hinge plates fused medially as a lightly excavate septalium (excavation running posteriorly to the cardinal process), supported by the median septum. Septalium anterior border V-shaped and either just reaching level of crural processes or extending anteriorly slightly beyond them (cardinal process, socket ridges and hinge plates illustrated in **Fig. 3 G, H**; specimen with longer septalium in **Fig. 3 I**). Brachidium illustrated from two specimens, one with narrower brachidium (**Fig. 3 I–K**) and one wider and longer (**Fig. 3 L–N**). Crura short, weakly diverging (from antero-posterior axis) or subparallel (on Holotype). Crural processes moderately long and pointed, directed ventrally (and slightly medially) (see **Fig. 3 J, N, Fig. 4 G, H**). Brachidium diploform ('campagiform'), descending branches broad and ribbon like, fused posteriorly with the crural process, and with short and thin lateral bands connecting with the median septum. Ascending branches and transverse band very high, forming a large hood/funnel, anterior-most extent of loop ~66%–75% dorsal valve length (see different aspects in **Fig. 3 I–N, Fig. 4 D, G, H**). Transverse band with pair of antero-lateral folds, demarcating a medial indentation of reduced height (see **Fig. 3 K**). Median septum thin, initially dropping in height anterior to hinge plates before rising to the highest point where the lateral bands connect, rapidly dropping off anterior to this but not extending beyond

brachial loop, terminating approximately 40%−65% dorsal valve length).

Ventral (pedicle) valve: Beak moderately small (length ~14%−17% overall length), suberect. Foramen subapical to transapical (posteriorly against border, 'marginate' per Thomson 1927), moderately large (diameter approximately 8%−10% overall valve length), permesothyridid, beak ridges poorly defined. Pedicle collar very short (little more than a ring in the foramen opening). Deltidial plates mostly exposed, fused (*i.e.*, as a symphytium) with little trace of a medial seam on material examined. Hinge teeth relatively small, bases not thickened (however, tooth−socket connection was very strong, and on the two specimens examined to illustrate brachidia, the hinge could not be disarticulated). Dental plates absent. Deltidial plates and hinge teeth illustrated in **Fig. 3 A, G, H**, **Fig. 4 C**, and others).

Soft tissue: Pedicle short (not extending beyond the beak), its end rough/papillate (**Supplementary Fig. 1 A**). Lophophore plectolophous (**Supplementary Fig. 1 B**). Gonad development apparent in some specimens, gonads narrow and confined to posterior half of valves (see **Fig. 3 A**).

Attachment substrata and epibiota: Approximately 36% of examined specimens were attached. Substrata varied but were small to large (size ≤ valve length) and included serpulid tubes, empty whole shells or worn fragments (including those of the brachiopod *Basiliolella colurnus*), and bryozoan colony fragments. Epibiota was mostly small encrusting sponges or brown films of microorganisms, the Holotype specimen had encrusted tubes on the ventral valve, possibly from Serpulid worms.

[1]Intraplicate (or plicosulcate) describes alternate folding, with dorsal ridge having a small median fold (relative to the stronger ventral folds flanking it), this is similar to parasulcate where the median fold is much stronger (and ventral folds weaker).

Specimens examined

Holotype. *C. furcifera* Holotype, east of Cape Byron (NSW), 12 ½ miles east of Cape Byron, 28.633°S, 153.866°E, 203 m, 10.xi.1902, AM C.19824.

Other material examined. 2 specimens, South of Maria Island, 42.7316°S, 148.2466°E, 98 m, *Rambler*Stn 75, 9.x.2014, TMAG E21827; 4 specimens, NE of Bermagui, 36.377°S, 150.248°E, 123−277 m, SS199405 Stn 172, 8.ix.1994, TMAG E21983; 5 specimens, off Pt Hicks, NE Bass Strait, 38.1967°S, 149.2717°E, 212−240 m, SS199305 Stn 115, 31.vii.1993, TMAG E22154; 1 specimen, NE of Flinders Island, eastern Bass Strait, 38.9508°S, 148.5014°E, 179−185 m, SS199305 Stn 54, 27.vii.1993, TMAG E22155; 14 specimens, off Pt Hicks, NE Bass Strait, 38.1917°S, 149.2599°E, 202−246 m, SS199305 Stn 181, 7.viii.1993, TMAG E22156; 1 specimen, off Bermagui, 36.4633°S, 150.3033°E, 215−220 m, SS199305 Stn 272, 15.viii.1993, TMAG E22157; 23 specimens, NE Bass Strait, 38.1933°S, 149.2599°E, 190−240 m, SS199305 Stn 191, 8.viii.1993, TMAG E22158 (Two specimens used as dry preparations of internal structures, given new registration number E22189); 1 specimen, southern NSW, 37.398°S, 150.298°E, 161−184 m, SS199405 Stn 107, 1.ix.1994, TMAG E22159; 1 specimen, NE Bass Strait, 38.1839°S, 149.2506°E, 158−180 m, SS199305 Stn 194, 8.viii.1993, TMAG E33640; 4 specimens, off Pt Hicks, NE Bass Strait, 38.1889°S, 149.2692°E, 230−240 m, SS199305 Stn 173, 6.viii.1993, TMAG E33644.

Remarks

C. Hedley (1905) of the Australian Museum (Sydney) described the new genus and species *Campages furcifera*, from a single specimen collected off Cape Byron on the 10th Nov 1902. The original description was limited, the genus only being defined by the form of its brachidium (later designated 'campagiform' after the genus). *C. furcifera* received little subsequent morphological assessment other than Cooper (1970) who briefly compared it to other species of the genus and Richardson (1979) who assessed the pedicle structure of the species.

The Holotype specimen of *C. furcifera* has dimensions 24 mm (length) and 17 mm (width) (Hedley, 1905) for a W%L of 70.8%. Cooper (1970) examined two *C. furcifera* specimens with W%L and T%L indices of 63%−65% and 65%−70% respectively (31.0 and 27.7 mm long; from off Gabo Island, Victoria, 210−265 m), these specimens and the Holotype were thus consistent with the range of indices for material examined herein. The morphology of the Holotype was also compared herein (see **Fig 4**), and it was found to generally be consistent with the examined material from the TMAG collections, however the folding was a bit stronger than what was observed on most TMAG specimens, the overall form was more triangular, and median septum didn't extend as far anteriorly.

Zezina (1981) reported the shell of a putative *C. furcifera* specimen collected off Bali (north-west of Australia, 8°49′S, 115°19′E, 202 m depth) and commented that *C. furcifera* may prove to be the senior synonym of *C. asthenia* Dall, 1920. Little comment can be made given that the shell Zezina examined was little more than a damaged dorsal valve missing the loop. However, Cooper (1970) differentiated *C. asthenia* by it having the widest point of the valves closer to the anterior end and thus with the anterior valve width equal or only slightly narrower than the mid-region (vs. widest midway along the valves in *C. furcifera*, per Cooper 1970, Plate 129C), *C. asthenia* also had a deeper antero-medial groove on the ventral valve. However, while the overall shape reported by Cooper (1970) was consistent with the *C. furcifera* from TMAG collections (which have a widest point midway), the Holotype of *C. furcifera* was distinctly widest at the anterior end of the shell (**Fig. 4 A, C**) as described
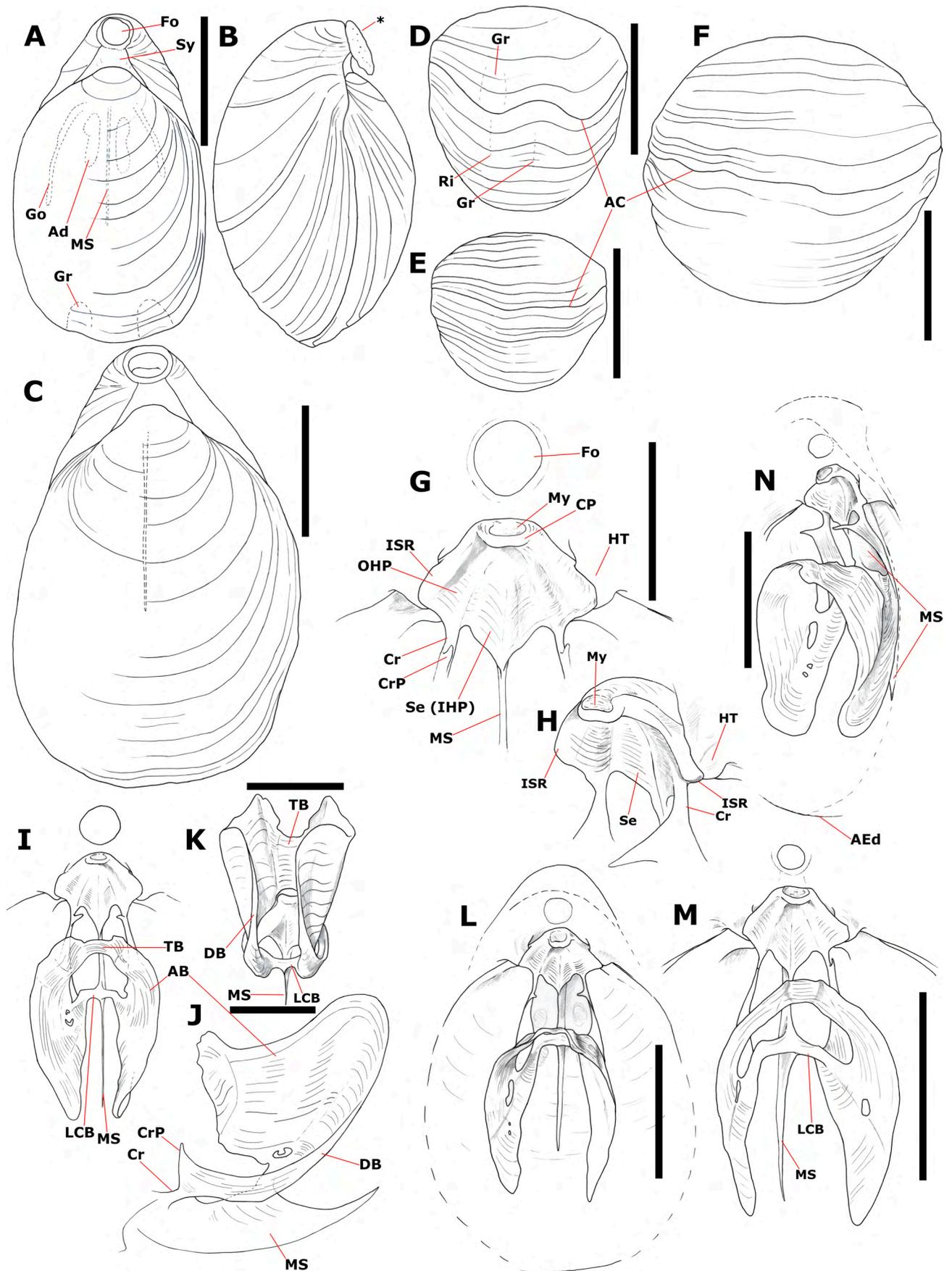
Fig. 3. *Campages furcifera* specimens. **A, B)** Dorsal and lateral aspects of average sized specimen (E22156; L=25.5 mm). **C)** Dorsal aspect of largest specimen (E21983; L=33.7 mm). **D–F)** Anterior aspects of three specimens with variable anterior commissure folding, well folded (**D**, same specimen as **A**), light folding (**E**; E22156; L=22.2 mm), and irregular folding (**F** same specimen as **C**). **G, H)** close-up aspects of cardinalia

and hinge teeth (looking at inside of dorsal valve with ventral valve lifted upwards) (E22189). **I–K**) ventral, lateral, and anterior aspects of brachidium from smaller specimen (E22189). **L–N**) Two ventral aspects (the first showing the outline of the dorsal valve) and a semi-lateral aspect of brachidium from a larger specimen (E22189). Abbreviations per Methods. Scale bars: 10.0 mm (**A–F, L–N**), 5.0 mm (**G, J, K; H** & **I** approximately same scale as **G** & **J** respectively).

