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The oldest brachiopods from the lower Cambrian of South Australia

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The morphology and organophosphatic shell structure of the paterinate brachiopod *Askepasma* is documented using new and previously collected specimens from the lower Cambrian of South Australia. Lack of adequately preserved material has seen the majority of paterinate specimens previously reported from South Australia referred to the genus *Askepasma* and treated under open nomenclature. Large collections of paterinates from the lower Cambrian Wilkawillina, Ajax, and Wirrapowie limestones in the Arrowie Basin, South Australia have prompted redescription of the type species *Askepasma toddense* and the erection of a new species, *Askepasma saproconcha* sp. nov. *Askepasma saproconcha* sp. nov. currently represents the oldest known brachiopod from the lower Cambrian successions in South Australia with a FAD in pre-trilobitic (Terreneuvian, Cambrian Stage 2, lower Atdabanian) strata in the basal part of the Wilkawillina and Wirrapowie limestones. *Askepasma toddense* predominantly occurs in *Abadiella huoi* Zone equivalent strata (Unnamed Cambrian Series 2, Stage 3, middle–upper Atdabanian) in the upper part of the lower Wilkawillina, Wirrapowie, and Ajax limestones. The shell microstructure of *Askepasma* suggests a proximal stem group position within the Brachiopoda and similarities with tommotiid taxa provides further evidence that the ancestry of crown group brachiopods is firmly entrenched within the Tommotiida.

Key words: Brachiopoda, Tommotiida, Paterinida, *Askepasma*, microstructure, Flinders Ranges, Arrowie Basin, lower Cambrian, South Australia.

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Introduction

Paterinates are one of the oldest brachiopod groups including the genera *Aldanotreta* and *Cryptotreta* (Pelman 1977) that were widespread during the early Tommotian within the transitional zone of the Siberian Platform (Pelman 1977; Ushatinskaya 2008). Although, their position as the oldest brachiopods has recently been challenged by the chemostratigraphic correlation of Mongolian sections placing the problematic kutorginid *Khasagtina* in the Nemakit–Daldy-

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nian (Kouchinsky et al. 2010; Maloof et al. 2010; see also Popov and Williams 2000: 214), the early origins of paterinates ensure that they are vital in our understanding of brachiopod evolution and phylogeny. Paterinates in general display a peculiar mosaic of morphological characteristics, linking them to both the linguliform and rhynchonelliform brachiopods (see Williams et al. 1998 for review). This has led to some uncertainty regarding their exact phylogenetic position within the Brachiopoda. Based on studies of the organophosphatic shell structure in paterinates, Williams et al. (1998) inferred that the group may have retained several plesiomorphies from the brachiopod stem group, such as attachment to the substrate by means of a cuticular pad from the ventral mantle, fused mantle lobes, vascula terminalia bifurcating peripherally and vestigial diductor muscles.

Of the early Tommotian Siberian species, only *Aldanotreta* was treated as a paterinid, until Pelman (1979) erected the Cryptotretidae to include *Cryptotreta*, assigning the new family to the Order Paterinida. Over the next two decades the family expanded to include three additional genera, *Salanygolina* Ushatinskaya, 1987; *Dzunarzina* Ushatinskaya, 1993; and *Askepasma* Laurie, 1986 following discoveries from the lower Cambrian of Mongolia (Ushatinskaya 1987, 1993) and Australia (Laurie 1986). However, the exact relationship between members of the Cryptotretidae is difficult to establish, with the majority of genera based on limited specimens, many of which are inadequately illustrated and require revision. A recent redescription of *Salanygolina* by Holmer et al. (2009) resulted in the placement of *Salanygolina* to a new family, the Salanygolinidae, based on the presence of a colleplax and an amalgam of chileate and paterinate character states. Williams et al. (1998) considered *Dzunarzina* to be synonymous with *Askepasma* and the reported presence of a possible ventral perforation in the type genus *Cryptotreta* places some doubt over its affinities (Holmer et al. 2009: 4). *Askepasma* displays characters typical of paterinids; however, the genus will be treated here with the family-level left open due to the uncertainties surrounding the status of the Cryptotretidae.

The paterinid genus *Askepasma* was erected by Laurie (1986) based on specimens from the lower Cambrian Todd River Dolostone in the eastern Amadeus Basin, Northern Territory, central Australia. Since then, specimens of *Askepasma* have featured in a number of taxonomic and biostratigraphic publications and on every occasion the specimens have been treated in open nomenclature. Ushatinskaya and Holmer in Gravestock et al. (2001: 122, pls. 15: 1–10, 16: 1–9) illustrated a number of etched specimens, from both the Stansbury and Arrowie basins of South Australia. The largely fragmentary collection displayed an apparent wide range of morphological variation prompting Ushatinskaya and Holmer in Gravestock et al. (2001) to refer to all specimens as *Askepasma*? sp. Holmer et al. (2006) analysed the organophosphatic shell structure of acid-etched *Askepasma* specimens from the Wirrapowie Limestone in the southern Arrowie Basin and referred the specimens to *Askepasma* sp., recognising morpho-

logical similarities with the specimens reported by Ushatinskaya and Holmer in Gravestock et al. (2001). In a review of Cambrian biostratigraphy in South Australia, Jago et al. (2006) reported the presence of two paterinid taxa, identified as *Askepasma* sp. A and sp. B, respectively. *Askepasma* sp. A was reported from the pre-trilobitic strata in the basal parts of the Wilkawillina and Wirrapowie limestones; the slightly younger *Askepasma* sp. B was reported to be restricted to *Abadiella huoi* Trilobite Zone equivalent strata in the upper part of the lower Wilkawillina Limestone (Jago et al. 2006). Peng et al. (2010: pl. 3: 1–12) described a new species of *Askepasma*, the first documentation of the genus outside of Australia, *A. transversalis* from the lower Cambrian Balang Formation of eastern Guizhou, extending the geographic range of the genus to include South China.

Balthasar et al. (2009) recently demonstrated a close similarity between the shell microstructure of paterinid brachiopods (*Askepasma* cf. *toddense*) and two early Cambrian tommotiid taxa, *Paterimitra* Laurie, 1986 and *Eccentrotheca* Landing, Nowlan, and Fletcher, 1980. The link between tommotiids and lophophorates is not a new concept having been suggested over 30 years ago (Bengtson 1977), an association that was predominantly based on morphological similarities between the two groups (Skovsted et al. 2009a). The microstructural similarities between the tommotiid taxa and *Askepasma* (Balthasar et al. 2009) together with morphological evidence from partially articulated scleritome material (Skovsted et al. 2008, 2009b, 2011) provided strong evidence that tommotiids constitute the basal stem group of the Brachiopoda. The unique shell microstructure shared by tommotiids and *Askepasma* left Balthasar et al. (2009) with little doubt that tommotiid sclerites represent the precursors of brachiopod shells. The purpose of this study is to resolve the taxonomic problems associated with the paterinid *Askepasma*, including a redescription of the type species, *Askepasma toddense,* and the erection of a new species, *Askepasma saproconcha* sp. nov. The shell microstructure of the genus is also documented and shows clear similarities to the shell microstructure of selected tommotiid taxa-strengthening the view that *Askepasma* and probably paterinids in general might better be interpreted as holding a position in the proximal stem group to all brachiopods.

