



Re-description of the deep-sea Australian Rhynchonellid brachiopod *Basiliolella colurnus* (Hedley, 1905) (Rhynchonellida: Basiliolidae)

Tristan Joseph Verhoeff

Tasmanian Museum and Art Gallery, Collections and Research facility, 5 Winkleigh Place, Rosny Park, Tasmania
7018 (Australia)

Corresponding author: tristan.verhoeff@utas.edu.au

Tristan Joseph Verhoeff  <https://orcid.org/0000-0001-5103-8592>



© Copyright of this paper is retained by its authors, who, unless otherwise indicated,
license its content under a CC BY 4.0 license

Abstract

The Rhynchonellid brachiopod species *Basiliolella colurnus* (Hedley, 1905), distributed along eastern Australia from Queensland to the northeastern Bass Strait, is re-described using new material compared to type specimens. The holotype and paratype material of *B. colurnus* is revealed to comprise old and thickened individuals, that had already died and been subject to weathering when Hedley (1905) described them. Comparison to this new material allows a better understanding of the morphology of this species to be achieved. Morphological variation in anterior commissure folding and plication in *B. colurnus* overlaps with that seen for *Basiliolella grayi* from off New Caledonia, however *B. colurnus* is distinguished by a tendency towards a flat-topped uniplicate folding with minimal to no plication (dentition). Furthermore, while both *B. colurnus* and *B. grayi* display ontogenetic change in older individuals with the crural bases becoming greatly swollen, *B. grayi* also has swelling of the hinge teeth bases, this is not seen in *B. colurnus*. *Basiliolella* specimens from Tonga are tentatively assigned to an undescribed species resembling *B. colurnus*.

Cite this paper as: Verhoeff TJ (2023). Re-description of the deep-sea Australian Rhynchonellid brachiopod *Basiliolella colurnus* (Hedley, 1905) (Rhynchonellida: Basiliolidae). *Australian Journal of Taxonomy* 44: 1–16. doi: <https://doi.org/10.54102/ajt.jfwuj>

<https://zoobank.org/References/17214CA5-B0DD-47F4-8E3E-79D03BF160E0>

Introduction

Australian waters contain a diverse assemblage of living brachiopod species (Phylum Brachiopoda). These species are often abundant, but their taxonomy and ecological importance remain poorly studied. One such relatively common brachiopod from the outer continental shelf and upper slope of eastern Australia is *Basil-*

iolella colurnus (Hedley, 1905), within order Rhynchonellida.

This species was first collected in 1902 when the Government hydrographer G.H. Halligan (with assistance of C. Hedley, Australian Museum) collected specimens off Wollongong and Cape Byron, and further material was collected in 1905 by Mr Hedley and Mr Petterd off Sydney (*vide* – Australian Museum records; AM C.18116,

C.19822, C.374080, & C.24375). Hedley published the description of *Hemithyris* (now *Basiliolella*) *columnus* using the specimen lot collected off Wollongong in 1902 (183 m depth) as the type series, and a specimen from this lot was selected as the holotype and illustrated (Hedley 1905, text fig. 7 & 8) (see **Fig. 1 A–C**). Problematically, Hedley's illustrations were apparently from an old, dead, and somewhat weathered specimen, and since then no description or illustration of *B. columnus* from Australian waters has been published, excepting two low resolution photographs of a specimen by Richardson (1997, fig. 19.7 e,f).

The closely related species, *Basiliolella grayi* (Woodward, 1855) is known from the south-western Pacific adjacent to Australia (recorded from New Caledonia and Chesterfield Islands, Norfolk Ridge, and off Fiji) (Woodward 1855; Laurin 1997; Bitner 2009; Bitner 2015). *Basiliolella grayi* is a variable species which unlike *B. columnus* often has strong plication (also referred to as being costate or dentate) superimposed on the same flat-topped uniplicate folding seen in *B. columnus* (Laurin 1997). The two species have never been critically compared, and to complicate matters Bitner (2019) recently identified putative *B. columnus* from off Tonga, well outside the expected range of the species. The poor original description of *B. columnus* may have hindered previous identification and assessment of *Basiliolella* species relative to each other.

This species and *Basiliolella* as a genus has had a complex taxonomic history. Thomson (1927) placed *Hemithyris columnus* in the Rhynchonellid genus *Aetheia* Thomson (1915) (spelled *Ætheia*) as it agreed with his definition of the genus in foramen, hinge teeth, and muscular pits, but differed in cardinalia with crural bases not meeting (i.e., lacking inner hinge plates). Cooper (1959) moved *H. columnus* and *Rhynchonella grayi* Woodward, 1855 into the genus *Eohemithyris* Hertlein & Grant, 1944 (previously a fossil genus with type species *E. alexi* Hertlein & Grant, 1944). Cooper (1959) regarded *Eohemithyris* as very similar to *Aetheia* but lacking inner hinge plates, and further considered *E. columnus* and *E. grayi* as extremely similar to *E. alexi* (though *E. grayi* was more strongly costate). A spelling change, *Eohemithyris* to *Eohemithyris*, was used by Cooper (1959) to make spelling consistent with *Hemithyris*, but since such a change is unjustified (per the ICZN) Ager (1965) insisted on the original spelling. Jean-Loup d'Hondt (1987) created the genus *Basiliolella* to accommodate his new species *B. ferox* Jean-Loup d'Hondt, 1987 collected off New Caledonia with dentate (costate) anterior commissures, reduced median septum, and thickened crural bases. d'Hondt apparently conducted his research without knowledge of the fossil *Eohemithyris* or living *E. grayi*, so when Laurin (1997) recognized similar material from New Caledonia as *Eohemithyris grayi* (Woodward, 1855), he synonymized d'Hondt's genus and species. During the preparation of the revised edition of the *Treatise*

on *Invertebrate Paleontology (Part H. Brachiopoda)* it was concluded by Savage *et al.* (2002) that the assigning of *H. columnus* and *R. grayi* into *Eohemithyris* (by Cooper, 1959) had been in error, with *Eohemithyris* only containing fossil taxa. As a result, d'Hondt's genus *Basiliolella* was resurrected as a name for the extant species, though *Eohemithyris* continued to be used for living species by some authors after the resurrection of *Basiliolella* (e.g., Zezina 2010).

In recent decades a large amount of material attributed to *B. columnus* has been collected, with a sizeable collection housed at the Tasmanian Museum & Art Gallery (TMAG). The aim of this research is to describe the morphology and variation of *B. columnus* in detail using this TMAG collection, and compare this to re-assessment of type material. This will allow assessment of how the Australian species compares to *B. grayi*, and secondarily permit a preliminary assessment of population structure, epibiota, and attachment.

Methods

The Tasmanian Museum and Art Gallery (TMAG), collections and research facility (Rosny Park, Tasmania), holds 19 specimen lots of *B. columnus* (comprising > 200 individual specimens), collected over 1993–2000 by the RV *Southern Surveyor* (SS), as part of the CSIRO south-east fisheries ecosystem structure surveys (SS199305 and SS199405) and the south-east marine biodiversity survey (SS200001) (CSIRO Data Trawler 2023). Collection equipment was epibenthic sled. TMAG specimens were examined in person, most were wet specimens (fixed and stored in 75% ethanol), and a small number were dry specimens. Photography and measurements were provided for specimens from the Australian Museum (AM), Sydney, namely holotype, paratype, and other specimens. The localities of specimens examined, as well as literature occurrences of the genus *Basiliolella*, are depicted on **Fig. 2**.

Specimens at TMAG (n = 148) were measured with calipers (length, width, and thickness) as per Verhoeff (2023), with width and thickness as percentages of valve length calculated (W%L and T%L) and size-frequency histograms constructed. Illustration of TMAG specimens was done by *Camera Lucida* (Leica MZ16 with drawing tube), and photography of some structures used a stacking camera macro-imaging setup and associated software (Passport linear actuator software, Visionary Digital; Capture One, Phase One; Zerene Stacker, Zerene Systems). Illustrations kept the ventral (pedicle) valve lowermost in lateral and anterior illustrations.

Valve ('shell') abbreviations: AC—anterior commissure, AdSc—adductor muscle scar, CP—cardinal process, Co—collar, Cr—crura, CrB—crural base, DL—dental lamellae (or plates), DP—deltidial plates, Fo—foramen, Gr—groove, HT—hinge tooth (teeth), IHP—inner hinge plate, ISR—inner socket ridge, LC—lateral commissure, MS—median septum, OHP—outer

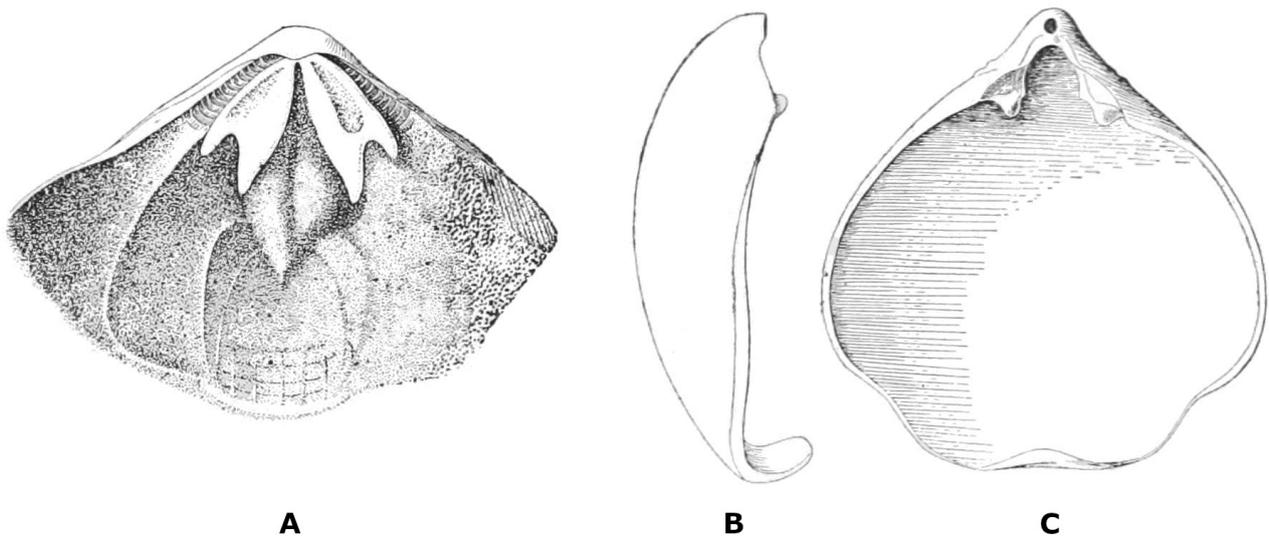


Figure 1. The holotype of *Basiliolella columnus* as illustrated by Hedley (1905), with a closeup of the dorsal valve cardinalia (A), lateral aspect of ventral valve (B), and dorsal (interior) aspect of ventral valve (C) depicted. This specimen was one of ~20 dead and generally disarticulated specimens collected in Aug 1902, 16 miles east of Wollongong, NSW, at 100 fathoms depth. The holotype (since registered as AM C.18116) was separated from the rest of this type material (AM C.374080).