Specimen	L	W	T	W%L	T%L	Attachment	Epibiota	Notes
E21827	26.0	15.65	15.05	60.2	57.9	Serpulid tube		
	26.05	17.0	16.0	65.3	61.4	Serpulid tube		
E21983	33.7	22.55	20.4	66.9	60.5			Illustrated
	29.1	16.7	16.6	57.4	57.0	Coral fragment		
	33.3	20.2	18.2	60.7	54.7			
	28.0	19.7	16.3	70.4	58.2			
E22154	26.1	15.35	17.8	58.8	68.2			
	27.0	17.4	16.2	64.4	60.0			
	24.5	14.1	14.6	57.6	59.59		Sponge	
	25.1	15.8	14.3	62.9	56.97			
E22155	27.35	19.1	16.05	69.8	58.7	Serpulid tube (~equal to L)		
E22156	32.3	21.1	19.5	65.3	60.4			
	26.0	14.85	16.2	57.1	62.3	Bryozoan frag		
	27.0	17.7	15.8	65.6	58.5			
	30.4	17.5	19.45	57.6	63.98	Shell fragment		
	29.5	18.5	17.0	62.7	57.6	Shell fragment		
	32.7	20.2	20.3	61.8	62.1	*Basiliolella colurnus* (dead)		
	28.0	16.0	16.8	57.1	60.0	*Basiliolella colurnus* (dead)		
	26.1	17.3	16.8	66.3	64.4			
	26.8	16.4	16.5	61.2	61.6			
	22.2	13.2	12.3	59.5	55.4			Illustrated
	28.4	17.55	17.1	61.8	60.2	Bryozoan fragment		
	25.45	14.7	15.6	57.8	61.3			Illustrated
	28.3	18.0	18.4	63.6	65.0			
	30.4	19.2	18.7	63.2	61.5			
E22157	29.3	17.1	18.2	58.4	62.1	Coral fragment		
E22158*	26.45	18.4	15.5	69.6	58.6	Gastropod shell	Sponge	
	27.7	19.0	16.8	68.6	60.6			
	29.5	18.3	17.85	62.0	60.5	*Basiliolella colurnus* (dead)		
	30.2	18.0	19.4	59.60	64.2			
	30.7	20.5	21.5	66.8	70.0		Sponge	
	31.7	22.25	19.9	70.2	62.8		Sponge	
	28.0	16.1	18.8	57.5	67.1			
	32.4	18.2	19.3	56.2	59.6			
	28.0	18.45	15.8	65.9	56.4			
	33.1	20.3	19.2	61.3	58.0			
E22159	32.35	18.75	20.15	57.96	62.3			
	24.45	17.9	12.9	73.2	52.8			
E33640	30.4	17.35	17.7	57.1	58.2	Bivalve fragment (~equal valve L)		
E33644	29.3	18.9	18.7	64.5	63.8			
	26.05	16.5	15.3	63.3	58.7			
	33.3	18.75	19.2	56.3	57.7	Coral fragment		
AM C19824	24	17	16**	70.8	66.7		Serpulid tubes(?)	Illustrated

Table 2. *Campages furcifera* **measurements, notes, and indices.** All measurements in mm.*=two specimens used for dry preparation of brachial loop (given new registration number E22189). **=approximate measurement as valves were disarticulated.
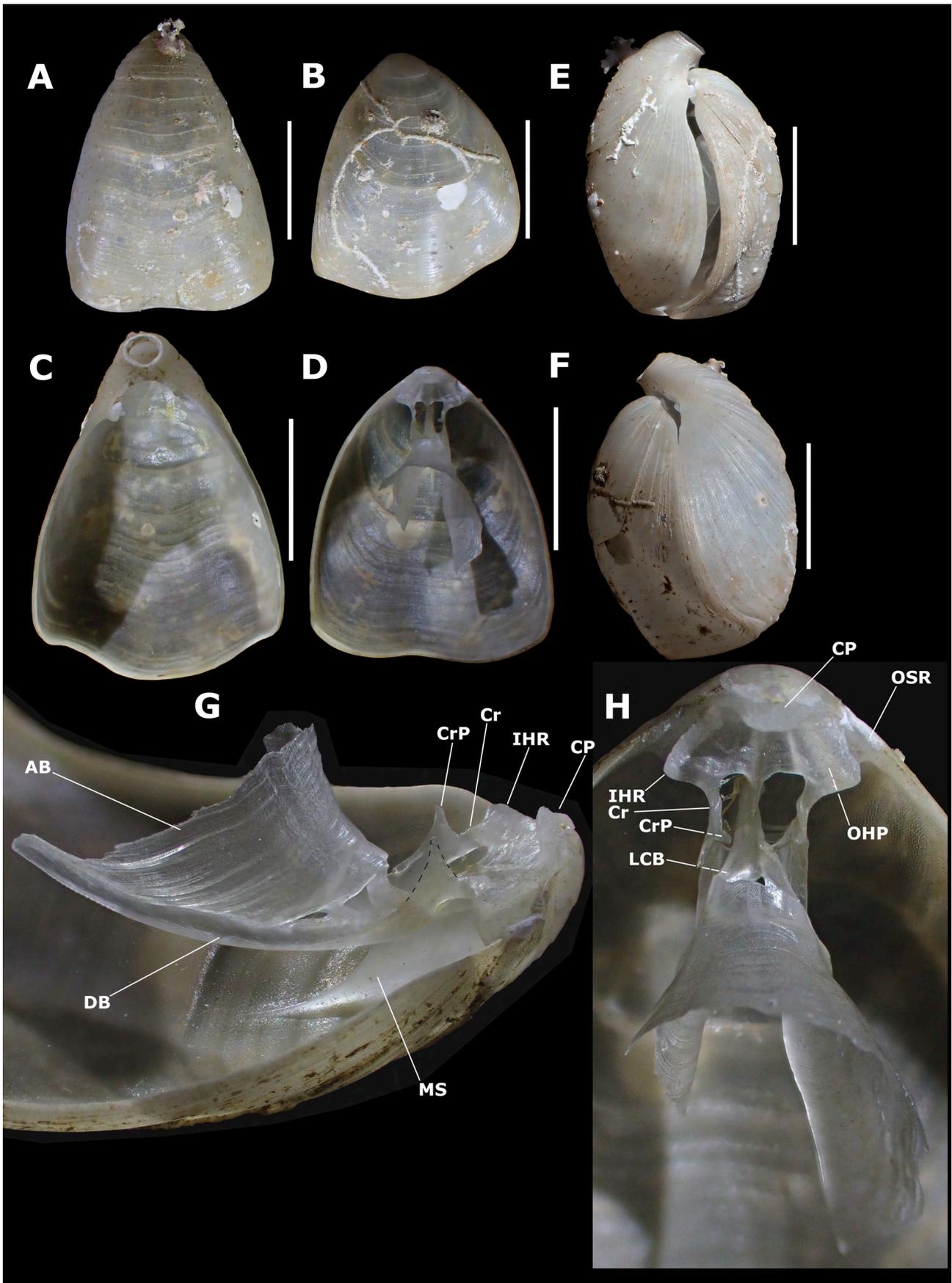
Fig. 4. *Campages furcifera* Holotype (AM C19824). **A**, **B**) external aspects of disarticulated ventral and dorsal valves. **C**, **D**) Internal aspects of ventral and dorsal valves. **E**, **F**) lateral aspects. **G, H**) semi-lateral and ventral aspect of brachidium–cardinalia complex. Abbreviations per Methods. Scale bars: 10.0 mm. Photography A.C. Miller, Copyright: Australian Museum (used with permission).

for *C. asthenia*, rendering the differences between the species uncertain.

The strong anterior folding of some *C. furcifera* specimens (per Hedley 1905 and Cooper 1970) has been used as a distinctive feature differentiating this species from others in the genus. Examination of material herein revealed that the extent of folding was highly variable. Therefore, the extent of folding doesn't consistently differentiate the local *Campages* species from other congeneric taxa.

Ultimately *C. furcifera* may either be more variable in its shape than previously realized, and likely a senior synonym of *C. asthenia*, or more than one species of *Campages* may be present in south-eastern Australia. At present the description of *C. furcifera* is simply adjusted to account for the variability of south-eastern Australian material and confirming synonymy of *C. asthenia* will be dependent on further morphological and ideally molecular study.

Bitner (2009, 2010, 2015) recorded *C. mariae* (Adams, 1860), previously known from the north-west Pacific, from around New-Caledonia (180–852 m depth), off north-eastern Australia. Compared to *C. furcifera*, *C. mariae* has more prominent external growth lines, and from literature measurements of seven specimens (Cooper 1970; Bitner 2010) it has proportionally greater width (W%L indices averaging 74.4%, range 67.8%–81.8%), but is otherwise very similar. Interestingly, *C. furcifera* has also been recorded from New Caledonia (d'Hondt 1987). However, the later work by Laurin (1997) (and confirmed by Bitner 2008) revealed that these specimens were *Fallax neocaledonensis* Laurin, 1997. This species is superficially similar in folding and brachidium to *C. furcifera*, but with a much more distinctly (and broadly) triangular outline and bearing hinge teeth supported by distinctive dental plates (absent in *Campages*). Yet, to further complicate matters, some specimens tentatively identified as *F. neocaledonensis* have been collected from eastern Australia (as will be discussed later) but occur at considerably greater depth than *C. furcifera*.

Interestingly, at least three *C. furcifera* specimens were attached to the empty valves of another brachiopod, *Basiliolella colurnus* (Hedley, 1905), and large amounts of dead *B. colurnus* shells were found with several of the *C. furcifera* lots (prior to sorting and registering). This indicates that these species may co-occur, but *Campages* utilizes *Basiliolella* shells as just one of several attachment substrates (along with bivalve and gastropod shells, and bryozoan fragments) on the shelly/rocky sands that it seems to inhabit.

Distribution: Examined material was collected from the outer shelf and upper slope from northern NSW, and south along the eastern Bass Strait and SE of Tasmania (see **Fig. 1 A**), within the distributional range specified by Richardson (1997) along the eastern, southern, and western coasts of Australia. Bathymetric range of specimens herein was 98–277 m, again within the known range of 48–439 m (Richardson 1997).

Genus *Dallina* Beecher, 1893

Type species: *Terebratula septigera* Lovén, 1846

Diagnosis: Small to large, triangular to subquadrangular in outline; lateral commissure curved towards dorsal valve, anterior commissure rectimarginate to paraplicate. Beak suberect to erect, without strong beak ridges; deltidial plates conjunct as a symphytium, partly exposed; foramen small to large, mesothyridid, attrite; hinge teeth small, dental plates absent; pedicle collar very short. Cardinalia lamellar with excavate inner and outer hinge plates separated by narrow well-developed crural bases, inner hinge plates a V-shaped septalium supported by median septum, inner socket ridges steeply inclined; cardinal process absent or produced as a very small rectangular plate folded (and not supported) anteriorly; median septum low anteriorly, extending beyond mid-valve; crura short, subparallel or weakly-diverging, crural processes large and pointed. Adult brachial loop teloform ('dalliniform'); lophophore plectolophous. (Modified from Emig 2022)

Genus description: As per diagnosis.

Dallina tasmaniaensis, sp. nov.

Fig. 5; Table 3

http://zoobank.org/urn:lsid:zoobank.org:act:10F319A7-641D-44FC-AC2A-D7834415D686

Holotype lodged with the Tasmanian Museum and Art Gallery, Tasmania (**TMAG E58673**), see specimens examined.

Diagnosis: Moderately large, thin shelled, and subtriangular *Dallina*, with relatively long beak, intraplicate anterior commissure (moderate folding), relatively broad symphytium, rectangular plate-like cardinal process, large crural processes supported by a straight-edged crura–descending branch junction, and relatively thick descending branches.

Etymology: Specific epithet '*tasmaniaensis*' after the island of Tasmania, around which much of the Type material was collected, combined with the Latin suffix '-ensis' forming an adjective from the toponym (*i.e.*, of/from Tasmania), neutral in gender.

Description

Overall valve form: Maximum valve length 24.2 mm (average 20.5 mm, SD 2.0, smallest 17.7 mm long). Valves wide, W%L averaging 88.1% (SD 5.1; range 78.9%–95.7%), and relatively thick, T%L averaging 63.8% (SD 3.0, range 58.7%–70.6%).