Institutional abbreviation.—SAMP, South Australian Museum, palaeontological collection, Adelaide, Australia.

Material, geological and geographical setting

The specimens of *Askepasma* described herein are derived from spot localities and samples collected along measured stratigraphic sections through transgressive to highstand system tract deposits in the Hawker Group (Gravestock and Cowley 1995; Gravestock and Shergold 2001; Zang 2002; Zang et
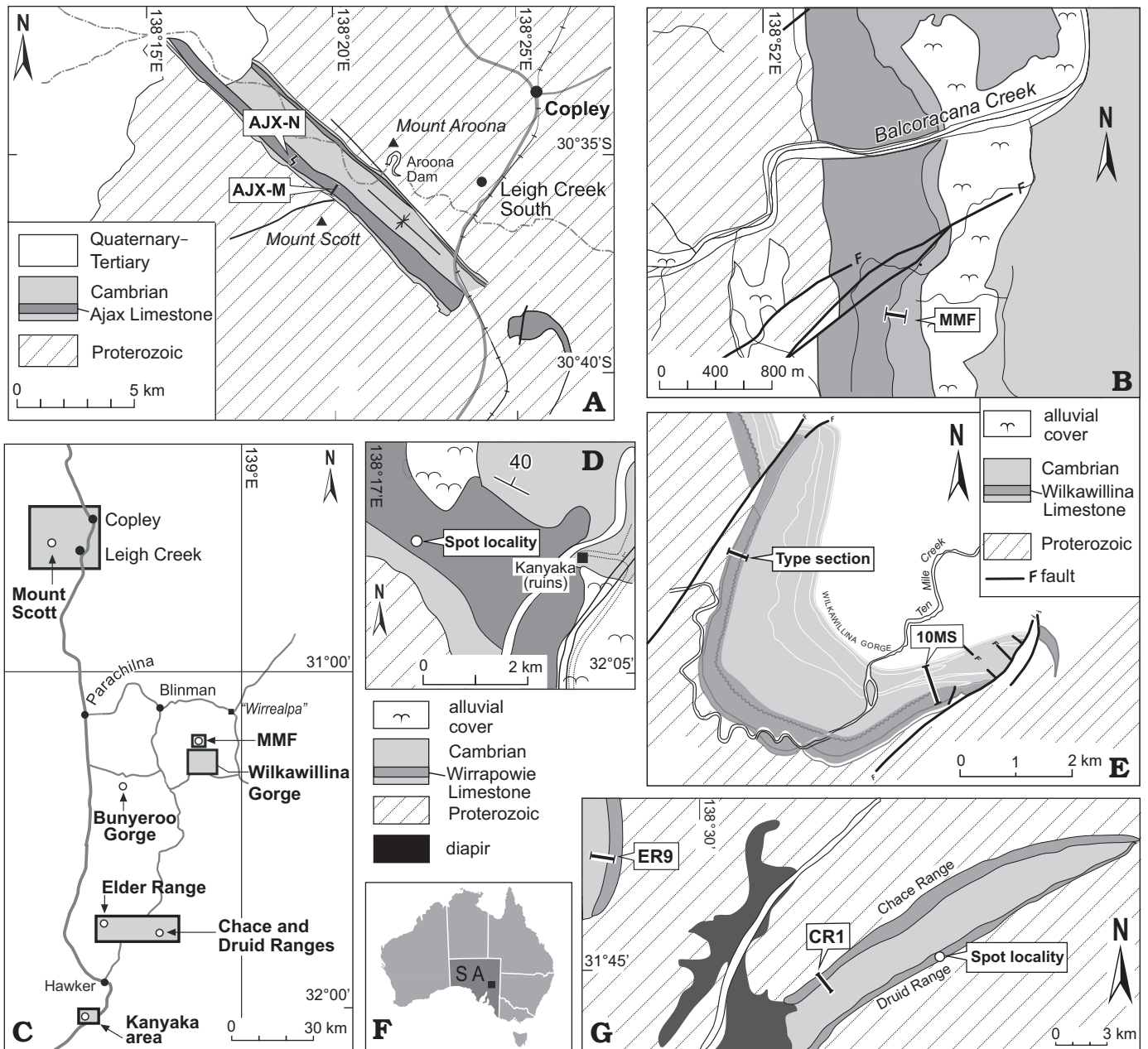
Fig. 1. Locality and geological maps showing position of sampled stratigraphic sections and spot localities. **A**. Mount Scott area with positions of sections AJX-M and AJX-N. **B**. Bunkers Range showing location of section MMF. **C**. Geographical position of localities in the Flinders Ranges. **D**. Location of spot sample taken near the Kanyaka ruins. **E**. Bunkers Graben, showing location of section 10MS and the Wilkawillina Type Section. **F**. General position of field area in South Australia. **G**. Chace, Druid, and Elder ranges, showing position of sections ER9 and CR1 and spot locality in the Druid Range.

al. 2004) that crop out in the Chace and Druid Range, Elder Range, Bunkers Range, Bunkers Graben and Mount Scott Range in the Arrowie Basin (Fig. 1). These thick carbonate-dominated successions predominantly represent shallow-water, carbonate platform (Wilkawillina, Wirrapowie, and Ajax limestones) through to transitional outer shelf environments (lowermost Mernmerna Formation). The majority of stratigraphic sections mentioned herein have previously been described in some detail by numerous authors (e.g., Paterson and Brock 2007; Skovsted et al. 2011; Topper et al. 2011a, b) and need only be summarised here.

Wilkawillina Limestone.—The specimens are derived from two main stratigraphic sections. The first locality is situated near the top of the Wilkawillina Limestone just below the "reddened" microstromatolitic horizon at sample horizon MMF/0.0 (*Abadiella huoi* Trilobite Zone). This stratigraphic level correlates with the base of the MMF section located approximately 1 km south of Balcoracana Creek on the eastern side of the Bunkers Range (base at coordinates: 31°11'38.4" S, 138°52'28.7" E; map datum: WGS84) (Fig. 1B). This horizon has also yielded articulated specimens of the tommotiids *Eccentrotheca* (Skovsted et al. 2008; 2011) and

