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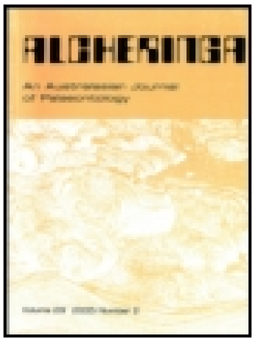

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# Kungurian (Cisuralian/Early Permian) brachiopods from the Snapper Point Formation, southern Sydney Basin, southeastern Australia

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# Kungurian (Cisuralian/Early Permian) brachiopods from the Snapper Point Formation, southern Sydney Basin, southeastern Australia

Sangmin Lee, G.R. Shi, Bruce Runnegar, and J.B. Waterhouse

**ABSTRACT**

Elements of a high-latitude (~60–70°S) and low-diversity early Kungurian (Cisuralian/Early Permian) brachiopod fauna have been sporadically reported from the sandstone-dominated Snapper Point Formation (SPF) in the southern Sydney Basin of southeastern Australia for more than a half-century, but a detailed description of this fauna is not yet available. In this paper we describe 12 brachiopod species and an indeterminate ingelarellid from the SPF, including one new species (*Tasmanospirifer jervisbayensis* sp. nov. Waterhouse & Lee). Though this brachiopod fauna is evidently associated with an interglacial stratigraphic interval, its taxonomic characteristics overall resemble those from stratigraphically bounding glacial intervals. This association is interpreted to indicate persistence and the strong endemic nature of the Permian Eastern Australian biogeographic province in high-latitude eastern Gondwana, regardless of glacial/interglacial climate states during the Cisuralian. Biostratigraphically, the SPF brachiopod fauna is divisible into two distinctive stratigraphic assemblages: the *Notospirifer* cf. *triplicata*–*Simplicisulcus* sp. Assemblage in the lower part of the formation and the *Johndearia brevis*–*Sulciplica transversa* Assemblage in the upper part, each distinguished by a set of unique species.

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Brachiopods; Kungurian; biostratigraphy; Snapper Point Formation; southern Sydney Basin; eastern Australia

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THE LOWER to Middle Permian strata of the southern Sydney Basin (SSB) in southeastern Australia are well known for containing widespread glacial deposits that characterize several glacial intervals (Crowell & Frakes 1971, Fielding *et al.* 2008, Waterhouse & Shi 2013), as well as prevalent and locally abundant marine protist and invertebrate fossils, such as brachiopods, bivalves, gastropods, echinoids, bryozoans, and foraminifera (e.g., Dana 1847, Laseron 1910, Dickins *et al.* 1969, Runnegar 1980, Scheibnerova 1982). As the list of references would suggest, many of these faunas have been referred to in various previous studies, but considerable amounts of the fossil materials remain undescribed. In the case of brachiopods, several previous studies described certain selected taxa (e.g., Campbell 1965, McClung 1978, Briggs 1998), but most of the Permian brachiopod assemblages remain to be documented in terms of systematic palaeontology.

This paper is a continuation of our effort to systematically and comprehensively document the rich and well-preserved Permian brachiopod assemblages from the SSB in southeastern Australia. Two previous studies already described the brachiopod assemblages from the two lowermost Permian formations in the basin: one assemblage from the basal Permian Wasp Head Formation (Cisterna & Shi 2014) and the other from the overlying Pebbley Beach Formation (Shi *et al.* 2020). Prior to these studies, eight terebratulide species, 16 spiriferide species (including 15 ingelarellids), two spiriferinide species, and 20 productide species had been described from the Permian of the SSB by Campbell (1965), Runnegar (1969), Armstrong (1970a), McClung (1978) and Briggs (1998). In the present paper, our principal aim is to describe the brachiopod fauna from the Snapper Point Formation (SPF) as a whole from new collections. In addition to the detailed taxonomy, we also discuss the age of the brachiopod fauna and implications for associated and previously proposed brachiopod biozones in light of the recent advancement concerning the Permian chronostratigraphy of the SSB.

## Geological setting

The Sydney Basin represents the southern part of a large, north–south trending, elongate sedimentary trough known as the Bowen-Gunnedah-Sydney Basin System, situated between the New England Fold Belt to the east and the Australian Craton to the west (Fig. 1A). During the Permian, the Sydney Basin was located in a high latitudinal region (~60–70°S) at the southeastern edge of Gondwana at the time (Powell & Li 1994, Veevers *et al.* 1994).

The Permian strata of the southern Sydney Basin (SSB) comprise both marine (Asselian to Capitanian) and non-marine (Capitanian to Changhsingian) successions, as well as intercalations of magmatic intrusions and relatively rare volcanic ash beds. The marine succession is well exposed along the coast between Batemans Bay and Wollongong where it is subdivided into two groups and seven

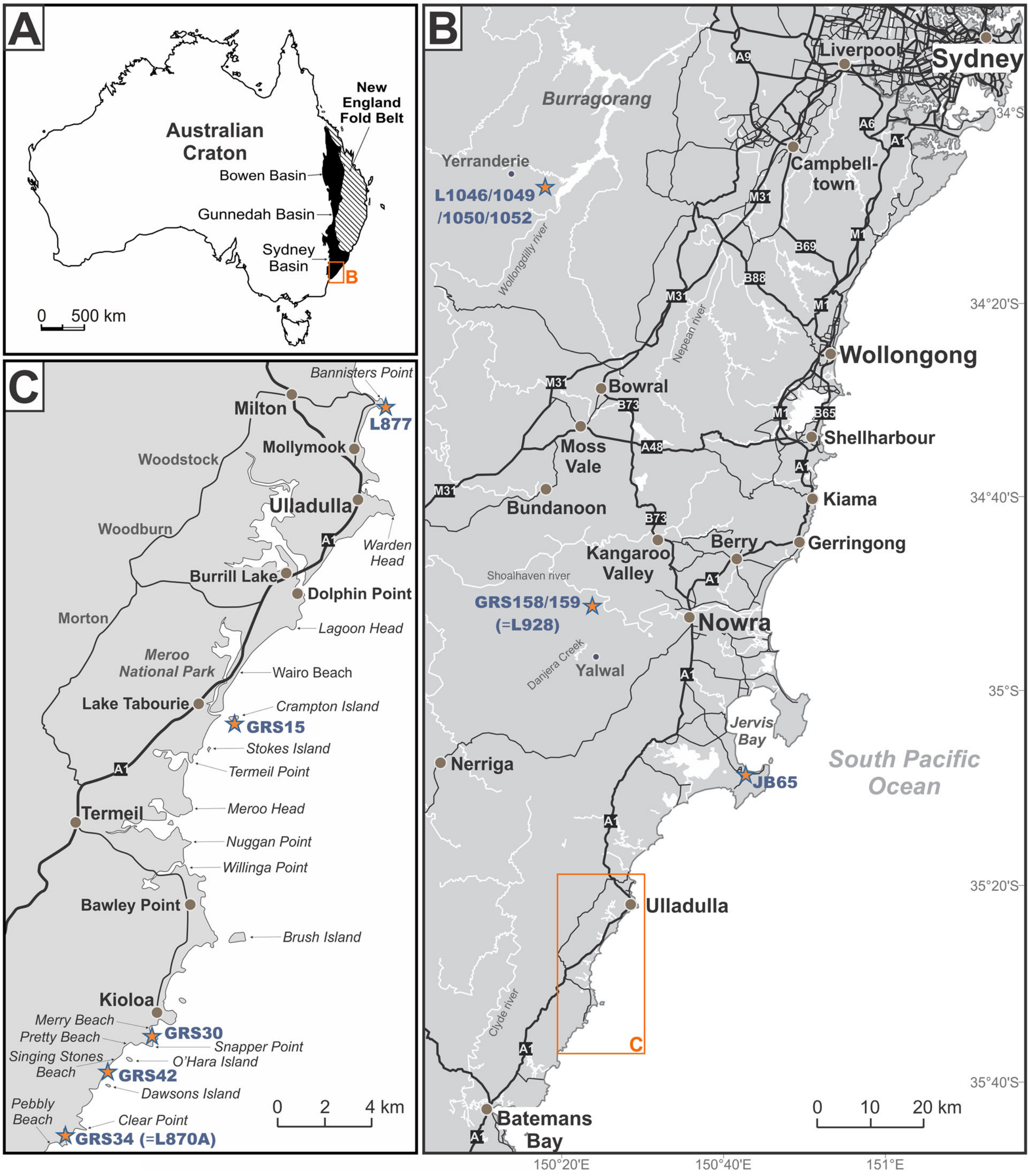

**Figure 1.** Location maps in this study. **A**, map showing the location of the Sydney Basin in Eastern Australia; **B**, map of fossil localities GRS158/159 (=L928) in Grassy Gully (North of Yalwal), JB65 in Jervis Bay, and L1046, L1049, L1050 and L1052 in the southwest of Burragorang Valley; **C**, detailed map of the coastal area between Pebbly Beach and Bannisters Point in South Coast, NSW and fossil localities GRS15, GRS30 (=L873), GRS34 (=L870A), GRS42 and L877. More detailed locality information is stated in Table 1.

formations; they are, in ascending order, the Wasp Head Formation (Talaterang Group), Pebbley Beach Formation, Snapper Point Formation, Wandrawandian Siltstone, Nowra Sandstone, Berry Siltstone, and Broughton Formation (the latter six formations comprise the Shoalhaven Group) (Gostin & Herbert 1973, Tye *et al.* 1996; Fig. 2). This marine succession is overlain by the Illawarra Coal Measures which mark the transition from marine to non-marine sedimentation.

The Snapper Point Formation (SPF), which has yielded the brachiopods described in this paper, was defined by Gostin & Herbert (1973) with its type section exposed along the low coastal cliffs between Clear Point and Crampton Island (~18 km apart in total; see Fig. 1C). In the type section at Clear Point, a pebbly conglomerate comprising the base layer of the SPF conformably overlies the top siltstone beds of the Pebbley Beach Formation (Figs 2, 3). Elsewhere in more inland areas, the SPF interdigitate with, and then

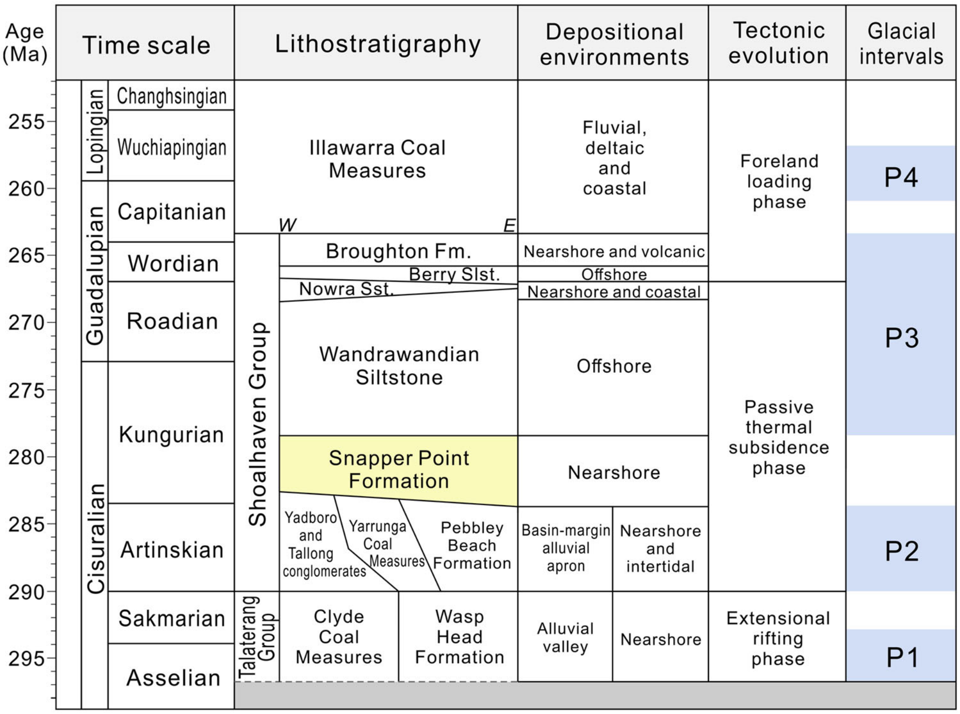

Figure 2. A chronostratigraphic framework showing the Permian lithostratigraphy, depositional environments, and tectonic stages of the Southern Sydney Basin, as well as the main glacial intervals (labelled as P1–P4) in the Eastern margin of Gondwana (lithostratigraphy, depositional environments and tectonic evolution follow Tye *et al.* 1996; glacial interval scheme from Fielding *et al.* 2008; the ages of the lithostratigraphic units and glacial episodes follow Shi *et al.* 2022a). Note that the Snapper Point Formation was deposited during the interglacial phase between two glacial intervals (P2 and P3).

overlies the Yadboro and Tallong conglomerates and the Yarrunga Coal Measures to the west (Tye *et al.* 1996; Fig. 2). Across the SSB, the SPF is overlain by the Wandrawandian Siltstone (Fig. 2), but their boundary is rarely exposed in the coastal sections.

The SPF mainly consists of fine- to coarse-grained sandstones, pebbly conglomerates, and minor siltstone interbeds (Fig. 3). The sandstones frequently include hummocky cross-stratification and cross-bedding, and the conglomerates are wave-rippled (Carey 1978, Tye *et al.* 1996), both suggesting a storm-influenced depositional environment on a shallow marine setting (see also Bann 1998, MacEachern *et al.* 2005, Bann *et al.* 2008, Luo *et al.* 2020).

## Materials and methods

Three fossil collections were described in this study, comprising one collection recently made by the authors (localities labelled with the prefix GRS), another collection loaned from the University of New England [originally collected by one of the authors (BR), labelled with prefix L], and the third and small collection came from the Geoscience Australia (originally collected by W.J. Perry and J.M. Dickins, labelled with prefix JB).

These three fossil collections were made from 11 different fossil localities over a period spanning more than a half-century. Some of the UNE L localities were later revisited and recollected by the authors (GRS and SL) adding more specimens to the original UNE collections but with nominally different but stratigraphically equivalent fossil locality numbers (e.g., GRS34 =L870A, GRS158/159 =L928). In this context, we note that the stratigraphy for one of the UNE L localities near the Burragorang Valley (L1052) remains unclear. Based on BR's original notes for the locality and our examination of its fossil materials, the specimens are considered to represent parts of the SPF, but it is plausible that the locality may be proved to belong to another stratigraphic unit (e.g., Nowra Sandstone; see Fig. 2).

All the fossil localities studied are marked on the maps (see Fig. 1B, C), and their relevant details (e.g., locations with GPS coordinates, stratigraphy, lithology, and preservation features) are fully described in Table 1.

### Repositories and institutional abbreviations

Types, figured, and other specimens examined in this study are deposited in the following institutions: Australian Museum (AM F), Sydney, Australia; Commonwealth Palaeontology Collection of Geoscience Australia (CPC), Canberra, Australia; University of New England (UNE F), Armidale, Australia; University of Queensland (UQF), Brisbane, Australia; United States National Museum of Natural History, Paleontological collection (USNM PAL), Washington, DC, USA; Sedgwick Museum (SM), Cambridge, UK; Natural History Museum (former British Museum) (BH), London, UK.

## Systematic palaeontology

Morphological terms and classifications adopted in this study follow Brunton *et al.* (2000) for productides, Carter *et al.* (2006) for spiriferides, Carter & Johnson (2006) for

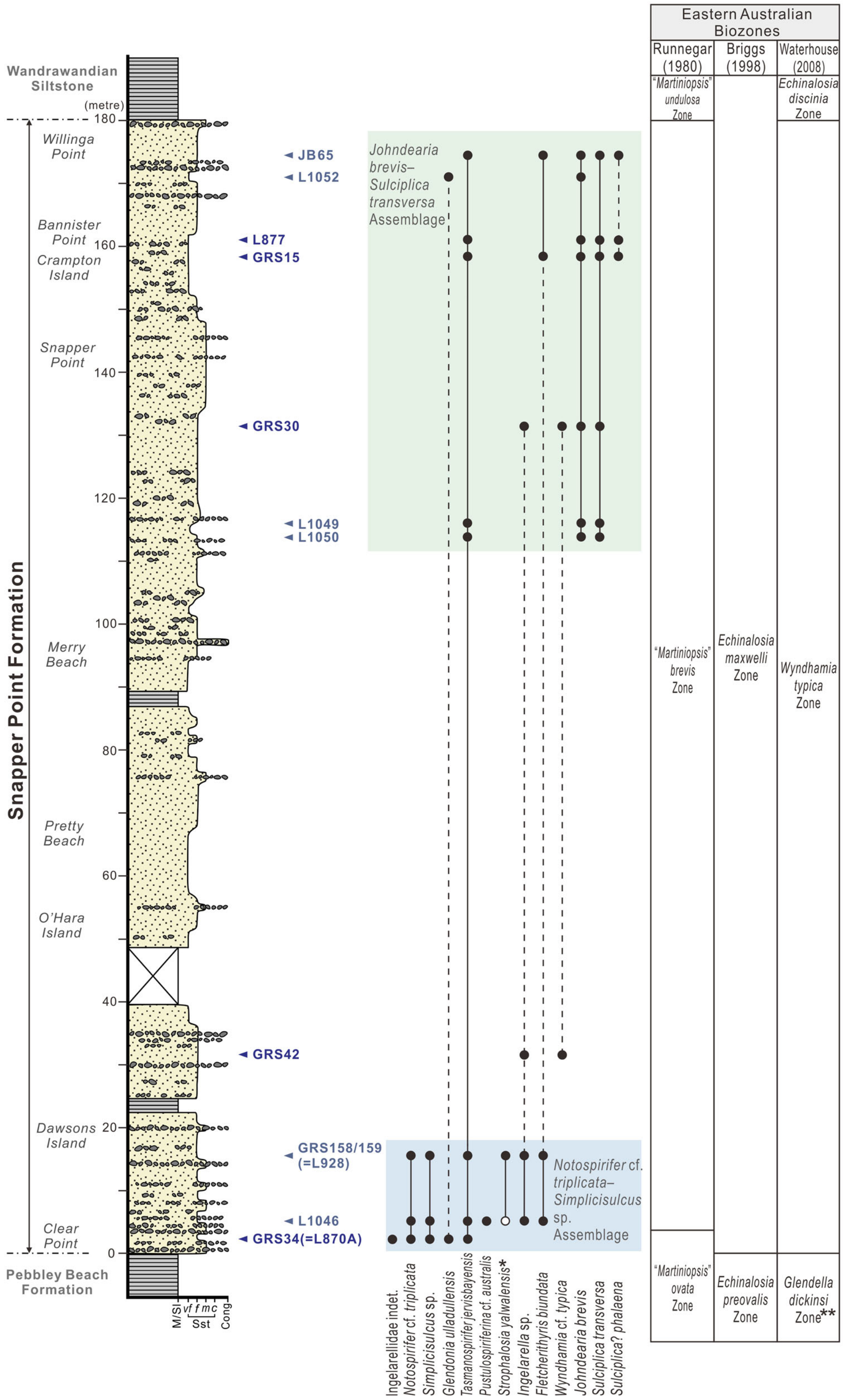

Figure 3. A composite columnar section of the Snapper Point Formation and our brachiopod biostratigraphic data, together with marine invertebrate biozones previously proposed in the formation. The column is drawn, based on the coastal outcrop exposures between Pebbly Beach and Bannister Point (see Fig. 1C) measured in Gostin & Herbert (1973, figs 9, 10). Abbreviations in the column: M, mudstone; Sl, siltstone; Sst, sandstone; vf, very fine; f, fine; m, medium; c, coarse; Cong, conglomerate. The relative stratigraphic positions of the inland fossil localities (in purple) are marked, according to Perry & Dickins (1952), Runnegar (1980), and UNE fossil locality records. **Strophalosia yalwalensis* is not found from the collection of L1046 in this study, but its occurrence was reported in Briggs (1998). **Waterhouse (2008) suggested *Glendella dickinsi* Zone at the Bowen Basin in Queensland, but no corresponding zone was identified from the Southern Sydney Basin.

Table 1. Detailed fossil locality information. The brief location of these localities is also marked on the map (Fig. 1B, C).

| Locality no. | Locality description | Stratigraphy (see also Fig. 3) | GPS coordinates | References | Lithology | Preservation of fossils |
|---|---|---|---|---|---|---|
| GRS15 | Southern cliff outcrop at Crampton Island | Upper part of the Snapper Point Fm. | 35°26′42.9″S 150°24′48.7″E | | Dark grey silty to fine sandstone | Brachiopod moulds concentrated in nodules |
| GRS30 | Coastal outcrop at Snapper Point | Upper part of the Snapper Point Fm. | 35°34′05.82″S 150°22′39.54″E | | Bright medium to coarse sandstone | Bivalves dominated; shell material remained |
| GRS34 (=UNE L870A) | Coastal outcrop exposed between Pebbly Beach and Clear Point | Base of the Snapper Point Fm. | 35°36′31.4″S 150°20′05.8″E | Runnegar 1980 | Yellowish fine to medium sandstone | Bivalves dominated; preserved as moulds |
| GRS42 | Coastal platform south of Singing Stones Beach | Lower part of the Snapper Point Fm. | 35°34′45.9″S 150°21′21.6″E | | Grey fine sandstone | Scattered brachiopod and bivalves shells on platform |
| GRS158/159 (=UNE L928) | Exposures on trail at Grassy Gully, west of Nowra | Lower part of the Snapper Point Fm. | 34°51′40.7″S 150°24′10″E | Runnegar 1980; Briggs 1998 | Yellowish silty to fine sandstone | Brachiopod moulds with abundant juvenile bivalve shells |
| GA JB65* | Quarry at the Jervis Bay naval base (1.5 km south from Captains Point) | Near top of the Snapper Point Fm. | 35°08′25.1″S 150°42′22.5″E | Perry & Dickins 1952; Runnegar 1980 | Grey fine to medium sandstone | Original brachiopod shells commonly remained |
| UNE L877 | Coastal outcrop at Bannisters Point in Mollymook | Upper part of the Snapper Point Fm. | 35°19′34.5″S 150°29′06.1″E | Runnegar 1980 | Dark grey silty to fine sandstone | Preserved as moulds |
| UNE L1046 | "The Sheepwalk", Burragorang | Near base of the Snapper Point Fm. | 34°09′25.4″S 150°17′12.5″E | Runnegar 1980; Briggs 1998 | Grey fine sandstone | Juvenile brachiopod and bivalve moulds dominated |
| UNE L1049 | Ridge running north from road to Tonalli Point, Burragorang | Upper part of the Snapper Point Fm. | 34°08′01.2″S 150°18′00.2″E | Runnegar 1980 | Yellowish silty to fine sandstone | Original brachiopod shells remained |
| UNE L1050 | Roadcut in Tonalli Point Road, Burracorang | Upper part of the Snapper Point Fm. | 34°08′23.5″S 150°17′34.9″E | Runnegar 1980 | Yellowish silty to fine sandstone | Original brachiopod shells remained |
| UNE L1052 | Another roadcut in Tonalli Point Road, Burracorang | Upper part of the Snapper Point Fm. | 34°08′19.5″S 150°18′43.0″E | Runnegar 1980 | Yellowish fine to medium sandstone | Preserved as moulds |

*The locality with the asterisk has not been visited by the present authors. The information about its locational/stratigraphic position is fully dependent on the references.

spiriferinides, and Lee *et al.* (2006) for terebratulides, unless mentioned. The application of Open Nomenclature terms (signs) is here practiced, following the recommendations of Sigovini *et al.* (2016).

We note that one of the authors (JBW) has different views on the family-level positions for some of the taxa described here. His classification scheme is available from Waterhouse (2013, 2015, 2016) and will not be repeated here.

Phylum BRACHIOPODA Duméril, 1806
Subphylum RHYNCHONELLIFORMEA Williams *et al.*, 1996
Class STROPHOMENATA Williams *et al.*, 1996
Order PRODUCTIDA Sarycheva & Sokolskaya, 1959
Suborder STROPHALOSIIDINA Waterhouse, 1975

### *Remarks*

The authorship issue for suborder Strophalosiidina in the revised Brachiopoda treatise volume 3 (Brunton *et al.* 2000, p. 565) had been raised by Waterhouse (2001, p. 52; 2002a, p. 39), but it was neither corrected nor even discussed in the last (supplementary) volume of the revised treatise (Brunton 2007, p. 2663). As a result, two different versions of authorship for the same suborder (Schuchert, 1913 vs. Waterhouse, 1975) have been inconsistently employed in subsequent taxonomic studies on strophalosiidines, causing continuous confusion. Therefore, we here clarify the authorship problem used in the treatise, seeking correct authorship of the suborder.