hinge plate, OSR—outer socket ridge, PaS—pallial septum, Pe—pedicle, Ri—ridge, So—socket, SoRi—socket ridges, Sy—symphytium (fused DP's). **Soft tissue abbreviations:** Ad—adductor muscles, an.st—anterior stem (of pallial sinus), an.st.2—secondary anterior stem, gon—gonad, lat.st—lateral stem (of pallial sinus), lat.st.2—secondary lateral stem, loph.arm—lophophore arm, Mo—mouth, post.stem—posterior stem (of pallial sinus), vas.med—vascula media (main stem), ves—vesiculae.

Results

Index comparisons and histograms: W%L and T%L indices for *B. columnus* specimens were visualized and fitted with linear regression equations. Both indices were modelled well by linear regression, W%L and T%L having R² values of 0.83 and 0.80 respectively (Fig. 3 A), though the very small number of smaller specimens reduced the fit. Both valve width and thickness increased proportionally with length, i.e., linearly, however valve width increased more rapidly than thickness for a given increase in valve length, reflected in the increased gradient of the W%L linear regression (0.947) compared to the T%L linear regression (0.565). Overall, this indicated that specimens with greater length tended to be proportionally wider and thinner compared to specimens with smaller length.

To assess population structure, size-frequency histograms were constructed for valve length (Fig. 3 B), width (Fig. 3 C), and thickness (Fig. 3 D). All three histograms were left-skewed, especially that for valve length. Overall, most specimens tended to occur within a narrow range of size with small specimens especially conspicuous in their rarity.

Epifauna: Approximately half of *B. columnus* specimens had notable epifauna on the valve exteriors, ~46% having encrusting bryozoans, ~6% having encrusting sponges, ~7% with possible serpulid tubes. The holotype and paratype material (which were dead when collected) also had epifauna consisting of bryozoans and serpulid tubes (see Fig. 6).

Attachment: Relatively few of the *B. columnus* specimens examined herein were attached, but attachment was always small fragments of worn shell, or small intact shells, consistent with a free-lying species living in coarse sands with high amounts of biogenic carbonates (worn down shell fragments). Richardson (1981, 1997) similarly noted that *B. columnus* was an unattached and free-lying species.

Discussion

Other than Hedley's (1905) illustrations, *Basiliolella columnus* has rarely been illustrated, and the type material has never been re-assessed before now. From examination of the type and paratype material herein, it is evident that this material, while conspecific with the TMAG material from south-eastern Australia, is non-representative of the morphology of many specimens (see description in following taxonomy section). The type and paratypes were old and thickened specimens, and already dead and weathered at capture, with the crura being worn away to simple points. Herein, the form of the crura of live specimens is confirmed to be falciform, with broadened truncated ends which are finely serrate distally, these and details of the collar and dental plates are illustrated for the first time. Most notable however is the lack of thickening on the crural bases on even larger specimens, and it would seem that only the few specimens that reach greater age experience such thicken-

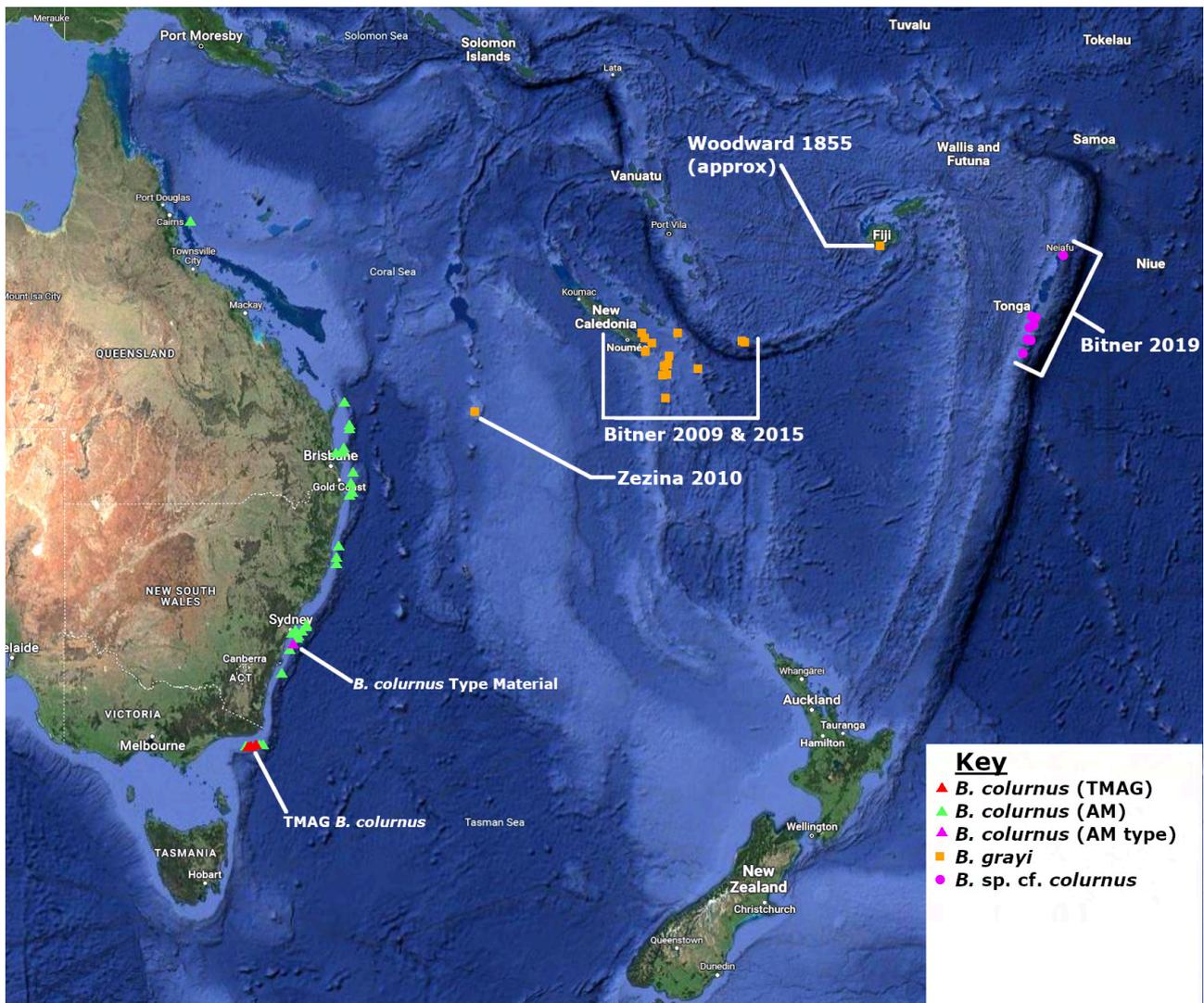


Figure 2. The locations of capture of *Basiliolella* specimens from literature and those studied herein. *B. colurnus* are represented by triangles (TMAG and AM specimens, with type specimens noted per Key), *B. grayi* by squares, and *B. sp. cf. colurnus* by circles. For some specimen groups the relevant literature is noted. Abbreviations: AM–Australian Museum, TMAG–Tasmanian Museum & Art Gallery.

ing. The ontogenetic history of *B. colurnus* would seem to involve progressive thickening of the crural bases on the oldest specimens, the swelling of these structures causing the paired bases to start coalescing medially and overgrowing the outer hinge plates laterally. Furthermore, W%L and T%L indices indicate that older and larger specimens increase in width more rapidly than they increase in thickness.

Type material for *B. colurnus* (AM C.374080), from which the holotype was selected, was found to comprise a mixture of two species, *Basiliolella* and a small punctate terebratulid taxon, however these non-rhynchonellid specimens were not described by Hedley and thus did not negatively affect his description.

The folding of the anterior commissure is more variable than previously appreciated in *B. colurnus*. The flat-topped uniplicate folding, without dentition (or secondary plication), has previously been regarded as

distinct from the anterior commissure of *Basiliolella grayi*, which often is distinctly dentate (the dentation being superimposed on the flat-topped uniplicate folding) (see Bitner 2009, fig. 3). Laurin (1997) examined hundreds of specimens of *B. grayi* from waters around New Caledonia, and found variation in the anterior commissure folding and plication encompassing the range of both *B. grayi* with the more exaggerated dentition and *B. colurnus* generally lacking this. Looking at the range of anterior commissure variation of *B. colurnus* examined herein, relative to New Caledonian *B. grayi* (see Fig. 4), it is apparent that while Australian specimens often generally lack secondary dentation, a small amount of this secondary plication does occur rarely, and likewise, *B. grayi* occasionally displays minimal to no plication. Laurin (1997) acknowledged that the thickness (swelling) of the hinge teeth bases was more exaggerated in the *B. grayi* specimen he examined (see Laurin 1997, fig. 7 A) compared to *B. colurnus*, but went on to