Paterimitra (Skovsted et al. 2009b). A second stratigraphic section, 10MS (Fig. 1E), is located on the south-eastern limb of the Bunkers Graben (base at coordinates: 31°17'42.8" S, 138°56'02.1" E; map datum: WGS84) close to the section line originally measured by Walter (1967: figs. 1, 2) and close to the eastern margin of the platform sequence where the upper Wilkawillina Limestone interfingers with the Mernmerna Formation as detailed by Clarke (1990: figs. 1–3). Specimens of *Askepasma toddense* occur in the Hideaway and Winnitinny Creek members of the Wilkawillina Limestone and extend into the lowermost Six Mile Bore Member of the overlying Mernmerna Formation. Trilobites are yet to be recorded from the Wilkawillina Limestone and lowermost Mernmerna Formation at section 10MS, with the first trilobite, *Eoredlichia shensiensis* Zhang, 1966 typifying the *Pararaia tatei* Zone occurring in the overlying Linns Springs Member of the Mernmerna Formation. *Askepasma toddense* co-occurs with characteristic *Abadiella huoi* Zone tommotiids, *Eccentrotheca helenia* Skovsted, Brock, Topper, Paterson, and Holmer, 2011, *Paterimitra pyramidalis* Laurie, 1986, and the tannuolind *Micrina etheridgei* (Tate, 1892) and based on the coeval faunal assemblage correlation with the *Abadiella huoi* Zone is most probable. *Askepasma* specimens do occur in the Wilkawillina Limestone in both the Bunyeroo Gorge Section (Fig. 1B) collected by David Gravestock in 1982 and the Wilkawillina Limestone Type Section (Fig. 1C) in the north-western Bunkers Graben originally collected by Brian Daily in 1969, however, specimens are fragmentary and none are illustrated herein.

A number of specimens were collected from the Wilkawillina Limestone at a single spot locality on the Narina road, south of Warragee Bore (coordinates: 31°01'20.892" S; 138°47'12.192" E; map datum: WGS84). The lack of trilobites at this locality suggests a pre-*Abadiella huoi* age.

Ajax Limestone.—Material is derived from two separate stratigraphic sections in the Mount Scott Ranges, central Flinders Ranges (Fig. 1A); AJX-M (base at coordinates: 30°35'49" S, 138°19'59.3" E; map datum: WGS84) and AJX-N (base at coordinates: 30°35'07.3" S, 138°18'56.5" E; map datum: WGS84). Both sections reveal a very similar outcrop succession, with AJX-N located approximately 2 km north-west of AJX-M (Fig. 1A). *Askepasma toddense* specimens are restricted to grey to buff coloured, thin nodular limestone beds that can be confidently equated with the *Abadiella huoi* Trilobite Zone due to the presence of the eponymous species (Topper et al. 2011a, b; Skovsted et al. 2011).

Wirrapowie Limestone.—Brachiopod specimens are primarily derived from two measured stratigraphic sections and

two spot localities through the Wirrapowie Limestone, southern Flinders Ranges. The first stratigraphic section, CR-1, was measured through the Wirrapowie Limestone and Mernmerna Formation in the Chace Range, southern Flinders Ranges (base grid coordinates: 31°44'38.8" S; 138°36'19.7" E) (Fig. 1G). The Wirrapowie Limestone in the Chace Range reaches a total thickness of 465 m and is dominated by massive, algal, mottled and ribboned carbonates. The first specimen of *Askepasma saproconcha* sp. nov. is recorded at 77 m above the base of the section and ranges basically through the entire Wirrapowie Limestone with the LAD at 449 m above the base of the section. The first trilobite, *Abadiella huoi*, representative of the *Abadiella huoi* Zone, is not recorded until 885 m above the base of the section with *Askepasma saproconcha* sp. nov., the tommotiid taxa, *Dailyatia*, *Kulparina*, and *Paterimitra* and indiscriminate phosphatic tubes the only taxa present in the pre-trilobitic Wirrapowie Limestone.

The second stratigraphic section, ER-9 (base coordinates 31°40'2.6" S; 138°26'11.5" E WGS84), was measured through the Wirrapowie Limestone and conformably overlying Mernmerna Formation cropping out on the eastern limb of a north plunging syncline in the northern Elder Range (Fig. 1G). The upper 47 m of massive, algal dominated, mottled and ribboned carbonates of the Wirrapowie Limestone was sampled at section ER-9, with all the paterinid specimens derived from the upper Wirrapowie Limestone. The lack of trilobite specimens throughout the ER-9 section hinders precise correlation, however, these beds do contain typical Atdabanian taxa including the tannuoliniid tommotiid *Micrina etheridgei* (Tate, 1892) and a coeval assemblage of bivalved arthropods considered by Topper et al. (2011b) to equate with the *Abadiella huoi* Zone.

Flat lying exposures of the upper Wirrapowie Limestone (pre *Abadiella huoi* Trilobite Zone) on the northern slope of the Druid Range (31°46'23.48" S, 138°35'44.48" E; map datum: WGS84) (Fig. 1G) yielded a diverse faunal assemblage including specimens of *Askepasma toddense*. The presence of *Kulparina* in the assemblage indicates that the strata are slightly older than the *Abadiella huoi* Zone (Skovsted et al. 2011). Additional Wirrapowie Limestone paterinid specimens are from a single locality a few miles south of Hawker and 1.4 km west of the ruins of Kanyaka Station, Flinders Ranges (Fig. 1D). Originally assembled by Brian Daily (kindly made available through Bert Rowell of Lawrence, Kansas), material from this specific spot locality has previously been documented by Holmer et al. (2006).

There are also specimens illustrated herein collected originally by the late Brian Daily in the 1970s. The specimens are from a range of localities across the Arrowie Basin. Unfortu-