Overall outline (dorso-ventrally) subtriangular, the widest point being near the anterior border which is

truncated (**Fig. 5 A–D**). Valves deeply biconvex, the ventral (pedicle) valve being deeper. Lateral commissure dorsally convex (curving towards the dorsal valve) (**Fig. 5 E**). Anterior commissure weakly to strongly intraplicate (plicosulcate), the dorsal valve with an antero-medial ridge with weak folding towards the dorsal valve flanked by two shallow grooves folding ventrally more strongly, creating an antero-medial groove on the ventral valve (see **Fig. 5 F**). On some specimens the overall folding (dorsally and ventrally) is weak to near absent (see **Fig. 5 G, H**). The folding sometimes creates two shallow indentations along the anterior margin (viewed dorso-ventrally, see **Fig. 5 B**).

Valves punctate, relatively smooth and thin, but with fine growth striae. Radial ribs/costae absent. Colouration beige, though several have a dark yellow or brown coating (see **Supplementary Fig. 1 C**).

Dorsal (brachial) valve: Cardinal margin angle obtuse (~118–135°). Cardinal process moderately developed, produced as a small rectangular plate, anteriorly folded from the dorsal umbo (with small myophore). Hinge sockets narrow and well defined. Inner socket ridges diverge at approximately 120° (relative to antero-posterior axis), anteriorly widened and steeply inclined towards the ventral valve (see **Fig. 5 I, J**, and lateral in **Fig. 5 K**). A gentle groove separates each inner socket ridge from each outer hinge plate, which are narrow and only slightly inclined. Crural bases separate the outer and inner hinge plates (bases narrow, outer edges not continuous with inner socket ridges). Inner hinge plates, inclined more than outer plates and meeting medially as an excavate septalium, supported by the median septum. Anterior edge of septalium forming a V-shape, extending anteriorly well beyond level of crural bases (but not reaching level of crural processes) (see **Fig. 5 I**). Crura relatively short, diverging only weakly, crural processes angled ventrally (ends directed slightly medial), large and pointed in lateral profile, dorsal edge of crura–descending branch junction straight (see **Fig. 5 I, K**, for ventral and lateral aspects respectively). Crural process located at ~20% dorsal valve length. Brachidium dalliniform (see **Fig. 5 J–L**), only attached by the crura (condition confirmed on two specimens, one illustrated), descending branches long, free from ascending branches for most of their length. Ascending branches wide, transverse band with pair of antero-lateral indentations/ridges (see **Fig. 5 K, L**). Median septum very high and thin posteriorly, dropping off abruptly in height at approximately ⅓ dorsal valve length (anterior to crural processes), then continuing as a low septum (slowly reducing in height), ending approximately ⅔ dorsal valve length (approximately at the anteriormost extent of the brachial loop) (see **Fig. 5 J, K** for ventral and lateral aspects of septum).

Ventral (pedicle) valve: Beak moderately small (length 14%–16% of overall length), suberect to erect. Foramen subapical (posterior edge is against the posterior border of the valve), moderately large (foramen diameter 11%–12% overall valve length), mesothyridid, beak ridges indistinct (partly visible, see **Fig. 5 M**). Pedicle collar short (as a ring within foramen). Deltidial plates are partly exposed, conjunct as a symphytium, medial seam where the plates abutted either visible (**Fig. 5 N, O**) or obscure (**Fig. 5 A, B**). Symphytium relatively broad (symphytium length 39%–46% its width). Hinge teeth at anterolateral corners of deltidial plates, relatively small compared to symphytium, squared, bases not especially thickened, dental plates absent (**Fig. 5 N, O**).

Soft tissue: Lophophore plectolophous. Pedicle very short (not extended beyond beak). Gonad development visible in some specimens, small and confined to posterior half of valves (see **Fig 5. D**).

Attachment substrata and epibiota: Specimens were generally lacking attachment substrata (other than one with a shell fragment) and lacking distinctive epibiota other than thin films of microorganisms perhaps giving a brown colour to some specimens.

Specimens examined

Holotype. 1 specimen, seamounts south of Tasmania, 44.2394°S, 147.2929°E, 1354–1414 m, IN2018_V06 Stn 169, 14.xii.2018, TMAG E58673.

Paratypes. 30 specimens, off Pt Hicks, NE Bass Strait, 38.4799°S, 149.5529°E, 1520–1527 m, SS200001 Stn 154, 18.iv.2000, TMAG E22119; 2 specimens, east of Flinders Is, eastern Bass Strait, 39.9155°S, 149.0884°E, 1557–1608 m, SS200001 Stn 256, 28.iv.2000, TMAG E22120; 15 specimens, off Pt Hicks, NE Bass Strait, 38.4784°S, 149.5566°E, 1426–1509 m, SS200001 Stn 158, 17.iv.2000, TMAG E22160 (one specimen used as a dry preparation of internal structures, given new registration number E22188); 5 specimens, seamounts south of Tasmania, 44.2969°S, 147.1149°E, 1712–1465 m, IN2018_V06 Stn 11, 24.xi.2018, TMAG E58675; 2 specimens, seamounts south of Tasmania, 44.2143°S, 146.2669°E, 1157–1353 m, IN2018_V06 Stn 74, 3.xii.2018, TMAG E58677.

Comparative material. Dallina triangularis Holotype [L=23.5 mm, W=21.0 mm, T=16.0 mm]. Kyushu coast, Japan, 31.2028°N, 129.8292°E, 402 m, S.S. _Soyo-Maru_ (Imperial Fisheries Institute, Tokyo), Stn 419, 15.vii.1929, TUM No. 56221 (Dry shell): _D. triangularis_ Paratype [L=20.0 mm, W=16.5 mm, T=12.7 mm], TUM No. 56779 (Dry shell; collected with Holotype).

Remarks

The specimens examined herein were attributed to _Dallina_ because of their overall shape and folding, the dalliniform brachidium only attached to the crura, fused deltidial plates, minimal trace of beak ridges, and the absence of dental plates.

Comparison to Atlantic species_: Dallina_ contains nine valid species (Emig 2022). _D. septigera_, _D. floridana_ (Pour-
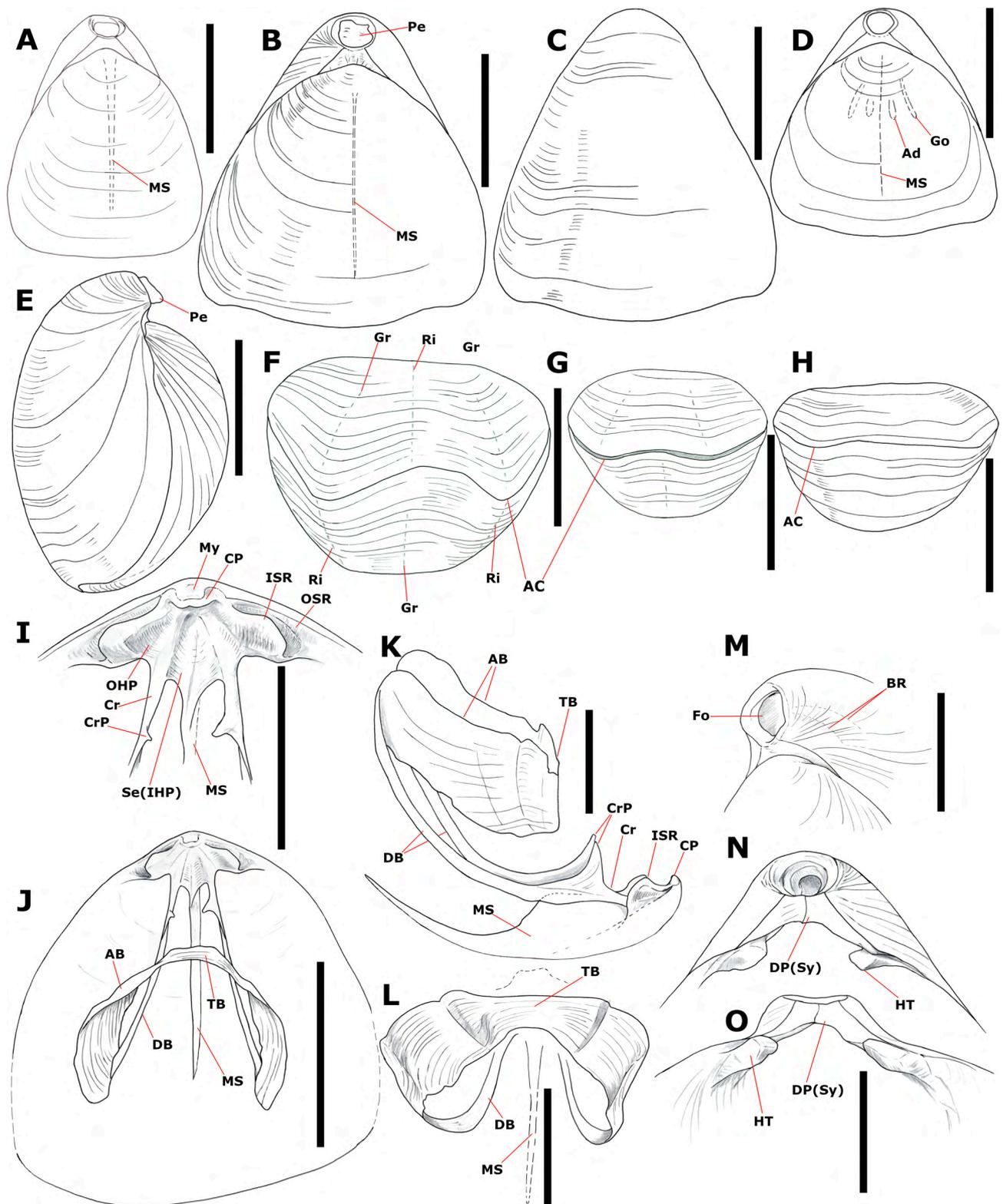
Fig. 5. *Dallina tasmaniaensis*, sp. nov. **A–D)** dorso-ventral aspects with dorsal aspect of Holotype (**A**; E58673; L=18.75 mm, T=11.0 mm), dorsal and ventral aspects of a larger specimen (**B, C**; E58675, L=23.7 mm, T=15.7 mm), and ventral aspect of specimen with gonad development (**D**; E58675, L=17.7 mm, W=16.7 mm). **E)** Lateral aspect of larger specimen (same specimen as **B**). **F–H)** anterior aspects depicting anterior commissure variation, specimen with well-developed folding (**F**, same specimen as **B**), reduced folding (**G**; E58673), and nearly absent folding (**H**, same specimen as **D**). **I–L)** Aspects of cardinalia and brachial loop, interior of dorsal valve, close-up of cardinalia (**I**), ventral aspect of brachial loop & cardinalia (**J**), lateral aspect of brachial loop & cardinalia (**K**), and anterior aspect of brachial loop (**L**) (E22188; L=23.6 mm). **M–O)** Beak and delthirium close-up, dorso-lateral aspect of beak (**M**; E58673), dorsal (**N**), and antero-dorsal (looking inside the beak) (**O**) aspects of delthirium and hinge teeth (**N**, **O**; E22188). Abbreviations per Methods. Scale bars: 10.0 mm (**A–H**, **J**), 5.0 mm (**I**, **K–O**).
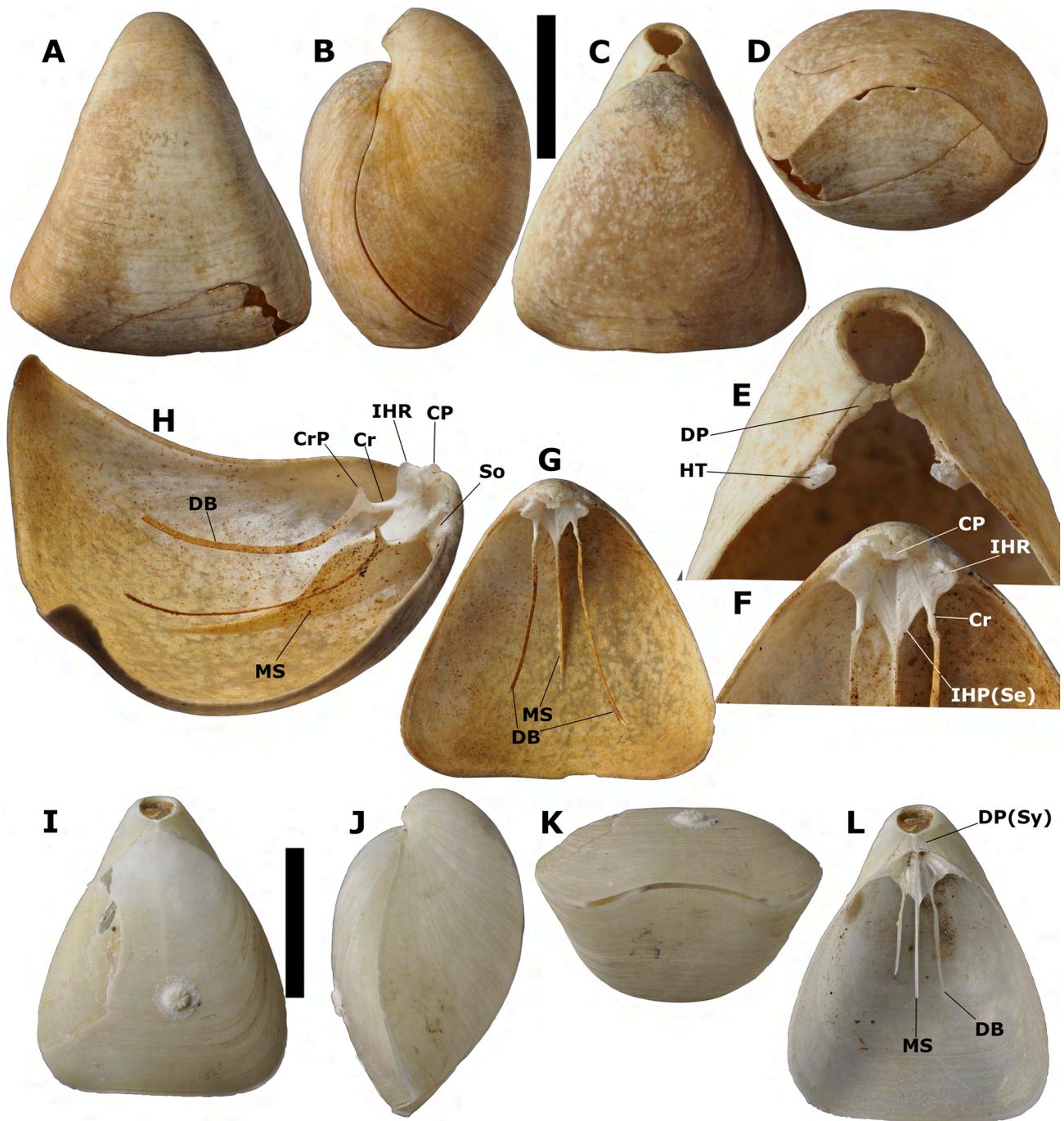
Fig. 6. *Dallina triangularis* type material. **A–H**) Holotype specimen (TUM No. 56221) with ventral (**A**), lateral (**B**), Dorsal (**C**), and anterior (**D**) aspects of whole specimen, followed by closeup of ventral valve delthirium (**E**), close-up of dorsal valve cardinalia (**F**), and interior aspects of the dorsal valve (**G, H**). **I–L**) Paratype specimen (TUM No. 56779), dorsal (**I**), lateral (**J**), and anterior (**K**), followed by dorsal aspect with part of damaged dorsal valve removed to reveal the cardinalia still connected at the hinge (**L**). Scale bars: 10.0 mm. Photography by Nemoto Jun, The Tohoku University Museum (used with permission).