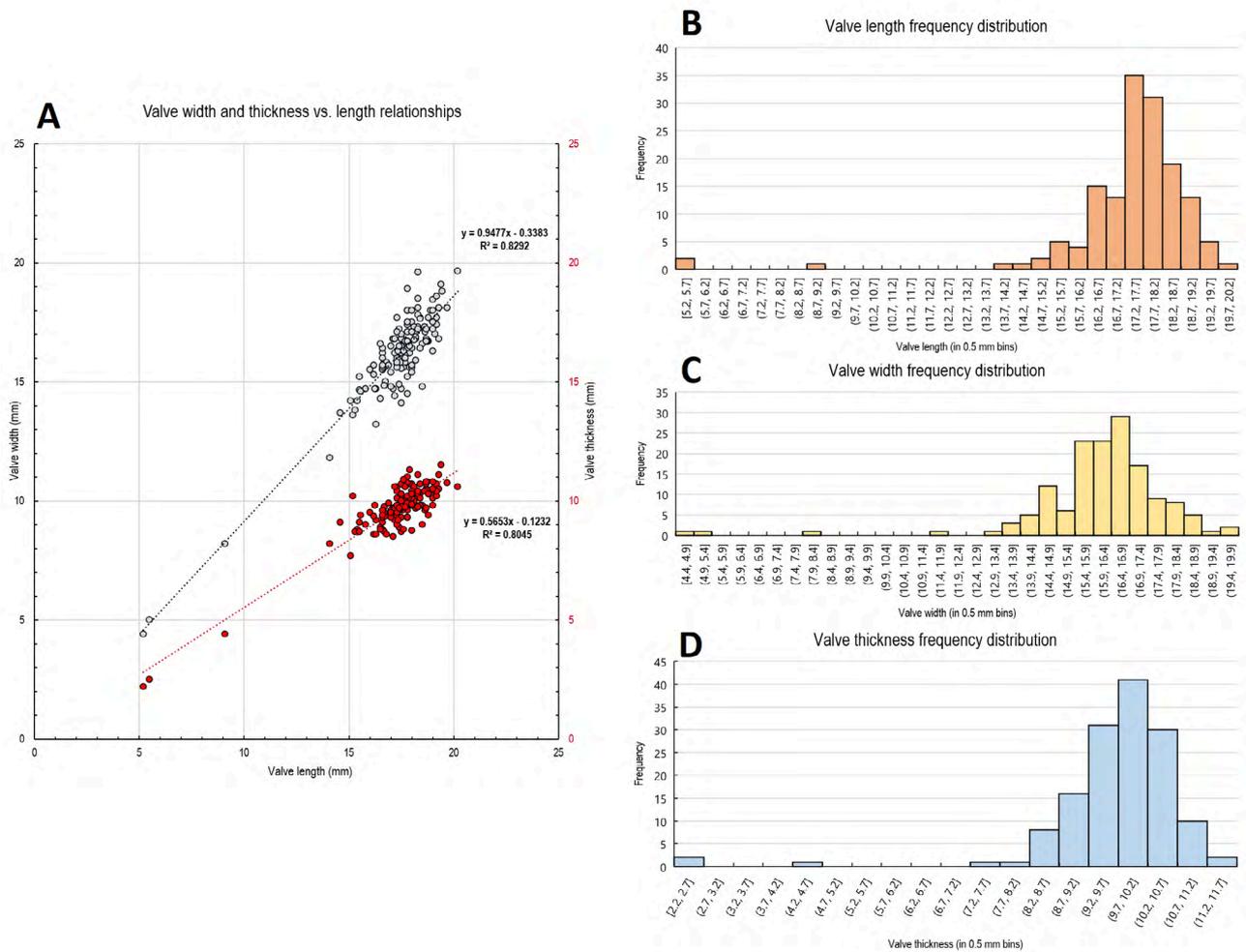


Figure 3. *Basiliolella columnus* analyses of morphometrics (n = 148 specimens from TMAG). **A)** relationships between valve width and thickness relative to valve length, linear regressions are fitted to each dataset (dashed lines) with equations and R2 values displayed. The width vs. length relationship uses grey points whereas thickness vs. length relationship uses red points. The y-axes at left and right are width and thickness respectively. **B–D)** size-frequency histograms of valve length (**B**), width (**C**), and thickness (**D**), measurements are grouped into 0.5 mm range bins for each histogram (size ranges being automatically generated, with minimum & maximum measurement for each bin listed along x-axis).

conclude (p. 423): “*Celles-ci devraient donc vraisemblablement être placées en synonymie, mais cette proposition ne peut être concrétisée ici, car tous les spécimens de collections, et notamment les types, n’ont pu être examinés*” = “These [*B. grayi* and *B. columnus*] should therefore probably be placed in synonymy, but this proposal cannot be concretized here, because all the specimens of collections, and in particular the types, could not be examined.”

Herein, the types of *B. columnus* have been compared along with more representative specimens, and while the overlap in commissure dentition is apparent, the synonymizing of the two species cannot be justified. Even though the commissure form of *B. columnus* is encompassed within the range seen in *B. grayi*, strong dentation (secondary plication) is seemingly frequent and typical of the New Caledonian and Fijian *B. grayi* (see Bitner 2009, fig 3; Bitner 2015, fig 2), whereas for *B. columnus*, out of the ~150 specimens examined only a

handful could be considered dentate, and these failed to reach the extent of dentition seen in typical *B. grayi*. In addition, the absence of thickening of the hinge teeth bases on older *B. columnus* also seems to differentiate this species from *B. grayi*.

Bitner (2019) recorded specimens from Tonga, which she designated as *B. columnus*, however this population is distinctly remote from the Australian population (see **Fig. 2**). The Tongan specimens have a broad and gentle uniplicate folding rather unlike the flat-topped folding typical of *B. columnus*. The median sinus or groove also causes a much more distinct antero-medial indentation (when viewed dorsally) (see Bitner 2019, fig 2. N–S). These specimens also had swollen crural bases as seen in older individuals of *Basiliolella* from Australia and New Caledonia. Given the disjunct distribution from other *Basiliolella* populations, and differences in morphology, the Tongan *Basiliolella* is herein regarded as a

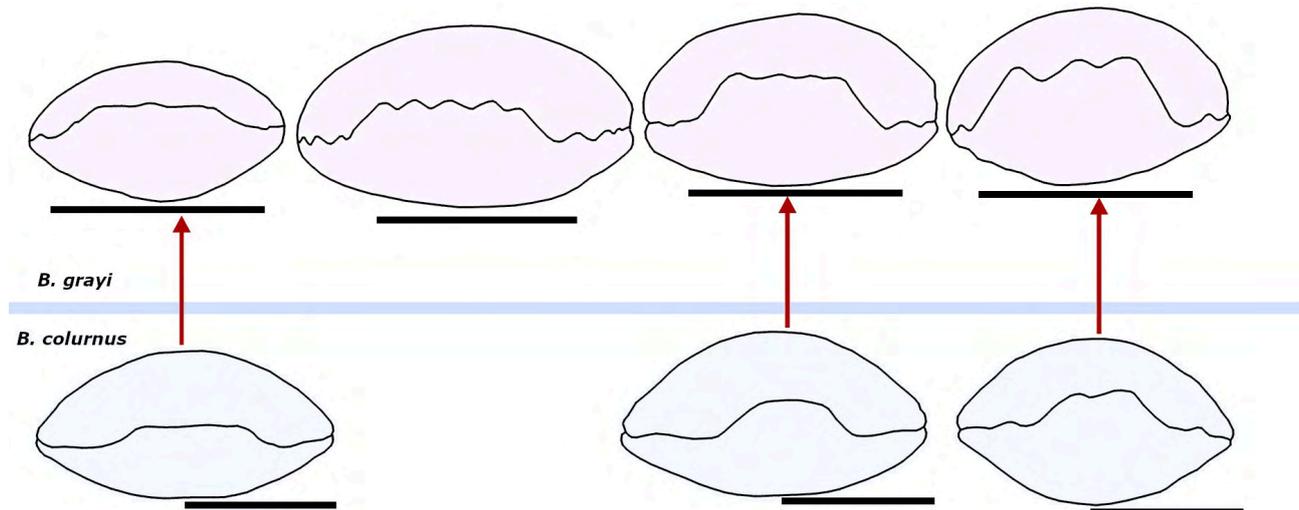


Figure 4. Comparison of anterior commissure folding and plication variation within *Basiliolella grayi* and *B. columnus*. Arrows show comparable folding between the two species, with the specimen at lower-right being one of the few *B. columnus* with plication similar to *B. grayi*. *B. grayi* redrawn from Laurin (1997, fig. 5 B, 6 A, D, E), *B. columnus* are simplifications from **Fig. 5** herein. Scale bars: 10.0 mm.

separate undescribed species with a superficial similarity to *B. columnus*, and is thus designated *B. sp. cf. columnus*. As the Tongan material was not directly examined, formally describing it as a new species was not possible in this contribution.

Size frequency distribution for *B. columnus* (length, width, and thickness) were all left-skewed distributions, a distribution seen for south-east Australian Dallinid brachiopods (Verhoeff 2023). This may be due to a sampling bias, smaller specimens being either missed by the equipment used, or simply not noticed when the crude benthic sled samples were initially sorted, but such distributions in brachiopods may also be due smaller individuals having disproportionately higher mortality or sporadic recruitment events (Brey *et al.* 1995; Baird *et al.* 2013).

The spirolophe lophophore of *B. columnus* when coiled occupied around half the internal space the valves, with each lophophore arm coiled with approximately 10 turns. The rhynchonellid *Notosaria nigricans* (Sowerby, 1846) has a similar lophophore to *Basiliolella*, and Hoverd (1985) reported that it could uncoil the lophophore, extending one or both arms beyond the valve. The rhynchonellid *Hemithiris psittacea* (Gmelin, 1790) could reportedly do the same (Ager 1987), but such behaviour would negate the filter feeding of the coiled lophophore and would probably be an indication of distress should they be observed in *Basiliolella*. The coiled lophophore of *N. nigricans* was also used for brooding, holding the eggs and hatched larvae between the filaments and brachial canal along the length of each coiled arm (Hoverd 1985), it remains to be seen if such brooding is conducted by *Basiliolella*.