It is evident that the subordinal name, 'Strophalosiidina' was, for the first time, applied by Waterhouse (1975, p. 4), and a similar scheme was later adopted by Brunton *et al.* (1995, 2000), especially in the point that the suborder is composed of three superfamilies (Strophalosioidea, Aulostegoidea and Richthofenioidea in modern terms). Although this fact was acknowledged by the authors of the treatise (Brunton *et al.* 2000, p. 351), they attributed the suborder to Schuchert (1913, p. 391) in which subfamily Strophalosiinae was established, possibly as a practice relating to Article 36.1 of the code of the International

Commission on Zoological Nomenclature (ICZN) (1999; both superfamily Strophalosiodea and family Strophalosiidae were attributed to Schuchert, 1913, by the article). It appears that Brunton *et al.* might regard the classification in Waterhouse (1975, 1978) as different from theirs, since Waterhouse's Strophalosiidina included two subfamilies (Echinoconchinae and Juresaniinae) positioned within another productide, suborder (Productidina) under their classification. Instead, Brunton *et al.* (2000) compared their scheme to (*sensu*) Lazarev (1989). However, Lazarev (1989) only described the oldest strophalosiidines of Devonian age (e.g., Strophalosiinae, Chonopectinae, Araksalosiidae), without providing any younger components of the suborder. In addition, the subfamily Strophalosiinae of Schuchert (1913), which was represented only by four genera (*Chonopectus* Hall & Clarke, 1892, *Strophalosia* King, 1844, *Aulosteges* von Helmersen, 1847, and *Etheridgina* Oehlert, 1887) and fully separated from Richthofeniidae, seems to be far from the subordinal scheme in Brunton *et al.* (2000). After all, it is obvious that the classification in Brunton *et al.* (1995, 2000) is not fully matched with any of the other schemes mentioned above, but the subordinal scheme for the Strophalosiidina is identical between Waterhouse (1978) and Brunton *et al.* (1995, 2000), in its composition with the strophalosioids, aulostegoids and richthofenioids. Further, Article 36.1 in ICZN (1999) applies only to family groups at the ranks of superfamily, family, subfamily, and tribe (subtribe), but not to suborder and higher ranks. Therefore, we suggest that the authorship for the suborder Strophalosiidina be given to Waterhouse (1975) who first used the name, with the subordinal definition subsequently provided by Waterhouse (1978, p. 20).

More recent publications (e.g., Waterhouse 2001, 2013) have redefined the suborder and its components since Brunton *et al.* (2000); however, they are not in consideration in this study.

Superfamily STROPHALOSIOIDEA Schuchert, 1913
Family STROPHALOSIIDAE Schuchert, 1913
Subfamily STROPHALOSIINAE Schuchert, 1913

**Strophalosia** King, 1844

1844 *Strophalosia* King, p. 313.
1966 *Strophalosia*; Brunton, p. 186.
1986 *Strophalosia*; Archbold, p. 98.
1998 *Strophalosia*; Briggs, p. 65.
2013 *Fimbrianalosia* Waterhouse, p. 216.
2013 *Crassispinosella* Waterhouse, p. 218.
2013 *Strophalosiaria* Waterhouse, p. 220.

### Type species

*Strophalosia gerardi* King, 1846, p. 92 from the Lopingian in Ladakh, Himalaya, NW India.

### Diagnosis

Weakly concavoconvex shell in medium size, with toothed articulation; outline transversely oval to subcircular; hinge less than maximum width. Prostrate to suberect spines on ventral valve but absent along hinge, no dorsal spines; concentric (more strictly, commarginal) ornamentation present and indistinct on both valves but more prominent on dorsal valve; capillae absent or weakly developed on dorsal valve (modified from Briggs 1998).

### Remarks

Despite limited preservation in type materials of *Strophalosia*, its morphological characteristics have been repeatedly investigated and/or discussed by various experts (e.g., King 1850, Davidson 1853, Hall & Clarke 1892, King 1938, Prendergast 1943, Muir-Wood & Cooper 1960, Waterhouse 1964, 2013, Brunton 1966, Archbold 1986, Briggs 1998), due to its importance as the representative of a very large group (suborder level). Therefore, the morphology of the type species has been sufficiently known (at least, in the shell external features) although relatively diverse diagnoses have been suggested for the genus. Its characteristic morphology includes a transversely oval outline, the maximum width around the mid-valve, prostrate and suberect spines developed only on the ventral external surface, and the dorsal external surface with concentric lamellae and dimples, as clearly confirmed by both Waterhouse (1964) and Brunton (1966).

*Heteralosia* King, 1938 has been commonly compared with *Strophalosia*, due to their similarity in shell external morphology (e.g., absence of dorsal spines); most of the taxonomic studies retained *Heteralosia* as a separate genus on the basis of their stratigraphical separation (Brunton 1966) or of minor morphological differences (Clarke 1969, Cooper & Grant 1975, Archbold 1986, Waterhouse 2013), whereas Briggs (1998) regarded it as a junior synonym of *Strophalosia*. We here provisionally retain *Heteralosia* as a separate genus from *Strophalosia* in its smaller shell size (Brunton 1966) and the absence of dimples on the dorsal shell surface (Waterhouse 2013), and note that the generic identity of *Heteralosia* and its relationships with other strophalosiine genera need to be further investigated, together with the validity of *Fortispinalosia* Waterhouse, 2013 (see below).

Western Australian species regarded as *Strophalosia* by Archbold (1986, 1991) and Archbold & Shi (1993; e.g., *S. irwinensis* Coleman, 1957 and *S. jimbaensis* Archbold, 1986) were later separated from *Strophalosia* and re-assigned to *Coronalosia* Waterhouse & Gupta, 1978 by Archbold & Simanauskas (2001; see also Briggs 1998) because of their possession of ventral hinge spines.

*Strophalosia* was split into several additional genera (e.g., *Fortispinalosia*, *Fimbrianalosia*, *Crassispinosella*, *Strophalosiaria*, and *Baikuralia*) by Waterhouse (2013), based on their minor morphological differences from the type species of *Strophalosia*. However, the validity of these new genera requires further study as the morphological differences recognized by Waterhouse could be accommodated as different species rather than different genera. Without revealing their phylogenetic relationships, the split of these possibly closely related species into different genera seems to be premature. Furthermore, it is notable that some of the characters used for the discrimination of the new genera in

Waterhouse (2013; e.g., development of dorsal capillae) were not clearly defined in the type species of *Strophalosia*. In light of these considerations, we regard *Fimbrianalosia*, *Crassispinosella*, and *Strophalosiaria* as junior synonyms of *Strophalosia* and the validity of *Fortispinalosia* and *Baikuralia* as a matter requiring further examination.

**Strophalosia yalwalensis** Briggs, 1998
(Figs 4A–V, 5)

1998 *Strophalosia yalwalensis* Briggs, p. 70, fig. 37A–I.

### *Diagnosis*

Medium-sized, weakly concavoconvex shell with transversely subcircular outline; hinge line narrower than shell maximum width; teeth and sockets distinct. Ventral valve without sulcus, ornamented with prostrate and suberect spines. Dorsal valve with irregularly distributed, indistinct dimples and concentric wrinkles. Ventral interior marked with spine tubes (tunnels); ventral adductor field elevated, reaching one-third to half of ventral disc length. Dorsal interior with bilobed but medially fused cardinal process connecting to distinct median septum; adductor scars clearly impressed; brachial ridges weak to moderately raised; small pits developed around dorsal adductor scars; tiny tubercles or ridges scattered around anterior margin (modified from Briggs 1998).

### *Neotype*

The specimen of a ventral external mould (AM F.96219) was originally collected from Grassy Gully (locality UNE L928) by one of the authors (BR) and it was later loaned and nominated as the holotype by Briggs (1998). However, the holotype specimen has neither been returned to the University of New England nor deposited in the Australian Museum (P. Smith personal communication 2022). Therefore, we here designate a well-preserved topotype specimen (a dorsal internal mould, AM F.158966) from the original UNE collection (but not included in Briggs 1998) as the neotype (Fig. 4A, B).

### *Referred material*

Twenty registered specimens (except the neotype): three ventral external moulds (AM F.158947–158949), 13 ventral internal moulds (AM F.158950–158962), three dorsal external moulds (AM F.158963–158965), and a dorsal internal mould (AM F.158967). Several unregistered specimens: fragmentary external and internal moulds.

### *Locality, unit and age*

Grassy Gully (GRS158/159 =L928), Burragorang Valley (L1046), and Yalwal (Elyard Hill); lower part of the Snapper Point Formation (early Kungurian), southern Sydney Basin (see also Briggs 1998, p. 70).

### *Description*

Shell medium-sized, ranging 18–39 mm in width and 15–27.5 mm in length (average 26.548 mm and 20.833 mm, respectively) (Fig. 5), 34 mm wide and 27.5 mm long in neotype; outline transversely subcircular, with width/length ratio ranging 1.021–1.550 (average 1.274); hinge line always narrower than maximum shell width at mid-shell, ranging 0.551–0.857 (average 0.760) of maximum width; lateral profile weakly concavoconvex; ears small, unclearly defined; cardinal extremities rounded.

Ventral valve gently to moderately convex, ranging 4–14 mm in thickness (average 8.781 mm) (Fig. 5), maximum convexity point variable from umbo to anterior to mid-valve; ventral disc broadly developed, without sulcus; ventral interarea wide, relatively low (3.5 mm high), nearly flat, horizontally striated; teeth distinct, hanging on interarea and diverging anterodorsally (Fig. 4G); ventral external surface covered with spines crudely arranged along concentric lines; spines fine, ∼0.4 mm in base diameter and seven to ten bases per 25 $\text{mm}^2$ on mid-disc, circular in cross-section, becoming coarser anteriorly, composed of interspersed prostrate and suberect series (in orientation), undeveloped along hinge; possible cicatrix at ventral umbonal region (Fig. 4P).

Dorsal valve flat to weakly concave on disc, becoming more concave and forming trail at anterior part of valve (2–3 mm apart from anterior margin) (Fig. 4K, L); dorsal median fold indistinct and low, developing from disc margin; dorsal interarea low (< 2 mm high), flat, horizontally striated (Fig. 4K); dorsal external surface ornamented commonly with dimples and concentric wrinkles; dimples small, shallow, randomly distributed on dorsal disc; concentric wrinkles indistinct, irregularly spaced but more populated on anterior part of valve; fine, anteriorly directing, low ridges and tube-like structures rarely developed along concentric rows on anterior surface (Fig. 4T–V); capillae undetected.

Ventral interior marked by elongate spine tubes most commonly on lateral sides of ventral disc (Fig. 4G); adductor muscle field slightly elevated, having thin median septum, variably elongate but generally reaching one-third to half of ventral disc length; impression of concentric lamellae visible on anterior part of ventral interior (Fig. 4F).

Dorsal interior with distinct sockets beside cardinal process; cardinal process bilobate but medially fused, directing posteroventrally or ventrally, anteriorly connected to median septum; median septum distinct, blade-like, up to 1 mm high from floor, extending anteriorly and reaching around 0.6 of dorsal valve length without interruption at adductor scars; socket ridges laterally branching out from base of cardinal process; lateral ridges absent or very weakly developed as lateral extension of socket ridges; dorsal adductor scars circular to heart-shaped in each, strongly impressed; brachial ridges weakly raised, broadly semicircular, occupying more than half of dorsal valve length; tiny pits disposed around adductor scars laterally along posterior part of brachial ridges; small tubercles or ridges (endospines) developed around anterior margin (Fig. 4B).

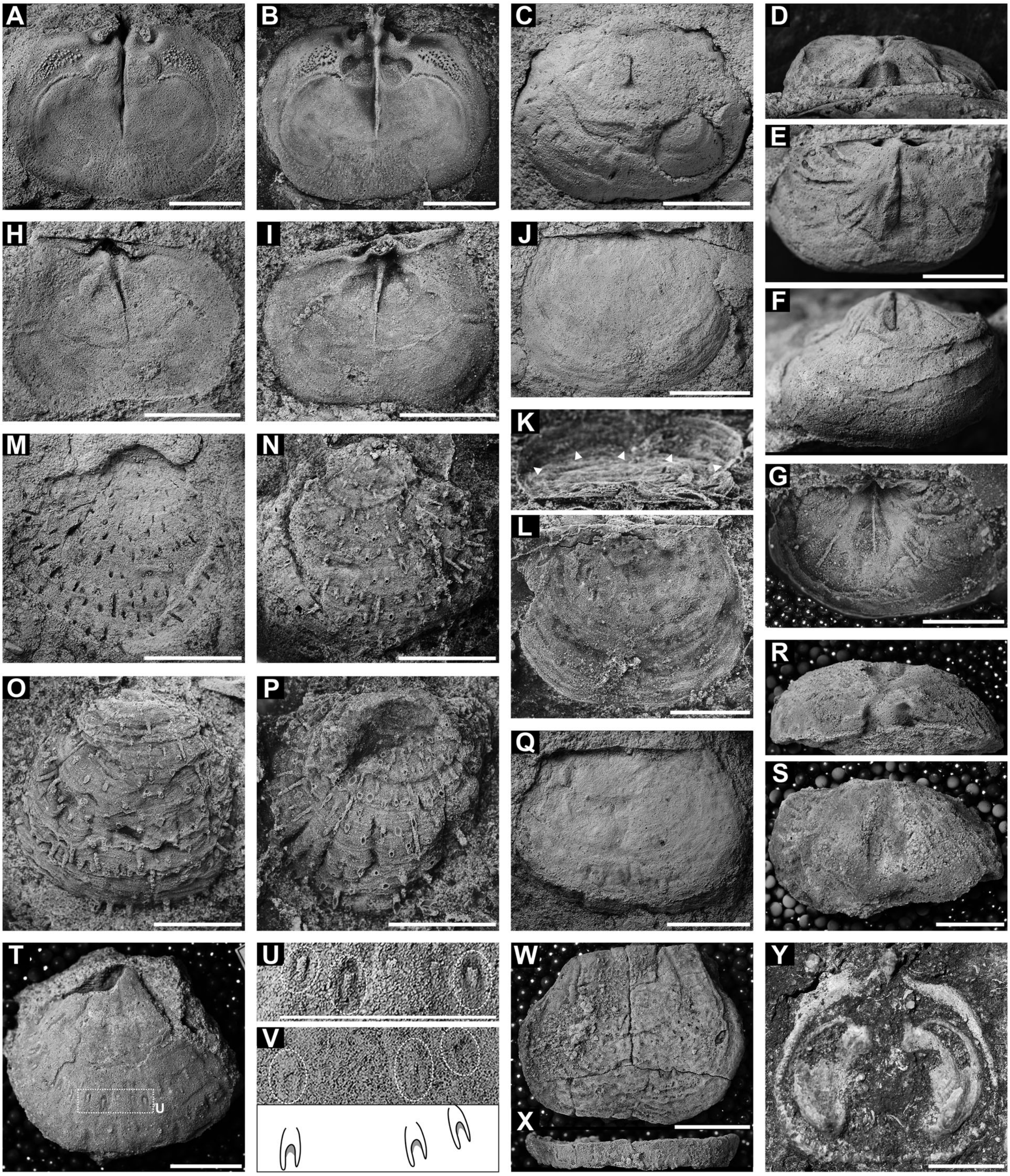

Figure 4. **A–V**, *Strophalosia yalwalensis* Briggs, 1998. **A, B**, a dorsal internal mould (AM F.158966, neotype) and its latex cast from L928; **C**, a ventral internal mould (AM F.158950) from GRS158; **D–G**, posterior, ventral and anteroventral views of a ventral internal mould (AM F.158951) and its latex cast from GRS159; **H, I**, a dorsal internal mould (AM F.158967) and its latex cast from GRS158; **J–L**, a dorsal external mould (AM F.158964) with posterior and dorsal views of its latex cast from GRS158, with white arrows indicating the boundary between the dorsal disc and trail (geniculation of dorsal exterior) on (K); **M, N**, a ventral external mould (AM F.158947)and its latex cast from GRS159; **O**, a latex cast of a ventral external mould (AM F.158948) from GRS158; **P**, a latex cast of a ventral external mould (AM F.158949) from GRS158; **Q**, a dorsal external mould (AM F.158963) from GRS158; **R, S**, posterior and ventral views of a ventral external mould (AM F.158952) from GRS159; **T**, a dorsal external mould (AM F.158965) from L928, with boxed area of (U); **U, V**, magnified view of boxed area in (T) and its latex cast, with white dashed ellipses indicating tube-like structures (possible dorsal spines or spine bases) and their schematic drawing. **W–Y**, *Wyndhamia* cf. *typica* (Booker, 1929). **W, X**, dorsal and anterior (dorsal-up) views of a weathered dorsal valve (AM F.158968) from GRS30; **Y**, a dorsal interior remains unregistered, preserved on rock platform (GRS42). All scales represent 10 mm.

## Remarks

These external/internal mould specimens with distinct toothed articulation are strongly matched with *Strophalosia yalwalensis* in most aspects. The representative morphological characteristics of the species, such as the two kinds of ventral spine orientation (prostrate or suberect), dorsal ornamentation composed of indistinct concentric wrinkles and dimples, elongate spine tubes on the ventral

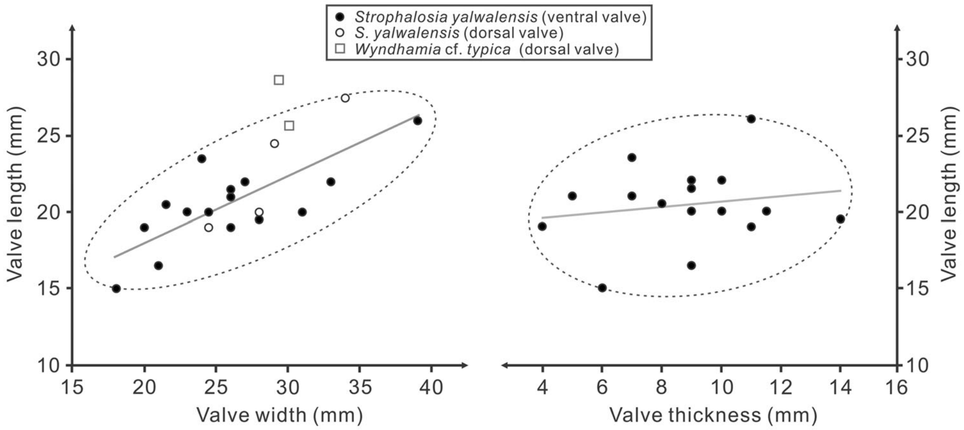

**Figure 5.** Shell measurements of two strophalosid species from the Snapper Point Formation: *Strophalosia yalwalensis* Briggs, 1998 and *Wyndhamia* cf. *typica* (Booker, 1929). The method of least squares is used for generating regression lines.

interior, and anterior extension of the dorsal median septum, are evidently identified in the specimens. This assignment is further supported by the fact that the specimens were also collected from the type locality of the species (Grassy Gully, UNE L928; see Briggs 1998). Despite the definite assignment to *S. yalwalensis*, we note that there are minor discrepancies about the morphology of the species between Briggs' (1998) description and our observation: (1) dimorphous nature of the ventral spines and (2) the development of small pits on the dorsal interior. Briggs (1998) differentiated the ventral spines of *S. yalwalensis* into two types, finer prostrate series (up to 0.4 mm in diameter) and coarser suberect series (up to 0.6 mm in diameter). However, the ventral spines in our specimens are mostly uniform in diameter size regardless of their orientation (either prostrate or suberect) if positioned on similar concentric rows in the valve (Fig. 4M–P; see also Briggs 1998, fig. 37A, B); a few prostrate spines appear to be preserved as much thinner forms in ventral external moulds, but they occupy only a very minor portion of the whole spines and can be a result of taphonomic effects. Also, the dorsal interiors in our specimens bear small but distinct pits around the adductor scars (Fig. 4A, B), which were neither described nor illustrated by Briggs (1998). These morphological differences may indicate some possible intraspecific variations or even taphonomic artefacts caused by preservational bias.

One of our dorsal external mould specimens exhibits rare fine, anteriorly directing, low ridges and tube-like structures along concentric rows on the anterior valve surface (Fig. 4T–V); they may be considered as possible traces of prostrate spines (or spine bases) of the dorsal valve. If these structures represent genuine dorsal spines (or spine bases), it would suggest that at least some individuals of *S. yalwalensis* might possess dorsal spines. If so, it would further indicate that some Permian strophalosiid taxa with dorsal spines (currently classified as dasyalosiines), such as *Echinalosia* Waterhouse, 1967 and *Wyndhamia* Booker, 1929, might have originated independently from strophalosiids that lacked dorsal spines (strophalosiines). Accepting this scenario, the current classification and phylogeny of strophalosiid genera would need to be reconsidered. It is noteworthy that Briggs (1998) also stated the possibility that some *Echinalosia* species (e.g., *Echinalosia mcclungi* Briggs, 1998) might be derived from *S. yalwalensis*.

Waterhouse (2013) placed *S. yalwalensis* in his new genus *Strophalosiaria* which was defined as having prostrate and suberect ventral spines, a wedge-shaped dorsal valve without an extended trail, and dorsal surface ornamentation composed of growth lamellae, dimples, and capillae. However, the morphology of *S. yalwalensis* is inconsistent with this diagnosis; both Briggs' (1998) description and our specimens demonstrate the presence of a geniculated trail on the external surface of the dorsal valve as well as the absence of dorsal capillae (although the possibility of this species possessing weak dorsal capillae cannot be completely ruled out).

As noted by Briggs (1998), *S. yalwalensis* share many features with *S. gerardi* from the Himalaya, including shell size, outline, and ornamentation as well as some key internal features. However, *S. gerardi* is distinguished by its large shell convexity. In addition, Brunton (1966) described that the dorsal median septum of *S. gerardi* is low and interrupted by adductor scars, in contrast with the high median septum in *S. yalwalensis* that clearly divides adductor scars (Fig. 4B). Waterhouse (2013) also stated that *S. gerardi* differs in having a longer trail, but one of our specimens appears to preserve an extended dorsal trail in *S. yalwalensis* (Fig. 4K, L).

Briggs (1998) originally reported *S. yalwalensis* from the Snapper Point Formation exposed at Grassy Gully (L928) and southwest of Burragorang Valley (L1046) (see Fig. 1C). However, none of his Burragorang specimens was illustrated. We have examined the remainder of the original UNE collection from these two localities, and we could only confirm *S. yalwalensis* from the Grassy Gully locality. Runnegar (1980) considered the *S. yalwalensis*-bearing horizon stratigraphically positioned near the base of the Snapper Point Formation, whereas Briggs (1998) regarded *S. yalwalensis* as a possible erosional remnant (recycled and redeposited from an older stratigraphic unit). This species has not been found in any other stratigraphic units including the underlying Pebbley Beach Formation (Shi *et al.* 2020) or, further below, the Wasp Head Formation (Cisterna & Shi 2014). Therefore, it is more likely that the restricted but locally abundant occurrence of *S. yalwalensis* in the lower part of the

Snapper Point Formation (early Kungurian) may suggest the occurrence of an endemic opportunistic species, probably occurring with the advent of the interglacial phase between P2 and P3 in the basin (Fig. 2).

Subfamily DASYALOSIINAE Brunton, 1966

### Remarks

Dasyalosiinae has been distinguished from Strophalosiinae, simply in the existence of spines on the dorsal valve (Brunton 1966, Brunton *et al.* 2000). However, as explained above, one of our *S. yalwalensis* specimens shows evidence of bearing dorsal spines (or spine bases) (Fig. 4T–V), raising the possibility that the acquisition of dorsal spines was likely to have happened in strophalosiine lineage multiple times. If it is true, the Dasyalosiinae could be a polyphyletic group.

Waterhouse (2001) subdivided the dasyalosiines into two subfamilies (Echinalosiinae and Dasyalosiinae), placing shells only with erect dorsal spines into the Echinalosiinae, and this was also followed in the classification of Strophalosiidina by Brunton (2007). However, this subdivision is not adopted here, because the development of dorsal spines and their phylogenetical significance within the strophalosiids need to be further investigated.

**Wyndhamia** Booker, 1929 (=Branxtonia Booker, 1929)

1929 *Wyndhamia* Booker, p. 24.
1929 *Branxtonia* Booker, p. 30.
1954 *Strophalosia*; Maxwell, p. 538.
1960 *Wyndhamia*; Muir-Wood & Cooper, p. 89.
1964 *Wyndhamia*; Waterhouse, p. 46.
1969 *Wyndhamia*; Clarke, p. 42.
1987 *Wyndhamia*; Archbold, p. 19.
1998 *Wyndhamia*; Briggs, p. 123.

### Type species

*Productus* (*Branxtonia*) *typica* Booker, 1929 [=*Strophalosia* (*Wyndhamia*) *dalwoodensis* Booker, 1929], from the Elderslie Formation (Kungurian) in Branxton, NSW, Australia.

Booker (1929) originally described three species, *Strophalosia* (*Wyndhamia*) *dalwoodensis*, *Strophalosia* (*Wyndhamia*) *valida*, and *Productus* (*Branxtonia*) *typica*, encompassing two new subgenera *Wyndhamia* and *Branxtonia*. However, all these three species were later revealed to be conspecific and subsequently synonymized as *Strophalosia typica* by Maxwell (1954). As explained by Briggs (1998, p. 123), the species name *typica* determined by Maxwell (1954) [as the First Reviser according to Article 24.2 in ICZN (1999)] should have precedence over *dalwoodensis*. On the other hand, since the (sub)genus *Branxtonia* was regarded as a junior synonym of *Wyndhamia* by Muir-Wood & Cooper (1960, p. 89), *Wyndhamia* has a priority as its genus name.

### Remarks

*Wyndhamia* (=*Branxtonia*) has been morphologically distinguished from *Strophalosia*, by its concentrically placed spine ridges, finer prostrate spines on the ventral valve (Muir-Wood & Cooper 1960), a wedge-shaped, anteriorly thickened dorsal valve (Waterhouse 1964), as well as the presence of dorsal spines. Additionally, Briggs (1998, p.125) also emphasized the development of coarse tubercles (pustules) on the anterior margin of the dorsal interior as a diagnostic character of *Wyndhamia*.

According to Briggs (1998, p. 125), *Echinalosia* resembles *Wyndhamia* in general morphological features but differs in its interspersed prostrate and erect ventral spines. On the other hand, Waterhouse (2001, p. 70) argued that *Wyndhamia* also bears prostrate and erect ventral spines, and thus suggested that the two genera are not distinguished by the presence/absence of erect spines but by their relative paucity. *Pseudostrophalosia* Clarke, 1970, possibly the closest genus to *Wyndhamia*, seems to be distinguished in having spines on the ears (Briggs 1998, Waterhouse 2001). Clarke (1970) originally attributed the occurrence of dendritic posterior ventral adductor scars as a key diagnostic character of *Pseudostrophalosia* but this feature has since been regarded as variable and insignificant (Waterhouse 1982, Archbold 1987).