tales, 1867), and *D. parva* Cooper, 1981 are all restricted to the North Atlantic (Zezina 2010). In *D. tasmaniaensis,* sp. nov. the cardinal process is higher and more developed than in *D. septigera* but lacks the small flanking elevations on the anterior face of the cardinal process depression noted on that species. The brachial loop also has thicker descending branches (but this may be variable). *D. septigera* was variable in shape (generally sub-

pentagonal but occasionally elongate triangular to equilateral triangular) (Atkins 1960), whereas all specimens of *D. tasmaniaensis,* sp. nov. were subtriangular (close to equilateral). *D. floridana* is triangular with similar folding but is smaller (largest 22 mm long and 25 mm wide), with the beak compressed laterally (rather than broad) and with 'Deltidium small, in two pieces' (*i.e.*, deltidial plates disjunct at a valve length of 22 mm)

Specimen	L	W	T	W%L	T%L	Attachment	Epibiota
E22119 †	18.8	15.8	11.7	84.04	62.23		
	20.0	18.4	NA	92	NA		
E22120	18.3	16.3	11.1	89.07	60.66		
	22.35	20.1	14.4	89.93	64.43		
E22160	20.8	18.2	12.6	87.50	60.58		
	20.4	18.9	14.4	92.65	70.59		
	23.6*	21.7	15.4	91.95	65.25		
	19.1	16.4	12.2	85.86	63.87		
	24.2	22.4	14.7	92.56	60.74		
	18.6	17.8	11.9	95.70	63.98		
E58673**	18.75	14.8	11.0	78.93	58.67		
E58675	23.7	20.8	15.7	88.14	66.53		
	17.7	16.75	10.85	94.63	61.30		
	19.75	17.6	12.65	89.11	64.05	Shell fragment	
	21.5	17.1	14.35	79.53	66.74		
E58677	20.35	17.3	13.1	85.01	64.37		
	20.6	16.8	13.6	81.55	66.02		

Table 3. *Dallina tasmaniaensis*, **sp. nov. measurements, notes, and indices.** All measurements in mm, NA = not assessable as valves damaged, † = contains further specimens too damaged to measure, *=specimen used for dry preparation of brachial loop (given new registration number E22188). ** = dry specimen (others in ethanol).

(Pourtalès, 1867). *D. floridana* is also restricted to the Gulf of Mexico(?) at shallow depths 64–724 m (Zezina 2010). Finally, *D. parva* Cooper, 1981 from the northeast Atlantic is also triangular (longer than wide), but is sulcate, and very much smaller as an adult (largest 11.0 mm long), the cardinal process not being described (Cooper 1981).

Comparison to Pacific and Southern Ocean species: The Pacific has a much larger number of *Dallina* species. *D. raphaelis* (Dall, 1870), *D. obesa* Yabe & Hatai, 1934, and *D. elongata* Hatai, 1940 were all described from off Japan, and all differ from *D. tasmaniaensis,* sp. nov. in having ovoid (quadrate-ovate) forms widest midway along the valves, much larger sizes (38.4, 31, & 38 mm long respectively), much shallower bathymetric ranges (all within 23–402 m depth), flatter lateral commissures (especially *D. obesa*), and thicker valves (Hatai 1940). *D. eltanini* Foster, 1974 (as well as *D. elongata*) is known from the far southern Pacific (Foster 1989), and in addition to differing with an ovoid to subpentagonal shape, it also has a sulcate anterior commissure (*vs.* variably intraplicate on other Pacific species). *D. eltanini*, *D. raphaelis,* and *D. elongata* interestingly share a moderately-developed cardinal process alike that seen in *D. tasmaniaensis,* sp. nov. (Foster 1974; Hatai 1940). Two problematic *Dallina* species (*D. simosensis* and *D. profundis*) are commented on in the discussion.

D. triangularis was described from two specimens collected off Japan (402 m depth). These type specimens (Holotype and Lectotype) were partly damaged (brachial loop ascending and transverse bands missing, some sections of valves cracked) but in good enough condition to allow comparison (see **Fig. 6**). Again, the overall triangular form, size, and ratios were similar. The primary differences between the *D. triangularis* Type specimens and *D. tasmaniaensis,* sp. nov. related to the beak, cardinal process, and brachial loop. In the former the beak is proportionally shorter (11%–14% vs. 14%–16%), with the symphytium proportionally narrower (symphytium length%width ~47.5%–57.9% vs. 39%–46%). On the *D. triangularis* Holotype the cardinal process is much more pronounced than in *D. tasmaniaensis,* sp. nov. (tapering and projecting more anteriorly, **Fig. 6 F**), and the anterior commissure folding of *D. triangularis* is far broader and stronger (especially on the Holotype). The form of the crura and brachidium descending branches are also rather different in *D. triangularis*, viewed semi-laterally (**Fig. 6 H**), the dorsal edge of the crura–descending branch junction (facing the inside of the valve) is distinctly indented, vs. straight in *D. tasmaniaensis,* sp. nov. (**Fig. 5 K**), with the crural processes also much shorter in *D. triangularis*. Specimens of these two species were similar in overall size (*D. tasmaniaensis* specimen with brachidium illustrated with L = 23.6 mm, similar in size to the 23.5 mm long *D. triangularis* Holotype), and thus brachidium and cardinal process differences were unlikely to be ontogenetic. Finally, the bathymetric range was also very different between the taxa (402 m vs. ~1100–1700 m for the southern Australian species).

D. triangularis is also known from putative material collected from the South China Sea (491–538 m), Lau Ridge off Fiji (416–1226 m), and Tonga Islands (356–367 m) (Bitner 2008; Bitner 2019; Bitner & Romanin 2018), but these specimens were only tentatively assigned to this species, and critical comparison of this material to both *D. triangularis* type material and *D. tasmaniaensis,* sp.

nov. will be needed. The South China Sea specimen was juvenile and similar to *D. triangularis* in overall shape and short beak (~10% overall length) (Bitner & Romanin 2018 fig 7A,B). The specimens from near Fiji and Tonga both had proportionally short beaks (beak length ~10%–13% overall length) with the Tonga specimen at 32.5 mm long exceeding any *D. triangularis* type material or *D. tasmaniaensis*, sp. nov. material, these specimens also had a much more pointed anterior edge, creating a 'diamond-like' shape (Bitner 2008 fig 16B–G; Bitner 2019 fig 7N), and may turn out to represent a distinct species.

Distribution: Continental slope from NE of the Bass Strait, eastern Bass Strait, and seamounts south of Tasmania (**Fig. 1 A**). Bathymetric range 1157–1712 m.

Genus *Jaffaia* Thomson, 1927

Type species: *Jaffaia jaffaensis* (Blochmann, 1910).

Diagnosis: Moderately large, ovoid to circular in outline; lateral commissure near straight, anterior commissure rectimarginate to lightly sulcate. Beak suberect; deltidial plates conjunct as symphytium, mostly exposed; foramen small, subapical, submesothyridid (or mesothyridid), attrite (beak ridges indistinct); hinge teeth large relative to symphytium, with swollen bases, dental plates absent; pedicle collar very short. Cardinalia lamellar, excavate inner and outer hinge plates separated by relatively thick crural bases, inner hinge plates form V-shaped septalium supported by median septum, inner socket ridges lightly inclined; cardinal process well-developed, supported anteriorly by a triangular ridge between the hinge plates, posteriorly facing myophore rounded to sub-pentagonal; median septum not reaching mid-valve, highest at junction with lateral connecting bands; crura short, subparallel, crural processes short and pointed. Adult brachial loop trabecular; lophophore plectolophous.

Genus description: As per diagnosis.

Remarks: Monotypic genus. Possibly synonymous with genus *Nipponithyris* Yabe & Hatai, 1934, per discussion section.

Jaffaia jaffaensis (Blochmann, 1910)

Fig. 7, 8; Table 4

Lectotype lodged with the Museum für Naturkunde, Berlin (ZMB Bra 956), see specimens examined.

Synonymy

Magasella jaffaensis Blochmann, 1910

Campages jaffaensis Hedley, 1911

Diagnosis: A dallinid with ovoid to circular outline, rectimarginate–lightly sulcate anterior commissure, subpentagonal myophore atop large anteriorly supported cardinal process, thick crural bases, V-shaped septalium, trabecular loop, and large hinge teeth with thickened bases and lacking dental plates.

Etymology: Both genus name and specific epithet are derived from the Type location, Cape Jaffa, South Australia, the Latin suffix '-ensis' added to form an adjective (*i.e.*, from Cape Jaffa).

Description

Overall valve form: Maximum valve length 23.4 mm (average 17.8 mm, SD 3.9, smallest 8.5 mm long). Valves wide, W%L index averaging 89.9% (SD 4.3; range 80.6%–97.6%), and relatively thin with thickness index T%L averaging 46.8% (SD 3.5; range 39.5%–54.8%).