Extant rhynchonellid brachiopods (Order Rhynchonellida) are united by having a greatly reduced lophophore

support (brachidium), comprising little more than the crura with the rest of the brachidium (descending, ascending, and transverse bands) absent (Schreiber *et al.* 2014). Rhynchonellida comprises 19 living genera in four recognized super-families (Emig 2023), with *Basiliolella* within super-family Pugnacoidea Rzhonsnitskaia, 1956 (containing Basiliolidae and extant genera *Basiliolella*, *Basiliola*, *Acanthobasiliola*, *Rhytirhynchia*, & *Striarina*) which forms a clade based on morphological characters (Schreiber *et al.* 2013). By contrast, the most complete molecular phylogeny of Rhynchonellida by Cohen & Bitner (2013) (12 species from 11 genera), found that other than Dimerelloidea, all rhynchonellid super-families were paraphyletic. Notably, *Basiliolella grayi* was nested within a clade containing *Basiliola*, *Parasphenarina*, and *Tethyrhynchia* (the latter two traditionally in super-family Norelloidea). This poor match between molecular and morphological phylogeny probably related to a high degree of neoteny and homoplasy (convergent evolution) of morphological features across Rhynchonellides.

The crura of extant rhynchonellids are broken into five groups: raduliform, canaliform, spinuliform, arcuiform, falciform, and maniculiform (Schreiber *et al.* 2013; Schreiber *et al.* 2014). The five traditional genera of Basiliolidae share a 'falciform' crural type, which is diagnostic of the family. This enables separation from other known Australian genera of Rhynchonellides, which have maniculiform type crura (*Cryptopora* and *Aulites*) or arcuiform type crura (*Neorhynchia*) (Schreiber *et al.* 2013). Australian *Cryptopora* and *Aulites* can also be distinguished by their much smaller size, flatter form in lateral profile, disjunct deltidial plates, and well-developed septal pillar. *Neorhynchia*, recently added to the Australian brachiopod fauna (Verhoeff 2023), is superficially similar to *B. columnus* in size and crura, but in addition to

the crura being arcuiform, it is separable on basis of disjunct deltidial plates on specimens of comparable size to *B. colurnus* (~10 mm long), more inflated lateral profile, and the anterior commissure being rectimarginate or folded in the opposite direction *B. colurnus* (sulcate with dorsal valve folding towards the ventral valve in *Neorhynchia*). *Basiliola* Dall, 1908 has yet to be recorded from Australian waters, but it is widely distributed globally has been reported from adjacent waters of the Indo-Pacific (*B. lucida* and *B. beecheri* from off New Caledonia; Laurin 1997), these taxa should be readily separated by their inflated valves (more rounded in lateral profile) and strongly arched, rather than flat-topped, folding along the anterior commissure. All non-rhynchonellid brachiopods in Australia can be easily separated from *B. colurnus* by presence of puncta.

Basiliolella colurnus seems to be a very abundant species along the eastern and south-eastern Australian outer shelf. At some RV *Southern Surveyor* stations *Basiliolella* was very abundant with many 100s of specimens captured at a single station. The commonality of this species was also attested to by Hedley (1905) who noted from surveys in NSW waters that "...every haul on the margin of the continental shelf has yielded single and broken valves". Interestingly, all records of *Basiliollella* (generally as *Eohemithyris*) are from either tropical or subtropical waters of the south-western Pacific (Tonga, Fiji, New Caledonia, and eastern Australia from Queensland, down as far south as the northeastern Bass Strait), the southernmost extent for *B. colurnus* off the north-eastern Bass Strait may be enabled by the warm waters of the Eastern Australian Current. The conspicuous absence of *Basiliolella* from southern Australia (including off eastern and southern Tasmania), areas well surveyed for brachiopods (Blochmann 1910; Richardson 1987; Verhoeff 2023), would seem to further imply that cold waters prevent the spread of this species to the far south-eastern and southern coasts of Australia.

Taxonomy

Phylum **BRACHIOPODA** Duméril, 1805

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

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

Order **Rhynchonellida** Kuhn, 1949

Super-family **Pugnacoidea** Rzhonsnitskaia, 1956

Family **Basiliolidae** Cooper, 1959

Genus ***Basiliolella*** d'Hondt, 1987

Genus *Basiliolella* d'Hondt, 1987

Type species: *Basiliolella ferox* d'Hondt, 1987 (by original designation) = *B. grayi* (Woodward, 1855)

Diagnosis: Small, subtriangular to subpentagonal in outline, smooth but sometimes with obscure marginal plicae; uniplication generally flat-topped, sometimes rounded; anterior commissure with or without variable dentition (secondary plication); beak small, straight to sub-erect; beak ridges sub-mesothyridid; foramen small, with well-developed collar extending below deltidial plates; deltidial plates conjunct as a symphytium; hinge teeth small, dental plates (lamellae) present but obscured in older individuals of some species due to swelling of hinge tooth base. Median septum reduced to a ridge or low keel; cardinal process absent or only weakly developed; outer and inner socket ridges well-developed, socket interiors with distinct corrugations or ridges; outer hinge plates small and narrow-triangular; crura falciform, distal ends broad and truncated, truncated edge with or without fine serration; crural bases variably thickened, increasingly swollen to medially coalescent in older individuals, overgrowing the outer hinge plates laterally; Inner hinge plates absent. Lophophore spirulophous.

Diagnosis modified from volume 4 of the Treatise on Invertebrate Paleontology (2002), and original diagnosis[1]

Etymology: Genus name alludes to a smaller form alike the sister genus *Basiliola* (-ella suffix indicating a diminutive form).

[1] Originally diagnosis (d'Hondt, 1987; p. 39): "*Basiliolidae à suture multiplissée du côté antérieur, à coquille lisse de forme triangulaire, à septum médian réduit à une carène très peu saillante. Crura renforcées à leur base. Crochet saillant submésothyride.*" = Basiliolidae with multi-fold commissure on anterior side, with smooth triangular-shaped shell, with a median septum reduced to a very slightly projecting ridge. Crura reinforced at their base. Beak projecting, sub-mesothyridid.

Genus description: As per diagnosis.

Basiliolella colurnus (Hedley, 1905)

Figs 5–8; Table 1.

Type specimen lodged (by Hedley 1905) at the Australian Museum, Sydney (AM C.18116).

Synonymy

Hemithyris colurnus Hedley, 1905

Ætheia colurnus: Thomson 1927

Eohemithyris colurnus: Cooper 1959, Zezina 1981, Zezina 2010 (with unjustified emendation to genus spelling)

Eohemithyris colurnus: Ager 1965, Richardson 1997

Eohemithyris colournus: Richardson 1981 (misspelling of specific epithet)

Basiliolella colurnus: Savage et al. (2002)

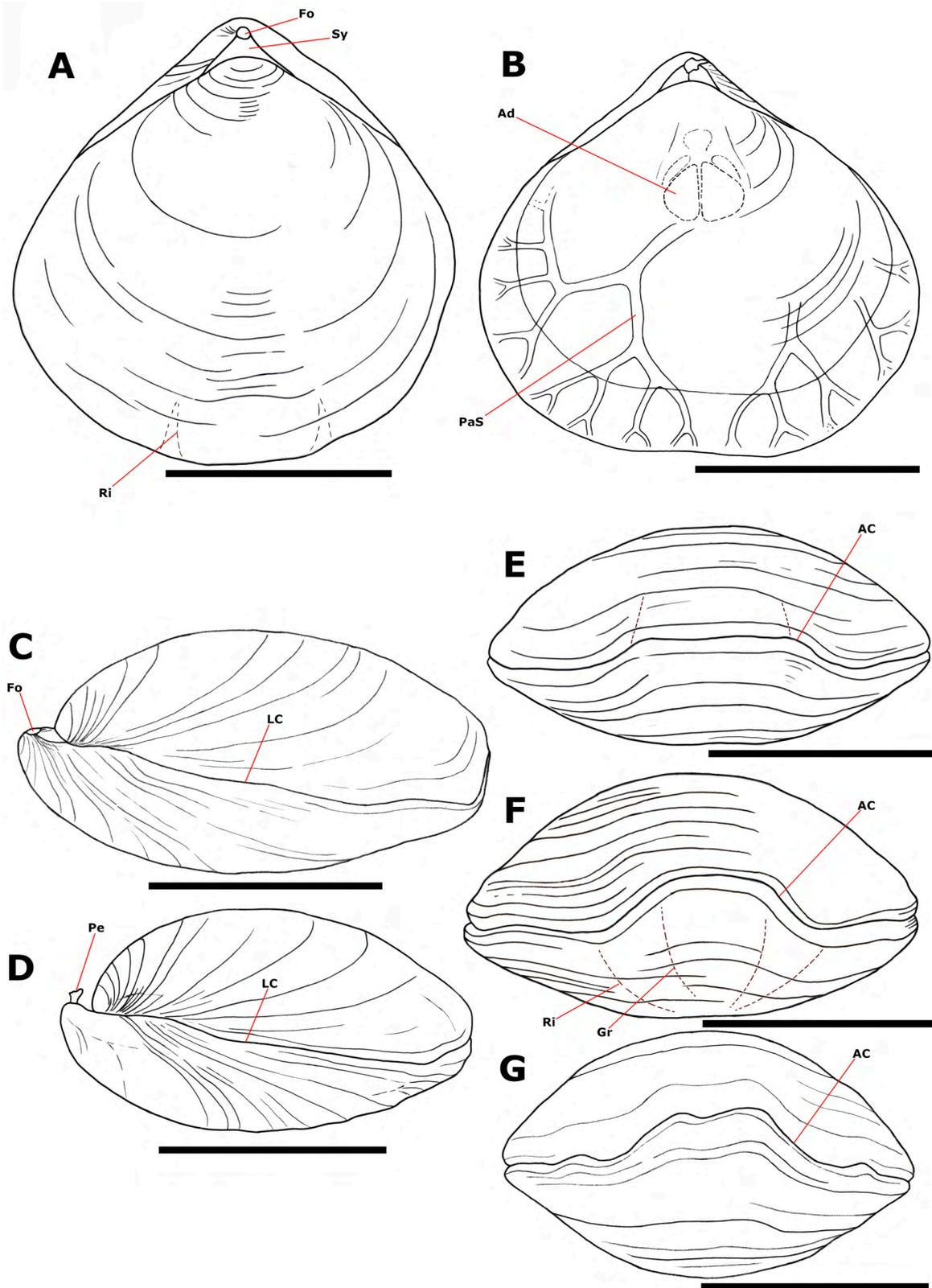


Figure 5. *Basiliolella colurnus* overall form and commissure variation (TMAG specimens). **A**) Dorsal aspect of large specimen (E22137; L = 20.2 mm, W = 19.6 mm). **B**) Dorsal aspect depicting pattern of pallial sinuses (within the mantle lining the dorsal valve), visible inside the valve by translucence (E22138; W = 19.6 mm). **C, D**) Lateral aspects of two specimens (**C**, same specimen as **A**; **D** E22138, L = 18.1 mm). **E–G**) Anterior aspects of three specimens to depict variability in anterior commissure folding: shallow and broad folding (**E**, same specimen as **B**), narrower and stronger folding (**F**, same specimen as **A**), and irregular or more ‘wavy’ folding (**G**, E22138, W = 18.1 mm). Abbreviations per Methods. Scale bars: 10.0 mm.