**Wyndhamia** cf. **typica** (Booker, 1929)
(Figs 4W–Y, 5)

### Referred material

Two specimens: a dorsal valve (AM F.158968) and a dorsal interior preserved on rock platform (unregistered).

### Locality, unit and age

Snapper Point (GRS30) and south of Singing Stones Beach (GRS42); Snapper Point Formation (early Kungurian), southern Sydney Basin.

### Description

Dorsal valve subquadrate in outline, equidimensional to slightly transverse (29.6–30.2 mm wide and 26–28.8 mm length with width/length ratio of 1.028–1.162; see Fig. 5), with maximum width at anterior to mid-valve, wedge-shaped in three-dimensional view, thickened anteriorly (1.8 mm thick at posterior area and 4.2 mm thick at anterior margin) (Fig. 4X), very gently concave and nearly flat externally; hinge narrower than maximum width (0.757 in ratio); dorsal external surface ornamented with anteriorly populated concentric wrinkles and dimples; spines not observed.

Dorsal interior surrounded by low but distinct marginal ridge with relatively coarse tubercles; sockets small but distinct, laterally open; cardinal process high, ventrally directing; median septum indistinctly developed, anteriorly reaching around 0.6 of dorsal disc length; dorsal adductor scars obscure; brachial ridges distinct, moderately raised, broadly semicircular, occupying more than half of dorsal disc length.

### *Remarks*

In spite of the weathered condition, these two dorsal specimens look very similar to *Wyndhamia typica* (Booker, 1929) originally from the Elderslie Formation in Branxton, NSW, particularly in a wedge-shaped dorsal valve with dimples on the external surface and coarse tubercles on the marginal ridge of the interior. One of the two specimens (AM F.158968) appears to have lost its ears and dorsal spines and to have a narrow hinge relative to its width at mid-valve (Fig. 4W), presumably due to poor preservation, just like the lectotype of *W. typica* from Branxton, NSW (Booker 1929, pl. 3, figs 1–3; illustrated also by Maxwell 1954, pl. 55, figs 9, 10; Muir-Wood & Cooper 1960, pl. 5, figs 11–13). Characteristically, this dorsal valve exhibits the thickened wedge-shape around the geniculation margin, a feature typical of *Wyndhamia* (=*Branxtonia*) (Waterhouse 1964). The other specimen of the dorsal interior (still buried in a rock platform in the south of Singing Stones Beach) clearly exhibits a stout cardinal process, distinct and moderately raised brachial ridges, and numerous coarse tubercles developed along the marginal ridge (from anterior to lateral sides) that correspond well with the morphology of a dorsal internal mould from "Egans Hill, Conjola" illustrated by Briggs (1998, fig. 64D), as well as with features of the lectotype (Maxwell 1954). Despite these similarities, we consider it premature to simply assign the specimens to *W. typica*, without the discovery of dorsal spines and of any ventral features. Therefore, this species is here regarded as an open nomenclature taxon but comparable with *W. typica*.

The dorsal valves of *Wyndhamia* cf. *typica* resemble those of *S. yalwalensis* from Grassy Gully not only in the general size and narrow hinge, but also in the dimples and concentric wrinkles ornamenting the dorsal external surface. But *S. yalwalensis* is generally more transverse in outline (Fig. 5) and has a longer dorsal trail (Fig. 4K, L). In addition, although *S. yalwalensis* bears numerous tubercles on the anterior part of the dorsal disc (Fig. 4A, B), they are clearly distinguished from the swollen tubercles developed along the marginal ridge of *W.* cf. *typica* (Fig. 4Y). The morphological similarities between the two species may suggest that *W. typica* was evolved from *S. yalwalensis*, especially in consideration of the possible traces of the dorsal spines in the latter. However, there is a notable difference between their dorsal spines: the prostrate dorsal spines appear to be possibly present in some specimens of *S. yalwalensis* (Fig. 4T–V), whereas *Wyndhamia* has been known to have only (sub)erect dorsal spines (Waterhouse 2001).

Class RHYNCHONELLATA Williams *et al.*, 1996
Order SPIRIFERIDA Waagen, 1883
Suborder SPIRIFERIDINA Waagen, 1883
Superfamily MARTINIOIDEA Waagen, 1883
Family INGELARELLIDAE Campbell, 1959

### *Diagnosis*

As the diagnosis by Archbold & Thomas (1986, p. 582).

### *Remarks*

Family Ingelarellidae is one of the most diversified brachiopod groups in the Permian of eastern Gondwana, particularly well preserved in eastern Australia and New Zealand. Since Campbell (1959, 1960, 1961) shed light on the identity of '*Martiniopsis*-like' brachiopods from the Permian of Queensland (all then assigned either to *Ingelarella* Campbell, 1959 or to *Notospirifer* Harrington, 1955) with the erection of a new subfamily Ingelarellinae, substantial studies on this group have followed (e.g., Waterhouse 1968, 1998, 2015, 2016, Armstrong 1970b, Runnegar & McClung 1975, McClung 1978, Archbold & Thomas 1986, Clarke 1987, 1992). This group, mainly defined by their commonality in shell micro-ornamentation with surface grooves arranged in quincunx (Fig. 6M–Q), originally included only three genera (*Ingelarella*, *Martiniopsis* Waagen, 1883, and *Notospirifer*) in Campbell (1959). However, numerous forms and morphological variations have been noted by subsequent taxonomic studies. According to Waterhouse (2016), more than 20 genera representing two different superfamilies (Ingelarelloidea Campbell, 1959 and Gerkispiroidea Carter, 1985) have been suggested for this group. Although some of the genera in Waterhouse (2016) need to be further examined to confirm their morphological distinctness, the majority of them seem to sufficiently hold their own morphological identities as valid genera. In order to demonstrate the morphological variations of the Permian ingelarellids and also to introduce brief criteria for their classification, we herein have attempted to provide our understanding of the characteristics and distinctions for 12 common eastern Australian Permian ingelarellid genera based on a careful review of literature as well as a detailed examination of some new material. The features highlighted in the illustrations (Fig. 6A–L) and in the complementary table (Table 2) are largely consistent with the descriptions given to these 12 genera by Waterhouse (1998, 2015, 2016).

The supra-generic classification of the ingelarellid taxa has also been controversial. Archbold & Thomas (1986) erected the family Ingelarellidae in which they included two subfamilies (Ingelarellinae and Notospiriferinae). Clarke (1992) proposed another subfamily (Glendoniinae) and added it to the Ingelarellidae. Waterhouse (1998) raised the Ingelarellidae to superfamily status (Ingelarelloidea), significantly revising the whole group with the suggestion of numerous new taxa.

In spite of the continuous studies on the ingelarellids, their origin and phylogeny remain poorly understood. The Ingelarellidae was commonly classified together with the Martiniidae, due to some common features shared (e.g., a generally oval outline, subdued lateral plications, and the existence of surface pits) (see Ivanova 1959, 1972, Pitrat 1965, Waterhouse 1971, Carter *et al.* 2006). However, the micro-ornamentation of the Martiniidae is poorly known (Waterhouse 1971, Carter 1974), hampering a clear understanding of its relationship and possible distinction from the Ingelarellidae or the Reticularioidea as noted by Sarycheva *et al.* (1963), Waterhouse (1971, 1978) and Grant (1976). Archbold & Thomas (1986) also emphasized the difficulty in

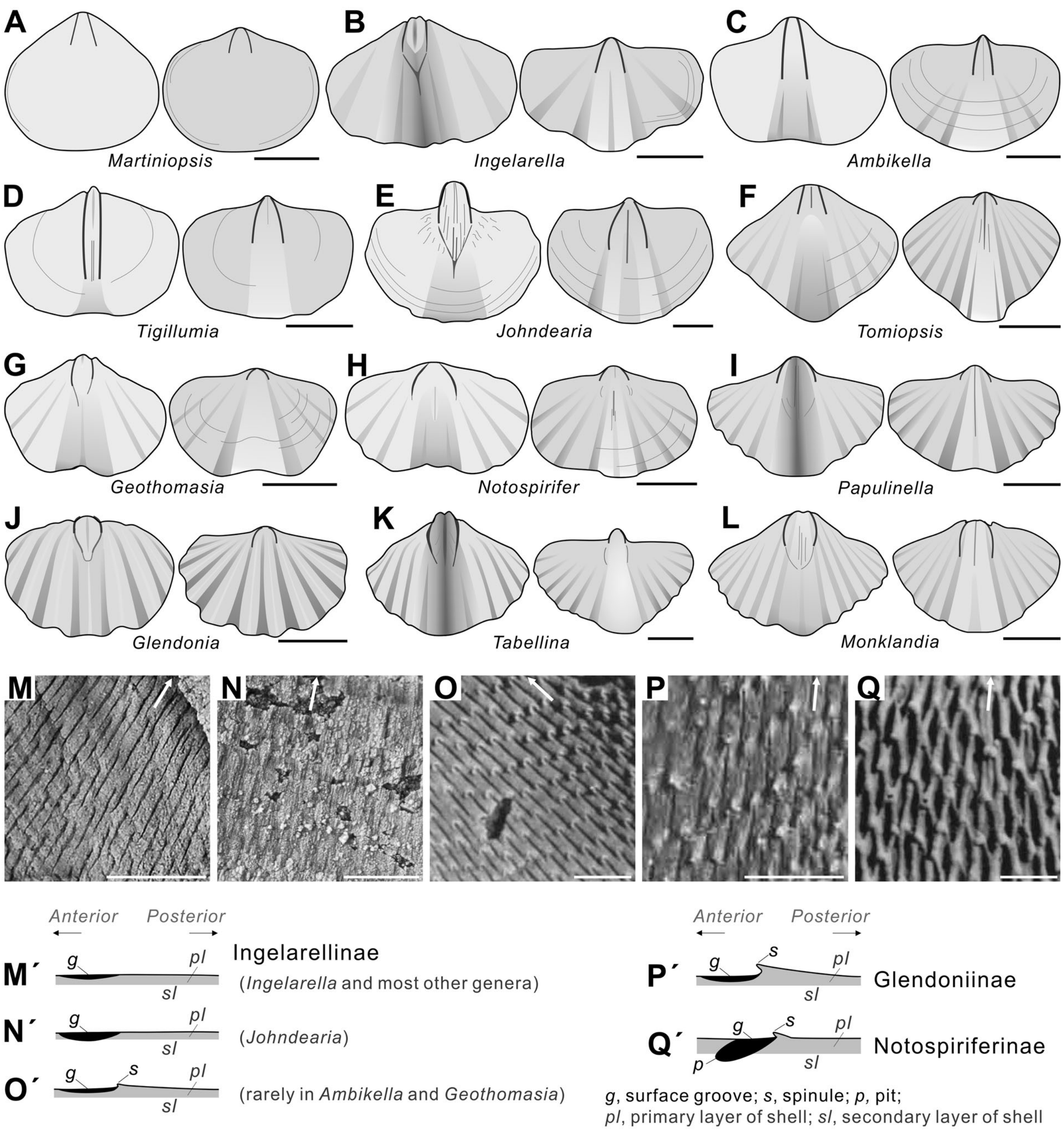

**Figure 6.** **A–L**, Schematic drawings of ingelarellid brachiopod genera in preservation as internal moulds (left, ventral valve; right, dorsal valve). These drawings are based on a representative specimen(s) selected for each genus. **A**, *Martiniopsis inflata* Waagen, 1883, fig. 7a, b for *Martiniopsis* Waagen, 1883; **B**, *Ingelarella* sp. in Waterhouse (2015, fig. 102B, C) for *Ingelarella* Campbell, 1959; **C**, *Ambikella ovulum* (Waterhouse, 1971, pl. 15, fig. 5; pl. 16, fig. 16) for *Ambikella* Sahni & Srivastava, 1956; **D**, *Tigillumia parallela* (Waterhouse, 1964) figured in Waterhouse (1968, pl. 13, figs 3, 6) for *Tigillumia* Waterhouse, 1998; **E**, *Johndearia isbelli* (Campbell, 1961, pl. 25, fig. 2a, b) for *Johndearia* Waterhouse, 1998; **F**, *Tomiopsis kumpani* (Yanishevsky, 1935) figured in Sokolskaya (1959) and again in Carter *et al.* (2006, fig. 1158.3a, b) for *Tomiopsis* Benediktova, 1956; **G**, *Geothomasia branxtonensis* (Etheridge, 1919) figured in Waterhouse (2015, fig. 113A, B) for *Geothomasia* Waterhouse, 1998; **H**, *Notospirifer gentilis* Waterhouse, 1983 figured in Shi *et al.* (2020, fig. 6E, L) for *Notospirifer* Harrington, 1955; **I**, *Papulinella hillae* (Campbell, 1961, pl. 27, figs 1a, 11b) for *Papulinella* Waterhouse, 1998; **J**, *Glendonia ulladullensis* McClung & Armstrong, 1978, pl. 1, figs 2, 3 for *Glendonia* McClung & Armstrong, 1978; **K**, *Tabellina denmeandi* (Campbell, 1961, pl. 23, fig. 7a, b) for *Tabellina* Waterhouse, 1986b; **L**, *Monklandia gympiensis* Waterhouse, 1998 figured in McClung (1978, pl. 3, figs 22, 23) for *Monklandia* Waterhouse, 1998. Scales for (A–L) represent 20 mm. More detailed morphological characters of the selected ingelarellid genera are also summarized in Table 2. **M–Q, M′–Q′**, Variation in micro-ornamentations on shell surfaces of the ingelarellids, with their sectional views. **M, M′**, shallow grooves without spinules in most taxa of the Ingelarellinae, represented by *Ingelarella atlanicha* (Kotljar in Licharew & Kotljar, 1978) figured in Shi *et al.* (2022b, fig. 5M); **N, N′**, relatively deep (reaching the fibrous secondary layer of shell) grooves without spinules in some species of *Johndearia*, represented by *Johndearia brevis* (McClung & Armstrong, 1975) figured in this study (shell internal surface with micro-ornamentation traces; see also Fig. 9E–H); **O, O′**, shallow grooves with low spinules in a few species of *Ambikella* and *Geothomasia*, represented by *Geothomasia profunda* (Campbell, 1961) figured in Armstrong (1970b, fig. 1I); **P, P′**, shallow grooves with high spinules in the Glendoniinae, represented by *Glendonia ulladullensis* McClung & Armstrong, 1978, pl. 1, fig. 22; **Q, Q′**, deep grooves (forming globose pits in the secondary layer of shell) with small spinules in the Notospiriferinae, represented by *Papulinella hillae* (Campbell, 1961) figured in Armstrong (1970b, fig. 1H). Scales 1 mm and white arrows for posterior direction in M–Q. The sectional drawings are based on Waterhouse (1967), Armstrong (1970b), and Clarke (1992). The images of O–Q are reproduced with permission.

**Table 2.** Morphological characteristics of Permian ingelarellid genera in eastern Australia.

| | | | | | | | | Micro-ornamentation (see also Fig. 6M–Q, M′–Q′) | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Ingelarellid genera | Shell size and outline | Sulcus | Fold | Ventral adminicula | Dorsal adminicula (tabellae) | Ventral median septum (tigillum) | Macro-ornamentation (plication) | Grooves arranged in quincunx | Pits (on secondary layer of shell) | C-shaped spinules |
| *Martiniopsis* Waagen, 1883 (Fig. 6A) | Small to medium, subovate | Weakly developed or absent | Insignificant or absent | Moderately long, thin, close-set, subparallel | Moderately long | Absent | No plica | Shallow, very narrow, elongate, with wider interspaces | Not developed | Absent |
| *Ingelarella* Campbell, 1959 (Fig. 6B) | Medium to large, transversely ovate | Well developed, broad, with subplicae or smooth | Relatively low, with shallow and broad groove on crest | Long, moderately spaced | Moderately long | Present | Weakly to moderately plicate on lateral slopes | Shallow, very narrow, elongate, with wider interspaces | Not developed | Absent |
| *Ambikella* Sahni & Srivastava, 1956 (syn. *Homevalaria* Waterhouse, 1986a; Fig. 6C) | Medium, transversely ovate | Well developed, with subplicae or smooth | Well developed, no median groove on crest | Moderate to long, moderately spaced, divergent | Shot and diverging or moderately long and subparallel | Absent | Weakly to moderately plicate on lateral slopes | Shallow, very narrow, elongate, sparsely spaced | Not developed | Mostly absent, but rarely with low spinules |
| *Tigillumia* Waterhouse, 1998 (Fig. 6D) | Small, transversely ovate | Weakly developed or absent, narrow | Weakly developed, having round crest | Long, close-set, subparallel | Long | Strongly developed | No plica | Shallow, very narrow, elongate, with wider interspaces | Not developed | Absent |
| *Johndearia* Waterhouse, 1998 (Fig. 6E) | Large, transversely ovate, posteriorly strongly thickened | Relatively broad, shallow, with smooth or subplicae | Low, round or with weak median groove on crest | Moderately long and spaced, subparallel | Moderately long and spaced | Absent | Smooth to weakly plicate on lateral slopes | Deep (reaching secondary layer of shell), narrow, elongate, closely spaced | Not developed | Absent |
| *Tomiopsis* Benediktova, 1956 (Fig. 6F) | Small to medium, transversely rounded | Moderately developed, with subplicae | Relatively low, with multiple subplicae on fold | Moderately long | Short, widely divergent | Absent | With low numerous plicae on lateral slopes | Relatively deep, narrow, strongly elongate, closely spaced | Not developed | Absent |
| *Geothomasia* Waterhouse, 1998 (Fig. 6G) | Small to medium, transversely ovate | Well developed, smooth or with subplicae | Round, low, generally smooth | Moderately long, close-set, subparallel | Short, widely divergent | Absent | Weakly plicate on lateral slopes | Shallow, narrow, elongate, closely spaced | Not developed | Mostly absent |
| *Notospirifer* Harrington, 1955 (Fig. 6H) | Small to medium, transversely subovate | Well developed, generally having subplicae | With weak median groove on crest or smooth | Moderately developed, divergent | Very short or absent | Absent | Weakly to moderately plicate on lateral slopes | Deep, relatively wide, shortly elongate, surrounded by narrow ridges | Developed | Small, knob-like |
| *Papulinella* Waterhouse, 1998 (Fig. 6I) | Medium to large, transversely subovate | Well developed, smooth | Mostly with median groove on crest | Moderately developed, divergent | Very short or absent | Absent | Moderately plicate on lateral slopes | Deep, relatively wide, shortly elongate, surrounded by narrow ridges | Developed | Small, knob-like |
| *Glendonia* McClung & Amstrong, 1978 (Fig. 6J) | Small to medium, transversely subovate to subrhomboidal | Narrow, with a single strong subplica | Consisting of two fold plicae | Moderately developed | Short to moderately long | Absent | With a few strong subangular plicae on lateral slopes | Relatively deep, narrow, strongly elongate | Not developed | High, robust |
| *Tabellina* Waterhouse, 1986b (Fig. 6K) | Medium to large, transversely subpentagonal | Broad, moderately developed, with subplicae | Round, relatively high, with rounded crest | Well developed, moderate to long | Very short or absent | Absent | With a few strong plicae on lateral slopes | Narrow, shortly elongate | Not developed | Thick, relatively low |
| *Monklandia* Waterhouse, 1998 (Fig. 6L) | Medium to large, slightly transverse | Broad, shallow, with two subplicae | Low nearly flat, having weak median groove on rest | Moderately long | Relatively long | Absent | Moderately to strongly plicate on later slopes | Relatively deep, narrow, shortly elongate | Not developed | Thin |

recognizing the superfamilial status for the Ingellarellidae and referred to the superfamily status of this group as being uncertain. Waterhouse (1998) elevated the ingelarellids to Ingelarelloidea and place the superfamily in the suborder Delthyridina, emphasizing similarities in internal plates. However, the fimbriate and pustulose micro-ornaments in Delthyridina clearly differ from the micro-ornamentation of the ingellarellids. In this study, recognizing more studies are required about the micro-ornamentations and their phylogenetic significance of the ingelarellids and other morphologically similar groups (e.g., martiniids and reticulariids), we provisionally place the Ingelarellidae into the Martinioidea, simply following Carter *et al.* (2006) which emphasized the similarity in overall morphology.

Subfamily INGELARELLINAE Campbell, 1959

### *Diagnosis*

Ingelarellidae with variable size; sulcus and fold variably developed, smooth or weakly plicate; lateral slopes with a few plicae or smooth; micro-ornamentation composed of shallow, elongate surface grooves arranged in quincunx, but generally without forming pits and spinules; ventral adminicula moderate to long; dorsal adminicula (tabellae) short to long; ventral median septum (tigillum) developed in a few genera (amended from Archbold & Thomas 1986, p. 584).

### *Remarks*

This subfamily is generally distinguished from other subfamilies of the Ingelarellidae by its micro-ornamentation composed only of shallow, elongate surface grooves without the formation of pits in the secondary layer of the shell and the development of c-shaped spinules at the posterior end of the grooves (see Fig. 6M–O, M′–O′; Table 2). As demonstrated in Campbell (1961) and Armstrong (1970b), a few species which were originally assigned to *Ingelarella* have small c-shaped spinules (protuberances) at the posterior tip of the surface grooves. Based on these observations, Archbold & Thomas (1986) considered the c-shaped spinules as a diagnostic character of *Ingelarella*, to distinguish it from another ingelarelline genus *Tomiopsis* Benediktova, 1956, which lacks such c-shaped spinules. However, Waterhouse (1986a, 1987) argued that the type species of *Ingelarella*, *I. angulata* Campbell, 1959, did not bear such spinules on the shell, through the examination of the topotype specimens. It was then concluded that the ingelarelline genera including *Martiniopsis*, *Ambikella* Sahni & Srivastava, 1956, *Tomiopsis*, and *Ingelarella* have all similar micro-ornamentation that do not bear the small c-shaped spinules (Waterhouse 1998).

Based on this conclusion, Waterhouse (1998) synonymized three genera (*Ingelarella*, *Ambikella*, and *Tomiopsis*), but considered that they still could remain as different subgenera within *Tomiopsis*. As explained in Waterhouse (1998, 2015, 2016), these (sub)genera are distinguishable in other morphological features (e.g., length of internal plates, characters of lateral plication, development of median furrow on the dorsal fold) (see also Fig. 6; Table 2). Using the external and internal features (instead of the micro-ornamentation), the present study includes the following genera in the subfamily: *Martiniopsis*, *Ingelarella*, *Ambikella*, *Tomiopsis*, *Tigillumia* Waterhouse, 1998, *Johndearia* Waterhouse, 1998, and *Geothomasia* Waterhouse, 1998 [several more genera were also included in the Ingelarellinae by Waterhouse (2015, 2016), but their generic distinctness needs to be further examined and validated].

**Ingelarella** Campbell, 1959

### *Type species*

*Ingelarella angulata* Campbell, 1959, p. 341 from the Ingelara Formation (Middle to Late Permian) in Dry Creek, Queensland, Australia.

### *Diagnosis*

Medium-sized, transverse shells generally with a few plicae; sulcus relatively broad and distinct; fold slightly elevated, with shallow, broad median furrow; lateral plications generally low and broad; micro-ornamentation ornamented by shallow, narrow, elongate grooves in quincunx, without spinules and pits; both ventral and dorsal adminicula relatively long; ventral median septum (tigilium) generally present.

### *Remarks*

This genus was originally proposed for the '*Martiniopsis*-like' (but generally with plicate shells) brachiopods from the Permian of eastern Australia by Campbell (1959). However, the identity of the genus was challenged, because some genera with similar morphologies (particularly, micro-ornament of elongate grooves arranged in quincunx and plicate lateral slopes), such as *Tomiopsis* from Russia, and *Ambikella* from India, had been suggested earlier. Archbold & Thomas (1986) supposed that these genera would be different from each other in the details of the micro-ornamentation, but this assertion was not supported by Waterhouse (1998), who after examining the topotype materials concluded that these three genera (*Ingelarella*, *Tomiopsis* and *Ingelarella*) have similar micro-ornamentation that do not bear the small c-shaped spinules.