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Fig. 2. Ventral valves of Cambrian paterinate brachiopod *Askepasma toddense* Laurie, 1986 from South Australia. **A**. SAMP47069, sample MMF0.0; exterior (A_1) and posterior (A_2) views. **B**. SAMP47070, spot sample Druid Range; interior (B_1) and oblique anterior (B_2) views. **C**. SAMP47071, sample AJX-M262.7; exterior view (C_1), close up of external micro-ornament (C_2). **D**. SAMP47072, sample AJX-M261.1; posterior (D_1) and lateral (D_2) views, close up of larval shell (D_3). **E**. SAMP47073, sample MMF0.0; interior view (E_1), oblique posterior view of ventral interarea (E_2). **F**. SAMP47074, sample AJX-M266; posterior view of ventral interarea (F_1), close up of ventral interarea, displaying pedicle callist (F_2). **G**. SAMP47075, sample MMF0.0; oblique lateral view of valve interior. **H**. SAMP47076, sample AJX-M263; posterior view of valve interarea. **I**. SAMP47077, sample ER9/10.8; juvenile valve exterior.
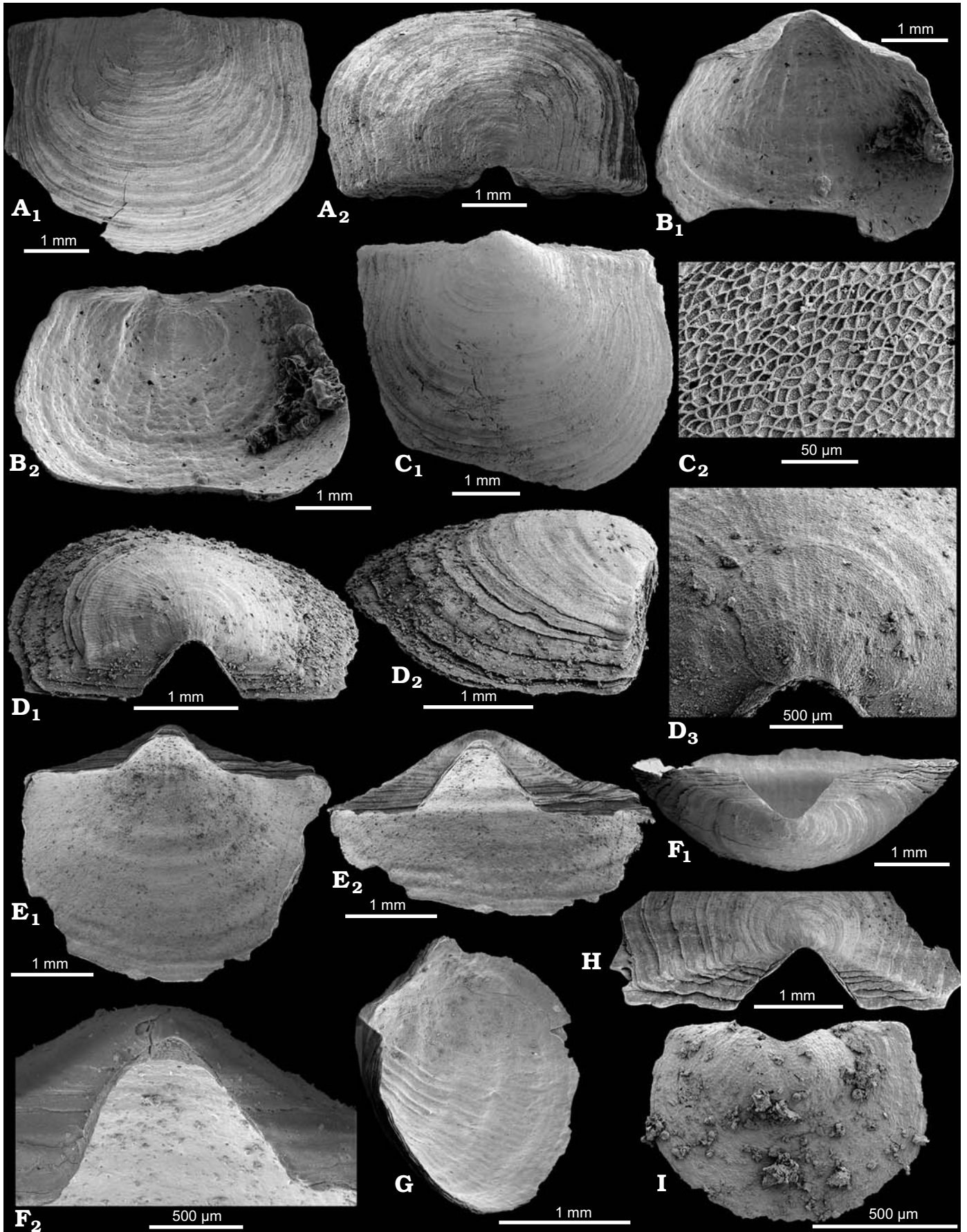
nately, there is no trace of the original field book used by Brian Daily to describe each locality in detail. Consequently, it is difficult to precisely locate and correlate most of these samples; however, the South Australian Museum Locality Register has provided us approximate locality details for each specimen and these are used to describe locality information for all illustrated specimens. The majority of these illustrated specimens are from a Wirrapowie Limestone spot sample taken north of Quorn, suspected to be near the Kanyaka spot locality documented by Holmer et al. (2006).

Systematic palaeontology

Phylum Brachiopoda Duméril, 1806

Class Paterinata Williams, Carlson, Brunton, Holmer, and Popov, 1996

Order Paterinida Rowell, 1965

Superfamily Paterinoidea Schuchert, 1893

Family uncertain

Remarks.—Originally assigned to the Paterinidae by Laurie (1986), the particular combination of characters displayed by *Askepasma* saw the genus reassigned to the Cryptotretidae (Williams et al. 1998; Holmer et al. 2006) joining three other genera *Cryptotreta* Pelman, 1977; *Aldanotreta* Pelman, 1977; and *Dzunarzina* Ushatinskaya, 1993. However, the relationship between each member of the Cryptotretidae is currently in a state of flux with the majority of genera based on only a few specimens that are inadequately figured and undoubtedly require revision (Holmer et al. 2009). *Dzunarzina* may be synonymous with *Askepasma* (see Williams et al. 1998) and the presence of a ventral perforation in the type genus *Cryptotreta* may see the genus reassigned to another family. With the taxonomic uncertainties surrounding the Cryptotretidae, the family-level assignment of *Askepasma* is herein left open pending revision of the Siberian taxa.

Genus *Askepasma* Laurie, 1986

Type species: *Askepasma toddense* Laurie, 1986; Atdabanian (lower Cambrian), Todd River Dolostone, Northern Territory, Australia.

Emended diagnosis.—Shell strophic, subquadrate in outline and ventribiconvex; ventral valve weakly to moderately sulcate, with well-defined, high, apsacline to cataclinide interarea, lacking a homeodeltidium, pedicle callist present; dorsal valve with weak to strong fold; dorsal interarea well defined, low, planar, anacline to cataclinide; with well-developed, small apical homeochilidium; shell ornamentation consisting of irregu-

lar concentric growth lines, microornamentation consisting of close-packed polygonal pits that penetrate the entire shell.

Remarks.—Despite the uncertainty surrounding the family, *Askepasma* does display a number of similar morphological characteristics to "cryptotretid" genera, *Aldanotreta*, *Cryptotreta*, and *Dzunarzina*. However, all three genera are monotypic and the detailed morphology of their respective type species is generally poorly known. *Aldanotreta sunnaginensis* Pelman, 1977 and *Cryptotreta neguertchenensis* Pelman, 1977 have only been documented from a few adjacent localities on the Siberian Platform and *Dzunarzina elenae* Ushatinskaya, 1993 from a single locality in western Mongolia with each species based on only a handful specimens. Discrimination between taxa is predominantly related to shell shape, inclination of ventral and dorsal interareas and the anterior commissure. For example, *Cryptotreta* and *Aldanotreta* are typically both transversely ovate, however, *Aldanotreta* is characterised by a broad sulcus and an apsacline ventral interarea whereas *Cryptotreta* is rectimarginate and with an orthocline ventral interarea (Pelman 1977; Laurie 2000). *Askepasma* is easily distinguished from all three genera by its overall shell shape, sulcation and ornamentation. Askepasma differs from *Aldanotreta* in possessing a low, dorsal interarea and a distinct micro-ornament of irregularly arranged polygonal pits (Fig. 2C$_2$). Askepasma is similar to *Aldanotreta* in that it is also invariably plicate, displaying a shallow and somewhat subdued fold in the dorsal valve (see Laurie 2000: fig. 86: 4c) similar to specimens of *Askepasma toddense* (Fig. 3). *Dzunarzina* bears a striking resemblance to *Askepasma*, the strong morphological similarities between the two genera has previously been noted by Williams et al. (1998), who suggested a possible synonymy of *Dzunarzina* with *Askepasma*. The distinctive polygonal ornament possessed by *Askepasma* has not been observed on specimens of *Dzunarzina* (Galina Ushatinskaya, personal communication 2011) and *Dzunarzina* also does not typically display a fold or sulcus, unlike specimens of *A. saproconcha* sp. nov. (Figs. 4, 5), however, lack of adequate material makes detailed comparison difficult.