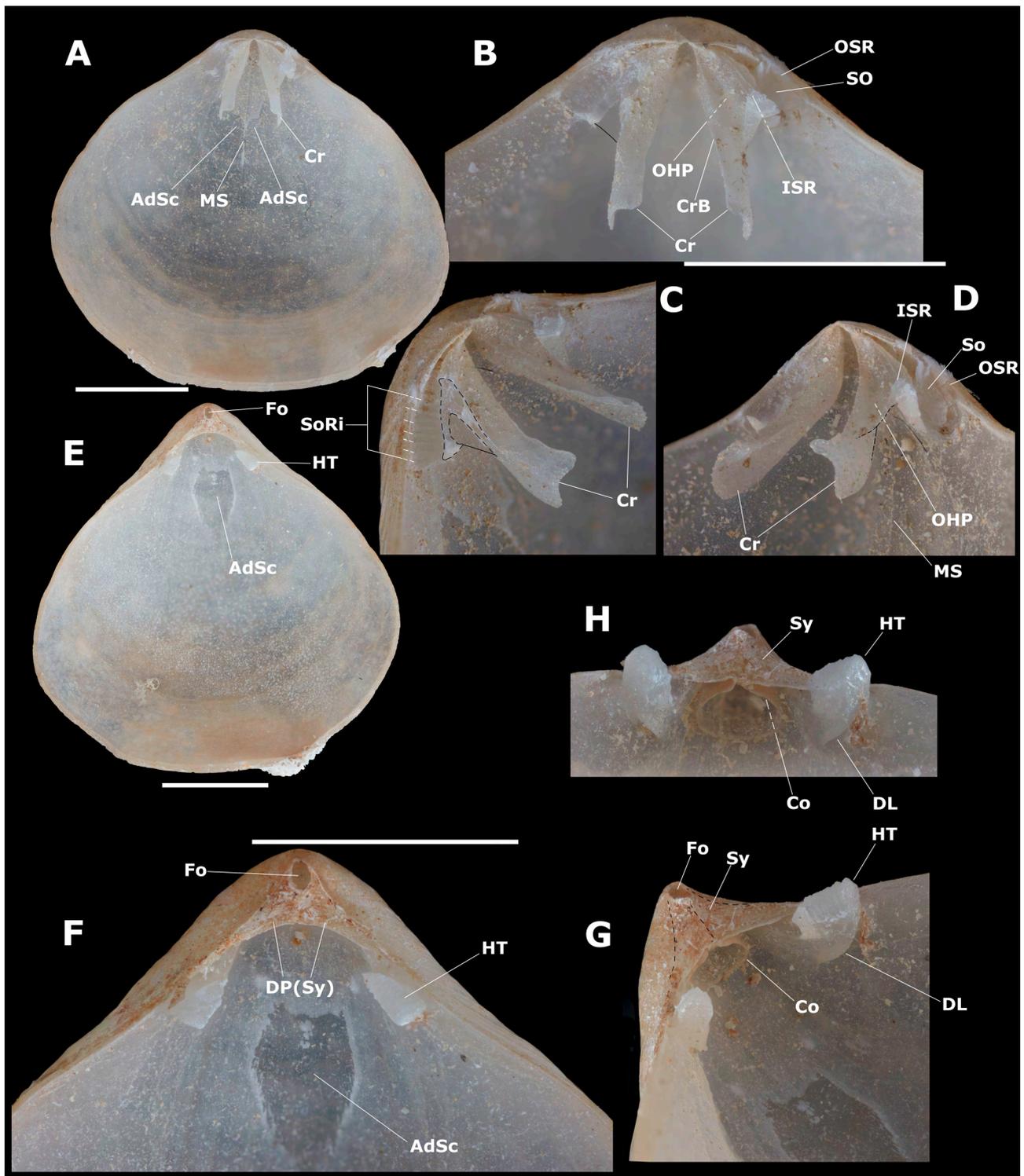


Figure 6. *Basiliolella columnus* valve interior details (TMAG E22144, L = 17.3 mm, W = 17.1 mm). **A)** Dorsal valve interior. **B)** Close-up of 'A' giving detail of cardinalia (ventral aspect). **C, D)** semi-lateral aspects of cardinalia, left image (C) shows internal socket ridges (due to ISR on that side being damaged). **E)** Ventral valve interior. **F)** close-up of 'E' depicting detail of the deltidium (or symphytium) and hinge teeth. **G, H)** semi-lateral (G) and semi-anterior (H) aspect of delthyrial structures and hinge teeth revealing deltidial plates and collar. Abbreviations per Methods. Scale bars: 5.0 mm.

Diagnosis: A *Basiliolella* with anterior commissure generally a simple flat-topped uniplicate fold directed into the dorsal valve, the fold spanning the medial third of valve width, rarely the commissure has subtle secondary plication (or dentition). Cura truncated ends with fine serration, crural bases only thickened/swollen in

old specimens; hinge teeth without swollen bases even in older specimens, with dental plates apparent.

Description

Overall valve form: Maximum valve length 20.2 mm, average length 17.4 mm, maximum valve width 19.7

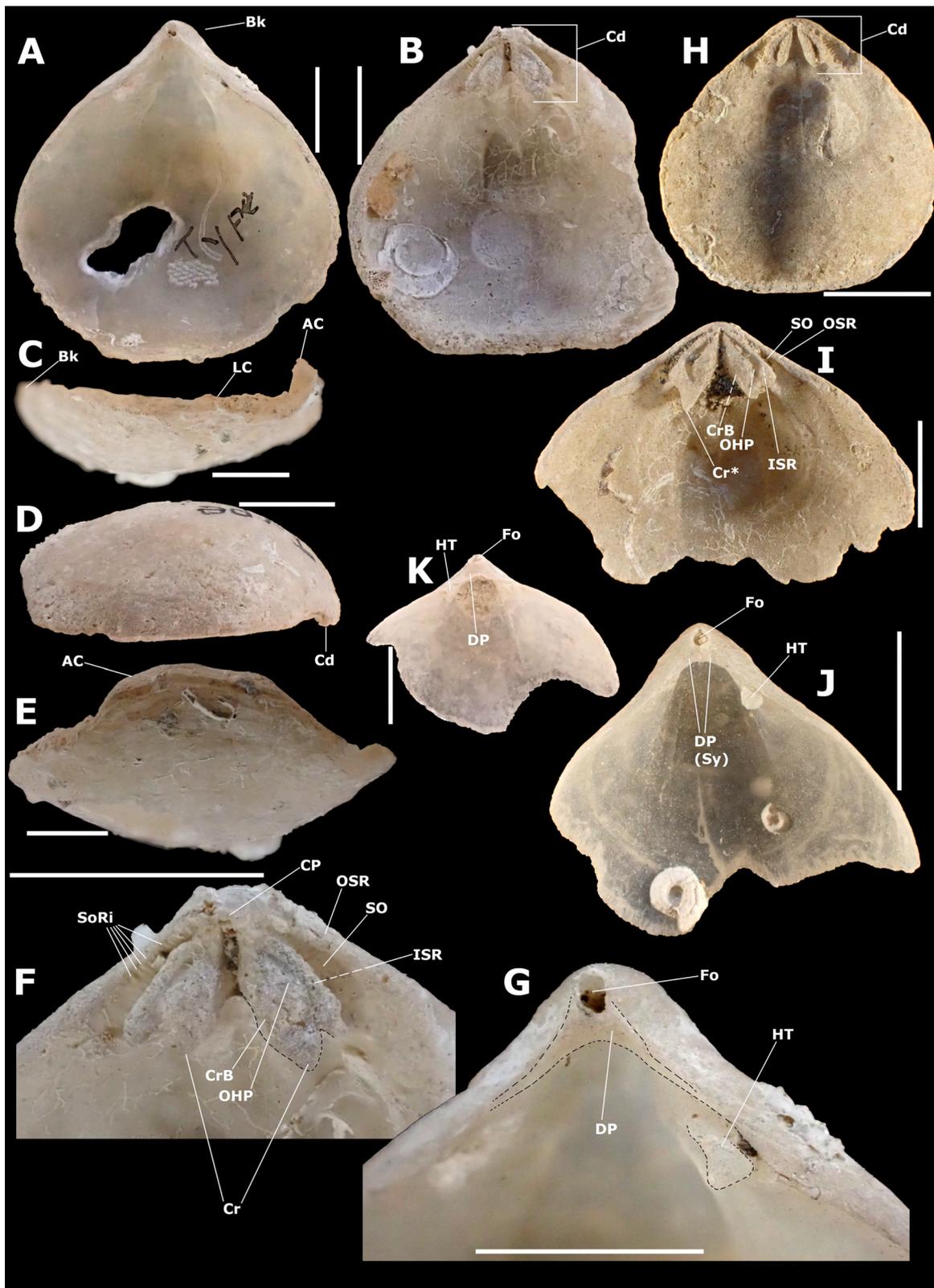


Figure 7. *Basiliolella columnus* type material and other comparative specimens from the Australian Museum. **A–G)** Holotype (AM C.18116) depicting ventral valve interior (**A**), dorsal valve interior (**B**), lateral aspect of ventral valve (**C**) and dorsal valve (**D**), anterior aspect of ventral valve (**E**), closeup of dorsal valve cardinalia structures (**F**), and closeup of ventral valve delthyrial structures (**G**). **H–J)** Paratype specimens (C.374080), dorsal valve interior and cardinalia detail from two specimens (**H**, **I**) and delthyrial details from fragmentary ventral valve (**J**). **K)** Putative *B. columnus* from off Cairns Queensland (C.374270), comprising a fragmentary ventral valve with the delthyrial structures depicted. Abbreviations per Methods. Scale bars: 5.0 mm. Photography by A.C. Miller, Copyright: Australian Museum, Sydney (used with permission).