Nevertheless, there seem to be substantial morphological differences between these three genera, as explained by Waterhouse (1998, 2015, 2016). Although *Ambikella* might be the closest genus to *Ingelarella*, the former differs in the absence of a median furrow on the dorsal fold (see Fig. 6C; Table 2). Also, a few species of *Ambikella* (including *Homevalaria* Waterhouse, 1986a later synonymized with *Ambikella*) bear low c-shaped spinules on their shell surface. The genus has been known generally from older strata than *Ingelarella* reported from Artinskian and younger rocks (Waterhouse & Shi 2010). *Tomiopsis* would be the oldest among the three genera, in consideration of its type species, *T. kumpani* (Yanishevsky, 1935), from the Lower Carboniferous of the Kuznets Basin. Based on the morphology of the type species, *Tomiopsis* is distinguished from *Ingelarella* by finer and more numerous plications and a distinct median septum on the dorsal floor (see Fig. 6F; Table 2). In addition,

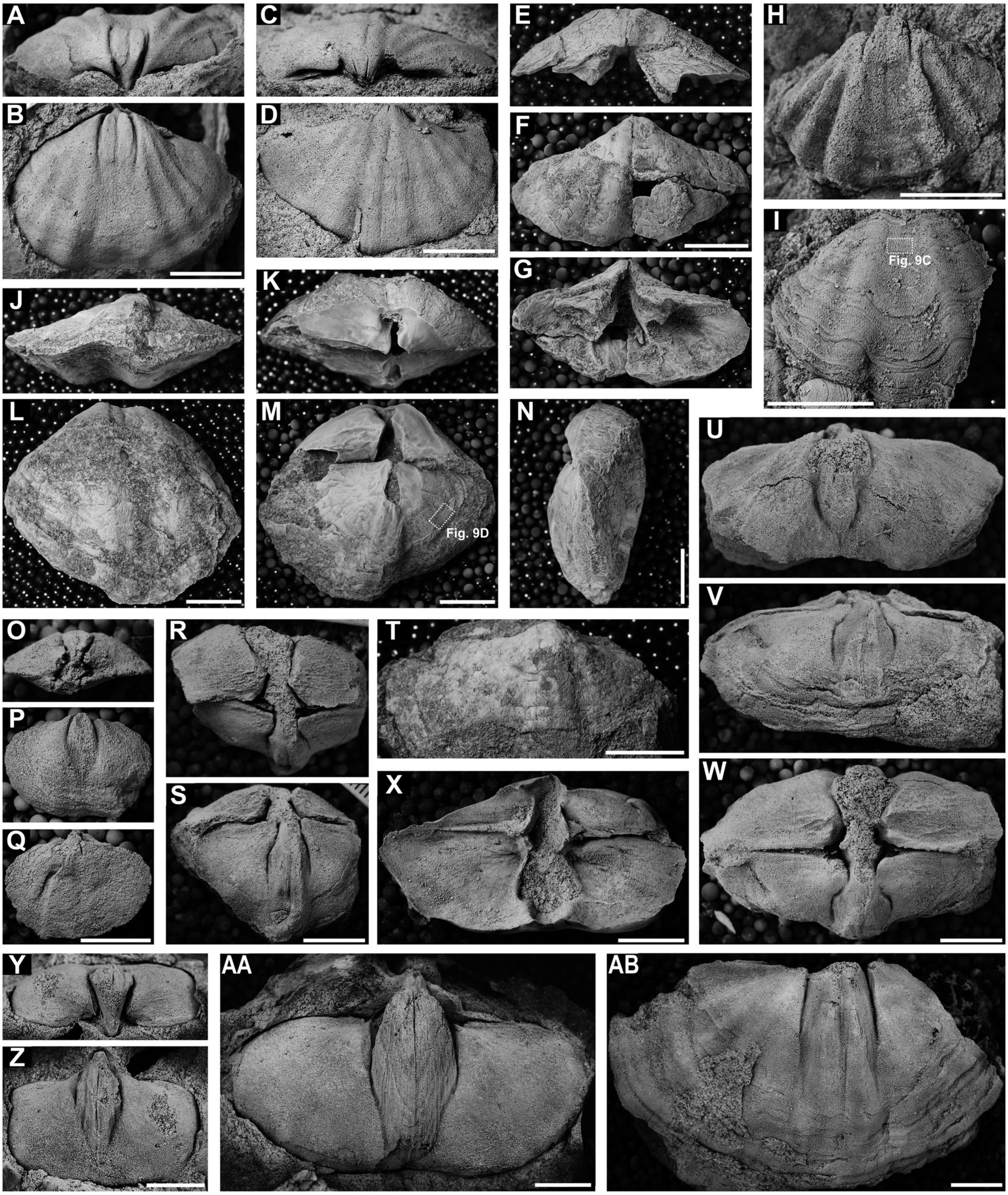

**Figure 7.** **A–N**, *Ingelarella* sp. **A, B**, posterior and ventral views of a ventral internal mould (AM F.158973) from L928; **C, D**, posterior and dorsal views of a dorsal internal mould (AM F.158976) from L928; **E–G**, posterior, ventral and dorsal views of an incomplete ventral valve (AM F.158970) from GRS30; **H**, a ventral internal mould (AM F.158974) from GRS158; **I**, a latex cast of a ventral external mould (AM F.158972) from L1046, with boxed area of Fig. 9C; **J–N**, anterior, posterior, ventral, dorsal and lateral views of a conjoined shell (AM F.158969) from GRS42, with boxed area of Fig. 9D in M. **O–AB**, *Johndearia brevis* (McClung & Armstrong, 1975). **O–Q**, posterior, ventral and dorsal views of an internal mould of a conjoined shell (AM F.158983) from L877; **R, S**, posterior and dorsal views of an internal mould of a conjoined shell (AM F.158984) from L877; **T**, a dorsal valve (CPC44471) from JB65; **U–X**, ventral, dorsal and posterior views of an internal mould of a conjoined shell (AM F.158985) and its latex cast (ventral up) from L877; **Y, Z**, posterior and ventral views of an internal mould of a ventral valve (AM F.158993) from L877; **AA**, a ventral internal mould (AM F.158994) from L877; **AB**, a dorsal internal mould (AM F.159000) from L877. All scales represent 10 mm.

*Tomiopsis* has been considered to have evolved through a different stock from those of *Ingelarella* and *Ambikella* (see Waterhouse 2015, fig. 6).

Campbell (1959, 1960, 1961) and McClung (1978) assigned all of the ingelarelline species from the Permian of eastern Australia (mainly of the Bowen Basin and Sydney Basin) to *Ingelarella*. These species have since been re-assigned to several genera (e.g., *Ambikella*, *Johndearia*, as well as *Ingelarella*) by Waterhouse (1998, 2015) following his significant review and revision of the ingelarellids.

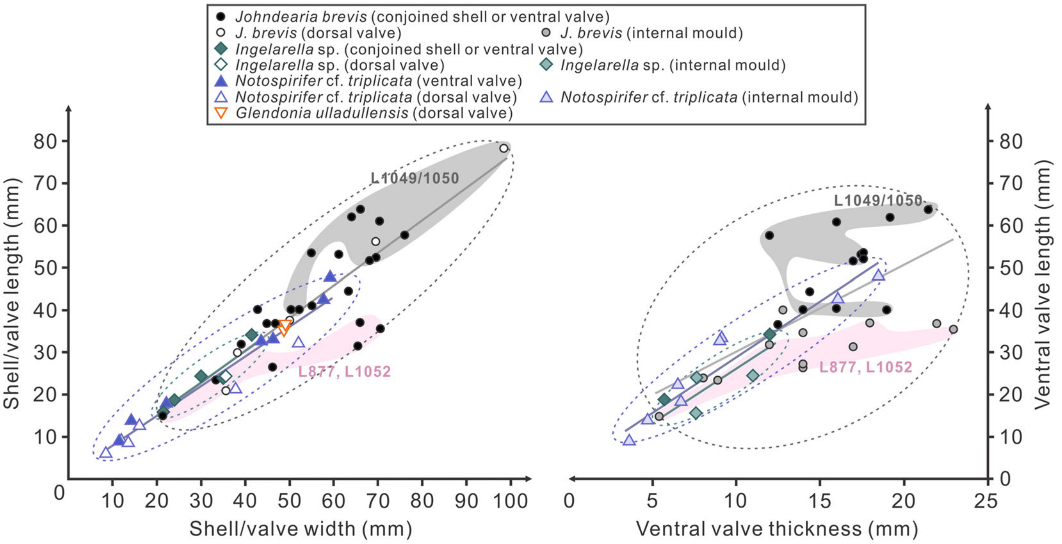

**Figure 8.** Shell measurements of four Ingelarellid species from the Snapper Point Formation: *Ingelarella* sp., *Johndearia brevis* (McClung & Armstrong, 1975), *Notospirifer* cf. *triplicata* Waterhouse, 2015 and *Glendonia ulladullensis* McClung & Armstrong, 1978. Shell thickness is measured only for ventral valves and internal moulds are distinguished from specimens with shell materials in the thickness measures (right graph). Shells of *J. brevis* collected from L1049/1050 localities (grey shade) appear to have a larger size and more equidimensional outline, whereas specimens from L877 and L1052 localities (pink shade) show a more transverse form. The method of least squares is used for generating regression lines.

## **Ingelarella** sp.
(Figs 7A–N, 8, 9A–D)

### *Referred material*

Eight registered specimens: a conjoined shell (AM F.158969), two ventral valves (AM F.158970, 158971), a ventral external mould (AM F.158972), three ventral internal moulds (AM F.158973–158975), and a dorsal internal mould (AM F.158976). Two unregistered specimens: fragmentary ventral valves from GRS42.

### *Locality, unit and age*

Snapper Point (GRS30), south of Singing Stones Beach (GRS42), Grassy Gully (GRS158/159 =L928), and Burragorang Valley (L1046); Snapper Point Formation (early Kungurian), southern Sydney Basin.

### *Description*

Shell medium-sized, ranging 21.7–41.4 mm wide (average 31 mm), 16.5–34.2 mm long (average 21.717 mm) (Fig. 8); outline subcircular, weakly transverse, with width/length ratio of 1.211–1.458 (average 1.297); lateral to anterior margins very rounded; hinge line consistently narrower than maximum shell width at slightly anterior to hinge, ranging 0.833–0.983 (average 0.873) of maximum width; ventribiconvex in lateral profile; cardinal extremities rounded.

Ventral valve moderately convex, with maximum convexity at umbonal region; ventral beak moderately incurved; ventral interarea moderately high, slightly concave to flat; delthyrium open, triangular, with delthyrial angle of 30–45°; sulcus well-formed, with angle of 30°, relatively shallow but deepening near anterior margin; lateral slopes ornamented by three pairs of low broad plicae in general, but sometimes more angular (Fig. 7H) or much weaker (Fig. 7L).

Dorsal valve weakly convex; dorsal interarea indistinct; fold distinct, weakly to moderately elevated, with broadly rounded crest medially incised by weak furrow; dorsal lateral slopes also with three pairs weak plicae.

Shell external surface macro-ornamented with concentric growth lamellae irregularly distributed on anterior part (Fig. 7I) and micro-ornamented by surface grooves; grooves shallow, narrow, elongate, arranged in quincunx, generally spaced, numbering generally seven or eight per 1 mm width at mid-shell (Fig. 9A–D).

Dental plates high, well-formed (Fig. 7G); ventral adminicula relatively closely spaced, moderately long, extending near to one-third of valve floor, surrounding ventral muscle field; muscle field strongly elongate oval, distinctly marked, medially divided by low ridge (Fig. 7B); ventral medium septum (tigillum) absent.

Dorsal interior poorly defined; dorsal adminicula closely spaced, short to moderately long; dorsal muscle field indistinct.

### *Remarks*

These medium-sized shells are sufficiently assignable to *Ingelarella*, even though they do not seem to show a ventral medium septum (tigillum) anterior to the muscle field. Like typical *Ingelarella*, they have three pairs of broad plicae on the lateral slopes, a distinctly developed sulcus, a median furrow on the dorsal fold, and anteriorly extended ventral adminicula. Their micro-ornamentation is also well-matched in the development of the shallow, narrow, elongate grooves arranged in quincunx (Fig. 9A–D). Nevertheless, this species is not coincident with any of the known *Ingelarella* species from the Permian of eastern Australia. Both the type species *I. angulata* and *I. plica* Campbell, 1961 are similar in the general shell size and lateral plications, but they have a much deeper and anteriorly wider sulcus and more

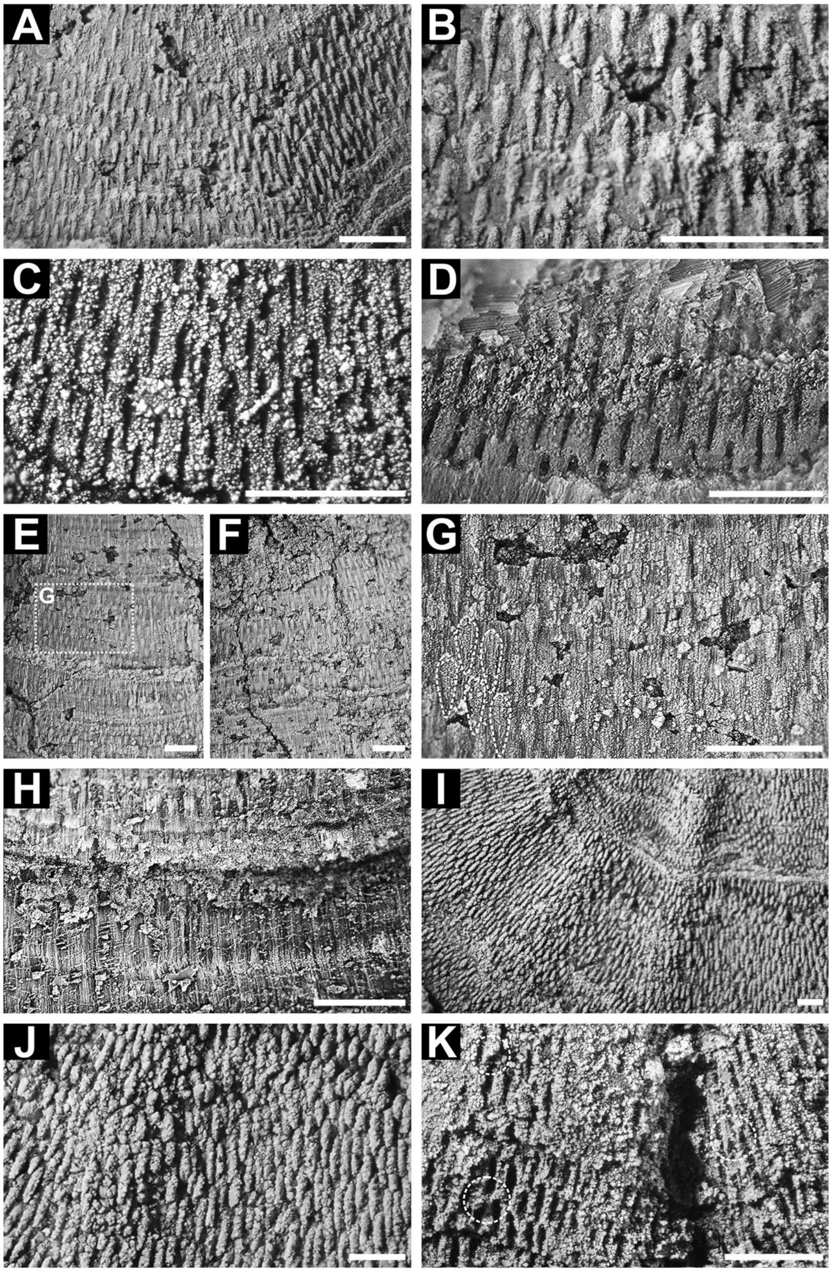

**Figure 9.** Shell micro-ornamentation of ingelarellid brachiopod species. **A–D**, *Ingelarella* sp. **A–C**, shell ornamentation traces remaining on a ventral external mould (AM F.158972) (A, B) and its latex cast showing an enlarged view of boxed area in Fig. 7I (C); **D**, elongate grooves on shell external surface (AM F.158969), magnification of boxed area of Fig. 7M. **E–H**, *Johndearia brevis* (McClung & Armstrong, 1975). **E, F**, shell internal surface bearing shell ornamentation traces (CPC44473), with boxed area of (G) in (E); **G**, magnified view of boxed area in (E), with white dashed lines indicating the extension of some elongate grooves remained in the secondary layer of the shell (but shown as shallow ridges in this internal view); **H**, latex cast of (E), but slightly different part from (G), showing the external features of the shell ornamentation. **I–K**, *Notospirifer* cf. *triplicata* Waterhouse, 2015. **I, J**, a dorsal external mould (AM F.159014), magnified views of boxed area in Fig. 12Q, showing deep grooves which form pits on the shell external surface; **K**, a latex cast of a dorsal external mould (AM F.159013), magnified views of boxed area in Fig. 12P, showing elongate grooves surrounded by ridges with some spinules (marked with dashed circles). All scales represent 1 mm.

elongated outline. *Ambikella plana* (Campbell, 1961) appears to be comparable with our specimens having reduced plications (Fig. 7F, L), but differs in the deep sulcus and the absence of median furrow on the fold.

The present species seems to be very similar to *Notospirifer* cf. *triplicata* Waterhouse, 2015, if the shell micro-ornamentation is not considered. Their shell sizes are comparable (see Fig. 8), and both generally have three pairs of relatively low and broad plicae on the lateral slopes. Considering the dorsal internal features known in the type species of two genera (see also Fig. 6B, H; Table 2), we have provisionally assigned the dorsal valves with short and divergent dorsal adminicula to *N.* cf. *triplicata*, and the others with closely spaced and nearly parallel dorsal adminicula to the present species. These assignments need to be confirmed once better-preserved specimens are acquired. The micro-ornamentation of *N.* cf. *triplicata* is distinguished from that of *Ingelarella* sp. in the formation of deep and swollen pits (Fig. 9I–K). *Ingelarella* sp. also exhibits a few similarities with *Johndearia brevis* also co-occurring in the Snapper Point Formation, especially in the general outline, relatively weak sulcus, and partially reduced plications. However, *J. brevis* is evidently distinguished by its large shell size (Fig. 8) as well as shell internal thickening (see below).

**Johndearia** Waterhouse, 1998

### Type species

*Ingelarella isbelli* Campbell, 1961, p. 181 from the Blenheim Formation (Wordian), in Homevale, Queensland, Australia.

### Diagnosis

Large shells smooth or with a few weak plicae; sulcus broad and shallow; fold with median furrow in general; shell interior commonly heavily thickened with callus; ventral adminicula slightly divergent to parallel; ventral muscle field large, elongate oval; dorsal adminicula (tabellae) moderately long.

### Remarks

This genus is distinguished from *Ingelarella* and other close allies by the large shell size and heavily thickened ventral valve. The strong morphological resemblances between these genera indicate that *Johndearia* evolved probably from a stock of *Ingelarella* (or *Ambikella*), as shown by Waterhouse & Shi (2010, fig. 6), and persisted as an endemic branch within eastern Australia.

The shell micro-ornamentation of *Johndearia* has been known to be identical to that of *Ingelarella*, based on the illustrations by Campbell (1961, pl. 25, figs 5b, 6). However, a few specimens of *Johndearia* from the Snapper Point Formation show fine radial (fibre-like) micro-structures combined with elongate grooves near their shell external surface (Fig. 6N) which might be related to the development of the large shell and extensive thickening in the genus.

**Johndearia brevis** (McClung & Armstrong, 1975)
(Figs 6N, 7O–AB, 8, 9E–H, 10, 11A–N)

1975 *Martiniopsis brevis* McClung & Armstrong, p. 232, fig. 2.
1975 *Martiniopsis brevis*; Runnegar & McClung, pl. 31.1, figs 26, 27.
1978 *Ingelarella brevis*; McClung, p. 46, pl. 2, figs 20, 21; pl. 5, figs 2–9; pl. 6, figs 1–12; pl. 7, figs 1–13.

### Diagnosis

Transversely suboval shells generally with a few weakly developed plicae; sulcus and fold mostly weakly developed, commonly with shallow median furrow on fold; ventral adminicula relatively short; dorsal adminicula variable, but generally well-spaced and of rather short extent; both ventral and dorsal muscle fields extensively elongate, distinctly incised on valve floor; surface grooves relatively deep, reaching secondary layer of shell.

### Holotype

UNE F14212 from UNE L845/1 locality, Elderslie Formation (Kungurian), Raymond Terrace, NSW, Australia.

### Referred material

Thirty-four registered specimens: six conjoined shells (AM F.158977–158982), four internal moulds of conjoined shells (AM F.158983–158986), seven ventral valves (AM F.158987–158992, CPC44467), nine ventral internal moulds (AM F.158993–158998, CPC44468–44470), two dorsal valves (AM F.158999, CPC44471), five dorsal internal moulds (AM F.159000–159003, CPC44472), and a fragmentary shell bearing shell surface ornaments (CPC44473).

### Locality, unit and age

Crampton Island (GRS15), Banisters Point (L877), southwest of lake Burragorang (L1049, 1050, 1052), and Jervis Bay (JB65); upper part of the Snapper Point Formation (early Kungurian), southern Sydney Basin. Wandrawandian Siltstone (late Kungurian to Roadian), southern Sydney Basin. Elderslie Formation (Kungurian) and Branxton Formation (*Fenestella* Shale, Roadian), northern Sydney Basin (McClung 1978).

### Description

Shell medium to large, ranging 21.3–98.4 mm wide (average 56.222 mm), 15–78.3 mm long (average 41.550 mm) in conjoined shell and either valve (Fig. 8); outline variable, from strongly transverse oval to circular or pentagonal, with width/length ratio of 1.026–2.076 (average 1.358); lateral to anterior margins very rounded; hinge line generally narrower than maximum shell width at slightly anterior to hinge or mid-shell, ranging 0.737–0.926 (average 0.830) of maximum width; biconvex in lateral profile, having maximum thickness of 32.2 mm in thickest conjoined shell; cardinal extremities obtuse to rounded.

Ventral valve moderately to strongly convex, generally maximum convexity at umbonal region, becoming flat anteriorly, but rarely geniculated dorsally near anterior margin (Fig. 10I); ventral beak moderately incurved; ventral interarea low, indistinctly bounded posteriorly; delthyrium triangular with delthyrial angle of 90° or higher, no delthyrial covering preserved; sulcus variably developed, mostly narrow and shallow, but moderately wide and deep in some specimens (Fig. 11B, D, E), no sulcal plication except sulcus-bounding plicae; lateral slopes mostly smooth without plication, but sometimes with two to three indistinct plicae (most commonly seven in adult stage) on each side.

Dorsal valve moderately convex, slightly less convex than ventral valve; dorsal interarea indistinct; fold commonly indistinct, narrow, weakly raised, but sometimes moderately broad and elevated; median furrow on fold variably developed, most commonly narrow and weakly incised, however more distinct and deeper in some specimens (Fig. 11N) and absent in others (Fig. 11F); dorsal lateral plications very similar to ventral ones.

Shell external surface strongly weathered, mostly only with concentric growth lamellae on anterior part (Fig. 10I,

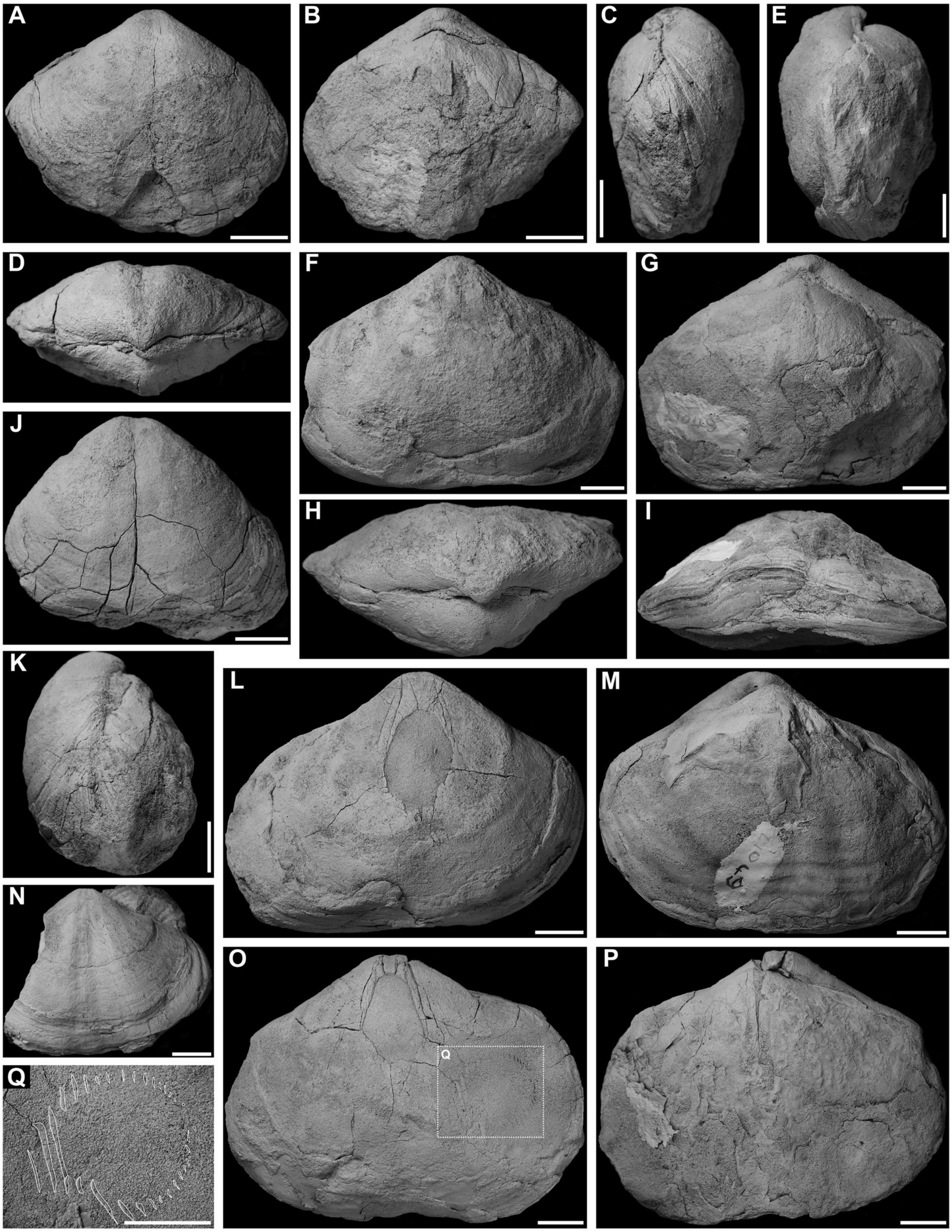

**Figure 10.** *Johndearia brevis* (McClung & Armstrong, 1975). **A–D**, ventral, dorsal, lateral and posterior views of a conjoined shell (AM F.158977) from L1050; **E–I**, lateral, ventral, dorsal, posterior, and anterior views of a conjoined shell (AM F.158978) from L1049; **J, K**, ventral and lateral views of a conjoined shell (AM F.158979) from L1050; **L, M**, ventral and dorsal views of a conjoined shell (AM F.158980) from L1050; **N**, a ventral valve (AM F.158987) from L1049; **O, P**, ventral and dorsal views of a conjoined shell (AM F.158981) from L1049, with boxed area of (Q); **Q**, magnified view of boxed area in (O), showing preserved spiralium (its outline marked with white lines). All scales represent 10 mm.