Askepasma toddense Laurie, 1986
Figs. 2, 3.

1986 *Askepasma toddense*; Laurie 1986: 449, figs. 5G, 11A–O.
1998 ?*Aldanotreta* sp.; Williams et al. 1998: 222.
1998 *Paterina*? sp.; Williams et al. 1998: 223, pls. 1: 1, 5: 6–8.
2001 *Askepasma*? sp.; Holmer and Ushatinskaya in Ushatinskaya and Holmer in Gravestock et al. 2001: 122, pls. 15: 1–10, 16: 1–9.
2006 *Askepasma* sp. B; Jago et al. 2006: fig. 4C, D.
2009 *Askepasma*; Balthasar et al. 2009: figs. 1C, F, H–J, 2E.

Material.—Consists of 20 illustrated specimens in addition to hundreds of dorsal and ventral valves.

Fig. 3. Dorsal valves of Cambrian paterinate brachiopod *Askepasma toddense* Laurie, 1986 from South Australia. **A**. SAMP41668, sample MMF0.0; exterior (A$_1$), oblique posterior (A$_2$), and lateral (A$_4$) views, close up of larval shell (A$_3$). **B**. SAMP47078, spot sample Druid Range; exterior (B$_1$) and posterior (B$_2$) views, close up of larval shell and broad notothyrium (B$_3$). **C**. SAMP47079, sample AJX-M256; exterior (C$_1$) and posterior (C$_2$) views, close up of dorsal interarea and broad notothyrium (C$_3$). **D**. SAMP47080, Druid Range spot sample; view of valve interior. **E**. SAMP47081, sample MMF0.0; lateral view (E$_1$), close up of interior showing submedian ridge (E$_2$). **F**. SAMP41667, sample MMF0.0; oblique posterior (F$_1$) and interior (F$_2$) views. **G**. SAMP47082, sample MMF0.0; view of valve interior. **H**. SAMP47083, sample ER9/10.8; view of juvenile valve exterior.
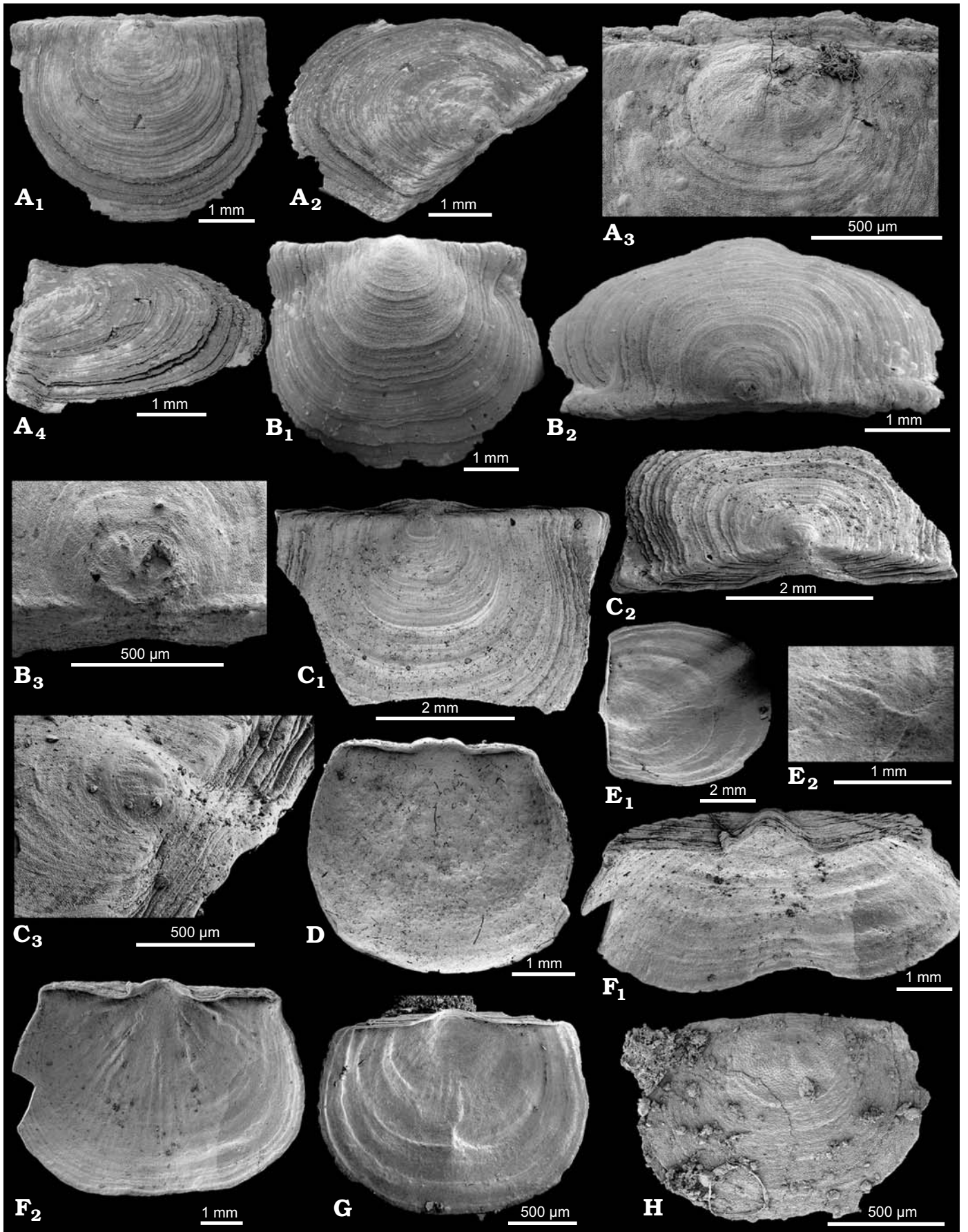
Emended diagnosis.—Shell strophic, subquadrate in outline and ventribiconvex; ventral valve rarely weakly sulcate, with well-defined, high, apsacline to catacline interarea, lacking a homeodeltidium; pedicle callist present; dorsal valve infrequently with weak to moderate fold; dorsal interarea well defined, low, planar, anacline to catacline; with well developed small, apical homeochilidium; shell ornamentation consisting of irregular concentric growth lines, ornamentation consisting of close-packed polygonal pits that penetrate the entire shell.