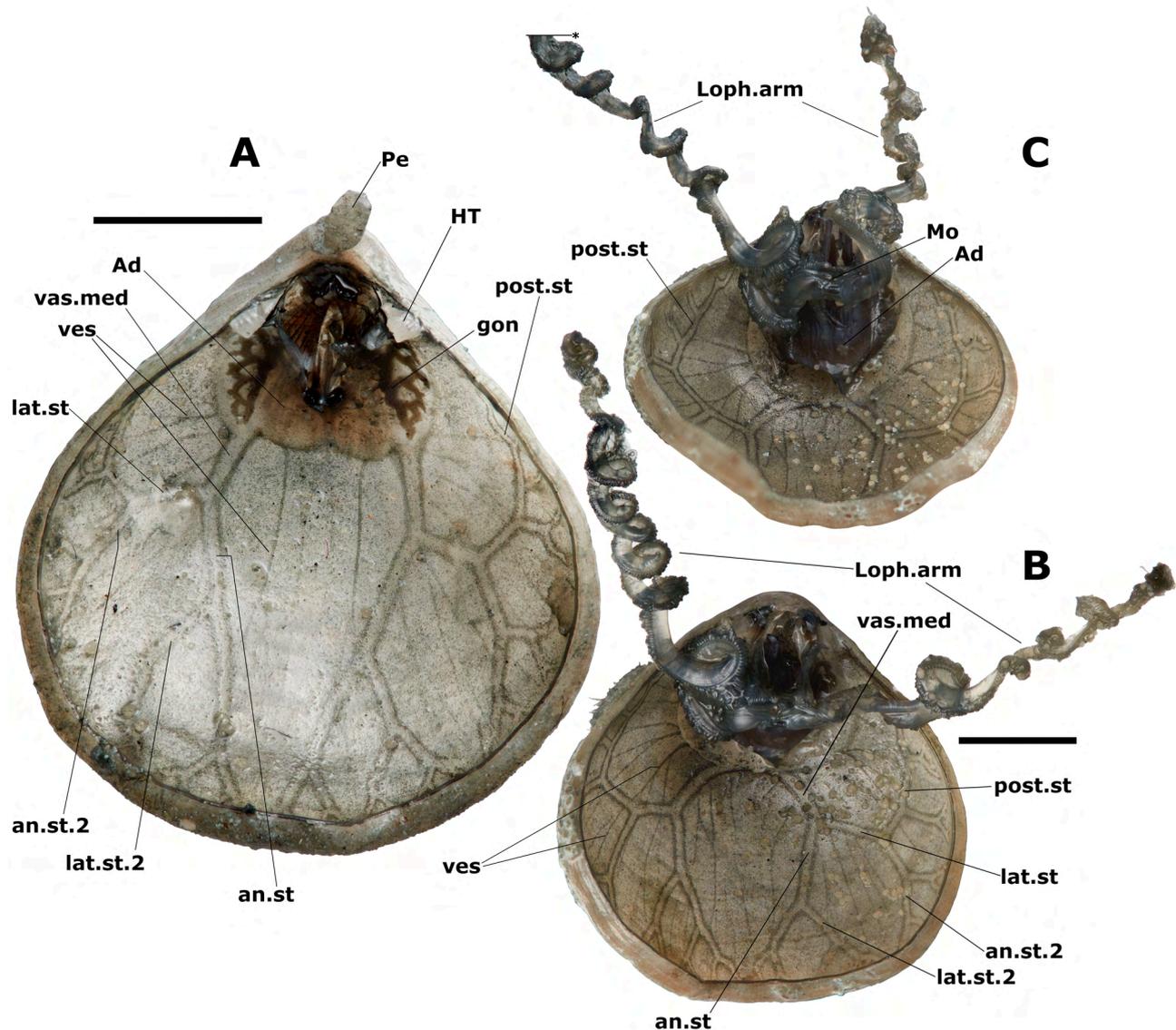


Figure 8. *Basiliolella columnus* lophophore and mantle details (TMAG E22142, L = 18.6 mm, W = 17.3 mm). Valves separated by cutting through adductor/diductor muscles and stained with chlorazol black to better contrast branching pattern of pallial sinuses. **A)** Ventral valve interior. **B)** Dorsal valve interior, with lophophore arms extended and lifted to expose mantle. **C)** similar aspect to 'B' with shell anterior edge elevated to better view mantle details at posterior end of shell. Abbreviations per Methods. Scale bars: 5.0 mm.

mm, average 16.1 mm. Valve width approximately equal to valve length, sometimes more or less, W%L averaging 92.8% (range 80.0%–107.1%, SD 4.65). Valve thickness approximately half valve length, T%L averaging 55.7% (range 42.3%–67.1%, SD 3.40). Maximum valve thickness 11.5 mm, average 9.7 mm.

Overall valve shape sub-pentagonal to rounded, widest approximately two thirds valve length, dorsal valve more rounded with the widest point closer to midway (**Figs 5 A, B, 6 E, 7 A, B**). Valves equally biconvex, not greatly inflated (thickness averaging 56% of length as stated earlier). Lateral commissure straight but descending slightly towards ventral valve anteriorly (**Fig. 5 C, D**). Anterior commissure generally flat-topped uniplicate, though variable, fold occupying medial ~third

of valve width, anterior edge folded towards the dorsal valve, the dorsal edge of this fold being truncated (flat-topped) (see **Fig. 5 E–G**), extent of folding various from subtle (**Fig. 5 E**) to more pronounced (**Fig. 5 F**); anterior commissure is either non-dentate (**Fig. 5 E, F**) or with some light dentition (or secondary plication) (**Fig. 5 G**); antero-medial groove on ventral valve (formed by uniplicate folding) shallow. On the type specimen the lateral and anterior commissure folding is comparable to TMAG material, straight along lateral commissure (**Fig. 7 C, D**), and with pronounced flat-topped uniplicate folding at anterior commissure (without dentition) (**Fig. 7 E**).

Valves impunctate, opaque or translucent on smaller specimens, colourless (cream or whitish). Fine to prominent growth striae present on smaller to moderately

Table 1. *Basiliolella columnus* measurements and notes for TMAG specimens. Epifauna attached to valve exteriors are recorded, while the notes column lists various attributes including any abnormalities, or if its pedicle was attached to an object. All measurements in mm.

Specimen lot	length	width	thickness	notes	Epifauna	Specimen lot	length	width	thickness	notes	Epifauna
E22122	16.6	16.2	NA	ventral valve	Bryozoan	E33495	18	15.6	10.1		Bryozoan
E21965	17.1	16.8	8.5	attached to shell fragment			18.3	17.3	9.75		
	18.8	16.7	9.4				18.7	16.8	10.7		Bryozoan
	17.8	14.5	9.8		Bryozoan		17.8	18	9.3		Bryozoan
	16.5	14.3	8.9		Bryozoan		17.85	16.6	10.1		Bryozoan & Serpulid
	5.5	5	2.5				18	15.4	9.8		Bryozoan
	5.2	4.4	2.2				17.8	17.5	10.75		Bryozoan
E21964	18.2	16.8	9.8		Bryozoan encrusting		15.5	14.65	9.1		Bryozoan
	17.8	18.9	9.6		Bryozoan encrusting		18	16.4	8.75		
	18.2	17.1	9.7		Bryozoan encrusting		18.1	17.3	10.6		Bryozoan
E21967	17.6	15.6	10				17.5	16.35	9.8		Bryozoan
E21966	16.2	15.7	8.6		Bryozoan & Serpulids	E22144	16.7	14.85	9.75		Bryozoan
	17.1	16.8	9.7		Bryozoan encrusting		18.3	17.2	10.2		
E22139	18	16.4	10.7		Bryozoan		18.7	16.7	9.7		
	18.4	17.7	10.3		Bryozoan		19	18.45	9.8		Bryozoan
	17.9	15.6	9.9		Bryozoan & Serpulids & sponge		18.3	17.8	10.3		
	15.1	14.2	7.7		Bryozoan		17.7	15.8	10.6		
	17.8	18	NA				19.3	18.1	11.1		
E22140	14.6	13.7	9.1				18	15.7	10.4		
	16.6	16.4	9.1		Bryozoan & Serpulids		17.5	15.55	9.3		Sponge
	18.7	16.7	10.5		Bryozoan		17.4	15.8	9.6		
	17.5	14.7	8.7	flat commissure	Serpulid		18.9	18	10.45		
	18.5	16.6	9.8		Bryozoan		19.3	16.8	10.5		
	14.1	11.8	8.2		Bryozoan		18.3	18.1	11.1		Bryozoan
	16.6	15.5	8.8		Serpulid		17.4	17.2	9.8		
	18.65	17.1	9.6		Bryozoan		17.6	16.5	10		Bryozoan
	15.8	14.7	9				18.3	17.2	10.4		
	15.4	14.2	8.8		Bryozoan		17.8	17.1	9.3		
	16	15.5	9.5		Bryozoan		17.5	16.8	10		
	16.6	15.5	9.3		Bryozoan		17.8	15.2	9.9		Sponge
	17.1	14.7	9.6		Bryozoan		17.5	16.5	10.7		Sponge
	17.8	16.3	9.8		Serpulid		18.3	18.5	10.4		Bryozoan & small coral(?)
E22121	17.8	16.4	9.8				16.2	15.3	9.35		Bryozoan
E33737	19.1	17	10.7		Sponge, Bryozoan, & Serpulid		16.7	15.6	9.5		Sponge
	19.2	17.4	10.7	deformed			17.5	14.1	9.7		Bryozoan
	18.2	16.9	9.7		Sponge & Serpulid		17.5	16.2	10		Bryozoan & sponge
	17.2	14.4	9.2		Sponge, Bryozoan, & Serpulid		16.25	14.7	9.8		
	17.8	16.7	9.8		Sponge & Bryozoan		15.55	14.6	9.4		
	9.1	8.2	4.4				15.3	13.8	8.7		
E33491	17.7	16.6	10.8		Bryozoan		17.5	17	10.3		
	17.5	16.8	10.2		Covered with encrusting sponge		15.5	15.2	8.7	attached to small gastropod shell	
	18.6	17.3	10.4		Some Bryozoan		18.4	16.4	10.7		
	19	17.2	10.1	asymmetric			19.4	19.1	11.5		
	18.4	16.4	9.8				17.7	16.7	10.6		
	17	14.8	9.6		Bryozoan		19.2	18.6	10.4		
	17.55	16	9.6				17.3	17.1	9.5		
	17.6	16.2	10		Bryozoan	E22142	16.6	16	9.6		Bryozoan
	17.9	16.2	10.7		Bryozoan encrusting		17.8	16.7	10.2	attached to shell fragment	
	17.3	16	9.4		Bryozoan		18	17.1	10.3		
	16.3	13.2	8.6		Bryozoan & Sponge		17.4	14.9	9.7		Bryozoan
E22141	19	16.3	10.8		Bryozoan		18.7	17.2	10.8		Bryozoan
	19.2	17.7	10.2		Bryozoan		16.8	15.8	8.6		Bryozoan
	17.2	16.8	9.7		Bryozoan		16.6	15.6	NA		
	18.5	14.8	9				17.45	15.8	9.85		Bryozoan
E22143	16.3	14.7	9.2		Bryozoan		17.3	15.6	9.8		
	17.4	15.9	8.9				17.3	15.8	10.1		
	17.3	16.3	9				18	18	9.85		
	19	17.5	10.4				17.7	16	9.75		
	15.2	13.6	10.2	flat commissure	Bryozoan		16.9	15.7	9.9		
	18.75	16.7	10.8		Bryozoan & small coral(?)		18.4	17.65	10.1	attached to small shell fragment	
	18.2	15.9	10.2		Bryozoan & Sponge		17.8	16.4	11		
	19.45	18.8	NA		Bryozoan		17	15.4	9.5		
	17.8	17.4	9.8		Bryozoan traces		16.6	15.7	9.4		
	16.7	15.8	8.7		Bryozoan encrusting		18.3	19.6	9.75		
	17.3	17.7	10.6		Bryozoan traces		17.2	16.8	10.6		
	16.75	15	9.35	flat commissure			17.5	16.5	10		
	17.3	15.75	10.4		Bryozoan traces		17.35	16.3	9.2		
	18.1	16.75	10		Bryozoan traces		18.8	17.7	10.3		
	17.6	16.8	8.8				19	18	10.5		
	17.2	16.2	9.7				17.9	16.5	11.3		
	17	16.5	9.3			E22137	19.7	18.1	10.75		
	17.7	16.1	NA				16.5	16.6	8.8		
	18	17.5	10.4		Bryozoan & Sponge		20.2	19.65	10.6		
							17.6	16.3	10.9		
							17.4	16.5	9.7		