Overall outline (viewed dorso-ventral) ovoid on smaller specimens to almost circular on larger specimens (**Fig. 7 A, B**). Laterally biconvex (valves near equal in depth). Lateral commissure near flat or gently curved towards ventral valve (see **Fig. 7 C–E**). Anterior commissure near rectimarginate in small and large specimens (**Fig 7 F**), but showing progressing degrees of being lightly sulcate in some specimens, the dorsal (brachial) valve bearing a very shallow median groove in its anterior half, the anterior edge curved ventrally into a low median ridge on the anterior half of the ventral (pedicle) valve (**Fig. 7 G**). The Lectotype specimen is comparable to the above, it being near circular in outline, with flat lateral commissure, and rectimarginate anterior commissure (**Fig. 8 A–D**).

Valves punctate. With distinct concentric growth striae, smooth on most specimens but becoming more pronounced and thickened (ridge-like) on older specimens. Radial ribs/costae absent. Colouration of valves cream or beige, one specimen with pink pigmentation (E21970) was possibly from pigmented animals it was stored with.

Dorsal (brachial) valve: Cardinal margin obtuse (~115–140°). Cardinal process well-developed, the myophore a roughly pentagonal platform (though more rounded-off and circular on some speicmens), angled posteriorly, with small lateral swellings, supported anteriorly by triangular ridge originating between inner hinge plates and rising posteriorly (see Cardinalia ventral aspect in **Fig. 7 H–K**). Sockets well demarcated by outer and inner socket ridges, inner socket ridges lightly inclined and thicker and larger distally. Outer hinge plates narrow (poorly defined), inclined less than the inner socket ridges. Crural bases notably large and wide, dividing outer and inner plates (and laterally converging with inner socket ridges). Inner hinge plates inclined more steeply than outer plates, meeting medially as an excavate septalium, supported by median septum. Anterior edge of septalium V-shaped, septalium short and not extending anteriorly beyond crural base. Crura short and sub-parallel. Crural processes short, pointed, angled medio-ventrally (ventral and semi-lateral aspects of crural processes **Fig. 7 H, K, J**). Crura proportionally

larger relative to the cardinalia on smaller specimens. Brachidium trabecular (**Fig. 7 I–L**), anterior-most extent of loop ~60%–70% dorsal valve length (loop proportionally longer in larger specimens, e.g., **Fig. 7 I, J**, and shorter in smaller specimens, **Fig. 7 K**). Median septum reducing in height anterior to septalium before rising to highest point at junction with brachial loop lateral connecting bands, then immediately reducing in height, terminating ~40%–50% dorsal valve length (see septum depicted in **Fig. 7 I, J**).

Ventral (pedicle) valve: Beak short (length approximately 8.5%–11% of overall valve length, proportionally smaller on larger specimens and *vice versa*), suberect. Foramen subapical (anterior to apex of beak), rounded and very small, but proportionally larger on smaller specimens and *vice versa* (diameter ~3%–5% of valve length), mesothyridid (closer to permesothyridid on some larger specimens), with beak ridges obscure and rounded (**Fig. 7 M**; **Supplementary Fig. 1 D**). Pedicle collar short. Deltidial plates mostly exposed, conjunct as a wide symphytium. Smaller individuals retain an irregular seam where the plates contact medially (**Fig. 7 M**), obscure on larger specimens but a thickened medial process remains on the inside face of the symphytium (**Fig. 7 N–P**). Hinge teeth large relative to symphytium, roughly triangular in outline, tooth bases swollen, proportionally larger on smaller specimens (see various aspects of teeth **Fig. 7 M–P**). Dental plates absent.

Soft tissue: Lophophore plectolophous. Gonads first noted on a specimen 12.7 mm long (**E21970**), distributed in four gonad lobes (2 on each valve), on the ventral valve the gonads are longer and each lobe V-shaped, on dorsal valve the lobes are shorter and straight. Gonads were either thin (**Fig. 8 F, G**) or greatly thickened (**Fig. 8 H, I**), presumably reflecting states of ripeness (though males and females were not distinguishable). Pedicle very short, not extending beyond beak (end papillate/rough).

Attachment substrata and epibiota: Attachment substrata for the pedicle were generally small fragments of dead shells (often gastropods), coral, and bryozoans. Regarding epibiota, < 20% of *J. jaffaensis* specimens examined had encrusting bryozoans growing on the valves.

Specimens examined

Lectotype. Off Cape Jaffa, South Australia, 165 m, ZMB Bra 956.

Paralectotype. Off Cape Jaffa, South Australia, 165 m, ZMB Bra 957 (dorsal valve missing).

Other material examined. ~40 specimens, southern Tasmania, 44.091°S, 146.698°E, 541 m, IN2018_V06 Stn 105, 8.xii.2018, TMAG E21968; 1 specimen, east Bass Strait, 38.92667°S, 148.46167°E [no depth], SS199405 Stn. 54, 27.viii.1994, TMAG E21970; 4 specimens, NE of Pedra Branca, southern Tasmania, 43.79°S, 147.62°E, 154 m, Stn UM 68.20, 9.i.1968, TMAG E21971 (two specimens

used as dry preparations of internal structures, given new registration number E22187); 2 specimens, NE Bass Strait, 38.2149–2029°S, 149.6625–6974°E, 395–402 m, SS200001 Stn 150, 17.iv.2000, TMAG E22115; 1 specimen, Great Australian Bight, 33.2545–2644°S, 130.7058–808°E, 130–134 m, SS200001 Stn 351, 10.v.2000, TMAG E22116; 1 specimen, Great Australian Bight, 33.2471–2552°S, 130.6376–6159°E, 141 m, SS200001 Stn 334, 10.v.2000, TMAG E22117; 1 specimen, east Bass Strait, 38.955°S, 148.5083°E, 179–185 m, SS199305 Stn 54, 27.vii.1993, TMAG E22161; 3 specimens, NE Bass Strait, 38.1622–1677°S, 149.6987–6852°E, 260–265 m, SS200001 Stn 199, 22.iv.2000, TMAG E22162; 1 specimen, southern Tasmania, 43.2626°S, 147.9664°E, 122 m, *Rambler* Stn 68, 20.iii.2014, TMAG E29043a; 14 specimens, southern Tasmania, 44.0417–0489°S, 146.3116–3071°E, 410–450 m, SS200702 Stn 32, 4.iv.2007, TMAG E55892. 5 specimens, eastern Tasmania, 42.7000–6333°S, 148.4000–4167°E, 450 m, SO3/84 Stn 78, 25.vi.1984, TMAG E22219.

Remarks

In 1906 Professor Friedrich J.W. Blochmann, at the University of Tübingen (Germany), loaned brachiopod material from the Adelaide Museum (now South Australian Museum) and described *Magasella jaffaensis*. Out of the three specimens examined by Blochmann, none was designated the Holotype, and some parts have gone missing, and so Lüter & Sieben (2005) re-assessed the type series to designate a Lectotype and Paralectotype at the Museum für Naturkunde (Berlin). Charles Hedley (1911) provided some additional illustrations of the brachial loop of this species (as it was damaged in the Type material) and recognized its similarity to *Campages*, but otherwise did not describe it.

The work herein clarifies the morphology of *Jaffaia* and confirms (amongst other detail) the form of the hinge teeth, absence of dental plates, the complex form of the cardinal process, and provides detail on how the beak shape and anterior commissure folding change on larger specimens.

When sorting specimens, some previous misidentifications had been made with juvenile *Magellania flavescens* (Lamarck, 1819) and *Anakinetica cumingi* (Davidson, 1852), these species may look superficially similar and should be expected when working on old specimen lots. Juveniles of the former can easily be identified by the presence of radial ribs (though these can be faint), while the latter has a much straighter cardinal margin, and proportionally longer and straighter beak.

Distribution: Specimens examined herein were collected from the outer continental shelf and upper slope of the eastern and north-eastern Bass Strait, off Southern Tasmania, and the Great Australian Bight (33.25–44.09°S, 130.63–149.7°E), at depths ranging from 122–541 m. This was within the distributional and
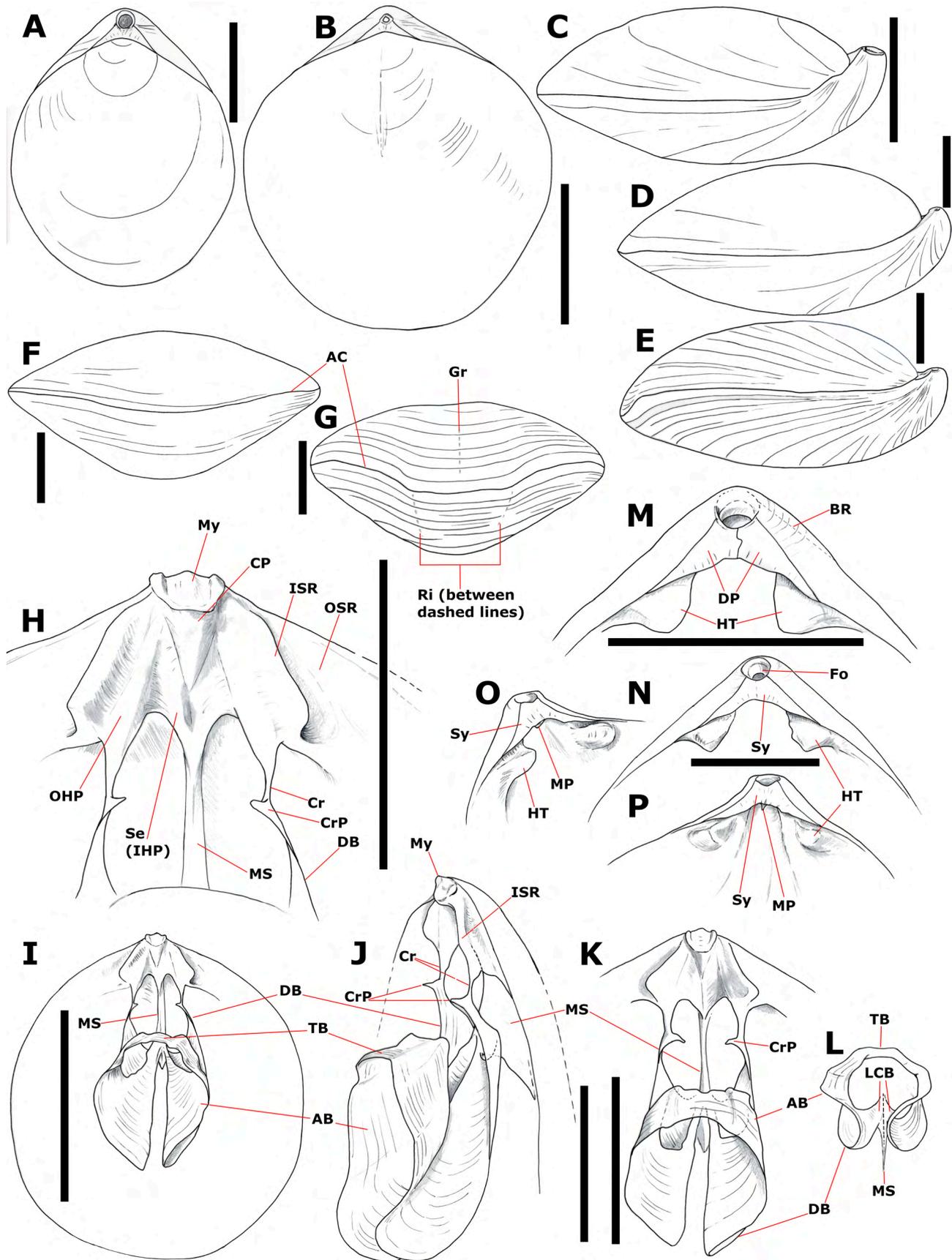
Fig. 7. *Jaffaia jaffaensis* specimens. **A, B**) dorsal aspects of a smaller specimen (**A**; E22187, L=13.9 mm) and larger specimen (**B**; E55892, L=23.1 mm). **C–E**) lateral aspects of small and large specimens (**C, D** are same specimens as **A, B** respectively) and specimen with stronger anterior folding (**E**; E55892, L=23.0 mm). **F, G**) anterior aspects of large specimen with minimal anterior commissure folding (**F**, same specimen as **B**) and another with stronger folding (**G**, same as **E**). **H–J**) Cardinalia (**H**) and ventral (**I**) and semi-lateral (**J**) aspects of brachial loop