J), but a few fragmentary shells also bearing surface grooves; grooves narrow, elongate, relatively deep, arranged in quincunx, numbering around five per 1 mm width at mid-shell, ornamented by radial lines (possibly fibrous secondary layer of shell or capillae) (Figs 6N, 9E–H).

Ventral interior strongly thickened posteriorly; dental plates relatively high; ventral adminicula high, moderately spaced, short to moderately long, anteriorly extending parallelly or at slightly divergent angle; ventral muscle filed strongly elongate oval, anteriorly extending to mid-valve floor, strongly bounded and impressed (therefore ventrally having much thinner shell; Fig. 10L, O), sometimes divided by low median ridge and marked by several vertical lines (Fig. 7AA); ventral median septum anterior to muscle field (tigillum) absent.

Dorsal adminicula moderately spaced, variably developed in length, from very short (Fig. 11H) to moderately long

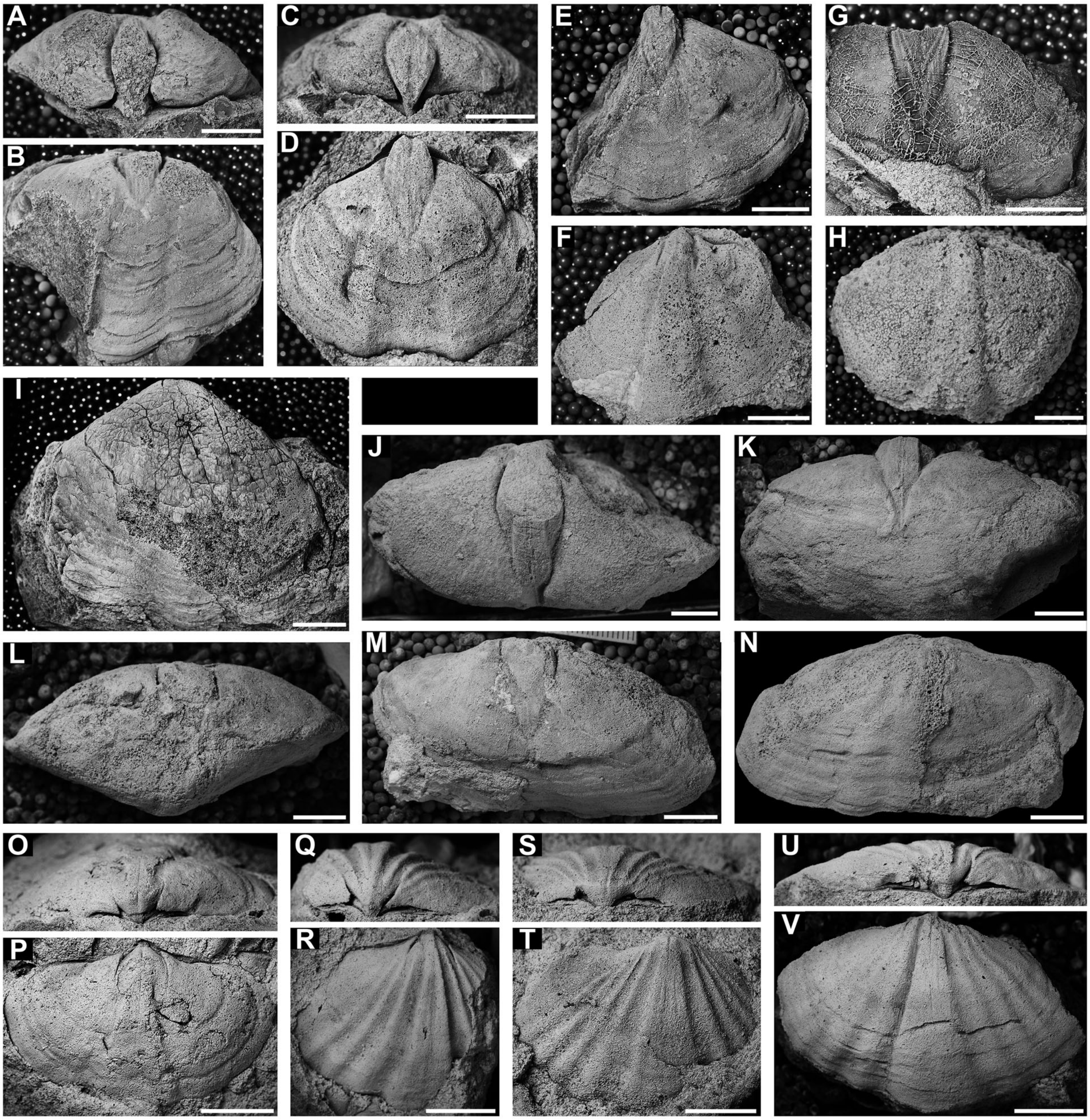

**Figure 11.** A–N, *Johndearia brevis* (McClung & Armstrong, 1975): **A, B**, posterior and ventral views of a ventral internal mould (CPC44468) from JB65; **C, D**, posterior and ventral views of a ventral internal mould (CPC44469) from JB65; **E**, a ventral internal mould (CPC44470) from JB65; **F**, a dorsal internal mould (CPC44472) from JB65; **G**, a ventral internal mould (AM F.158995) from GRS15; **H**, a dorsal internal mould (AM F.159001) from GRS30; **I**, a ventral valve (CPC44467) from JB65; **J, K**, ventral and anterior views of a ventral internal mould (AM F.158996) from L1052; **L–N**, posterior, ventral and dorsal views of internal mould of a conjoined shell (AM F.158986) from L1052. **O–V**, *Notospirifer* cf. *triplicata* Waterhouse, 2015. **O, P**, posterior and dorsal views of a dorsal internal mould (AM F.159015) from L928; **Q, R**, posterior and dorsal views of a dorsal internal mould (AM F.159016) from L928; **S, T**, posterior and dorsal views of a dorsal internal mould (AM F.159017) from L928; **U, V**, posterior and dorsal views of a dorsal internal mould (AM F.159018) from L928. All scales represent 10 mm.

(anteriorly reaching one-third of valve length; Fig. 7AB); dorsal muscle field relatively distinct, elongate, narrow, extending to near mid-valve floor; dorsal median septum sometimes distinctly developed (Fig. 7S, AB).

### *Remarks*

A large suite of specimens representing *Johndearia brevis* from the Elderslie Formation in the northern Sydney Basin were described and figured by McClung (1978). Our specimens from the Snapper Point Formation are well suited to this species, also demonstrating a similar range of morphological variation discussed in McClung (1978). For example, the shell outline varies from a strongly transverse form to a relatively equidimensional one, and the variety of forms is generally correlated to their locality and therefore differences in lithology (Fig. 8), suggesting possible environmental impacts (e.g., grain size as habitat substrate) on its morphology. As another notable intraspecific variation, the fold on the dorsal valve seems to carry a very shallow median furrow, which is seldom long and deep, and in other specimens, is entirely absent. This implies some deviation from the typical *Johndearia*, which, in the type species as well as other forms, carries a well-defined median furrow along the dorsal fold. Given that a significant portion of *J. brevis* specimens lacks a median furrow on the dorsal fold, it is likely that the species might represent a variant of typical *Ambikella*, which was more common in Lower Permian faunas of eastern Australia and had a simple rounded fold-crest.

*Johndearia brevis* strongly resembles *J. isbelli* (Campbell) both internally and externally. McClung (1978) separated these two species by the latter's large shell size and longer dorsal adminicula, but the relatively large morphological variation of *J. brevis* commonly makes the distinction difficult at a population level; i.e., some specimens of *J. brevis* from the Snapper Point Formation are as large as or even larger than *J. isbelli* specimens measured in Campbell (1961, Table 2; see also Fig. 8), and the anteriorly extended form of dorsal adminicula is frequently detected in *J. brevis* (Fig. 7AB). It indicates that the species separation might have relied more on their stratigraphic disparity. In addition to the supposed differences, we have observed possible capillae associated with elongate grooves in a few shell fragments of *J. brevis* from the Snapper Point Formation (Figs 6N, 9E–H), possibly as a more substantial feature that distinguishes the species from younger *Johndearia* species. However, there is a possibility that these capillae-like structures might represent the fibrous secondary layer of the brachiopod shells. If so, the elongate surface grooves seem to reach the secondary layer of the shell in *J. brevis* (Fig. 6N′), which implies its significant difference from other ingelarelline genera in the shell micro-ornamentation (see Archbold & Thomas 1986). The development of the unusual micro-ornamentation might also be linked to the heavy shell thickening in the species. The genuine identity and consistency of the micro-structures as well as their origin need to be further examined with the collection of additional specimens that better preserve the shell external surface.

*Johndearia brevis* marked the inception of a lineage prominent in the mid-Permian (since Kungurian) and extending into the Lopingian of eastern Australia and New Zealand (Waterhouse & Shi 2010). According to some authorities, it gave rise to *Johndearia undulosa* (Campbell, 1961), from beds above the Tiverton Formation in the Bowen Basin. Both Runnegar & McClung (1975, pl. 31, fig. 1) and McClung (1978) envisaged *J. brevis* as preceding *J. undulosa*, which seems to have longer and more strongly developed dorsal adminicula. McClung (1978) reported possible *J. undulosa* from the top of the Elderslie Formation. But Waterhouse (2001, p. 100) pointed out that *Ingelarella cessnockensis* McClung, 1978 was likely to be a junior synonym of *J. brevis*, as the former is also found in the Elderslie Formation, overlapping with *J. brevis* in stratigraphic range. Furthermore, *J. undulosa* was found in the Freitag Formation of the Bowen Basin together with *Wyndhamia typica*, as described by Waterhouse (2001, p. 72, pl. 5, figs 12–16, ?17), and *W. typica* is also found in the Elderslie Formation. Allied *Wyndhamia* is found in the Grange Mudstone and lower Malbina Formation (Kungurian) of the Tasmania Basin, with reported *J. brevis* (Clarke & Banks 1975, Waterhouse 2001).

McClung (1978) and Runnegar (1980) thought that *J. brevis* occurs from or near the base of the Snapper Point Formation, therefore regarding most of the formation as belonging to the "*Martiniopsis*" *brevis* Zone (according to the biozonation by Runnegar & McClung 1975). However, our biostratigraphic data shows that *J. brevis* first appeared in the upper part of the Snapper Point Formation, thus underlining the need to reconsider the stratigraphic extent of the "*M.*" *brevis* Zone in the formation.

Subfamily NOTOSPIRIFERINAE Archbold & Thomas, 1986

### Diagnosis

As the diagnosis by Archbold & Thomas (1986, p. 584).

### Remarks

This subfamily is mainly distinguished from the Ingelarellinae by its micro-ornamentation consisting not only of surface grooves but also of spinules and pits (Fig. 6Q′). Armstrong (1970b) demonstrated that the micro-ornamentation of *Notospirifer* has small spinules and deeper grooves that form pits in the secondary layer of the shell (see also Fig. 6Q). In comparison, the micro-ornamentation of *Ingelarella* and its close allies is represented by superficial shallow grooves which do not form pits (see Fig. 6M′–O′).

Archbold & Thomas (1986) included *Glendonia* McClung & Armstrong, 1978 in the Notospiriferinae, as the genus was known to develop relatively deep surface grooves (McClung & Armstrong 1978). However, as explained by Clarke (1992), the grooves of *Glendonia* do not form pits and are restricted to the primary layer (see Fig. 6P′). Consequently, Clarke (1992) proposed another subfamily (Glendoniinae), based on the micro-ornamentation of *Glendonia* (see below).

Three notospiriferine genera have been known only from the Permian of eastern Australia and New Zealand, including *Notospirifer*, *Papulinella* Waterhouse, 1998 (see Fig. 6H, I; Table 2), and *Farmerella* Clarke, 1992.

**Notospirifer** Harrington, 1955

### Type species

*Spirifer darwini* Morris, 1845, p. 279, from the Muree Sandstone (Guadalupian) in Glendon, NSW, Australia.

### Diagnosis

Small to medium-sized shells with transverse outline; sulcus with subplicae; fold with median furrow; lateral slopes with relatively strong plicae in general; micro-ornamentation consisting of deep globose pits penetrating secondary layer of shell and low c-shaped spinules; ventral adminicula moderately developed, divergent; dorsal adminicula (tabellae) very short or absent.

### Remarks

Although *Notospirifer* is clearly distinguished from *Ingelarella* (and other allies) in the micro-ornamentation

Figure 12. A–T, *Notospirifer* cf. *triplicata* Waterhouse, 2015. **A, B**, posterior and ventral views of a ventral internal mould (AM F.159004) from L1046; **C, D**, posterior and ventral views of a ventral internal mould (AM F.159005) from L928; **E, F**, posterior and ventral views of a ventral internal mould (AM F.159006) from GRS34; **G, H**, posterior and ventral views of a ventral internal mould (AM F.159007) from L1046; **I, J**, posterior and ventral views of a ventral internal mould (AM F.159008) from L928; **K**, a juvenile ventral internal mould (AM F.159019) from L1046; **L**, a juvenile dorsal internal mould (AM F.159020) from L1046; **M**, a juvenile dorsal internal mould (AM F.159021) from L1046; **N**, a dorsal internal mould (AM F.159022) from GRS158; **O, P**, a dorsal external mould (AM F.159013) from L1046 and its latex cast, with boxed area of Fig. 9K in (P); **Q, R**, a dorsal external mould (AM F.159014) from L928 and its latex cast, with boxed area of Fig. 9I in (Q); **S, T**, posterior and ventral views of a ventral internal mould (AM F.159009) from GRS158. **U–X**, *Glendonia ulladullensis* McClung & Armstrong, 1978. **U, V**, posterior and dorsal views of a dorsal internal mould (AM F.159027) from L1052; **W, X**, anterior and lateral views of a dorsal valve (AM F.159026) from L870A. **Y, Z**, Ingelarellidae indet., posterior and ventral views of a ventral internal mould (AM F.159028) from GRS34. **AA–AH**, *Simplicisulcus* sp. **AA, AB**, posterior and ventral views of a ventral internal mould (AM F.159031) from GRS34, with a white arrow indicating the remnant of the connecting plate joining the dental plates and ventral adminicula on (AB); **AC, AD**, posterior and dorsal views of a dorsal internal mould (AM F.159035) from GRS34; **AE, AF**, posterior and dorsal views of a dorsal internal mould (AM F.159036) from L1046; **AG**, a latex cast of a ventral external mould (AM F.159030) from GRS34; **AH**, a latex cast of a dorsal external mould (AM F.159033) from GRS34. Scales for A–R represent 5 mm, whereas others (S–AH) are 10 mm.

characteristics (deep grooves forming pits in the secondary layer of the shell; Fig. 6Q′), their separation is sometimes not easy because of the preservation nature that the micro-ornamentation is commonly weathered or abraded. Also, it has been generally considered that the lateral plications of *Notospirifer* are more strongly developed than those of *Ingelarella*, but some species of *Notospirifer* (e.g., *Notospirifer gentilis* Waterhouse, 1983) are represented by low and broad plicae on the lateral slopes and, therefore, the external features of a few *Notospirifer* species might be indistinguishable from those of *Ingelarella*. However, the internal plates between these two genera appear to be more distinguished; the ventral adminicula of *Notospirifer* extend divergently on the ventral floor, and the dorsal adminicula are very shortly developed or absent (see Fig. 6H; Table 2).

Waterhouse (1998) separated *Papulinella* from *Notospirifer* by an absence of subplicae on the sulcus, combined with the possession of stronger lateral plications. A Tasmanian genus *Farmerella* has been known to superficially resemble *Glendonia*; Clarke (1992) regarded its type species *Farmerella exoporosa* Clarke, 1992 and *Glendonia duodecimcostata* (M'Coy, 1847) as homeomorphic forms. However, the micro-ornamentation of *Farmerella* is nearly identical to that of *Notospirifer*, both containing deep and globose pits.

**Notospirifer** cf. **triplicata** Waterhouse, 2015
(Figs 8, 9I–K, 11O–V, 12A–T)

### Referred material

Twenty-two registered specimens: nine ventral internal moulds (AM F.159004–159012), two dorsal external moulds (AM F.159013, 159014), and 11 dorsal internal moulds (AM F.159015–159025).

### Locality, unit and age

South of Clear Point (GRS34 =L870A), Grassy Gully (GRS158/159 =L928), and Burragorang Valley (L1046); lower part of the Snapper Point Formation (early Kungurian), southern Sydney Basin.

### Description

Shell small to medium, ranging 8.8–59 mm wide (average 30.362 mm), 7–42.7 mm long (average 23.440 mm) (Fig. 8); outline transversely oval, with width/length ratio of 1.021–1.458 (average 1.257); hinge line generally narrower than maximum shell width at slightly anterior to hinge, ranging 0.849–0.899 (average 0.866) of maximum width; ventribiconvex in lateral profile; cardinal extremities rounded to obtuse.

Ventral valve moderately convex, with maximum convexity at umbonal region; sulcus distinct, shallow, moderately broad, with angle of around 30°, bearing two weak subplicae; lateral slopes commonly ornamented by three or four pairs of low broad plicae, but weakly marked on shell interior.

Dorsal valve weakly convex; fold distinctly developed, weakly to moderately elevated, with nearly flat crest (Fig. 12P, R); median furrow on fold present; lateral plications on dorsal slope also composed of three to four pairs of plicae, but more distinct and angular than ventral ones.

Shell surface with concentric growth lamellae irregularly distributed (Fig. 12O–R); micro-ornamentation composed of pits and spinules; pits numerous, elongate, relatively short, deep (Fig. 9I–K); spinules tiny, developed at posterior edge of each pit (Fig. 9K).

Ventral adminicula moderately long, generally diverging with angle of 50–60°, posteriorly surrounding ventral muscle field; muscle field elongate oval, weakly to moderately marked, anteriorly reaching near to mid-valve floor (Fig. 12T).

Dorsal adminicula short, widely divergent; ctenophoridium relatively narrow, bearing about ten platelets; dorsal median septum indistinctly developed; dorsal muscle field faintly impressed.

### Remarks

This species is generally well-matched with *Notospirifer triplicata* Waterhouse, 2015 from the lower Tiverton Formation (Sakmarian) in the Bowen Basin. Both are characterized by the medium size in adults, three pairs of lateral plicae on the lateral slopes, a broadly rounded dorsal fold, and a shallow median furrow on the crest. The most significant difference between the two species lies in the strength of the lateral plications; *N. triplicata* exhibits strongly plicate lateral slopes, whereas the ventral internal moulds from the Snapper Point Formation present significantly subdued impressions of the lateral plicae. In addition, it seems that *N. triplicata* has a more deeply developed sulcus. However, the subdued impression of the lateral plications in the ventral mould specimens might be a result of the ventral interior thickening. It is also noteworthy that *N. gentilis* reported from the upper part of the Pebbley Beach Formation (which underlies the Snapper Point Formation; Fig. 2) by Shi *et al.* (2020) also exhibits the subdued lateral plications in its ventral internal mould specimens. This implies that the species of *Notospirifer* in the southern Sydney Basin might develop thicker ventral valves through shell internal thickening than the species in the Bowen Basin. Unfortunately, our specimens do not include any ventral valve showing well-preserved external features of the ventral plications, hampering a more detailed comparison.

Subfamily GLENDONIINAE Clarke, 1992

### Diagnosis

As the diagnosis by Clarke (1992, p. 75).

### Remarks

Like the Notospiriferinae, this subfamily is a group of the ingelarellid taxa that have small c-shaped spinules (Fig. 6P), but whose surface grooves do not form any globose pits penetrating the secondary layer of the shell (Fig. 6P′) [Carter *et al.* (2006, p. 1762) stated that the Glendoniinae forms pits, but it is incorrect]. Four genera, *Glendonia*, *Tabellina* Waterhouse, 1986b, *Monklandia* Waterhouse, 1998 (see Fig. 6J–L; Table 2) and *Birchsella* Clarke, 1987, have been considered to form the subfamily (see Waterhouse 1998).

*Kelsovia* Clarke, 1990 was proposed as a genus of the Glendoniinae by Clarke (1992), but it was later synonymized with *Tabellina* by Waterhouse (1998). Carter *et al.* (2006) listed *Homevalaria* as a valid genus of the subfamily. However, *Homevalaria* was synonymized with *Ambikella* by Waterhouse (2015, p. 150) who considered the development of 'fine c-shaped spinules' in the type species of *Homevalaria* (*Ingelarella ovata* Campbell, 1961) as features formed by weathering rather than true micro-ornamentation. Two Permian genera from New Zealand, *Wairakispirifer* Waterhouse, 1998 and *Mesopunctia* Waterhouse, 1998, were also assigned to the Glendoniinae by Gourvennec & Carter (2007), but these genera were originally proposed as members of another subfamily Mesopunctiinae Waterhouse, 1998 and their affinities to the Glendoniinae seem to be questionable.

**Glendonia** McClung & Armstrong, 1978

### Type species

*Glendonia ulladullensis* McClung & Armstrong, 1978, p. 3, from the Wandrawandian Siltstone (Kungurian-Roadian) in North Head, Ulladulla, NSW, Australia.

### Diagnosis

As the diagnosis by McClung & Armstrong (1978, p. 2).

### Remarks

This genus fundamentally differs from most other ingelarellid genera in having the shell surface micro-ornamentation with robust c-shaped spinules at the posterior margin of elongate grooves (Fig. 6P). Notwithstanding this micro-ornamentation feature, *Glendonia* is also clearly distinguishable by its globular appearance with a strong shell convexity, narrow median (sub)plica on the sulcus, and relatively angular and coarse lateral plications (Fig. 6J).

**Glendonia ulladullensis** McClung & Armstrong, 1978
(Figs 6P, 8, 12U–X)

1877 *Spirifer duodecimcostata*; de Koninck, pl. 12, fig. 4a.
1888 *Spirifer oviformis*; Johnston, pl. 11, fig. 2.
1978 *Glendonia ulladullensis* McClung & Armstrong, p. 3, pl. 1, figs 1–13, 21, 22; pl. 2, figs 1–6.

### Holotype

An internal mould of a conjoined shell (UQF57510) from the Wandrawandian Siltstone in North Head, Ulladulla, NSW, Australia was designated as the holotype by McClung & Armstrong (1978).

### Referred material

Two registered specimens: a fragmentary dorsal valve (AM F.159026) and a dorsal internal mould (AM F.159027).

### Locality, unit and age

South of Clear Point (GRS34 =L870A) and Burragorang Valley (L1052); Snapper Point Formation (early Kungurian), southern Sydney Basin. Wandrawandian Siltstone (late Kungurian to Roadian) in southern Sydney Basin. Belford Formation (Roadian) in northern Sydney Basin. Blenheim Formation (Moonlight Sandstone, Wordian) in Bowen Basin (Runnegar & McClung 1973, McClung & Armstrong 1978).

### Description

Dorsal valve medium-sized (48.5 mm wide and 36.35 mm long on average; Fig. 8), semicircular in outline, with relatively strong convexity (15.05 mm in average height of dorsal valve); hinge line slightly narrower than maximum shell width at around one-third of valve length; fold distinct, moderately elevated, anteriorly diverging with angle of 35°, bearing two strongest plicae divided by median furrow; median furrow on fold relatively distinct, deeply incised in one valve (Fig. 12U, V) but shallow in the other valve (Fig. 12W); lateral plications distinct, subangular, three or four on each side, commencing near dorsal beak.

Shell external surface mostly weathered, but traces of concentric growth lamellae still partially remaining.

Dorsal interior with very short, weakly divergent dorsal adminicula (Fig. 12U, V); ctenophoridium probably narrow, but platelets not preserved.

### Remarks

Despite the limited material (dorsal valves only), these specimens appear to be safely assignable to *Glendonia ulladullensis*, suggested by their strong shell convexity, slightly subangular and thick lateral plications, and a distinct median furrow on the dorsal fold. It is noteworthy that the median fold furrow in one of the dorsal valves (Fig. 12W) collected from the base of the Snapper Point Formation is less strongly developed than in the other dorsal valve from the upper part of the formation (see Fig. 3).

The occurrence of *G. ulladullensis* from the Snapper Point Formation implies that the species first appeared in the early Kungurian or even earlier, although it flourished during the late Kungurian to Roadian mainly in the southern Sydney Basin (McClung & Armstrong 1978).

**Ingelarellidae** indet.
(Fig. 12Y, Z)

### Referred material

Two registered specimens of ventral internal moulds (AM F.159028, 159029).

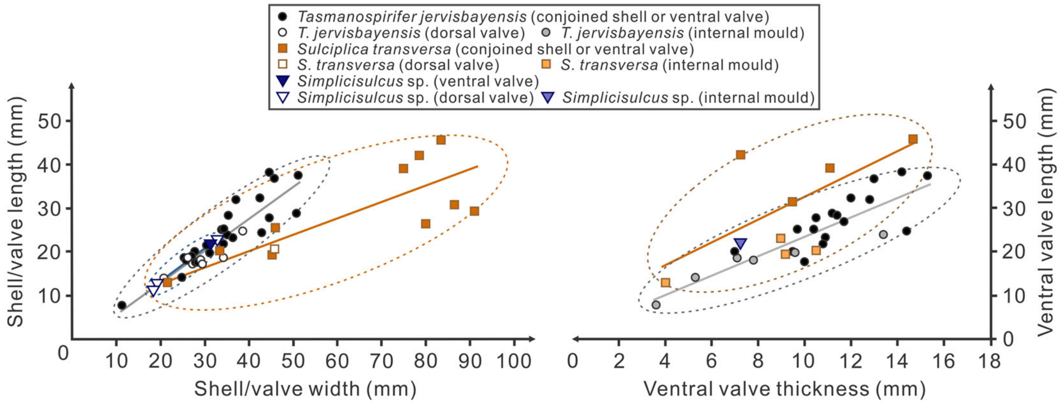

**Figure 13.** Shell measurements of three spiriferoid species from the Snapper Point Formation: *Simplicisulcus* sp., *Tasmanospirifer jervisbayensis* sp. nov. Waterhouse & Lee, and *Sulciplica transversa* (Waterhouse, 1968). The method of least squares is used for generating regression lines.