sized specimens (Fig. 5), older thickened specimens with surface roughened and striae obscured except some near anterior commissure where they are more pronounced (Fig. 7 C–E).

Dorsal valve interior: *Cardinalia* illustrated for TMAG specimen in Figure 6 A–D. Cardinal margin approximately 112–116°. Cardinal process essentially absent, a small medial depression at posterior umbo being the

likely point of diductor muscle attachment (some thickening occurs at this area in the older type specimens; Fig. 7 F). Sockets with well-developed outer and inner socket ridges, each inner ridge forming an angled corner antero-laterally. Sockets with strong corrugation or internal ridges (matching corresponding grooves on ventral valve teeth). Outer hinge plates forming narrowly triangular and concave plates between each inner

socket ridge and crural base. Inner hinge plates absent (leaving V-shaped cavity between crural bases). Crural bases diverge at approximately 34° on TMAG specimens, outer hinge plates attached along outer faces of crural bases (see **Fig. 6 D**); beyond hinge plate crura are relatively short ('free length' ~40% the total length of the crura back to their point of origin near the umbo) and curve slightly medially. Crura 'falciform', laterally compressed, concave along their inner face, distally broad and truncated, the truncated edge being slightly serrated.

On the holotype and paratype material (**Fig. 7 F-I**), which represent older and thickened specimens, the crural bases have become greatly thickened and swollen, postero-medially coalescing, and laterally overgrowing the outer hinge plate (the plate forming a narrow groove between the swollen crural base and the inner socket ridge). On the type material the free crura were weathered away (likely as the specimens were already dead and/or disarticulated when collected), therefore Hedley (1905) only illustrating the crura as short points (see **Fig. 1 A**).

Median septum reduced to a fine and low ridge, extending less than a third the dorsal valve length (just visible in **Fig. 6 A, C, D**).

Ventral valve interior (see **Fig. 6 E-H**): Beak small, length (posterior to dorsal valve) 8%–9% of total valve length, straight-suberect. Beak ridges sub-mesothyridid (but not readily apparent). Foramen tiny and trans-sub apical. Deltidial plates small and medially conjunct as a symphytium, often with a medial seam still visible where the plates meet. Symphytium very short (in antero-posterior axis), yet relatively wide, forming a thin edge leading towards the hinge teeth, mostly exposed. Where they contact medially the deltidial plates fold ventrally to form a large and tubular collar running posteriorly to the foramen (below the deltidial plates) (see **Fig. 6 G, H**). Hinge teeth small, with dorsal faces ovoid-rectangular and bearing series of ridges (matching ridges or corrugations in the dorsal valve sockets). Teeth supported by dental plates (or lamellae) (see **Fig. 6 G, H**).

On holotype and paratype material (**Fig. 7 G, J**) the delthyrial area is similar, deltidial plates conjunct with medial seam visible (paratype **Fig. 7 J**) or obscured (holotype **Fig. 7 G**), with the beak ridges slightly more visible, and the hinge teeth more worn.

Soft tissue (illustrated in **Figure 8**): Pedicle short, not extending much beyond beak. Lophophore spirolophous, comprising a pair of elongate arms, each coiled into a spiral. When coiled the lophophore takes up only half the valve length, but when fully extended each arm (from where the crura attach) is approximately 2× the dorsal valve length. Muscle attachment fields reach ~35% ventral valve length from beak, ~40% the dorsal valve length (from posterior end).

Pallial sinuses on both ventral and dorsal valves have essentially the same pattern and comprise a pair of well-developed vascula media originating from the antero-lateral edges of the main coelomic cavity for each valve, as well as multiple fine 'vasculae' (ves) radiating from the coelomic cavity. On each valve the main stems of vascula media (vas.med) diverge anteriorly (their bases being closer together on the dorsal valve), each then branches into a main anterior stem (an.st) which heads anteromedially in an arcing path to the anterior valve edge. The first (most posterior) lateral stem given off by each vascula media (lat.st) branches into another anteriorly directed stem (an.st.2) and a posterior stem (post.st) arcing back almost as far as the hinge. Further anteriorly along the an.st a second lateral stem (lat.st.2) can be defined. Each of these stems give off shorter lateral stems which in turn branch again before they reach the valve edge.

Gonads comprise four small patches, 2 per valve (more apparent on ventral valve, see **Fig. 8 A**). On the ventral valve they extend ~33% the valve length from the beak, each comprising a branching structure with an ovoid outline, positioned lateral the adductor muscles.

Material examined

TMAG material examined

E22122, 38°11.6'S, 149°17.2'E, 249 m, RV *Southern Surveyor*, SS199305 Stn. 171, 6.viii.1993; **E21965** & **E22121** (7 specimens), 38°11.8–11.4'S, 149°16.0–17.1'E, 210–220 m, RV *Southern Surveyor*, SS199405 Stn. 83, 29.viii.1994; **E21964** & **E33737** (9 specimens), 38°11.6'S, 149°16.9'E, 230 m, RV *Southern Surveyor*, SS199305 Stn. 173, 6.viii.1993; **E21967** & **E22144** (100–200+ specimens), 38°11.6'S, 149°15.6'E, 190–240 m, RV *Southern Surveyor*, SS199305 Stn. 191, 8.viii.1993; **E21966** & **E22140** (16 specimens), 38°11.2'S, 149°15.2'E, 158–180 m, RV *Southern Surveyor*, SS199305 Stn. 194, 8.viii.1993; **E22139** (5 specimens), 38°10.3'S, 149°38.2'E, 245 m, RV *Southern Surveyor*, SS199305 Stn. 204, 9.viii.1993; **E33491** (11 specimens), 38°11.5'S, 149°16.3'E, 217 m, RV *Southern Surveyor*, SS199305 Stn. 190, 8.viii.1993; **E22141** (10 specimens), 38°10.1'S, 149°37.9'E, 245 m, RV *Southern Surveyor*, SS199305 Stn. 206, 9.viii.1993; **E22143** (~50 specimens), 38°11.5'S, 149°15.6'E, 202–246 m, RV *Southern Surveyor*, SS199305 Stn. 181, 7.viii.1993; **E33495** (~30+ specimens), 38°11.5'S, 149°15.6'E, 180 m, RV *Southern Surveyor*, SS199305 Stn. 193, 8.viii.1993; **E22142** (24 specimens), 38°11.8'S, 149°16.3'E, 212–240 m, RV *Southern Surveyor*, SS199305 Stn. 115, 31.vii.1993; **E22137** (5 specimens), 38°9.7–10.4'S, 149°39.0–37.3'E, 224–280 m, RV *Southern Surveyor*, SS200001 Stn. 198, 22.iv.2000.

AM material examined

Holotype. **AM C.18116**, 16 miles east of Wollongong, 34°25'S, 151°15'E, 183 m, viii.1902.

Paratypes. **AM C.374080**, ~20 fragmentary and disarticulated valves (some not *B. columnus*), collection as per holotype (C.18116) which was separated from this lot.

Other material. **AM C.19824**, 12 ½ miles east of Cape Byron, 28°38'S, 153°52'E, 203 m, 10.xi.1902; **AM C.374270**, off Cairns, Queensland, 17°9.60–9.70'S, 146°42.00–42.40'E, 613–668 m, HMAS *Kimbla*, 13.x.1981; **AM C.219803**, Lord Howe Shelf, Tasman Sea, 31°44.27'S, 159°4.43'E, collected University of Wollongong x.1998.