Description.—Shell ventribiconvex, subquadrate in outline (maximum width 6.2 mm, maximum length 5.1 mm) with maximum width approximately mid-length. Hinge line straight. Ventral valve moderately to strongly convex, with maximum convexity at umbo (Fig. 2). Lateral slopes flattened, broad with a shallow sulcus developed in the anterior half of the valve, although not always present. Larval shell (maximum width 642 μm), generally rounded and bulbous with four lobes (Fig. $3A_3$). Ventral interarea well-defined, high and varies from apsacline to catacline. Delthyrium open, width of delthyrium is 1.5 to 1.92 times the height of the delthyrium (e.g., Fig. 2D–F) with the apex occupied by a large depressed pedicle callist (Fig. $2F_2$). Dorsal valve weakly convex to flattened, infrequently with weak to moderate fold (Fig. 3). Dorsal interarea well-defined, low and varies from anacline to hypercline (Fig. $3A_2$, B_2, C_2). Notothyrium broad, closed entirely by a convex (weak to strong), triangular homeochilidium (Fig. $3A_3$, B_3, C_3). Post larval shell external ornament of well developed, irregularly spaced, concentric growth lamellae bearing a ornamentation of hexagonally close-packed, deep hemispherical pits (width of pits range from 4 to 10 μm, maximum depth of pits 5 μm), separated by high walls (Figs. $2C_2$, 6A). Larval shell covered by irregular shallow, polygonal pits, separated by low, rounded walls (Fig. $3A_3$, B_3). Larval shell ornament frequently not well developed, giving a wrinkled appearance. Ventral and dorsal interior with variably developed ridges, typically two, primary submedian ridges diverging anteriorly at approximately 10–15° (Fig. $3F_2$). Some ventral valves display a series of ridges (up to 9) diverging anteriorly from the pedicle callist (Fig. 2G). Dorsal interior may also display a slightly more prominent, submedian ridge, towards the anterior half of the valve (Fig. $3E_2$, G). Juveniles are ventribiconvex, rarely with any fold or sulcus present (Figs. 2I, 3H). Juvenile ventral valves are weakly to moderately convex

with interareas moderately high and nearly always procline (Fig. 2I). Dorsal valves of juveniles, flattened with poorly defined interareas and almost always orthocline (Fig. 3H). Ornament is the same as in adult specimens. Shell microstructure displays a rhythmic succession of alternating thin heavily mineralised compact laminae (around 5 μm thick; Fig. 7) and thicker less strongly mineralised laminae (Fig. 7) with prominent elliptical cavities (Figs. 6C, 7D). Lateral margins thickened with thin lamellae extensions giving a frayed or hook-like appearance (Figs. 6B, 7D).

Remarks.—The genus *Askepasma* was originally erected on the basis of eighteen specimens recovered from the lower Cambrian Todd River Dolostone in the Northern Territory of Australia (Laurie 1986). The collection of *Askepasma toddense* from the lower Cambrian of the Arrowie Basin currently consists of hundreds of dorsal and ventral valves and within the assemblage there is a wide range of ontogenetic and morphological variation, primarily in inclination of the interarea and prominence of the dorsal fold. Dorsal valves for instance, display a variation in the inclination of the dorsal cardinal area from hypercline to anacline (compare Fig. 3B and Fig. 3C). Ventral valves predominantly display a slightly concave, apsacline interarea (Fig. $2D_2$), rarely showing variation to a catacline and procline inclination of the ventral cardinal area. Juveniles though, almost always exhibit a procline ventral interarea (see Fig. 2I) with the interarea in dorsal valves poorly developed (Fig. 3H). Ventral valves rarely display sulcation, however dorsal valves invariably display a weak to moderate fold that is developed in the anterior half of the valve (Fig. 3B, F). Such morphological variation is present in individual samples as well as throughout stratigraphic sections and is herein treated as intra-specific variation.

Ushatinskaya and Holmer in Gravestock et al. (2001: 122) described a largely fragmentary assemblage from various Arrowie and Stansbury basin localities, noting the particular wide range of morphological variation within the collection, specifically shell shape and sulcation. Despite documenting isolated valves and fragments from five different localities, Ushatinskaya and Holmer in Gravestock et al. (2001: 122, pls. 15: 1–10, 16: 1–8) only illustrated specimens from the Ajax Limestone, Mount Scott Range and a single specimen from the Parara Limestone retrieved from drill core SYC-101 (Ushatinskaya and Holmer in Gravestock et al. 2001: pl. 16: 9). Despite illustrated specimens (Ushatinskaya and Holmer in Gravestock et al. 2001: 122, pls. 15: 1–10, 16:

Fig. 4. Ventral valves of Cambrian paterinate brachiopod *Askepasma saproconcha* sp. nov. from South Australia. **A**. SAMP47084, sample CR1-136, Chace Range; view of valve exterior. **B**. SAMP41646, sample CR1-136, Chace Range; exterior (B_1) and posterior (B_2) views, close up of larval shell (B_3). **C**. SAMP47085, spot sample near Kanyaka ruins; plan (C_1), oblique posterior (C_2), and oblique lateral (C_3) views of valve exterior. **D**. SAMP47086, Wilkawillina spot sample taken 2.5 miles North-northwest of Point Well (originally labelled P14556J), plan view of valve exterior. **E**. SAMP47087, spot sample taken north of Quorn, near Kanyaka ruins (originally labelled P14559O); oblique lateral view of valve exterior. **F**. SAMP47088, spot sample taken north of Quorn, near Kanyaka ruins (originally labelled P14559M); anterior view of articulated valves showing pronounced fold and sulcus. **G**. SAMP 47089, spot sample near Kanyaka ruins; posterior view showing high interarea and pedicle callist (G_1), oblique lateral view of dorsal valve interior (G_2), plan view of dorsal valve interior (G_3). **H**. SAMP47090, spot sample near Kanyaka ruins; plan view of dorsal valve interior (H_1), close up of ventral interarea (H_2) displaying depressed pedicle callist. **I**. SAMP47120, CR1-77, Chace Range; detail showing shell structure. **J**. SAMP47121, CR1-77, Chace Range; close up of polygonal ornament.
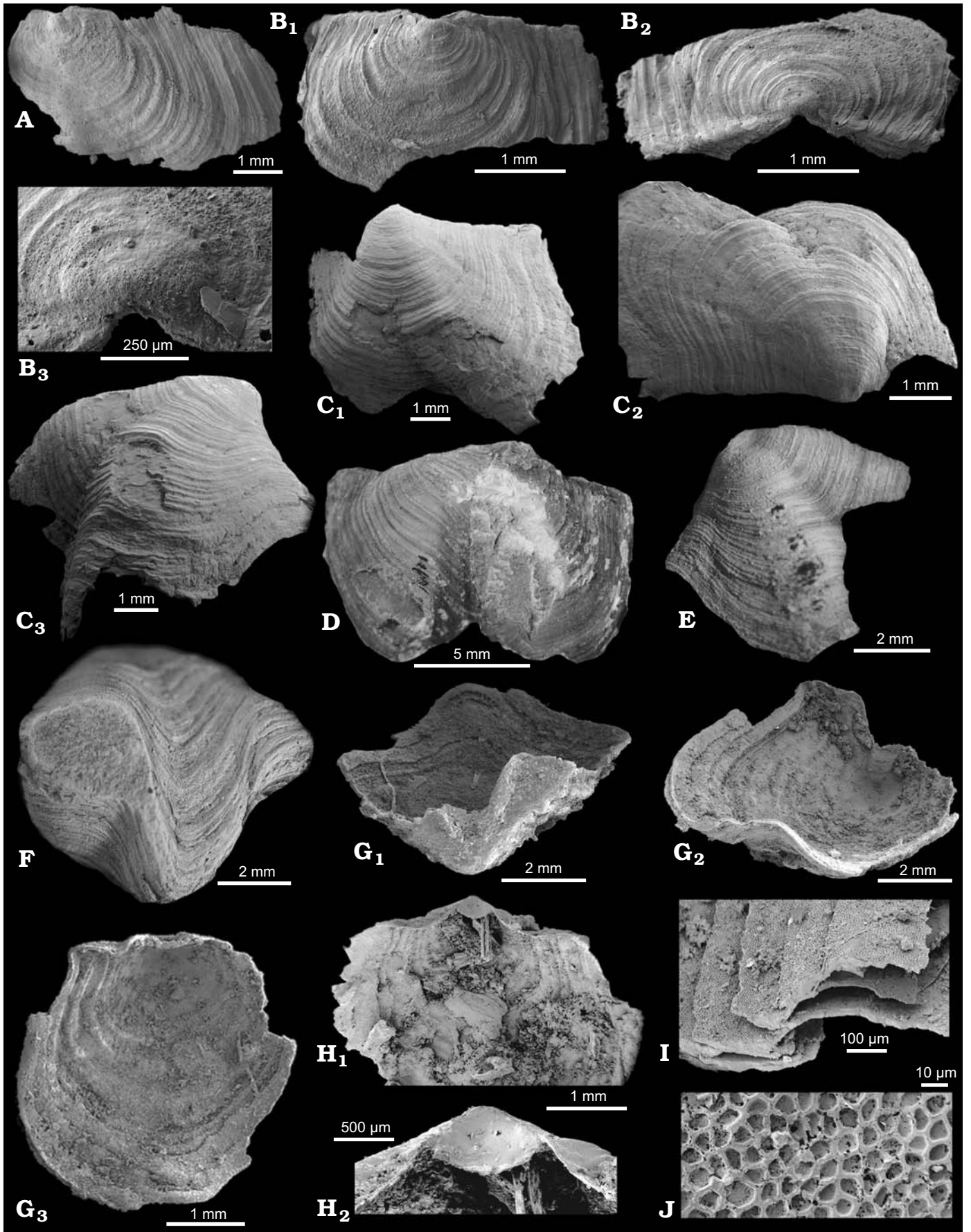
1–9) displaying morphological variation all individuals fit within the scope of *Askepasma toddense* and whilst it is possible that their collection contained specimens of *Askepasma saproconcha* sp. nov. without further information its presence is difficult to confirm.

In a biostratigraphic review of the Cambrian of South Australia, Jago et al. (2006: fig. 4C, D) illustrated two specimens of *Askepasma toddense*, there referred to as *Askepasma* sp. B from *Abadiella huoi* Zone equivalent strata in the shallow-water setting of the Wirrealpa Hinge Zone, specimens that are re-illustrated here (Fig. 3A, F). Unlike *Askepasma saproconcha* sp. nov. which is restricted to pre-trilobitic strata, *Askepasma toddense*, ranges from immediately below the base of the *Abadiella huoi* Zone into the upper Atdabanian where it co-occurs with other linguliform brachiopods, such as *Eoobolus*, *Eodicellomus*, and *Kyrshabaktella* (Jago et al. 2006). The stratigraphic separation of the two species suggests use in further biostratigraphic studies and may be used to facilitate correlation across Cambrian basins in Australia.

Peng et al. (2010: 372, pl. 3) recently documented a new species of *Askepasma* from the lower Cambrian Balang Formation in Eastern Guizhou. *Askepasma transversalis* Peng, Zhao, Qin, Yan, and Ma, 2010 represents the first occurrence of the genus outside of Australia extending its geographic range to South China. *Askepasma transversalis* shares many similarities with the type species and is characterised by a straight hinge line, well-defined dorsal and ventral interareas with a wide delthyrium capped by a large pedicle callist. The main morphological difference between the two species is the prominent pedicle beak displayed by *A. transversalis* (Peng et al. 2010: pls. 3, 6, 9). Differences in preservation between the Chinese and Australian material makes comparison difficult; the Chinese material is represented by crack out specimens deposited in deep-water, shelf to slope environment of the Balang Formation (Peng et al. 2010). *Askepasma transversalis* is also slightly younger than *A. toddense* with the Balang Formation of mid to late Botomian age (*Palaeolenus–Megapalaeolenus* Assemblage zones) (see Steiner et al. 2007).

Geographic and stratigraphic range.—Lower Cambrian (middle–upper Atdabanian, Cambrian Series 2, Stage 3–4?), Ajax Limestone (Mount Scott Range), Wilkawillina Limestone (Bunyeroo Gorge, Ten Mile Creek, and Bunkers Range), Wirrapowie Limestone (Druid Range and Elder Range), Mernmerna Formation (Ten Mile Creek) and Parara Limestone (Horse Gully and SYC-101).

Askepasma saproconcha sp. nov.

Figs. 4, 5.

2006 *Askepasma* sp. A; Jago et al. 2006: 414, fig. 4A, B.
2006 *Askepasma* sp.; Holmer et al. 2006: 3, fig. 2a–h.

Etymology: From the Greek *sapro*, rotten and *concha*, shell. In reference to the weakly phosphatised shell that easily disintegrates when submerged in acid and the subsequent disappointment of a worker having spent hours in the acid room only to retrieve nothing but fragments from the resulting residues.

Type material: Holotype: SAMP47091 (Fig. 5A) from Wirrapowie Limestone, originally collected by Brian Daily from a spot locality north of Quorn, supposedly near the Kanyaka ruins, Southern Arrowie Basin. Paratypes: SAMP47085 (Fig. 4C), SAMP47087 (Fig. 4E), SAMP47088 (Fig. 4F), SAMP47089 (Fig. 4G), SAMP47092 (Fig. 5B), SAMP47093 (Fig. 5C) and SAMP47095 (Fig. 5E) from Wirrapowie Limestone, spot locality near the Kanyaka ruins, southern Arrowie Basin. SAMP47084 (Fig. 4A) and SAMP41646 (Fig. 4B) from Wirrapowie Limestone, Chace Range, sample CR1-136. SAMP47086 (Fig. 4D) from the Wilkawillina Limestone, 4.4 km Northwest of Point Well, Arrowie Basin.