of a larger specimen (E22187; L=18.7 mm). **K, L**) Cardinalia and brachial loop of a smaller specimen (E22187; L=14.0 mm, same specimen as **A**) with ventral aspect (**K**) and anterior aspect of the loop (**L**). **M–P**) Closeup aspects of beak, delthirium and hinge teeth from a smaller specimen (**M**, same specimen as **A**) and a larger specimen (**N–P**, same as **H–J**). Abbreviations per Methods. Scale bars: 5.0 mm (**A**, **C–H, J, K, M, N, P**), 10.0 mm (**B, I**).
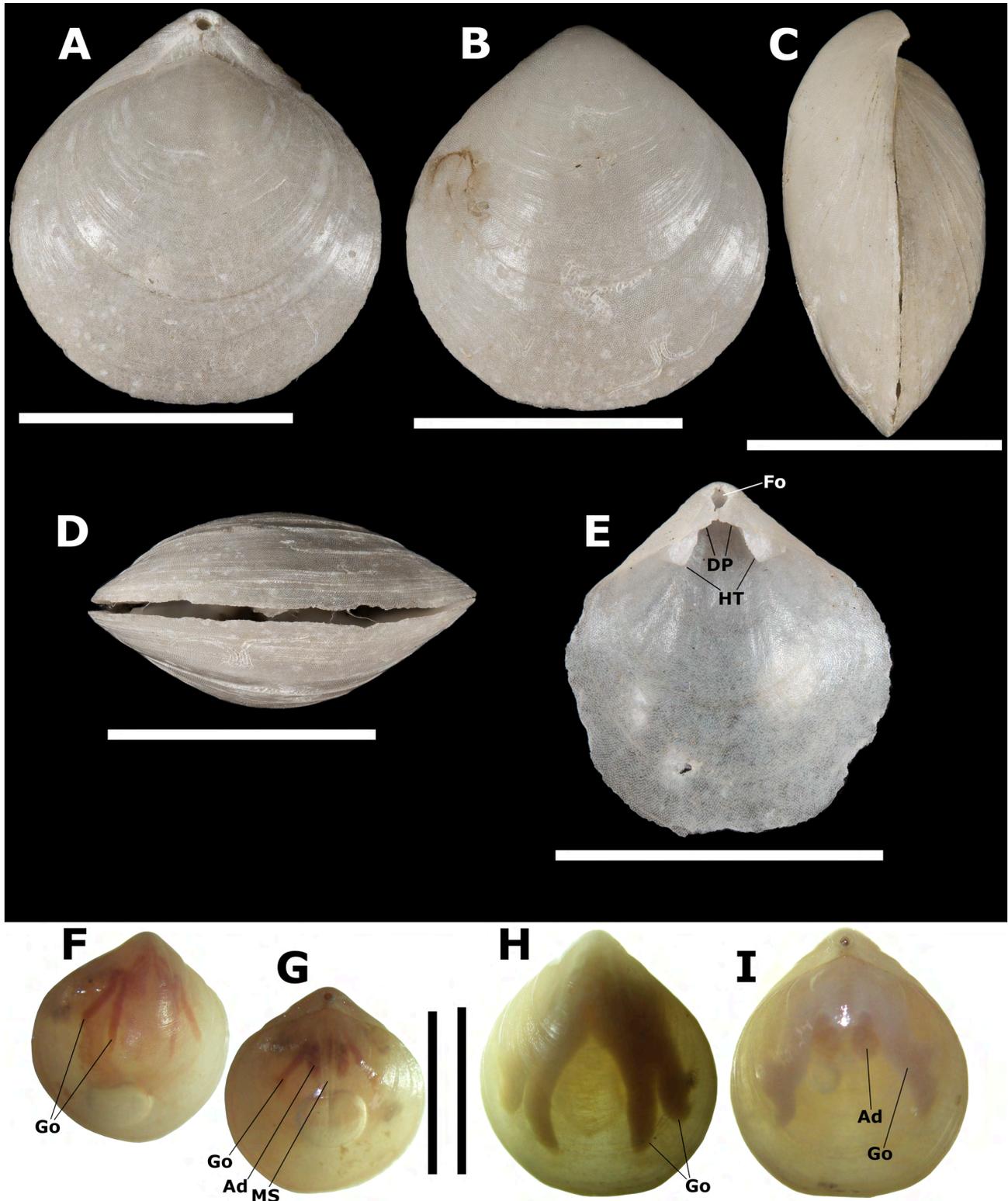
Fig. 8. *Jaffaia jaffaensis* Type material and gonad development. **A–D**) Lectotype (ZMB Bra 956) with dorsal (**A**), ventral (**B**), lateral (**C**), and anterior (**D**) aspects. **E**) Paratype (ZMB Bra 957) interior of ventral valve. **F–I**) Differences in gonad development, specimen with reduced development (**F, G**; E21970; L=12.7 mm), and specimen with high development (**H, I**; E21971; L=16.2 mm), ventral and dorsal aspects are left and right respectively. Scale bars: 10.0 mm. Photography (**A–E**) by Hwa Ja Götz, Museum für Naturkunde Berlin (used with permission).

Specimen	L	W	T	W%L	T%L	Attachment	Epibiota	Notes
E21968	21.25	19.9	10.5	93.65	49.41		Encrusting bryozoans	
	14.4	13.3	6.9	92.36	47.92	Shell fragment		
	21.3	19.45	9.75	91.32	45.77	Bryozoan fragment	Encrusting bryozoans	
	17.35	14.85	8.5	85.59	48.99		Encrusting bryozoans	
	21.45	20.5	9.8	95.57	45.69			
	19.6	18.0	8.9	91.84	45.41		Encrusting bryozoans	
	19.0	16.5	9.5	86.84	50.0		Encrusting bryozoans	
	18.0	16.3	8.7	90.56	48.33			
	18.0	16.4	8.7	91.11	48.33	Gastropod fragment		
	18.5	17.1	8.4	92.43	45.41			
	17.8	16.8	9.45	94.38	53.09	Scaphopod fragment	Encrusting bryozoans	
	12.3	11.2	5.2	91.06	42.28	Gastropod fragment		
	20.2	18.75	9.3	92.82	46.04	Gastropod fragment		
	10.0	9.0	4.4	90.0	44.0	Gastropod fragment		
	13.4	12.4	5.3	92.54	39.55			
E21970	12.7	12.1	5.5	95.28	43.31			Illustrated
E21971	16.9	14.2	7.3	84.02	43.19			
	16.2	14.2	8.35	87.65	51.54			Illustrated
	13.9**	11.2	6.2	80.58	44.60			Illustrated
	18.65**	15.1*	8.15	80.97	43.70			Illustrated
E22115	8.5	7.3	4.0	85.88	47.06	Gastropod fragment		
	15.6	13.5	7.0	86.54	44.87			
E22116	18.2	16.2	8.6	89.01	47.25	Bryozoan fragment		
E22117	13.0	11.2	5.8	86.15	44.62			
E22161	14.9	12.9	6.6	86.58	44.30	Shell fragment		
E22162	13.3	11.15	5.4	83.83	40.60	Coral(?) fragment		
	13.7	11.35	6.4	82.85	46.72			
	9.95	8.5	4.25	85.43	42.71			
E29043a *	12.4	10.8	4.9	87.10	39.52			
E55892	23.4	21.6	11.1	92.31	47.44			
	21.7	20.4	10.55	94.01	48.62			
	22.9	21.0	12.2	91.70	53.28		Encrusting bryozoans	
	23.1	21.75	10.5	94.16	45.45			Illustrated
	21.1	20.6	10.4	97.63	49.29			
	21.7	20.0	9.45	92.17	43.55			
	23.0	20.0	10.4	86.96	45.22			Illustrated
	23.4	22.05	11.3	94.23	48.29		Encrusting bryozoans	
	21.45	19.3	11.7	89.98	54.55		Encrusting bryozoans	
	21.4	18.85	11.1	88.08	51.87			
	20.3	19.0	9.4	93.60	46.31		Encrusting bryozoans	
	19.8	18.6	9.8	93.94	49.49			
	19.8	17.95	8.5	90.66	42.93			
	19.0	17.5	9.0	92.11	47.37			
E22219	17.7	15.3	8.8	86.44	49.72			Brown colour
	19.1	18.55	8.9	97.12	46.60			
	17.55	16.5	8.4	94.02	47.86			
	21.1	17.55	10.0	83.18	47.39			
	19.8	16.7	NA	84.34	NA			
ZMB Bra 956	14.6	13.5	8.0	92.47	54.79			Illustrated

Table 4. *Jaffaia jaffaensis* **measurements, notes, and indices.** All measurements in mm, * = dry specimen (others in ethanol). **=specimen used for dry preparation of brachial loop (given new registration number E22187).

bathymetric ranges recorded Richardson (1997), southern, eastern, and western Australian coasts, 67–550 m.

Genus *Fallax* Atkins, 1960

Type Species: *Fallax dalliniformis* Atkins, 1960.

Diagnosis: Moderately sized, valves smooth, elongate ovate to subpentagonal in outline, biconvex; lateral commissure curved towards dorsal valve, anterior commissure rectimarginate to parasulcate. Beak low, erect; deltidial plates conjunct in adults as symphytium, exposed; foramen small, permesothyridid, beak ridges rounded; hinge teeth somewhat small relative to symphytium, bases not swollen, dental plates present, lamellar and straight; pedicle collar broad, sessile, impunctate. Cardinalia lamellar, inner and outer hinge plates well developed, crural bases not well-differentiated, inner hinge plates form short septalium (shortest medially, anterior border indented or flat) supported by median septum; inner socket ridges lightly inclined; cardinal process not differentiated (absent); median septum extending anteriorly about ¾ valve length; crura short, subparallel, crural processes short. Adult brachial loop diploform (campagiform); Lophophore plectolophous (lophophore and mantle finely spiculate). (Modified from Atkins 1960, Emig 2022).

Genus description: As per diagnosis.

Fallax neocaledonensis Laurin, 1997

Fig. 9; Table 5

Holotype lodged (by Laurin, 1997) with the Muséum National d'Histoire Naturelle, Paris (MNHN-IB-2009-196).

Diagnosis: Per description.

Description

Full measurements were not obtained from this material (photographs and limited measurements provided), and only a simplified description is given.

Overall valve form: Valve length 15.1–21.2 mm (average 17.6 mm). Valves broad, W%L averaging 97% (range 92.6%–103.5%), and relatively thick (T%L 57.6%–61.5%). Overall shape triangular (near equilateral) and thus broadest anteriorly. Valves biconvex, ventral valve slightly deeper. Lateral commissure curved towards dorsal (brachial) valve. Anterior commissure weakly intraplicate (plicosulcate), similar to *Dallina tasmaniaensis,* sp. nov., the folding creates two shallow indentations along the anterior margin. Valves punctate, slightly translucent, white. Relatively smooth with fine growth striae (radial markings absent). Overall form illustrated in **Fig. 9 A–G**, and **Supplementary Fig. 1 E–H**.

Dorsal (brachial) valve: Interior detail depicted in **Fig. 9 H–M**. Cardinal process largely absent (small V-shaped indent anterior to the umbo being the diductor attach-ment point). Hinge sockets well developed, inner socket ridges strongly diverging and steeply inclined (outer corners triangular). Outer hinge plates slightly grooved, demarcated from inner hinge plates by crura (crura laterally continuous with the outer hinge plates, and without a well-defined base). Inner hinge plates proportionally smaller, fused medially as excavate septalium, supported by median septum. Septalium shortest medially and thus indented at anterior border almost to level of the sockets. Crura short and broad in lateral profile, subparallel (or slightly diverging). Crural processes short and pointed, directed ventrally and slightly medially. Brachidium diploform, descending branches ribbon like, broadly fused posteriorly with crural processes and with short lateral connecting bands to the median septum. Ascending and transverse bands forming hood/funnel, loop being relatively small (compared to *C. furcifera*) with its anterior-most extent just short of 50% dorsal valve length. Median septum thin, dropping in height anterior to septalium before rising to junction with lateral connecting bands, before rapidly dropping off anterior to this and fusing with valve floor at just over 50% the dorsal valve length.