Distribution: Hedley (1905) recognized three collection sites for *B. columnus* off central NSW and northern NSW coasts off eastern Australia (183–203 m depth). Zezina (2010) recorded distribution as eastern Australia from Cape Byron to Gabo Island (28° to 37°S) at 188–203 m. Richardson (1997) recorded a similar range, but erroneously recorded the bathymetric range as 974–1125 m. Zezina (1981; p. 11) recorded a single *B. columnus* from the eastern Bass Strait (38°12'S, 149°40'E, 200–300 m), noting it to be the most southern record of the species. All TMAG specimens were recorded from this southernmost region of the species' range (all collected from between 38°10'–12'S, 158–280 m, *i.e.*, the northeastern Bass Strait).

The collection voyages by the RV *Southern Surveyor*, from which the TMAG *B. columnus* specimens came from, also collected large numbers of brachiopods around eastern and southern Tasmania, as did more recent voyages by the RV *Investigator* (see Verhoeff 2023). Yet, despite these collecting efforts no *B. columnus* specimens were identified from stations south of ~38°12'S, and as was covered in the discussion, it would seem that *B. columnus* is limited in its southwards distribution along eastern Australia by the decreasing water temperatures.

The AM specimen **C.374270** from off Cairns, Queensland (613–668 m), was the northernmost occurrence of *B. columnus*, at ~17°10'S, well separated from all other specimens along the Queensland and NSW coasts, occurring from 24°S. However, this specimen was a fragment of a ventral valve (see **Fig. 7 K**), and while consistent with *Basiliolella*, the inability to confirm the anterior commissure form rendered this identification tentative only.

Further putative "*Eohemithiris*" specimens from the Lord Howe Rise (Tasman Sea) were also briefly investigated (**C.219803**). However, these specimens were very small and not unambiguously assignable to *Basiliolella*.

Overall, *B. columnus* has been recorded with confidence over a bathymetric range of 150–300 m along eastern Australia from off K'gari, Queensland to the northeastern Bass Strait (latitude 24°S–38°12'S). Records of *B. columnus* from off Tonga (Bitner 2019) are herein assigned to an undescribed *Basiliolella* sp. (*B. sp. cf. columnus*, per discussion), while an AM specimen from the Solomon Islands (**C.395898**) has yet to be investigated.

Disclosures

Conflicts of Interest: The author declares no conflict of interest.

Declaration of Funding: This research did not receive any specific funding.

Acknowledgments

The author would like to thank TMAG Zoology staff for allowing access to their brachiopod collection and generously allowing usage of TMAG laboratory spaces and equipment, particular thanks are due to Dr Kirrily Moore (Assistant Curator), Dr Simon Grove (Senior Curator, Invertebrate Zoology), and Dr Cathy Byrne (Senior Curator, Zoology). Thanks are due also the Australian Museum, Sydney, particularly Allison C. Miller (Collection Manager, Malacology) who provided excellent photography of type material and other specimens. The author acknowledges the use of the Atlas of Living Australia (<https://ror.org/018n2ja79>), which proved invaluable in assessing specimen records and distribution. Lastly, the author wishes to thank the two reviewers, Dr Jeffrey Robinson and another anonymous, for their valuable comments that significantly improved the final manuscript.

References

- Ager DV (1965) Mesozoic and Cenozoic Rhynchonellacea. In: Moore RC (Ed.), *Treatise on Invertebrate Palaeontology. Part H. Brachiopoda*. University of Kansas Press.
- Ager DV (1987) Why the rhynchonellid brachiopods survived and the spiriferids did not: a suggestion. *Palaeontology* **30**, pp. 853–857.
- Atlas of Living Australia (2022) *Eohemithyris columnus* occurrence download at <https://doi.org/10.26197/ala.72017179-abd7-44ed-a9cd-2c3fed08e569> Accessed 22 July 2022.
- Baird MJ, Lee DE, Lamare MD (2013) Brachiopod *Liothyrella neozelanica* Thomson, 1918 from Doubtful Sound, New Zealand. *Biological Bulletin* **225**, pp. 125–136.
- Bitner MA (2009) Recent Brachiopoda from the Norfolk Ridge, New Caledonia, with description of four new species. *Zootaxa* **2235**, pp. 1–39. Doi: <https://doi.org/10.5281/zenodo.190398>
- Bitner A (2015) Checklist of recent brachiopod species collected during the Terrasses and Exbodi cruises in the New Caledonian region, SW Pacific. *ZooKeys* **537**, pp. 33–50.
- Bitner MA (2019) Recent brachiopods from the Tonga Islands, SW Pacific: taxonomy and biogeography. *Research in Paleontology and Stratigraphy [Rivista Italiana di Paleontologia e Stratigrafia]* **125**, pp. 587–608.

- Blochmann F (1910) New Brachiopods from South Australia (paper presented by Verco, J.C.). *Transactions and Proceedings and Report of the Royal Society of South Australia* **34**, pp. 89–99. [+plates XXVII & XXVIII].
- Brey T, Peck LS, Gutt J, Hain S, Arntz WE (1995) Population dynamics of *Magellania fragilis*, a brachiopod dominating a mixed-bottom macrobenthic assemblage on the Antarctic shelf. *Journal of the Marine Biological Association of the United Kingdom* **75**, pp. 857–869.
- Brodie JW (1965) Capricorn Seamount, south-west Pacific Ocean. *Transactions of the Royal Society of New Zealand: Geology* **3**, pp. 151–158.
- Cohen BL, Bitner MA (2013) Molecular phylogeny of rhynchonellide articulate brachiopods (Brachiopoda, Rhynchonellida). *Journal of Paleontology* **87**, pp. 211–216.
- Cooper GA (1959) Genera of tertiary and recent Rhynchonelloid brachiopods. *Smithsonian Miscellaneous Collections* **139**, pp. 1–90.
- CSIRO Data Trawler (2023) NCMI Information and Data Centre, survey data downloaded from: https://www.cmar.csiro.au/data/trawler/survey_details.cfm?survey=SS199305, https://www.cmar.csiro.au/data/trawler/survey_details.cfm?survey=SS199405, & https://www.cmar.csiro.au/data/trawler/survey_details.cfm?survey=SS200001 Accessed 2023.
- D'Hondt J-L (1987) Observations sur les Brachiopodes actuels de Nouvelle-Calédonie et d'autres localités de l'Indo-Pacifique. *Bulletin du Muséum National d'Histoire Naturelle. Paris, 4th series* **9**(Section A, No. 1), pp. 33–46.
- Emig CC (2023) Order *Rhynchonellida* on BrachNet. Accessed at <http://paleopolis.rediris.es/BrachNet/CLASS/Rhynchonellida.htm> on 31 Aug 2023.
- Hertlein LG, Grant US (1944) The Cenozoic Brachiopoda of western North America. *Publications of the University of California at Los Angeles in Mathematical and Physical Sciences* **3**, pp. 1–236.
- Hedley C (1905) Mollusca from one hundred and eleven fathoms, east of Cape Byron, New South Wales. *Records of the Australian Museum* **6**, pp. 41–54.
- Hoverd WA (1985) Histological and ultrastructural observations of the lophophore and larvae of the brachiopod, *Notosaria nigricans* (Sowerby 1846). *Journal of Natural History* **19**, pp. 831–850.
- Laurin B (1997) Brachiopodes récoltés dans les eaux de la Nouvelle-Calédonie et des îles Loyauté, Matthew et Chesterfield. In 'Résultats des Campagnes MUSORSTOM Vol. 18'. (Ed A Crosnier). *Mémoires du Muséum national d'Histoire naturelle. Série A, Zoologie* **176**, pp. 411–471.
- Lee DE (1978) Cenozoic and recent rhynchonellide brachiopods of New Zealand: Genus *Aetheia*. *Journal of the Royal Society of New Zealand* **8**, pp. 93–113. Doi: <https://doi.org/10.1080/03036758.1978.10419419>
- Richardson JR (1981) Brachiopods and pedicles. *Paleobiology* **7**, pp. 87–95.
- Richardson JR (1987) Brachiopods from carbonate sands of the Australian shelf. *Proceedings of the Royal Society of Victoria* **99**(1), pp. 37–50.
- Richardson JR (1997) Chapter 19 Brachiopods (Phylum Brachiopoda). In: Shepherd SA, Davies M (Eds.), *Marine Invertebrates of Southern Australia. Part III*. Government Printer: Adelaide, Australia, pp. 999–1027.
- Schreiber HA, Bitner MA, Carlson SJ (2013) Morphological analysis of phylogenetic relationships among extant rhynchonellide brachiopods. *Journal of Paleontology* **87**, pp. 550–569.
- Schreiber HA, Roopnarine PD, Carlson SJ (2014) Three-dimensional morphological variability of Recent rhynchonellide brachiopod *crura*. *Paleobiology* **40**, pp. 640–658.
- Savage NM, Manceñido MO, Owen EF, Carlson SJ, Grant RE, Dagensand AS, Dong-Li S (2002) Pugnacoidea. In: Kaesler RL (Ed.), *Treatise on Invertebrate Paleontology. Part H. Brachiopoda Revised. Volume 4*. Geological Society of America and University of Kansas, Colorado and Lawrence, Kansas, pp. 1165–1218.
- Thomson JA (1915) The Genera of Recent and Tertiary Rhynchonellids. *Geological Magazine*, decade 6 **2**, pp. 387–392.
- Thomson JA (1927) Brachiopod morphology and genera (recent and Tertiary). *New Zealand Board of Science and Art* **7**, pp. 1–338.
- Verhoeff TJ (2023) New records and descriptions of recent Australian brachiopods (Terebratulida, Dallinidae and Aulocothyropsidae; and Rhynchonellida, Frieleidae). *Australian Journal of Taxonomy* **11**, pp. 1–29. Doi: <https://doi.org/10.54102/ajt.hplgy>
- Woodward SP (1855) Description of a new species of recent *Rhynchonella*. In: Davidson T (Ed.), A few remarks on the Brachiopoda. *Annals and Magazine of Natural History (series 2)* **16**, pp. 429–445.
- Zeina ON (1981) Recent deep-sea brachiopoda from the western Pacific. *Galathea Report* **15**, pp. 7–20.
- Zeina ON (2010) Check-list of Holocene brachiopods annotated with geographical ranges of species. *Paleontological Journal* **4**, pp. 1176–1199.



This paper was typeset using Prince

www.princexml.com