### *Locality, unit and age*

South of Clear Point (GRS34 =L870A); the base of the Snapper Point Formation (early Kungurian), southern Sydney Basin.

### *Remarks*

These two fragmentary ventral internal moulds present a few characteristics of the ventral valves, such as a relatively narrow sulcus, subangular lateral plications (three or four plicae on each lateral slope), and well-spaced ventral adminicula. Combined with these features, the possible trace of a median plica very faintly remaining on the sulcus (of an unfigured specimen) might imply a possible affinity to *Glendonia* or allied taxa. However, *Glendonia ulladullensis* occurring in the same locality (GRS34 =L870A) is not comparable at all, as it has much broader lateral plications. Further, the material is too limited for us to make any comment on shell outline, convexity or shell micro-ornamentation.

Superfamily SPIRIFEROIDEA King, 1846
Family TRIGONOTRETIDAE Schuchert, 1893
Subfamily NEOSPIRIFERINAE Waterhouse, 1968

**Simplicisulcus** Waterhouse, 2002b

### *Type species*

*Neospirifer arthurtonensis* Waterhouse, 1968, p. 28 from the Earnvale Member (Wuchiapingian), Bagrie Formation in Arthurton, New Zealand.

### *Diagnosis*

Small shell with narrow hinge and obtuse cardinal extremities; costae unequal, forming fasciculation; dental plates and ventral adminicula joined by connector plate (see Waterhouse 2016, p. 8, for the definition) below delthyrium.

### *Remarks*

*Simplicisulcus* appears to demonstrate the characteristics both of Spiriferidae King, 1846 and Neospiriferinae (or some taxa of Trigonotretinae). According to Waterhouse (2016), this genus is similar to the Spiriferidae in having internal plates, including a connector plate that joins the dental plates and ventral adminicula, whereas it externally exhibits well-developed and fasciculate plicae, like the Neospiriferinae. Waterhouse (2016) transferred the genus (together with *Spiriferalaria* Waterhouse, 2002b) to the Spiriferidae, emphasizing the presence of the connector plate. However, it is unclear why the connector plate is so significant in the classification and phylogeny of spiriferoids. Here, we prefer to retain the genus within the Neospiriferinae in view of its strong fasciculation, until the classification of the spiriferoids is fully reviewed.

**Simplicisulcus** sp.
(Figs 12AA–AH, 13)

### *Referred material*

Nine registered specimens: a ventral external mould (AM F.159030), two ventral internal moulds (AM F.159031, 159032), two dorsal external moulds (AM F.159033, 159034) and four dorsal internal moulds (AM F.159035–159038).

### *Locality, unit and age*

South of Clear Point (GRS34 =L870A); lower part of the Snapper Point Formation (early Kungurian), southern Sydney Basin.

### *Description*

Shell relatively small, 31.2 mm wide, 21.9 mm long, and 7.4 mm high in largest ventral valve (Fig. 13); outline transverse, with width/length ratio of 1.425; hinge line shorter than maximum width generally at one-third of shell length; lateral profile biconvex; cardinal extremities obtuse.

Ventral interarea moderately high; sulcus moderately deep, narrow anteriorly diverging at 25°, with three simple costae; ventral lateral slopes bearing five pairs of plicae, innermost pair of plicae developed parallelly to sulcus without invading sulcus anteriorly.

Dorsal interarea very low; fold narrow, slightly elevated, bearing four low costae at anterior part (Fig. 12AH); dorsal lateral slopes with four pair of plicae.

Costation unequal, forming fascicles (by two or three costae); ventral fascicles (plicae) commonly having additional (bifurcating) costa on more lateral side of each plication at posterior part of valve (Fig. 12AG); dorsal costation less regular, generally branching at anterior part (Fig. 12AH).

Ventral interior with low dental plates; ventral adminicula short, well-spaced, joined by connector plate (Fig. 12AB); delthyrial plate absent; ventral muscle field distinctly impressed, elongate oval, posteriorly bounded by ventral adminicula, anteriorly reaching more than half of shell length (Fig. 12AB).

Dorsal interior with relatively narrow ctenophoridium; ctenophoridium not elevated, bearing six to eight platelets (Fig. 12AC–AF); dorsal adminicula (tabellae) absent; dorsal muscle scars obscure.

### Remarks

These specimens (all moulds) are incomplete and exhibit limited features, but do preserve remnants of the connector plate (Fig. 12AB), and in outline come close to *Simplicisulcus concentricus* (Waterhouse, 1987, p. 21) from the Brae Formation (Kungurian) of the Bowen Basin. As in this species the cardinal extremities are obtuse, the sulcus and fold narrow, and the innermost pair of ventral plicae do not enter the sulcus. However, costae are finer and more numerous in *S. concentricus*, when compared to our material. The fasciculation formed by the unequal costae on the lateral slopes in our external mould specimens appears to be compatible with that of *Grantonia hobartensis* Brown, 1953 from the Berriedale Limestone (Artinskian) in Tasmania, but it is certain that the Tasmanian trigonotretine species does not have any connector plate in its ventral interior.

Subfamily TRIGONOTRETINAE Schuchert, 1893

**Tasmanospirifer** Waterhouse, 2016

### Type species

*Tasmanospirifer clarkei* Waterhouse, 2016, p. 254 from the Berriedale Limestone (Artinskian) in Tasmania, Australia.

### Diagnosis

Medium-sized, slightly transverse shell generally with rounded cardinal extremities; sulcus and fold with a few (sub)plicae; lateral slopes with subangular to rounded plicae; delthyrium open; shell surface ornamented with growth lamellae and, possibly, capillae; ventral valve variably thickened, with or without apical callus (umbonal callosity); dental plates supported by short ventral adminicula; ctenophoridium narrow; dorsal adminicula (tabellae) absent (amended from Waterhouse 2016, p. 253).

### Remarks

*Tasmanospirifer* was mainly defined with some specimens originally referred to as *Spirifer tasmaniensis* Morris, 1845 from the Permian of Tasmania by Waterhouse (2016). This genus exhibits the shell outline and interior structures comparable with those of *Trigonotreta* Koenig, 1825, but is distinguished by simple plications without fasciculation. As noted by Waterhouse (1968) and Clarke (1979) in which *S. tasmaniensis* was regarded as *Sulciplica* Waterhouse, 1968, the shell plication of *Tasmanospirifer* is nearly identical to that of *Sulciplica*. However, *Tasmanospirifer* is distinguishable in having a much less transverse outline and, possibly, less thickened ventral valve than *Sulciplica*.

The diagnosis of *Tasmanospirifer* is slightly expanded here with our specimens that exhibit little to no considerable shell thickening. The Tasmanian species of the genus are all known to have a strongly thickened ventral valve (especially, at the posterior part) with a well-developed apical callus, whereas the ventral valves of the new species from the Snapper Point Formation are not strongly thickened (see below). However, in spite of the distinct difference in the development of ventral thickening (and apical callus), the new species is still considered to belong to *Tasmanospirifer*, because of similarities in all other diagnostic features of the genus.

*Tasmanospirifer* was originally proposed only with two Permian species from Tasmania, *T. clarkei* and *T. tasmaniensis* (Morris), by Waterhouse (2016). However, more shells with a weakly transverse outline and simple plications are known from the Permian deposits of Tasmania as well as of other basins in eastern Australia (e.g., Waterhouse 1987, Clarke 1990), and some of these species (e.g., *Spirifera stutchchburii* Etheridge, 1892 and *Sulciplica subglobosa* Clarke, 1990) seem to be assignable to *Tasmanospirifer*. The present study describes a new species of the genus from the Snapper Point Formation, confirming its occurrence also in the southern Sydney Basin. In consideration of all these occurrences, it is very likely that *Tasmanospirifer* was distributed across eastern Australia during the Permian.

Waterhouse (2016) regarded *Tasmanospirifer* as a member of Georginakingiidae Waterhouse, 2004, which was separated from Trigonotretidae, together with *Sulciplica*. However, we prefer to place both genera within the Trigonotretidae (Trigonotretinae), following the classification scheme of Carter *et al.* (2006).

**Tasmanospirifer jervisbayensis** sp. nov. Waterhouse & Lee (Figs 13, 14, 15A–Q)

### Diagnosis

Relatively small, weakly transverse shell with five to seven, subangular to rounded plicae on each lateral slope; sulcus narrow, having median (sub)plica; fold moderately elevated, with two median (sub)plicae divided by median furrow; lateral plications narrow, rounded to subangular, mostly simple and very rarely bifurcated (costate); ventral valve weakly thickened, without apical callus; growth lamellae subimbricate, distinct on anterior shell surface; dorsal median septum present.

### Etymology

Named after the type locality of the species at Jervis Bay, NSW, Australia.

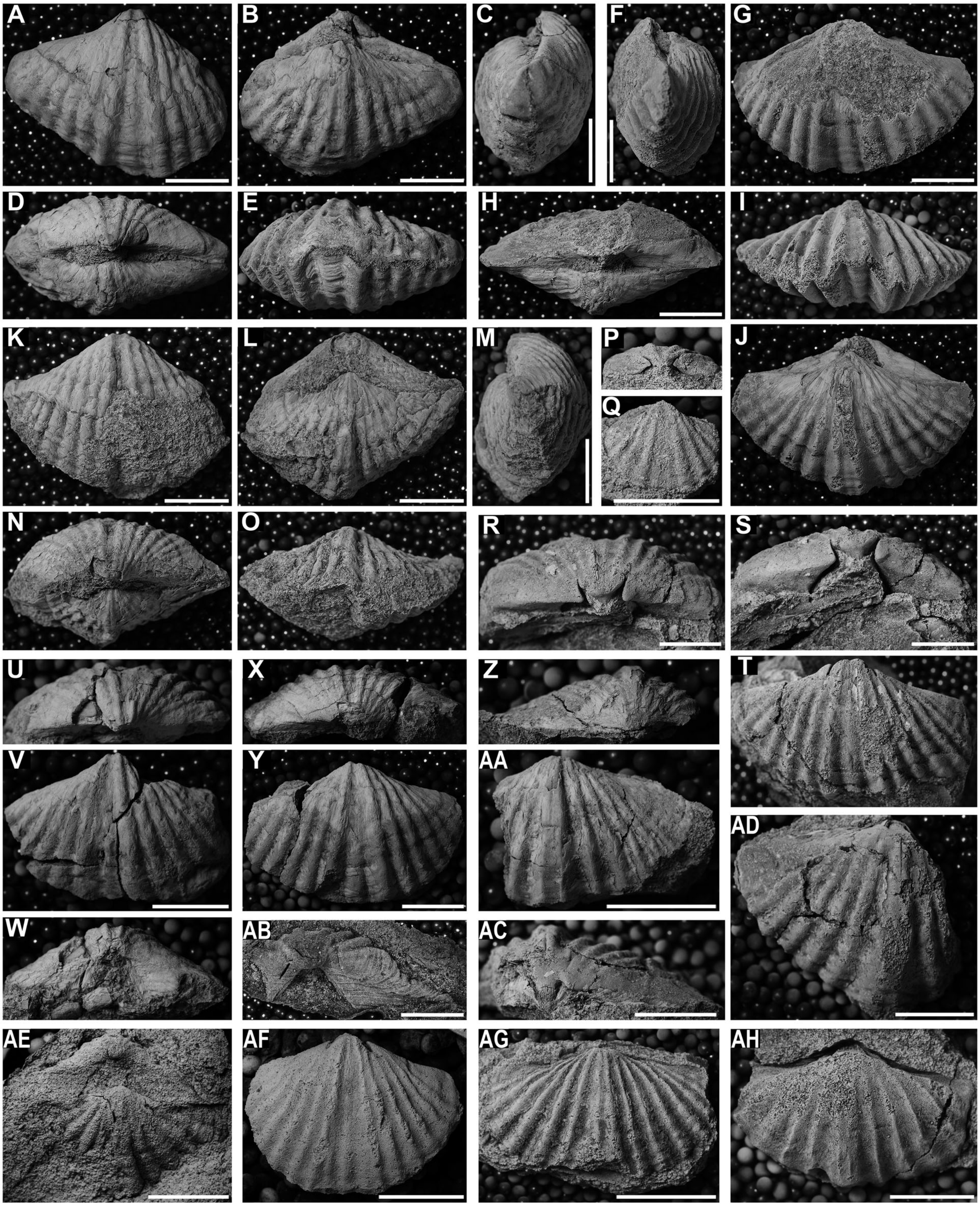

**Figure 14.** *Tasmanospirifer jervisbayensis* sp. nov. Waterhouse & Lee. **A–E**, ventral, dorsal, lateral, posterior and anterior views of a conjoined shell (CPC44474, holotype) from JB65; **F–J**, lateral, ventral, posterior, anterior and dorsal views of a conjoined shell (CPC44475, paratype) from JB65; **K–O**, ventral, dorsal, lateral, posterior and anterior views of a conjoined shell (CPC44476, paratype from JB65); **P, Q**, posterior and ventral views of a juvenile ventral internal mould (AM F.159053) from L1046; **R–T**, posterior, dorsal and ventral views of a ventral internal mould (CPC44483) from JB65; **U–W**, posterior, ventral and dorsal views of a ventral valve (CPC44477) from JB65; **X, Y**, posterior and ventral views of a ventral valve (CPC44478) from JB65; **Z, AA**, posterior and dorsal views of a dorsal valve (CPC44485) from JB65; **AB**, latex cast of a ventral external mould showing its open delthyrium (AM F.159051) from GRS34; **AC, AD**, posterior and dorsal views of a dorsal valve (CPC44486) from JB65; **AE**, latex cast of an external mould of a conjoined shell (AM F.159048) from L877; **AF**, a ventral internal mould (AM F.159054) from L928; **AG**, a dorsal internal mould (AM F.159061) from GRS158; **AH**, a dorsal internal mould (AM F.159060) from GRS34. All scales represent 10 mm.

### *Holotype and paratypes*

A well-preserved conjoined shell (CPC44474) from an old quarry at Jervis Bay (locality JB65) is designated as the holotype (Fig. 14A–E). Also, two other conjoined shells (CPC44475, 44476) from the same locality are designated as paratypes (Fig. 14F–J, Fig. 14K–O, respectively).

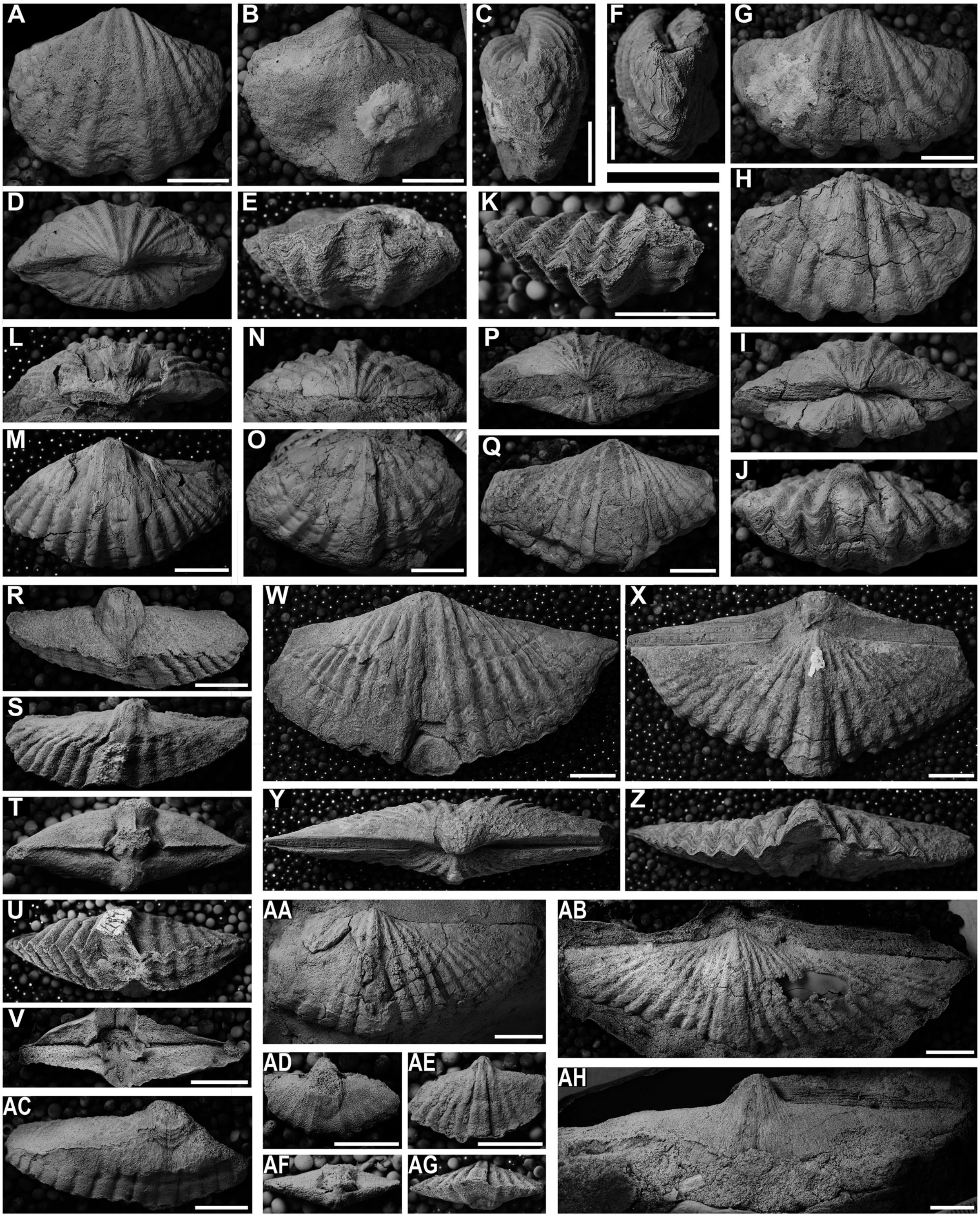

**Figure 15.** **A–Q**, *Tasmanospirifer jervisbayensis* sp. nov. Waterhouse & Lee. **A–E**, ventral, dorsal, lateral, posterior and anterior views of a conjoined shell (AM F.159039) from L1049; **F–J**, lateral, ventral, dorsal, posterior and anterior views of a conjoined shell (AM F.159040) from L1050; **K**, anterior view of a fragmentary conjoined shell (AM F.159041) from GRS15; **L, M**, posterior and ventral views of a ventral valve (CPC44479) from JB65; **N, O**, posterior and dorsal views of a dorsal valve (AM F.159058) from L1049; **P, Q**, posterior and ventral views of a conjoined shell (AM F.159042) from L1050. **R–AH**, *Sulciplica transversa* (Waterhouse, 1968). **R–V**, ventral, dorsal, posterior and anterior views of an internal mould of a conjoined shell (AM F.159069) and its latex cast from L877; **W–Z**, ventral, dorsal, posterior and anterior views of a conjoined shell (AM F.159065) from L1050; **AA**, a dorsal valve (AM F.159079) from L1050; **AB**, a latex cast of an external mould of a conjoined shell (AM F.159067) from L877, showing its dorsal exterior and ventral interarea; **AC**, a ventral view of an internal mould of a conjoined shell (AM F.159070) from L877; **AD–AG**, ventral, dorsal, posterior and anterior views of an internal mould of a conjoined shell (AM F.159071) from L877; **AH**, a ventral internal mould (AM F.159078) from 877. All scales represent 10 mm.

### Referred material

Thirty-eight registered specimens (except the holotype and paratypes): nine conjoined shells (AM F.159039–159047), an external mould of a conjoined shell (AM F.159048), eight ventral valves (AM F.159049, 159050, CPC44477–44482), two ventral external moulds (AM F.159051, 159052), seven ventral internal moulds (AM F.159053–159057, CPC44483, 44484), five dorsal valves (AM F.159058, CPC44485–44488), a dorsal external mould (AM F.159059), and five dorsal internal moulds (AM F.159060–159064).

### Locality, unit and age

South of Clear Point (GRS34 =L870A), Crampton Island (GRS15), Bannisters Point (L877), Grassy Gully (GRS158/159 =L928), Burragorang Valley (L1046, 1049, 1050), and Jervis Bay (JB65); Snapper Point Formation (early Kungurian), southern Sydney Basin.

### Description

Shell small to medium-sized, ranging 27–51.1 mm in width, 19–38.2 mm in length (Fig. 13), and 17.1–21.3 mm in thickness of conjoined shells; outline weakly transverse in general, with width/length ratio ranging 1.156–1.760 (average 1.455); hinge line straight, slightly narrower than greatest width in general; maximum width commonly at slightly anterior to hinge; lateral profile biconvex; cardinal extremities obtuse in general but very rarely weakly alate.

Ventral valve moderately convex, maximum convexity at umbonal region, generally with very weakly incurved ventral beak; ventral interarea moderately high, generally reaching one-fifth of valve length, slightly concave, bearing distinct horizontal striations (Fig. 14AB); delthyrium triangular with delthyrial angle around 70–80°, open without any delthyrial covering; sulcus distinct, generally narrow, shallow but deepening anteriorly, consistently with distinct but low median subplica, lacking additional lateral subplicae; lateral slopes with five to seven plicae (most commonly seven in adult stage) on each side; lateral plications distinct, narrow, rounded to subangular, mostly simple but very occasionally bifurcated in some specimens (Fig. 14AF, AH).

Dorsal valve moderately convex, similar to or slightly less convex than ventral valve; dorsal interarea weakly developed; fold distinct, narrow, moderately raised, bearing two subplicae medially divided by very distinct median furrow (extending from dorsal umbo to anterior edge); dorsal lateral plications identical to ventral ones.

Shell external surface ornamented by concentric growth lamellae; growth lamellae commonly not distinct, but becoming densely spaced, relatively distinct and subimbricate near anterior margin of shell (Fig. 15H), having around 10 lamellae per 5 mm length near anterior margin; capillae absent or not preserved.

Ventral interior weakly (or not) thickened; dental plates moderately long, supported by short, diverging ventral adminicula (with divergent angle of 50–60°) on ventral floor; external shell plications fully reflected on valve floor; ventral muscle field elongate oval, weakly marked, posteriorly bounded by ventral adminicula, anteriorly reaching posterior to mid-valve.

Dorsal interior with crural plates; ctenophoridium relatively narrow, bearing 13 platelets (Fig. 14AC); dorsal median septum low and short but clearly developed at posterior part, reaching one-fifth to one-fourth of dorsal floor (Fig. 14AD); dorsal muscle field unclear.

### Remarks

These weakly transverse shells with plications from the Snapper Point Formation have peculiar characteristics both externally and internally, distinguished from all other trigonotretine taxa. Some external features of these specimens, such as the narrow and simple plication, narrow sulcus and fold, and shell surface ornamentation dominated by growth lamellae, are almost identical to those of *Sulciplica transversa* Waterhouse, 1968 in our collection, probably suggesting their close relationship (also, mostly occurring together; see Fig. 3). However, *S. transversa* is readily distinguished not only by a few external characters (much more transverse outline with alate cardinal extremities, indistinctly developed median plica, and extra lateral subplications on the dorsal fold), but also by internal characters (strongly thickened ventral interior with apical callus and strongly marked ventral muscle field) (see below). Another possible species of *Sulciplica* in this study (*Spirifer phalaena* Dana, 1849) is also comparable with the present species in general external features but differs in the micro-ornamentation composed of strongly imbricate growth lamellae and tiny capillae.

As a novel species of *Tasmanospirifer*, *T. jervisbayensis* is evidently separated from other species of the genus. *Tasmanospirifer clarkei* Waterhouse is different in its much wider sulcus bearing three or more subplicae (costae) as well as in more common bifurcation (and intercalation) on lateral plications (see Clarke 1979, pl. 4, figs 1–4, 9), and *T. tasmaniensis* has also a wider sulcus bearing more subplicae (see Clarke 1979, pl. 4, figs 5–8). An older possible species of *Tasmanospirifer* also from Tasmania, *T. subglobosa* (Clarke, 1979), is similar to *T. jervisbayensis* in having a narrow sulcus bearing a single median subplica, but its dorsal fold lacks any subplication. Another Tasmanian species, *Sulciplica crassa* Clarke, 1979, also resembles *T. jervisbayensis* in having a distinct median subplica on the sulcus and simple lateral plications, but it is clearly distinguishable in its thicker lateral plications as well as in the presence of capillae (radial lirae). In addition, apart from the external morphological differences mentioned above, *T. jervisbayensis* can be clearly distinguished from all the other species in lacking shell thickening and apical callus at the ventral interior.