Ventral (pedicle) valve: Beak relatively small, suberect. Foramen subapical, small (diameter approximately 7%–8% overall valve length). Possibly mesothyridid, but beak ridges poorly defined, rounded. Pedicle collar reduced to a ring within foramen. Deltidial plates mostly exposed, fused as symphytium (seam present where the plates fused medially) (**Fig. 9 N, P**). Hinge teeth well-developed, relatively small, bases not thickened. Dental plates present, lamellar, straight, connecting to floor of valve (**Fig. 9 O, P**).

Soft tissue: Pedicle thin, short to relatively elongate (extending beyond foramen, greater than beak length). Lophophore not preserved on material examined.

Attachment substrata and epibiota: Three specimens were attached to small rocks (size < half valve length). Valves free of epibiota.

Specimens examined

5 specimens, SE of Brisbane, Queensland, 27.933°S, 154.050°E, 967 m, FRV *Kapala*, 6.xi.1978, AM C.153071; 2 specimens, off Smoky Cape, NSW, 31.300°S, 153.350°E, 1334 m, 22.ix.1969, AM C.153078.

Remarks

Australian Museum specimen lots (**C.153071** and **C.153078**), were collected from southern Queensland and northern NSW coasts (967–1334 m) and identified by the late brachiopod expert Joyce Richardson as *Fallax* sp. in 1987. Initially it was suspected that these specimens would be further *Dallina* material, but they were found to not only have a campagiform loop, but lacked a cardinal process seen in *C. furcifera* and most importantly had distinctive dental lamellae. The overall form of the valves and the internal structures closely matched those
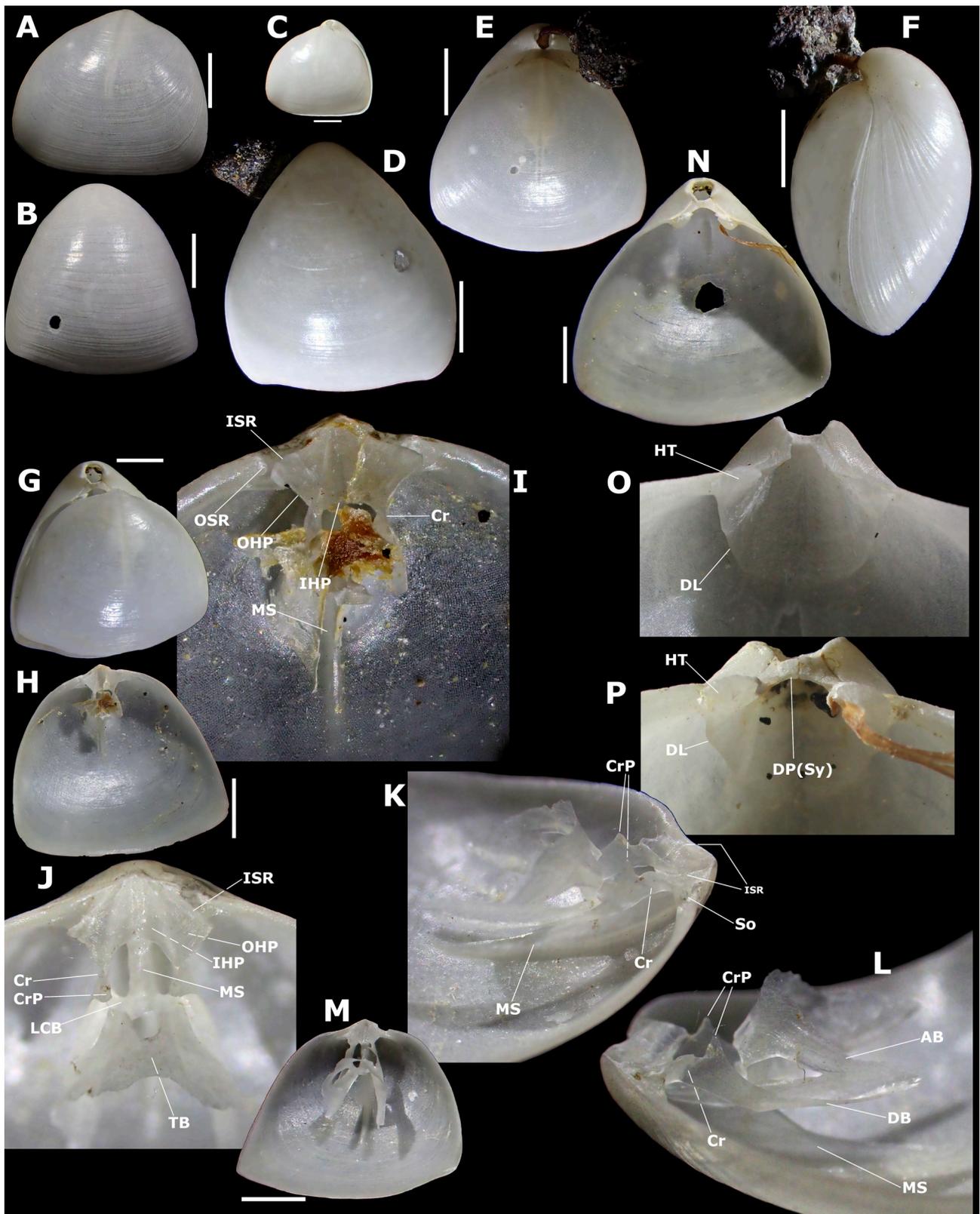
Fig. 9. *Fallax neocaledonensis*. **A–C**) external aspects of disarticulated specimen (C153071, L = 17.6 mm), dorsal valve exterior (**A**), ventral valve exterior (**B**), and semi-lateral dorsal aspect of the specimen with the valves reconnected (**C**). **D**, **E**) ventral and dorsal aspects of specimen with pedicle attachment (C153071, L = 17.1 mm). **F**) lateral aspect of specimen with attachment (C153071, L = 18.6 mm). **G–I**) detail of larger specimen with damaged brachial loop (C153078, L = 21.2 mm), dorsal aspect of whole specimen (**G**), dorsal valve interior (**H**), and detail of cardinalia of same (**I**). **J–M**) dorsal valve interior depicting good condition cardinalia–brachidium complex (C153071, L = 17.6 mm), dorsal closeup of cardinalia and brachidium (**J**), right–left semi-lateral aspects of same (**K, L**), and brachidium relative to whole dorsal valve interior (**M**). **N–P**) dorsal valve interior and delthirium detail, whole valve interior (**N**), and closeup of delthirium (two specimens), angled to

expose teeth supports (**O, P**) (**N & P** from C153071, L = 17.6 mm; **O** from C153078, L = 21.2 mm). Abbreviations per Methods. Scale bars: 5.0 mm. Photography A.C. Miller, Copyright: Australian Museum (used with permission).

Specimen	L	W	T	W%L	T%L	Attachment	Notes
C153071	17.6	17.7	NA	101%	NA		Disarticulated
	15.1	15.0	8.7	100%	57.6%		
	16.0	14.8	NA	92.6%	NA	Small rock (?)	Dorsal valve broken
	17.1	16.1	NA	94.3%	NA	Small rock (?)	
	18.6	16.9	11.4	91%	61.5%	Small rock (?)	
C153078	21.2	22.0	NA	103.5%	NA		Disarticulated
	25.4	22.1	15.8	87.1%	62.2%		**Possibly** *Dallina* (?)

Table 5. *Fallax neocaledonensis* **measurements, notes, and indices.** All measurements in mm (but more approximate as limited measurements were provided and others calculated from these). NA = not assessable as valves were disarticulated or suitable measurements/ photos were not provided.

described by Laurin (1997) for *Fallax neocaledonensis*, collected around New Caledonia, but without detailed comparison to Type material, this identification must be treated as tentative. This is the first confirmation of *Fallax* and family Aulacothyropsidae from Australian waters. However, the larger specimen in AM lot **C153078** (L = 25.4), is excluded from the above description as it differs from the other specimens and may be comparable to *Dallina*. Its narrower form (W%L = 87%), considerably larger and more circular foramen (diameter 11.5% overall length), and light beige-brown colouration (rather than white) are all consistent with *D. tasmaniaensis,* sp. nov. (**Supplementary Fig. 1 I–K**).

F. neocaledonensis is distributed widely around New Caledonia, Fiji, and Tonga (Bitner 2009, 2015, 2019), and if conspecific these Australian specimens would represent a considerable range extension for the species. Zezina (2010) recorded a tentative *Fallax* sp. from the Arafura Sea (off northern Australia, 7°34′S, 132°44′E, 390 m depth). Zezina (1981) originally recorded this same specimen as '*Campages* (?) sp.' but given its lack of cardinal process she was hesitant in this placement, and while its loop was presumably diploform ("the loop joins the septum near the middle of its length") no comment was made on the dental plates.

The triangular form and diploform brachidium of this species may represent a point of confusion with *C. furcifera* and *D. tasmaniaensis,* sp. nov., however these putative *F. neocaledonensis* were collected from considerably greater depth than *C. furcifera* (< 439 m vs. 967–1334 m). It can be distinguished from both of these species by the presence of dental plates, a septalium shortest medially and indented at its anterior border (rather than longest medially forming a V-shape), and from *Dallina* is clearly distinguished by its diploform rather than teloform loop.

Neorhynchia strebeli (Dall, 1908)

Fig. 10; Table 6

Lectotype (per Cooper 1972) is lodged with the National Museum of Natural History, Washington (USNM 110741).

Synonymy

Hemithyris strebeli Dall, 1908

Neorhynchia profunda Cooper, 1972

'*Neorhynchia*' *abyssa* Cooper, 1972 [as a misspelling of *Notorygmia abyssa*]

Diagnosis: Suboval, subtrigonal, to pentagonal; biconvex to slightly ventribiconvex, typically sulcate (but sometimes uniplicate or rectimarginate), smooth and impunctate; broad but deep, arcuate anterior commissure; beak short, hypothyridid; foramen moderate, deltidial plates disjunct. Crura short, gently arcuiform. Lophophore spirolophous. (Modified from Emig 2022). Genus is monotypic and so the diagnosis is for the genus also.

Etymology: Specific epithet in honour of German malacologist Dr. Hermann Wilhelm Strebel (1834–1914).

Description

Overall valve form: Maximum valve length 14.6 mm (average 13.4 mm, SD 0.96, smallest specimen 12.1 mm long). Valves rather wide with some specimens having width equal to valve length, W%L average 92.8% (SD 6.3, range 82.7%–100.7%). Valves with moderate thickness, T%L averaging 55.0% (SD 3.9, range 50.0%–61.6%).

Overall valve shape rounded subtriangular, widest point slightly anterior to mid-valve. Valves equally biconvex, or with the dorsal (brachial) valve slightly deeper. Lateral commissure flat or slightly curved towards the ventral (pedicle) valve. Anterior commissure variably sulcate, anterior edge folded slightly or moderately towards the ventral valve (**Fig. 10 A–F**). Dorsal valve with median

groove very shallow. Valves impunctate, translucent, and largely colourless. Relatively smooth but with fine growth striae.

Dorsal (brachial) valve: Cardinal margin approximately 110−112°. Cardinalia illustrated in **Fig. 10 G–K**. Cardinal process largely absent, a thin transverse ridge marking its place, with a small depression at the posterior end of the cardinalia possibly serving as the diductor muscle attachment (?). Sockets with outer and inner socket ridges well developed (inner ridge antero-laterally rounded or angular), the sockets slightly corrugated. Outer hinge plates broad and concave, bordered medially by cural bases. Inner hinge plates absent. Crura short and arcuiform (flattened; broader and truncated distally in lateral profile), diverging strongly at approximately 60°. Median septum a faint and low ridge, approximately restricted to the posterior 20%−30% of the dorsal valve length.