These specimens all assigned here to *T. jervisbayensis* have been collected from multiple geographical localities and stratigraphic horizons of the Snapper Point Formation, and the different populations separated by the localities and/or horizons seem to show minor but noticeable morphological differences. The type locality (JB65) specimens are characterized by thin, slightly subangular lateral plications, while the Burragorang (L1049, 1050) specimens have slightly thicker and rounded plications on their lateral slopes. Also, it seems that possibly older specimens from the lower stratigraphic horizons (GRS34, GRS158/159, L928, L1046) exhibit bifurcations on the plication more commonly than the younger shells from the higher horizons (JB65, GRS15, L877, L1049/1050; see Fig. 3). These slight dissimilarities in morphology (mainly, on plications) are regarded simply as intraspecific variations presumably caused by different evolutionary pathways and/or different local ecological habitats.

**Sulciplica** Waterhouse, 1968

1968 *Sulciplica* Waterhouse, p. 25.
2016 *Angulispirifer* Waterhouse, p. 255.

### *Type species*

*Sulciplica transversa* Waterhouse, 1968, p. 25 from the Broughton Formation (Westley Park Sandstone Member, Wordian) at Black Head, Gerringong, NSW, Australia.

### *Diagnosis*

Medium to large, moderately to strongly transverse shell with alate cardinal extremities; sulcus and fold relatively narrow, having a few (sub)plicae; lateral slopes with numerous, mostly simple plicae; delthyrium posteriorly occluded by bulbous apical callus; posterior part of ventral valve strongly thickened. Shell interior with dental plates and ventral adminicula, but no dorsal adminicula. Shell external surface commonly with growth lamellae and capillae, forming subcancellate micro-ornamation; lamellae subimbricate.

### *Remarks*

According to Clarke (1987, 1990), most of the species assigned to *Sulciplica* (and *Tasmanospirifer*) from the Permian of Tasmania consistently have capillae (radial lirae) commonly forming cancellate micro-ornamentation on the shell external surface, together with growth lamellae. Unlike the Tasmanian species (possibly except *Sulciplica*? *phalaena*), our specimens from the Snapper Point Formation do not bear any capillae; their shell surface is ornamented only by growth lamellae, particularly at the anterior part of the shell surface. Unfortunately, we cannot make a conclusion about the question if this dissimilarity in micro-ornamentation was caused by genuine morphological difference or by preservation effects. Therefore, the micro-ornamentation characters have not been used for the classification of *Sulciplica* species, even though they are fully described and discussed below.

Waterhouse (2016) proposed *Angulispirifer* with *Spirifer phalaena* Dana as the type species. However, the morphology of *S. phalaena* appears to be sufficiently covered with the diagnosis of *Sulciplica* (although its micro-ornamentation still requires further investigation; see below) and, consequently, the genus is here synonymized with *Sulciplica*.

**Sulciplica transversa** Waterhouse, 1968
(Figs 13, 15R–AH, 16A–I)

1845 *Spirifer vespertilio*; Morris, p. 282, pl. 17, figs 1, 2; non pl. 17, fig. 3.
1849 *Spirifer vespertilio*; Dana, p. 685, pl. 2, fig. 3a–c.
1965 "*Spirifer*" aff. *vespertilio*?; Waterhouse & Vella, p. 66, pl. 3, figs 1, 2, 4, 5.
1968 *Sulciplica transversa* Waterhouse, p. 27, pl. 16, figs 1, 4.
1983 *Sulciplica transversa*; Waterhouse & Jell, p. 243, pl. 2, figs 2, 3.
1987 *Sulciplica transversa*; Clarke, p. 269, figs 6–8.

### *Diagnosis*

Strongly transverse shell with eight or more plicae (up to 16) on each lateral slope; plication narrow, rounded to subangular, generally simple but very occasionally bifurcated unequally; ventral interarea relatively high; growth lamellae distinct on anterior shell surface.

### *Holotype*

A specimen (USNM PAL 3596) from the Broughton Formation (Westley Park Sandstone Member, Wordian) at Black Head, Gerringong, NSW, Australia. This specimen was originally illustrated as *Spirifer vespertilio* Sowerby by Dana (1849, pl. 2, fig. 3a, b).

### *Referred material*

Nineteen registered specimens: two conjoined shells (AM F.159065, 159066), two external moulds of conjoined shells (AM F.159067, 159068), four internal moulds of conjoined shells (AM F.159069–159072), three ventral valves (AM F.159073–159075), two ventral external moulds (AM F.159076, 159077), three ventral internal moulds (AM F.159078, CPC44489, 44490), a dorsal valve (AM F.159079), a dorsal external mould (AM F.159080), and a dorsal internal mould (AM F.159081).

### *Locality, unit and age*

Snapper Point (GRS30), Crampton Island (GRS15), Banisters Point (L877), Burragorang Valley (L1049, 1050) and Jervis Bay (JB65); upper part of the Snapper Point Formation (early Kungurian), southern Sydney Basin. Wandrawandian Siltstone (late Kungurian to Roadian), Nowra Sandstone (Roadian), and Broughton Formation (Wordian) in southern Sydney Basin. Malbina Formation (Member E, Wordian), Marra Formation (Wordian), Mistletoe Sandstone (Wordian), and Ferntree Formation (Wuchiapingian) in Tasmania Basin (Clarke 1973, 1987). Blenheim Formation (Wordian to Wuchiapingian) in Bowen Basin (Waterhouse & Jell 1983).

### *Description*

Shell medium to large, ranging 21.6–91.5 mm in width, 13–45.6 mm in length (Fig. 13); outline strongly transverse, with width/length ratio ranging 1.640–3.155 (average 2.203); hinge line straight, coincident with greatest width; lateral profile slightly ventribiconvex; cardinal extremities generally alate in adult stage (Fig. 15X).

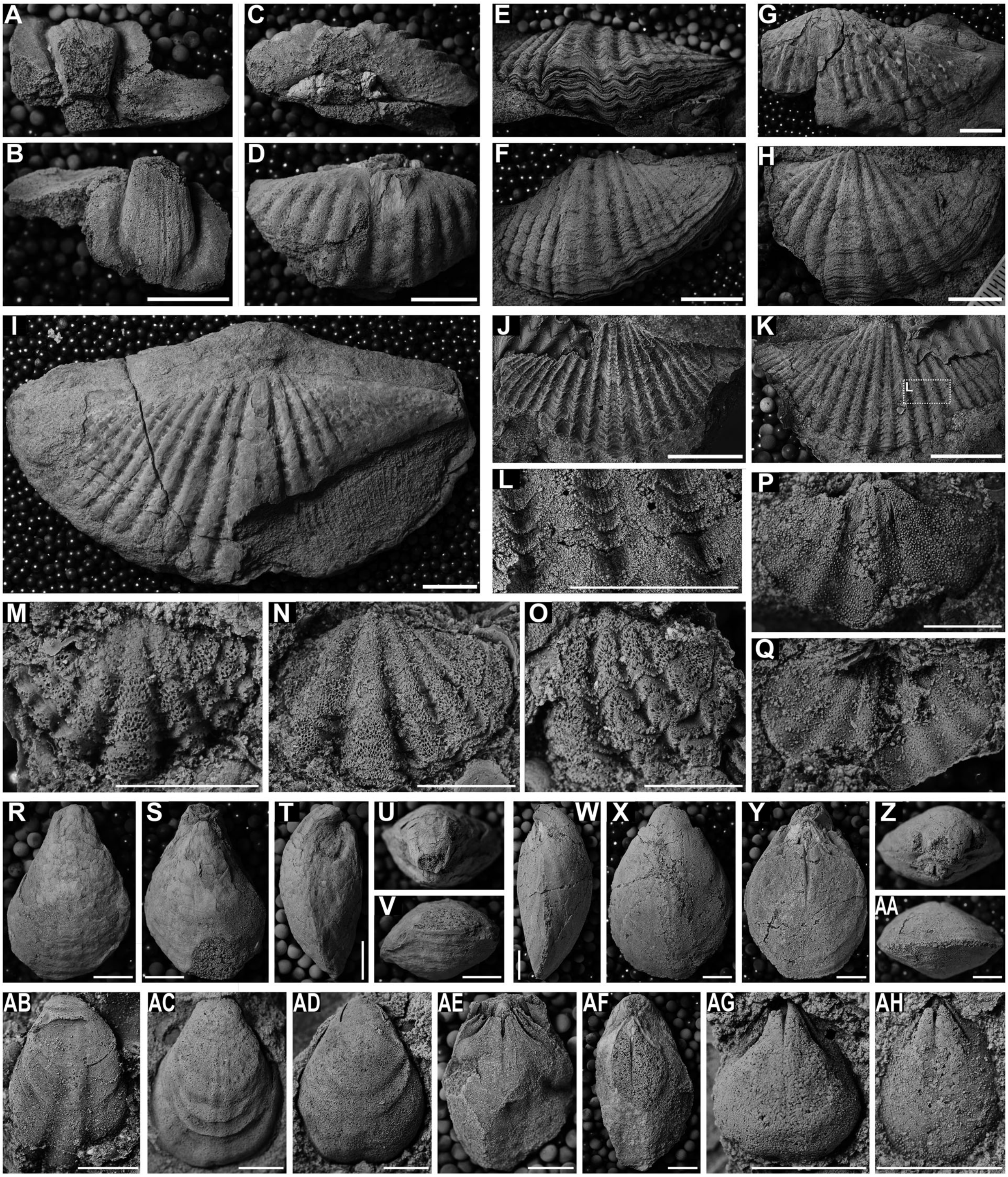

**Figure 16.** **A–I**, *Sulciplica transversa* (Waterhouse, 1968). **A, B**, posterior and ventral views of a fragmentary ventral internal mould (CPC44489) from JB65; **C, D**, posterior and ventral views of a fragmentary ventral internal mould (CPC44490) from JB65; **E, F**, anterior and dorsal views of a latex cast for an external mould of a conjoined shell (AM F.159068) from GRS15; **G**, a ventral valve (AM F.159073) from L1050; **H**, a latex cast of a dorsal external mould (AM F.159080) from L877; **I**, a dorsal view of a conjoined shell (AM F.159066) from L1050. **J–L**, *Sulciplica*? *phalaena* (Dana, 1849). **J, K**, a ventral external mould (AM F.159082) and its latex cast from GRS15, with boxed area of (L); **L**, magnified view of boxed area in (K). **M–Q**, *Pustulospiriferina* cf. *australis* (Maxwell, 1964). **M**, a latex cast of a dorsal external mould (AM F.159083) from L1046; **N**, a latex cast of a dorsal external mould (AM F.159084) from L1046; **O**, a latex cast of a dorsal external mould (AM F.159085) from L1046; **P, Q**, a dorsal internal mould (AM F.159086) and its latex cast from L1046. **R–AH**, *Fletcherithyris biundata* (M'Coy, 1847). **R–V**, ventral, dorsal, lateral, posterior and anterior views of a conjoined shell (CPC44491) from JB65; **W–AA**, lateral, ventral, dorsal, posterior and anterior views of a conjoined shell (CPC44494) from JB65; **AB**, a ventral external mould (AM F.159090) from L1046; **AC**, a ventral internal mould (AM F.159092) from L928; **AD**, a ventral internal mould (AM F.159093) from L1046; **AE**, a dorsal view of an internal mould of a conjoined shell (AM F.159088) from GRS15; **AF**, a dorsal view of a conjoined shell (CPC44492) from JB65; **AG**, a dorsal internal mould (AM F.159100) from L1046; **AH**, a dorsal internal mould (AM F.159101) from L1046. Scales for A–K represent 10 mm, whereas others (L–AH) are 5 mm.

Ventral valve weakly to moderately convex, with slightly incurved beak; ventral interarea moderately to strongly high, reaching one-sixth to one-fifth of valve length, slightly concave, bearing distinct horizontal striations and small pits (Fig. 15X, Y, AH); delthyrium triangular, probably open; sulcus very narrow, shallow to moderately deep, generally having three subplicae (median subplica indistinct); lateral slopes ornamented by numerous plicae (8–16, but generally up to 12 on each side); plications distinct, rounded to subangular, mostly simple without bifurcation or intercalation.

Dorsal valve weakly convex, nearly flat except median fold at posterior part, becoming more convex near anterior margin of lateral slopes; dorsal interarea very low, faintly developed; fold distinct, slight to moderately elevated, with rounded fold crest, bearing two or four subplicae medially divided by median furrow; median furrow on fold shallow, continuously developed from dorsal umbo to anterior edge; dorsal plications identical to ventral ones.

Shell external surface ornamented by concentric growth lamellae; growth lamellae indistinct at posterior part, but becoming distinct, densely spaced and imbricate near anterior margin, having 10–12 lamellae per 5 mm length at anterior margin (Fig. 16E); capillae absent or not preserved.

Ventral interior posteriorly strongly thickened with apical callus; dental plates weakly developed, supported by short to moderate ventral adminicula; external shell plications reflected on anterior part of valve floor; ventral muscle field distinctly incised, elongate oval in outline, with weak striations, anteriorly extending anterior to mid-valve in general; no median septum on ventral floor.

Dorsal interior with short socket plates, without dorsal adminicula (tabellae); spiralia strongly developed, laterally directed, around 30 whorls on each side (Fig. 16I); dorsal muscle field indistinct; dorsal median septum absent.

### *Remarks*

This species is probably conspecific with *Spirifer vespertilio* Sowerby, 1844. However, the original materials of Sowerby's species were neither illustrated nor properly described and, further, they have been known to be missing (see Waterhouse & Vella 1965). Morris (1845) also reported *S. vespertilio* from the Permian of Tasmania, applying Sowerby's name. However, Morris's (1845) specimens seem to represent two different species: *Sulciplica transversa* (pl. 17, figs 1, 2) and *Sulciplica*? *phalaena* (pl. 17, fig. 3) in this study (see below). After all, owing to the ambiguity of Sowerby's original species, Waterhouse (1968) abandoned the name *vespertilio* and replace it with *Sulciplica transversa*, based on the specimens of Dana (1849, pl. 2, fig. 3a, b).

Morris (1845, p. 282, pl. 17, fig. 6) documented another Tasmanian species that has a strongly transverse outline, *Spirifer avicula* Sowerby, 1844. Although it closely resembles *S. transversa* in outline, the specimen of Morris (1845) is distinguished in the fasciculate plication as well as in the absence of a median furrow on the dorsal fold. Based on these features, Clarke (1987) assigned *S. avicula* to *Fusispifer* Waterhouse, 1966 belonging to the Neospiriferinae.

*Sulciplica transversa* has been reported commonly from Guadalupian deposits in eastern Australia, and our specimens from the Snapper Point Formation of the early Kungurian age may represent the earliest occurrence of this species. It is very likely that these strongly transverse shells were evolved from a population of *Sulciplica* sp. reported from the underlying Pebbley Beach Formation by Shi *et al.* (2020, fig. 3R–3V). These shells are also characterized by relatively narrow, simple plicae and two additional lateral subplicae on the fold, but their dorsal fold lacks a distinct median furrow at the anterior part. There is no doubt that *S. transversa* from the Snapper Point Formation is conspecific with its younger Tasmanian representatives figured by Clarke (1987, figs 6–8), but it is still distinguishable by relatively minor differences, such as the dorsal fold with a less distinct median furrow and ventral interarea only with horizontal striations, as well as the absence of capillae (consequently, not yielding cancellate micro-ornamentation).

An older (Asselian or Sakmarian) Tasmanian species *Sulciplica crassa* Clarke, 1990 (p. 64, fig. 8), resembles *S. transversa*, in having a relatively narrow sulcus with three subplicae in general, but *S. crassa* has a less transverse outline and thicker and fewer plications on the lateral slopes. *Tasmanospirifer subglobosa* (Clarke, 1990), also from Tasmania, is comparable to *S. transversa* in our collection, because it lacks capillae on the shell surface. However, its relatively equidimensional outline appears to indicate its closer affinity to *Tasmanospirifer*. *Spirifer phalaena* Dana, 1849 which is temporarily assigned to *Sulciplica* (see below), is similar to *S. transversa* in general features but differs in the less transverse outline and strongly imbricate growth lamellae on the whole shell surface.

**Sulciplica? phalaena** (Dana, 1849)
(Fig. 16J–L)

1845 *Spirifer vespertilio*; Morris, p. 282, pl. 17, fig. 3; non pl. 17, figs 1, 2.
1849 *Spirifer phalaena* Dana, p. 685, pl. 2, fig. 4.
?1965 "*Spirifer*" *phalaena*; Waterhouse & Vella, p. 67, pl. 3, fig. 6.
?1968 ?*Licharewia phalaena*; Waterhouse, p. 24, pl. 16, fig. 2.
1983 *Sulciplica* cf. *phalaena*; McClung, p. 66.
2016 *Angulispirifer phalaena*; Waterhouse, p. 255, fig. 328.

### *Diagnosis*

Moderately transverse shell with 11 to 12 plicae on each lateral slope; plication narrow, subangular, simple; sulcus narrow, bearing median (sub)plica; fold with two (sub)plicae divided by median furrow; growth lamellae strongly imbricate, regularly spaced through whole shell surface; capillae present.

### *Lectotype*

A dorsal valve (BM 8588) from the Malbina Formation (E Member, Wordian) in Eagle Hawk Neck, Tasmania, designated by Waterhouse & Vella (1965). This specimen was

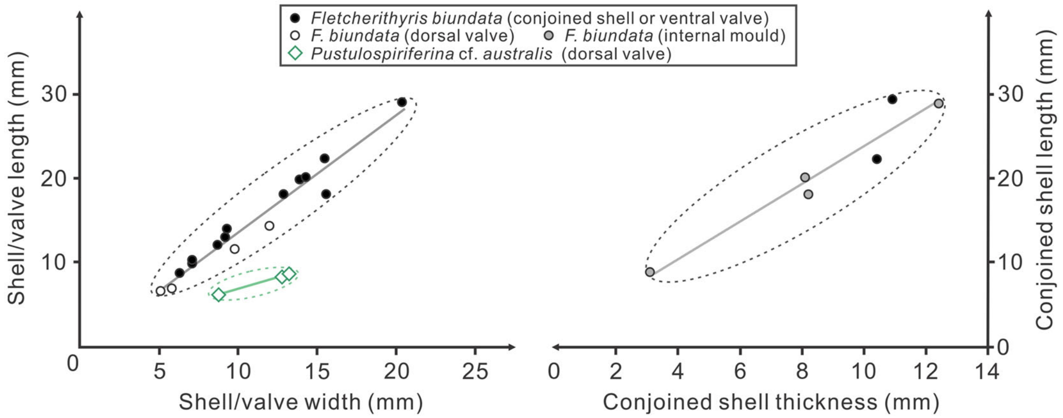

**Figure 17.** Shell measurements of *Pustulospiriferina* cf. *australis* (Maxwell, 1964) and *Fletcherithyris biundata* (M'Coy, 1847) from the Snapper Point Formation. The method of least squares is used for generating regression lines.

originally figured as *Spirifer vespertilio* Sowerby by Morris (1845, pl. 17, fig. 3).

### *Referred material*

A single registered specimen of a ventral external mould (AM F.159082), with a few unregistered fragmentary shells from the localities GRS15, L877, and JB65.

### *Locality, unit and age*

Crampton Island (GRS15), possibly Banisters Point (L877) and Jervis Bay (JB65); upper part of the Snapper Point Formation (early Kungurian), southern Sydney Basin. Broughton Formation (Wordian), southern Sydney Basin (Dana 1849). Malbina Formation (Wordian) in Tasmanian Basin (Morris 1845). GSQ Eddystone 1 core (Intervals B and C) in the Denison Trough in Bowen Basin (McClung 1983). Flowers Formation (Kungurian or Wordian?) of Parapara Group in Nelson, New Zealand (Waterhouse & Vella 1965).

### *Description*

Ventral valve medium-sized (>32 mm wide and 18.2 mm long in ventral external mould), weakly convex; outline moderately transverse, with width/length ratio of 1.8 or higher; hinge relatively extended; sulcus weakly developed, very narrow, bearing distinct median (sub)plica; lateral plications narrow, subangular, mostly simple without bifurcation or intercalation, with 11 or 12 plicae on each side; micro-ornamentation composed of concentric growth lamellae and capillae over whole external surface (Fig. 16J, K); growth lamellae strongly imbricate, regularly spaced in general, having 8–10 lamellae per 5 mm length at mid-valve to anterior margin; capillae fine, very thin, repeatedly interrupted by growth lamellae, weakly preserved only on tiles of imbricate lamellae at interspaces between plicae (Fig. 16L).

### *Remarks*

This species, represented by a single ventral external mould (and a few shell fragments) in our collection, is characterized by its moderately transverse outline, narrow sulcus with a distinct median (sub)plica, and micro-ornamentation composed of distinctly imbricate growth lamellae and weak capillae over the whole shell surface. These features appear to be evidently coincident with those in a dorsal valve referred to as *Spirifer vespertilio* Sowerby by Morris (1845, pl. 17, fig. 3; also illustrated in Waterhouse 2016, fig. 328). The dorsal valve of Morris (1845) was differentiated from *S. vespertilio* and proposed as *Spirifer phalaena* by Dana (1849). Much later, *S. phalaena* was questionably assigned to *Licharewia* Einor, 1939 by Waterhouse (1968), and then to *Angulispirifer* by Waterhouse (2016). However, *S. phalaena* is evidently impunctate and has distinct plication and strongly imbricate growth lamellae which have never been documented in *Licharewia*. In addition, *Angulispirifer* is here considered as a junior synonym of *Sulciplica* (see above).

The narrow and simple plication as well as the narrow sulcus and fold in *S. phalaena* may suggest a possible affinity both to *Sulciplica* or *Tasmanospirifer*. It appears that *S. phalaena* shows an intermediate form between these two genera; its sulcus with a median plica is more approachable to *T. jervisbayensis*, whereas the subangular plication and relatively extended hinge look closer to *S. transversa*. We provisionally assign the species to *Sulciplica*, as the transverse outline is more comparable with *Sulciplica*. *Sulciplica crassa* Clarke, 1990 from the Sakmarian of Tasmania is considerably comparable with *S.*? *phalaena* in the moderately transverse outline and distinct median subplica on the sulcus, but the Sakmarian species of Tasmania has a more convex shell, much coarser plications, and probably more continuous capillae.

There is also a possibility that *S.*? *phalaena* might be more related to another spiriferide group, due to its unique characteristics in shell ornamentation. The micro-ornamentation preserved in our external mould demonstrates distinctly imbricate growth lamellae across the whole shell surface and minute capillae lying on each of the imbricate lamellae (Fig. 16L), which is readily different from those of

*S. transversa* and *T. jervisbayensis* from the Snapper Point Formation in our collection; these two latter species do not bear any capillae on their shell surface, and their growth lamellae are never distinct as much as those of *S.*? *phalaena* (see above). The shell micro-ornamentation of *S. transversa* and its relatives from Tasmania is all known to be dominated by a cancellate pattern, as fully described and illustrated by Clarke (1987, 1990), and they appear to be also inconsistent with that of *S.*? *phalaena*. The shell micro-ornamentation of *S.*? *phalaena* may imply its possible relationship to some taxa of Paeckelmanelloidea Ivanova, 1972 (e.g., *Pterospirifer* Dunbar, 1955, see pl. 22, fig. 23).

Order SPIRIFERINIDA Ivanova, 1972
Suborder SPIRIFERINIDINA Ivanova, 1972
Superfamily PENNOSPIRIFERINOIDEA Dagys, 1972
Family PUNCTOSPIRIFERIDAE Waterhouse, 1975

**Pustulospiriferina** Watehouse in Waterhouse, Campbell & Williams, 1983

### *Type species*

*Punctospirifer etheridgei* Armstrong, 1970c, p. 317 from the Tiverton Formation (Artinskian), in Homevale, Queensland, Australia.

**Pustulospiriferina** cf. **australis** (Maxwell, 1964)
(Figs 16M–Q, 17)

### *Referred material*

Four registered specimens: three dorsal external moulds (AM F.159083–159085) and a dorsal internal mould (AM F.159086).

### *Locality, unit and age*

Burragorang Valley (L1046); lower part of the Snapper Point Formation (early Kungurian), southern Sydney Basin.

### *Remarks*

These four fragmentary specimens exhibit only features of the dorsal valve including small valve size (8.6–13.3 mm wide and 6.5–8.9 mm long; Fig. 17), a transverse valve outline (1.323–1.547 in the ratio of valve width/length), narrow fold with nearly flat crest, three plicae on each dorsal lateral slope, and shell surface covered by distinct growth lamellae and coarse punctae. The dorsal interiors are characterized by a low median septum anteriorly extending to one-third of the valve length and low, slightly divergent dorsal adminicula (Fig. 16P, Q). The punctae are coarsely developed on the external shell surface (Fig. 16M–O), whereas they are preserved in much finer forms on the internal floor (Fig. 16Q). There is also a tendency that they become coarser anteriorly in the external shell. However, these patterns in punctation size might be caused by preservation effects. The density of punctation seems to be relatively consistent among the specimens as well as between the external and internal shells, showing 20–35 punctae per 1 $\text{mm}^2$ in the anterior part to mid-valve.

These morphological characteristics are likely to indicate a close affinity to *Pustulospiriferina*. Among a few species of the genus mainly reported from the Bowen Basin, *Pustulospiriferina etheridgei* (Armstrong, 1970c) from the Tiverton Formation (Artinskian) is comparable in shell ornamentation and punctation density, but it differs in more transverse outline as well as in more plicated lateral slopes. ?*Pustulospiriferina lirata* Waterhouse, 1987 from the Elvinia and Rose's Pride formations (Artinskian?) is also similar in general features but is distinguished in its larger shell size and more densely developed growth lamellae. *Pustulospiriferina australis* (Maxwell, 1964) from the Burnett Formation (Sakmarian) appears to be the most similar to these punctate shells in having a weakly transverse outline, three plicae in each lateral slope, and a low median septum on the dorsal floor.