Ventral (pedicle) valve: Beak small, proportionally larger on smaller specimens and *vice versa* (length posterior to dorsal valve ~9%−12% of total valve length), variably straight to suberect. Foramen hypothyridid, collar short; deltidial plates small and disjunct, triangular, mostly exposed (see **Fig. 10 L, M**). Hinge teeth prominent and large relative to delthirium, supported by thin dental plates (see **Fig. 10 N**).

Soft tissue: Not in good condition on the few specimens examined, pedicle short (not extending beyond the beak posteriorly) and lophophore spirolophe (consistent with Zezina 2015) though poorly preserved).

Attachment substrata and epibiota: Specimens examined were lacking attachment substrates and epibiota.

Specimens examined

3 specimens, SE of Pt Hicks, NE Bass Strait, 38.4784°S, 149.5566°E, 1426−1509 m, SS200001 Stn 158, 17.iv.2000, TMAG E22183; 1 specimen, seamounts south of Tasmania, 44.2969°S, 147.1149°E, 1712−1465 m, IN2018_V06 Stn 11, 24.xi.2018, TMAG E22182; 3 specimens, seamounts south of Tasmania, 44.2394°S, 147.2929°E, 1354-1414 m, IN2018_V06 Stn 169, 14.xii.2018, TMAG E58672; 2 specimens, seamounts south of Tasmania, 44.2143°S, 146.2669°E, 1157-1353 m, IN2018_V06 Stn 74, 3.xii.2018, TMAG E21963.

Comparative material. Abyssothyris wyvillei, 1 specimen [L=12.2 mm, W=11.2 mm, T=6.5 mm], NE Bass Strait, 38.4784°S, 149.5566°E, 1426−1509 m, SS200001 Stn 158, 17.iv.2000, TMAG E22184.

Remarks

The sulcate anterior commissure, hypothyridid foramen, crura and septum form, and impunctate valves, all supported the assigning of material examined herein to *Neorhynchia*. This material was collected from the continental slope north-east of the Bass Strait, and from seamounts off southern Tasmania (**Fig. 1 A**), 1157−1712

m depth, apparently representing the first record of this genus from Australian waters. Interestingly, several specimens were captured with *Dallina tasmaniaensis,* sp. nov. (**E22160** & **E58675**), and a putative *Abyssothyris wyvillei* (Davidson, 1878) (**TMAG E22184**, see comparative material; **Fig. 10 O, P**), indicating sympatric distribution with these species.

Other Rhynchonellid order brachiopods previously recorded from southern Australia are *Aulites brazieri* (Crane, 1886), *Cryptopora gnomon* Jeffreys, 1869, and *Basiliolella colurnus* (Hedley, 1905). *Aulites* and *Cryptopora* occur in Australia over similar depth to *Neorhynchia* (31–1143 and 974–1125 m respectively; Richardson 1997) but can be distinguished by their high median septum (septal pillar) roughly midway along dorsal valve, as well as differences in the crura. *B. colurnus* has a uniplicate anterior commissure (ventral valve anterior folding into the dorsal valve—opposite to *Neorhynchia*) and lives far shallower. TMAG has 19 lots of *B. colurnus*, all recorded over a bathymetric range of 158–280 m (slightly expanding the 188–203 m bathymetry range recorded by Zezina 2010). The Rhynchonellid genera *Grammetaria* Cooper, 1959 and *Basiliola* Dall, 1908 have been recoded adjacent to Australia (New Caledonia, per Laurin 1997), but should be readily distinguishable if they are ever recorded from Australia. The Terebratulid order *Phaneropora galatheae* Zezina, 1981 is externally alike *Neorhynchia* and occurs locally from 399–1463 m depth, but again has a septal pillar and is punctate (unlike the Rhynchonellids), and is substantially smaller than *Neorhynchia* (Richardson 1997). Finally, Cooper (1927) notes *N. strebeli* as very similar in external form to the Terebratulid brachiopod *Abyssothyris wyvillei* (Davidson, 1878), however, while these species co-occurred herein *A. wyvillei* was also clearly distinguishable by the presence of puncta, as well as conjunct deltidial plates, and absence of median septum.

N. strebeli is broadly distributed throughout the Pacific Ocean from 2560–4513 m depth (Zezina 2010). Records from the western Pacific are limited, Cooper (1927) noted a 15 mm long *N. strebeli* from *Challenger* Station 184, south of New Guinea (2560 m), while Laurin (1997) described a 12.3 mm long specimen captured at L'Île-des-Pins (2660 m depth), eastern Coral Sea, and referred to another captured further south in the New Caledonia basin (2930 m). Barnes & Peck (1997) recorded further specimens from the Weddell Sea, Antarctica (814 m), with maximum length 22.1 mm, with Foster (1989) recording it from the far southern Pacific (42−63°S, 74−128°W).

The size range (no more than 14.6 mm) of this Australian *N. strebeli* material was comparable to that described by Cooper (1927) and Laurin (1997) from the western Pacific. The bathymetric range (1426–1712 m) was within the range expected (when considering Barnes & Peck 1997 and Zezina 2010). Considering how widespread this species is in the Pacific Ocean, it is
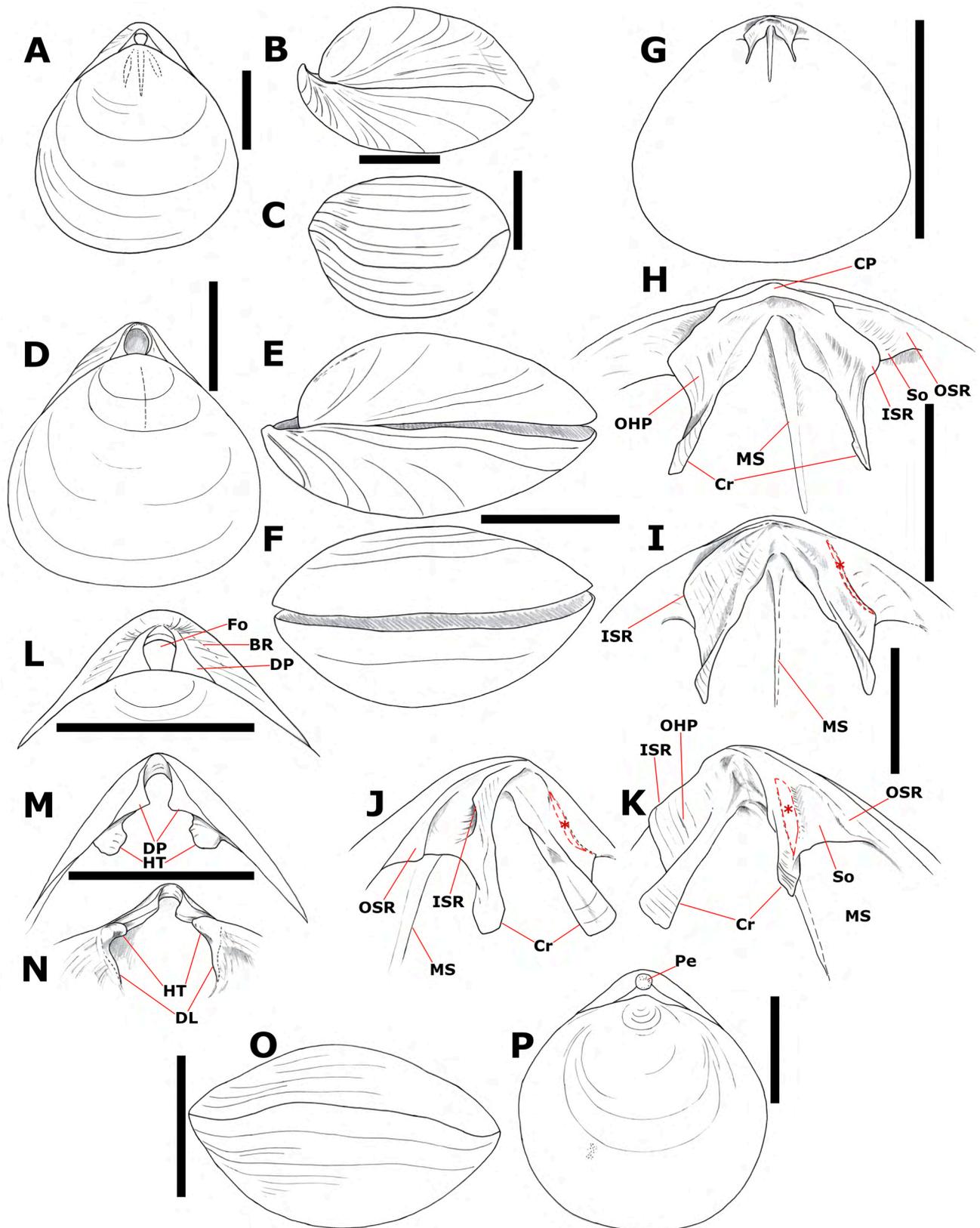
Fig. 10. *Neorhynchia strebeli* and comparative material. **A–C**) Dorsal, lateral, and anterior aspects of a thicker specimen with sub-erect beak (E22183; L=14.6 mm). **D–F**) Dorsal, lateral, and anterior aspects of a smaller specimen with straighter beak (E22182; L=12.1). **G, H**) interior of dorsal valve (ventral aspect), depicting whole valve (**G**), and close-up of cardinalia (**H**) (E21963; L=12.7). **I–K**) Cardinalia close-up ventral aspect (**I**) and left and right semi-lateral aspects from another specimen highlighting cardinalia variation (E22183; L = 13.8 mm). **L**) Dorsal closeup of beak (same specimen as **A–C**). **M, N**) Dorsal aspect (**M**) and antero-dorsal aspect (**N**) of delthirium and beak interior, depicting hinge teeth and dental plates (lamellae) (same specimen as **I–K**). **O, P**) *Abyssothyris wyvillei* comparative material collected with *N. strebeli*, anterior (**O**) and dorsal (**P**) aspects (E22184; L=12.2 mm, T=6.5 mm). Abbreviations per Methods with '*' marking site of broken-off 'ISR' (on

I–K demarcated by dashed red outline). Scale bars: 10.0 mm (**G**), 5.0 mm (**A–E**, **L**, **M**, **O**, **P,** with **F** & **N** approximately same scale as **E** & **M** respectively), 2.0 mm (**H, I,** with **J** & **K** approximately same scale as **I**).

Specimen	L	W	T	W%L	T%L	Notes
E22183	14.5	12.0	8.3	82.76	57.24	
	14.6	12.6	9.0	86.30	61.64	Illustrated
	13.8	11.8	7.3	85.51	52.90	Illustrated
E22182	12.1	11.7	6.4	96.69	52.89	Illustrated
E58672*	13.1	12.5	NA	95.42	NA	disarticulated
	12.2	11.7	7.0	95.90	57.38	
	13.8	13.5	6.9	97.83	50.00	
E21963	14.2	14.3	7.5	100.70	52.82	
	12.7	12.0	NA	94.49	NA	Disarticulated (dorsal valve L = 11.3 mm). Illustrated

Table 6. *Neorhynchia strebeli* measurements, notes, and indices. All measurements in mm, NA = not assessable as valves were disarticulated, * = dry specimens (others in ethanol).

unsurprising that it would eventually be collected from Australia. Cooper (1972) recognized two species of *Neorhynchia*, describing material from the north-eastern Pacific as *N. profunda* Cooper, 1972, diagnosed by having a consistently greater length than width (the Type material of *N. strebeli* having greater width than length). Later authors have not recognized this species, likely as *N. strebeli* is far more variable than initially realized, but in any case, *N. profunda* W%L indices (79.6%–97.9%; *fide* Cooper 1972) fit the W%L indices of the Australian material. Databases (*e.g.*, WoRMS 2022b) also list a *Neorhynchia abyssa* Cooper, 1972, however while Cooper (1972) described the Terebratulid *Notorygmia abyssa* Cooper, 1972 (since synonymized under *Macandrevia diamantina* Dall, 1895), he did not describe a *Neorhynchia* with this name. Instead, Cooper (1927; p.5) contained a single usage of '*Neorhynchia abyssa*' when listing locality data, apparently little more than a typographic mistake for *Notorygmia abyssa* which was mistakenly copied into databases.

Disclosures

Acknowledgments

SupplementaryData

Supplementary Figure 1. Uploaded to Zenodo: https://doi.org/10.5281/zenodo.7262574

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