In spite of the closeness to *P. australis* in the morphology of the dorsal valve, a more adequate comparison is still difficult in view of the paucity of ventral valve and shell micro-ornamentation. Furthermore, the development of shell micro-ornamentation (e.g., capillae, lamellae, and micro-spines) in the species of *Pustulospiriferina* and allied taxa needs to be examined further and more clearly defined for understanding their classification and phylogenetic relationship.

Order TEREBRATULIDA Waagen, 1883

Suborder TEREBRATULIDINA Waagen, 1883
Superfamily DIELASMOIDEA Schuchert, 1913
Family DIELASMATIDAE Schuchert, 1913
Subfamily DIELASMATINAE Schuchert, 1913

**Fletcherithyris** Campbell, 1965

1961 *Fletcherina* Stehli, p. 452 (*non* Lang, Smith & Thomas, 1955).
1965 *Fletcherithyris* Campbell, p. 24.

### *Type species*

*Terebratula amygdala* Dana, 1847, p. 152 (non Catullo, 1846, p. 90) from the Broughton Formation (Westley Park Sandstone Member, Wordian) at Black Head, Gerringong, NSW, Australia (= *Atrypa biundata* M'Coy, 1847).

### *Remarks*

According to Campbell (1965), terebratulides in the Permian of Australia mostly consisted of a few dielasmoid genera which belong either to Dielasmatidae (with dental plates) or to Gillediidae Campbell, 1965 (without dental plates). Among the dielasmatids, the dominant genus is *Fletcherithyris*. This genus is morphologically characterized by its small to medium size, rectimarginate to sulciplicate anterior commissure, well-developed pedicle collar and dental plates, inner hinge plates forming a septalium and a median septum, terebratuliform loop with an incomplete transverse band, and coarse and less densely distributed punctae.

*Fletcherithyris* is superficially indistinguishable from *Dielasma* King, 1859. However, as demonstrated by Stehli (1961) and Campbell (1965), *Fletcherithyris* has its inner hinge plates generally joining to form a septalium on a dorsal median septum. In contrast, the inner hinge plates of *Dielasma* either separately fuse with the dorsal floor or form a sessile setalium without a median septum (Campbell 1965). A Carboniferous cryptonelloid genus *Girtyella* Weller, 1911 has similar cardinal structures with *Fletcherithyris* in having hinge plates supported on a dorsal median septum (see Campbell 1965, text-fig. 6), but the loop of *Girtyella* has a complete transverse band which is missing in *Fletcherithyris*. A genus from the Permian of Western Australia, *Hoskingia* Campbell, 1965, also resembles *Fletcherithyris* in having inner hinge plates which medially join on the dorsal floor and form a setalium, as well as in the absence of a transverse band in the loop. However, *Hoskingia* is much larger than *Fletcherithyris* and, further, it was later classified into Beecheriidae Smirnova, 2004, owing to its weakly developed outer hinge plates. Another Western Australian genus, *Yochelsonia* Stehli, 1961, is distinguished both from *Fletcherithyris* and *Hoskingia*, in a sub-triangular outline, non-labiate foramen, and a loop with a transverse band.

Some other dielasmoid genera without dental plates from Australia and New Zealand, such as *Gilledia* Stehli, 1961, *Paragilledia* Waterhouse in Shi *et al.*, 2020, *Maorielasma* Waterhouse, 1964 (gillediids), *Pseudodielasma* Brill, 1940, and *Marinurnula* Waterhouse, 1964 (pseudodielasmatids), are also comparable with *Fletcherithyris* in external morphology. However, apart from the absence of dental plates, their inner hinge plates never form a septalium supported on a dorsal median septum as in *Fletcherithyris*; the inner hinge plates of *Gilledia*, *Paragilledia*, *Pseudodielasma*, and *Marinurnula* are either absent or joined directly to the dorsal floor, and those of *Maorielasma* are united on the floor forming a sessile septalium without a median septum (see Campbell 1965, text-fig. 1).

Campbell (1965) suggested that the density of punctae could be useful in the taxonomy of terebratulides, in contrary to Percival (1916) who argued that the density of punctae was significantly variant even within a species. According to the punctae measurement of Campbell (1965, p. 8), *Fletcherithyris* has 35–180 (mean 90) punctae per 1 mm$^2$ area, whereas *Dielasma* and *Girtyella* have 150–350 (mean 250) and 180–400 (mean 280) punctae, respectively. Campbell (1965) also considered that the difference in punctation density would be controlled by water temperature because all Australian genera seemed to have much lower punctation densities than Permo-Carboniferous warm-water taxa. Although this interpretation needs to be further investigated, we have confirmed that the size and density of punctae are very consistent among our specimens of *Fletcherithyris*, partially supporting the view of Campbell (1965).

**Fletcherithyris biundata** (M'Coy, 1847)
(Figs 16R–AH, 17)

1847 *Terebratula amygdala* Dana, p. 152 (*non* Catullo, 1846).
1847 *Atrypa biundata* M'Coy, p. 231, pl. 13, fig. 9, 9a.
1849 *Terebratula amygdala*; Dana, p. 682, pl. 1, fig. 2a–c.
1961 *Fletcherina amygdala*; Stehli, p. 453, pl. 61, figs 7, 10, 11, 14, 15, 19–22.
1965 *Fletcherithyris amygdala*; Campbell, p. 26, pl. 3, figs 1–6; pl. 6, figs 11–34; text-figs 7–9.
1982 *Fletcherithyris biundata*; Waterhouse, p. 82, pl. 15, figs e, j; pl. 17, figs a, c.
1987 *Fletcherithyris biundata*; Waterhouse, p. 46, pl. 13, figs 12–16.
1987 *Fletcherithyris biundata*; Clarke, p. 284, fig. 19.

### Diagnosis

As the diagnosis by Campbell (1965, p. 26).

### Nomenclature

This species was originally proposed as *Terebratula amygdala* by Dana (1847). However, as the name *T. amygdala* was preoccupied by Catullo (1846, p. 90), Dana's species name is invalid. This invalidity was first recognized by Finlay (1927, p. 533) in which *Dielasma sacculum bensoni* was proposed as the replacement name for *Dielasma sacculum* (Martin) var. *amygdala* (Dana) described by Dun & Benson (1920, p. 347). [Based on the renaming proposal, Waterhouse (1982, 1987) regarded the species name *bensoni* Finlay, 1927 as the replacement for *amygdala* Dana, 1847 (non Catullo).] However, regardless of the proposal of Finlay (1927), *Atrypa biundata* M'Coy, 1847 (certainly conspecific with *T. amygdala* Dana and proposed a few months later than Dana's species) seems to have a priority for its replacing name, according to Article 23.3.5 of ICZN (1999) that *"the Principle of Priority requires that if a name in use for a taxon is unavailable or invalid, it must be replaced by the next available name from among its synonyms"*. Therefore, *Fletcherithyris biundata* (M'Coy, 1847) is here regarded as the valid name for the species, as in Waterhouse (1982, 1987) and Clarke (1987).

According to Campbell (1957), the terebratulide specimens from the Burindi Group in NSW (Carboniferous) referred to *D. sacculum* var. *amygdala* by Dun & Benson (1920), clearly differ from *T. amygdala* Dana (=*Fletcherithyris biundata*) and the Burindi Group specimens were assigned to *Balanoconcha elliptica* Campbell, 1957.

### Lectotype

Two different lectotypes were historically proposed for this species. A conjoined shell (USNM PAL 3597 b) from the Broughton Formation (Westley Park Sandstone Member, Wordian) in Black Head, Gerringong, NSW, Australia was designated as the lectotype of *T. amygdala* Dana (non Catullo) by Campbell (1965, pl. 6, figs 15–18; see also Dana 1849, pl. 1, fig. 2a–d). Later, due to the invalidity of Dana's species, Waterhouse (1982) designated another lectotype

(SM E10590) among the specimens of *Atrypa biundata* M'Coy, 1847 (figured in pl. 13, fig. 9, 9a) also collected from the Broughton Formation in Black Head.

It is certain that *amygdala* Dana (non Catullo) was and is a real (if invalid) taxon, and that its type specimen (lectotype) was fixed earlier by Campbell (1965), even though the name of the species has changed to *biundata* M'Coy. Therefore, it seems that the lectotype selected by Campbell (1965; USNM PAL 3597b) should have a priority as the type specimen of *F. biundata* if the synonym is agreed upon.

### Referred material

Twenty-three registered specimens: three conjoined shells (CPC44491–44493), an external mould of a conjoined shell (AM F.159087), four internal moulds of conjoined shells (AM F.159088, 159089, CPC44494, 44495), two ventral external moulds (AM F.159090, 159091), seven ventral internal moulds (AM F.159092–159098), a dorsal external moulds (AM F.159099), and five dorsal internal moulds (AM F.159100–159104). Several unregistered specimens: small fragmentary external and internal moulds preserved on slabs from L1046.

### Locality, unit and age

Grassy Gully (GRS158/159 =L928), Burragorang Valley (L1046), Jervis Bay (JB65), and Crampton Island (GRS15); Snapper Point Formation (early Kungurian), southern Sydney Basin. Black Head in Gerringong; Broughton Formation (Westley Park Sandstone Member, Wordian), southern Sydney Basin. Jerrawangala; probably Wandrawandian Siltstone (late Kungurian to Roadian), southern Sydney Basin. Bank of Hunter River in Glendon Homestead; Muree Sandstone (Guadalupian), northern Sydney Basin. Font Hill Shaft near Maitland; lower part of Branxton Formation (Wordian), northern Sydney Basin (Campbell 1965). Southeast Queensland; Barfield and Flat Top formations (late Kungurian to Roadian), southern Bowen Basin (Waterhouse 1987). Yellow Point, Birchs Bay; Abels Bay Formation (Wordian to Capitanian), Tasmania Basin (Clarke 1987). Letham Burn (GS6071) in Southland, New Zealand; upper Mangarewa Formation (Capitanian) (Waterhouse 1982).

### Description

Shell small to medium-sized, ranging 6.3–20.4 mm in width, 8.8–29.3 mm in length, and 3.1–12.5 mm in thickness of conjoined shells (Fig. 17); outline elongate oval, with width/length ratio ranging 0.664–0.867 (average 0.718); maximum shell width generally anterior to mid-shell; lateral profile biconvex, with slightly sinuate lateral commissures; anterior commissure rectimarginate to weakly sulciplicate.

Ventral valve moderately to strongly convex, with maximum convexity at umbonal region; foramen round, permesothyrid and labiate, around 3.1 mm in width diameter in adult specimens, directing posterodorsally; ventral umbo narrow, suberect; median fold absent or weakly developed in general; ventral shell surface commonly ornamented by a few concentric lamellae (or wrinkles) more populated anteriorly (Fig. 16AC, AD); punctae relatively coarse, consistently developed across valve, generally numbering 50–60 per 1 $mm^2$ on mid-valve surface.

Dorsal valve similarly or slightly less convex than ventral valve, with uniform convexity across valve; median sulcus indistinct, weakly developing only when ventral median fold exists; shell ornamentation of dorsal valve identical to ventral one.

Ventral interior with strongly developed pedicle collar; dental plates formed variably, from closely spaced, parallel to slightly divergent ones (Fig. 16R) to widely spaced, strongly divergent (Fig. 16AD), but generally reaching one-sixth of whole valve length; muscle scars and pallial markings ill-defined.

Dorsal interior with highly developed inner socket ridges forming deep sockets; inner hinge plates medially uniting to form septalium consistently supported on median septum (Fig. 16Y); length of septalium around one-fifth of dorsal valve length; height of septalium (and median septum) from valve floor increasing anteriorly; median septum becoming rapidly low at anterior margin of septalium and further anteriorly extending to mid-valve floor (Fig. 16Y, AE–AG); muscle scars lacrimate in outline, weakly defined laterally and anteriorly, reaching mid-valve floor (Fig. 16AF–AH).

### Remarks

The specimens in hand can be comparable with *Fletcherithyris biundata* in shell size and convexity, rectimarginate to weakly sulciplicate anterior commissure, narrowly developed ventral umbo, and well-developed pedicle collar and dental plates. Moreover, all our dorsal internal mould specimens consistently exhibit the formation of a septalium supported on a median septum on the dorsal floor (see Fig. 16Y, AF–AH). Additionally, the punctation density of our specimens (50–60 punctae per 1 $mm^2$ in adult specimens) is also well-matched with that of *F. biundata* given by Campbell (1965; 40–60). It is also worth noting that Campbell (1965, p. 32) included some specimens from Jervis Bay (all numbered AM F263) in *F. biundata* and these specimens likely came from the same locality as our GA JB65, in consideration of the fact that our JB65 collection was originally made by J.M. Dickins (see Perry & Dickins 1952) and many of Campbell's (1965) materials were supplied by him.

Campbell (1965) also described three other species of *Fletcherithyris* from the southern Sydney Basin, including *F. canni* Campbell, 1965, *F. illawarrensis* Campbell, 1965, and *F. parkesi* Campbell, 1965. The morphology of these species is considerably overlapped with that of *F. biundata* and they are distinguishable only in minor morphological differences. *Fletcherithyris canni* probably from the lower part of the Nowra Sandstone (Roadian; see Fig. 2) at Culburra Headland (now Penguin Head) has a broader outline and its septalium seems to be positioned more highly from the dorsal floor and relatively shorter in length. *Fletcherithyris illawarrensis* from the Wandrawandian Siltstone (late

Kungurian to Roadian; see Fig. 2) at Wyro (Lagoon Head) is distinguished in its stronger shell convexity and in having more distinct ventral fold and dorsal sulcus which consequently form uniplicate anterior commissure. *Fletcherithyris parkesi* was reported to have come from a wide range of localities in the Sydney, Bowen and Tasmania basins; it is characterized by the most strongly plicated shell among all of the *Fletcherithyris* species, featuring a strongly sulciplicate anterior commissure. Most of our specimens from the Snapper Point Formation can be evidently separated from the three species, while a few external mould specimens of disarticulated valves from L1046 preserve somewhat stronger plication (Fig. 16AB). Although these more plicated specimens might suggest their possible affinity to *F. parkesi*, they are here considered as intraspecific variations within *F. biundata*, owing to the absence of shells showing distinctly sulciplicate anterior commissure (which is another diagnostic characteristic of *F. parkesi*).

*Fletcherithyris farleyensis* Campbell, 1965 from the Farley Formation (Artinskian) of the northern Sydney Basin at Farley, NSW, appears to be most similar to *F. biundata*. All external features of *F. farleyensis* are nearly identical to those of *F. biundata*, but the former is different internally in having a sharply V-shaped septalium in cross-section and a lower dorsal median septum. *Fletcherithyris farleyensis faba* Campbell, 1965 and *F. burdenae* Waterhouse, 2015, both from the Tiverton Formation (Sakmarian) of the northern Bowen Basin, also resemble *F. biundata* in general features, but they have a more flattened umbonal region on their ventral valve. *Fletcherithyris galbina* Waterhouse, 1982 from the upper Mangarewa Formation (Capitanian) in New Zealand, is comparable in size but differs in having a less convex and more elongated shell.

Our discovery of *F. biundata* from the Snapper Point Formation probably records the oldest occurrence of this species, suggesting that it may have dwelled in the southern Sydney Basin, at least, since the early Kungurian. Because there were other pre-existing species of *Fletcherithyris* (e.g., *F. farleyensis*, *F. burdenae*, and *F. parkesi* during Sakmarian to Artinskian) in other basins of eastern Australia, it is likely that *F. biundata* was evolved from one of the congeneric species *via* migration to the southern Sydney Basin. If Campbell's (1965) interpretation that *F. biundata* and *F. farleyensis* belonged to the same stock of *Fletcherithyris* lineage is correct, *F. biundata* might have originated from a population of *F. farleyensis* since the population migrated southward probably with the transition from glacial (P2) to interglacial interval around the Artinskian–Kungurian boundary (see Fig. 2).

## Results

Based on 188 fossil brachiopod specimens examined (see Supplemental material for the details of registered specimens), a total of 12 species belonging to 11 genera and an indeterminate ingelarellid are identified from the Snapper Point Formation (SPF).

### Stratigraphic correlations of the SPF brachiopods

For the biostratigraphic correlation of the brachiopod species, a composite columnar section of the SPF (Fig. 3) was prepared from the stratigraphic logs by Gostin & Herbert (1973, figs 8–10). The stratigraphic positions of the coastal fossil localities between Clear Point and Bannister Point (GRS15, GRS30, GRS34 =L870A, GRS42, L877; see Fig. 1C) were directly marked on the composite column, whereas the stratigraphic positions of the inland fossil localities (GRS158/159 =L928, L1046, L1049, L1050, L1052, JB65; see Fig. 1B) were shown as approximately equivalent levels in the composite columnar section based on the correlations by Runnegar (1980) as well as from our fieldwork experience. As a result, each of the fossil localities is considered to represent a unique biostratigraphic horizon (Fig. 3), and the succession of these fossil localities collectively constitutes the most comprehensive brachiopod biostratigraphic sequence known to date for the SPF. As an exception, the stratigraphic positions of two UNE localities (L1049 and L1050, both in the Burragorang Valley) are considered to be at the nearly same horizon in the relatively upper part of the SPF (see Fig. 3), although Runnegar originally noted that these localities were geographically separated. We grouped these two localities together because the lithology, species contents, and preservation features shown in the fossil materials from both localities are identical (see Table 1).

### Two brachiopod assemblages recognized from the SPF

According to our composite biostratigraphic occurrence chart (Fig. 3), most of the brachiopod horizons are distributed stratigraphically either in the lower part of the formation or in the upper part. And these lower and upper brachiopod-bearing parts are distinctly separated by an extensive (>100 m thick) scarcely fossiliferous interval in the middle which is dominated by coarse sandstones and pebbly conglomeratic layers.

The lower part of the SPF contains four brachiopod fossil horizons (localities), GRS34 (=L870A), L1046, GRS158/159 (=L928), and GRS42, in ascending order. Except for the uppermost horizon in the lower part (GRS42) which provided only a few shells (three registered specimens), the other three horizons share several species which form a brachiopod assemblage for the lower part of the formation. Among nine brachiopod species that were found in the three horizons of this assemblage, three species (*Notospirifer* cf. *triplicata*, *Simplicisulcus* sp., and *Tasmanospirifer jervisbayensis*) occur in all of the horizons, and two species (*Ingelarella* sp. and *Fletcherithyris biundata*) were discovered from the two upper ones [L1046 and GRS158/159 (=L928)] (Fig. 3). *Strophalosia yalwalensis* is identified only from the locality GRS158/159 (=L928) in this study, but it was also reported from the locality L1046 by Briggs (1998). Because some of these common species (*T. jervisbayensis*, *Ingelarella* sp. and *F. biundata*) in the lower part of the formation are also found in the localities representing the upper part, the other species (*N.* cf. *triplicata*, *Simplicisulcus* sp. and, possibly, *S. yalwalensis*) can be considered the more characteristic species of these horizons. This brachiopod assemblage from the lower part of the SPF is therefore named *Notospirifer* cf. *triplicata*–*Simplicisulcus* sp. Assemblage.

This assemblage also contains a few extra brachiopod taxa. *Pustulospiriferina* cf. *australis* and Ingelarellidae indet. were each discovered exclusively from a single locality, GRS34 and L1046, respectively (Fig. 3). *Glendonia ulladullensis* was found rarely from L870A in the lower part and L1052 in the upper part of the SPF; it is a common species in the overlying Wandrawandian Siltstone (McClung & Armstrong 1978).

The upper assemblage of the SPF is composed of six brachiopod fossil horizons including the stratigraphically well-defined localities among the coastal outcrops (GRS15, GRS30, L877 and JB65), as well as inland localities of L1049/1050 and L1052 whose stratigraphic position is less certain (Fig. 3). Most of these fossil horizons are clearly distinguished from those in the lower part of the SPF in bearing two unique species, *Johndearia brevis* and *Sulciplica transversa*. Therefore, the brachiopod assemblage from these upper horizons is here named the *Johndearia brevis*–*Sulciplica transversa* Assemblage. In addition to the two most representative species, *Sulciplica*? *phalaena* seems to also occur only from this assemblage (three uppermost horizons; see Fig. 3).

On the other hand, two species common in the *N.* cf. *triplicata*–*Simplicisulcus* sp. Assemblage (at the lower part of the SPF), *T. jervisbayensis* and *F. biundata*, are frequently found in the *J. brevis*–*S. transversa* Assemblage (Fig. 3). In addition, the stratigraphic range of *Ingelarella* sp. generally found in the lower assemblage also extends to the bottom of the upper assemblage (GRS30), as is *G. ulladullensis* found in L1052.

Finally, it is notable that *Wyndhamia* cf. *typica*, represented by two specimens, is found only in two fossil localities (GRS30 and GRS42) in the middle part of the SPF, without demonstrating any strong association with either of the two brachiopod assemblages described above.

## Discussion

### Age assignment

The overall age of the Snapper Point Formation (SPF) has been constrained to the early Kungurian, based on a SHRIMP U-Pb zircon age of 278.9 ± 3.7 Ma recently obtained from a syndepositionally intruded magmatic body (Shi *et al.* 2022a). Thus, the age of the SPF brachiopod fauna is also deemed to be early Kungurian. This age assignment is different to Metcalfe *et al.* (2015) and Smith *et al.* (2017) who both assigned the SPF to the Roadian based on palynobiostratigraphy, and to Garbelli *et al.* (2019) who proposed a late Kungurian-Wordian age range for the SPF based on strontium isotope values from Permian brachiopod shells.

### Biozonal correlations

Based on occurrences of some selected common and diverse brachiopod taxa in the Permian of eastern Gondwana margin (e.g., strophalosids and ingelarellids), several biozonal schemes have been contrived. For example, Runnegar & McClung (1975) suggested 10 biozones for the Permian of eastern Australia on the basis of the supposed ingelarellid lineage. Briggs (1998) proposed 21 biozones mostly with strophalosid brachiopods. Waterhouse (2008) suggested a more complicated biozonation scheme that adopts different subzones for different basins and geographic areas, utilizing both brachiopod and bivalve faunas.

Despite the scarcity of fossils in the SPF, the biozone schemes of the previous studies were also applied to the formation. Runnegar & McClung (1975) and Runnegar (1980, fig. 20.1) suggested that two biozones would be placed in the SPF: the "*Martiniopsis*" *ovata* Zone to the base of the SPF and "*Martiniopsis*" *brevis* Zone to the remaining (upper) stratigraphic interval. On the other hand, the entire SPF was ascribed to the *Echinalosia maxwelli* Zone by Briggs (1998) and to the *Wyndhamia typica* Zone by Waterhouse (2008), respectively (see Fig. 3).

The determination of early Kungurian age for the SPF, based on a SHRIMP U-Pb zircon age of 278.9 ± 3.7 Ma (Shi *et al.* 2022a), has significant implications for constraining the ages of the biozones. Assuming a validity for their correlations, the ages of all the brachiopod biozones would be constrained in the early Kungurian, although the biozone from the basal part of the SPF ("*M.*" *ovata* Zone) could originate in the late Artinskian (as the zone starts from the middle part of the underlying Pebbley Beach Formation).

Combined with the age constraints, our biostratigraphic results indicate that some minor revisions or re-interpretations would be required for the biozones in the SPF. Runnegar (1980, fig. 20.1) regarded the "*M.*" *brevis* Zone as commencing from near the bottom of the SPF; however, our result demonstrates that the lower boundary of this biozone (represented by the first occurrences of *Johndearia brevis*) needs to be moved to the upper part of the SPF, to coincide with the stratigraphic commencement of the *J. brevis*–*S. transversa* Assemblage (Fig. 3). On the other hand, the underlying "*M.*" *ovata* Zone that was thought to immediately underlie the "*M.*" *brevis* Zone in the southern Sydney Basin (SSB) by Runnegar (1980) has not been confirmed by this study. The "*M.*" *ovata* Zone was shown to occur between the middle part of the Pebbley Beach Formation and the base of the SPF in the SSB by Runnegar (1980, fig. 20.1), but "*Martiniopsis*" *ovata* (considered as *Ambikella ovata* in this paper) is, in fact, neither present in the Pebbley Beach Formation (see Shi *et al.* 2020) nor found in the SPF, despite the report of McClung (1978) mentioning the rare occurrence of this species in the Pebbley Beach Formation.

Briggs (1998) reported the occurrences of *Strophalosia yalwalensis* and *Wyndhamia typica* in the SPF, placing the entire SPF into a single strophalosid biozone known as the *E. maxwelli* Zone. Although the recognition of this zone in the SPF is supported by our study, it is worth noting that *S. yalwalensis* is found only in the lower part of the SPF while *W. typica* rarely occurs only in the middle part (Fig. 3). Therefore, it would be difficult to conclude that the SPF corresponds to the *E. maxwelli* Zone. In this context, a similar note should also be mentioned with regard to the *W. typica* Zone of Waterhouse (2008) that was proposed to accommodate the brachiopod fauna of the entire SPF and considered to be of Kungurian age. Obviously, this claim also cannot be fully supported by the present study as the eponymous species (*W. typica*) is absent in the *Notospirifer* cf. *triplicata*–*Simplicisulcus* sp. Assemblage (Fig. 3). [However, it needs to be noted also that both Briggs (1998) and our study have not identified any *Wyndhamia* among the specimens collected from the Grassy Gully locality (L928), whereas Waterhouse (2001) considered some of them as *W. typa*.] In short, regardless of either designating the brachiopod fauna of the SPF to the *E. maxwelli* Zone or the *W. typica* Zone, it is apparent that the fauna as a whole is stratigraphically heterogeneous and, at least locally, contains two distinct assemblages.

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## Supplemental data

Supplemental data for this article is available online at https://10.1080/03115518.2022.2151045.

## Zoobank UUID

http://zoobank.org/E97CBD9E-B48F-443E-8FF6-29D7E1B00331.

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