Type locality: Wirrapowie Limestone, spot locality north of Quorn, near Kanyaka ruins, Arrowie Basin.

Type horizon: Spot Locality in the Wirrapowie Limestone.

Diagnosis.—Shell strophic, uniplicate, subquadrate in outline and ventribiconvex; ventral valve strongly convex with maximum convexity at umbo and with well developed high apsacline interarea; delthyrium is wide and triangular lacking homeodeltidium and restricted by pedicle callist; dorsal valve convex with well-developed median fold and well-defined anacline to catacline interarea; ornamentation consisting of concentric lines only; ornament consisting of close-packed polygonal pits that penetrate the entire shell. Partially mineralised shell with inner surface commonly lacking mineralisation.

Description.—Shell ventribiconvex, subquadrate in outline (maximum width 2.39 cm, maximum length 2.04 cm) with maximum width at approximately mid-length. Hingeline straight. Ventral valve strongly convex, with maximum convexity at umbo. Lateral slopes flattened, broad with a well-defined, sharp, sulcus developed in the anterior half of the valve (Fig. 4C–F, G). Dorsal valve weakly to moderately convex with well-defined fold developed in the anterior half of the valve (Fig. 5A, B, D_3). Ventral interarea well-defined, moderately high and varies from apsacline to catacline. Delthyrium open and wide, with an obtuse delthyrial angle (114–115°), width of delthyrium is 3 to 3.2 times the height of the delthyrium (e.g., Fig. $4B_2$) with an obvious pedicle callist (Fig. $4G_3$, H). Dorsal valve moderately to strongly convex (Fig. 5). Dorsal interarea well-defined and low to

Fig. 5. Dorsal valves of Cambrian paterinate brachiopod *Askepasma saproconcha* sp. nov. from South Australia. **A**. SAMP47091, spot sample taken north → of Quorn, near Kanyaka ruins (originally labelled P14559V); oblique anterior (A_1) and anterior (A_2) views, oblique plan view showing pronounced fold (A_3), oblique lateral (A_4), plan (A_5), and lateral (A_6) views. **B**. SAMP47092, spot sample near Kanyaka ruins; plan view (B_1), lateral view showing median fold (B_2), and anterior view showing pronounced median fold (B_3). **C**. SAMP47093, spot sample taken north of Quorn, near Kanyaka ruins (originally labelled P14559Y); plan view of valve exterior. **D**. SAMP47094, spot sample taken north of Quorn, near Kanyaka ruins (originally labelled P14559P); plan view (D_1), posterior view of dorsal interarea (D_2), and posterior view showing pronounced fold (D_3). **E**. SAMP47095, spot sample near Kanyaka ruins; plan view of valve exterior (E_1), oblique lateral (E_2) and anterior (E_3) views.
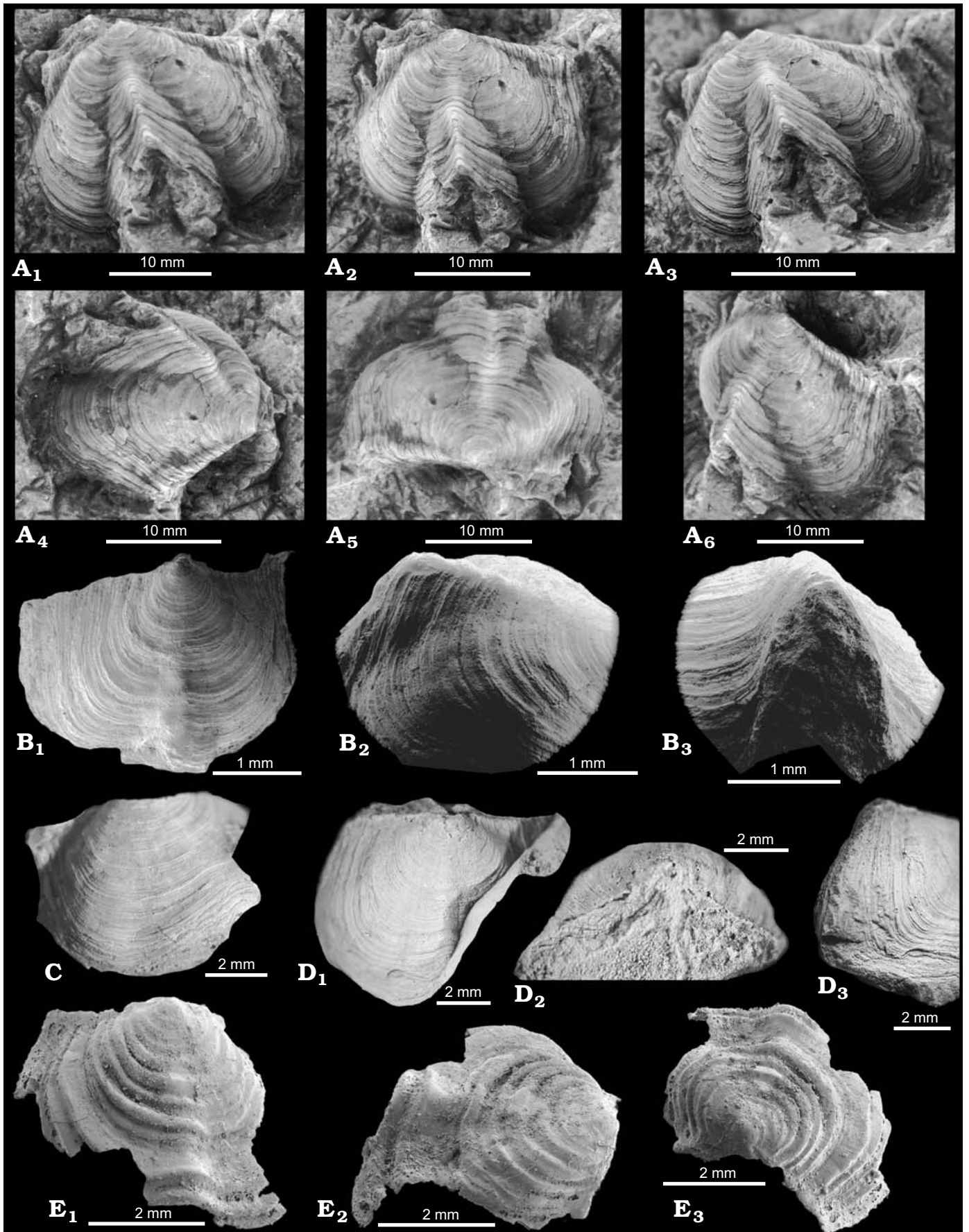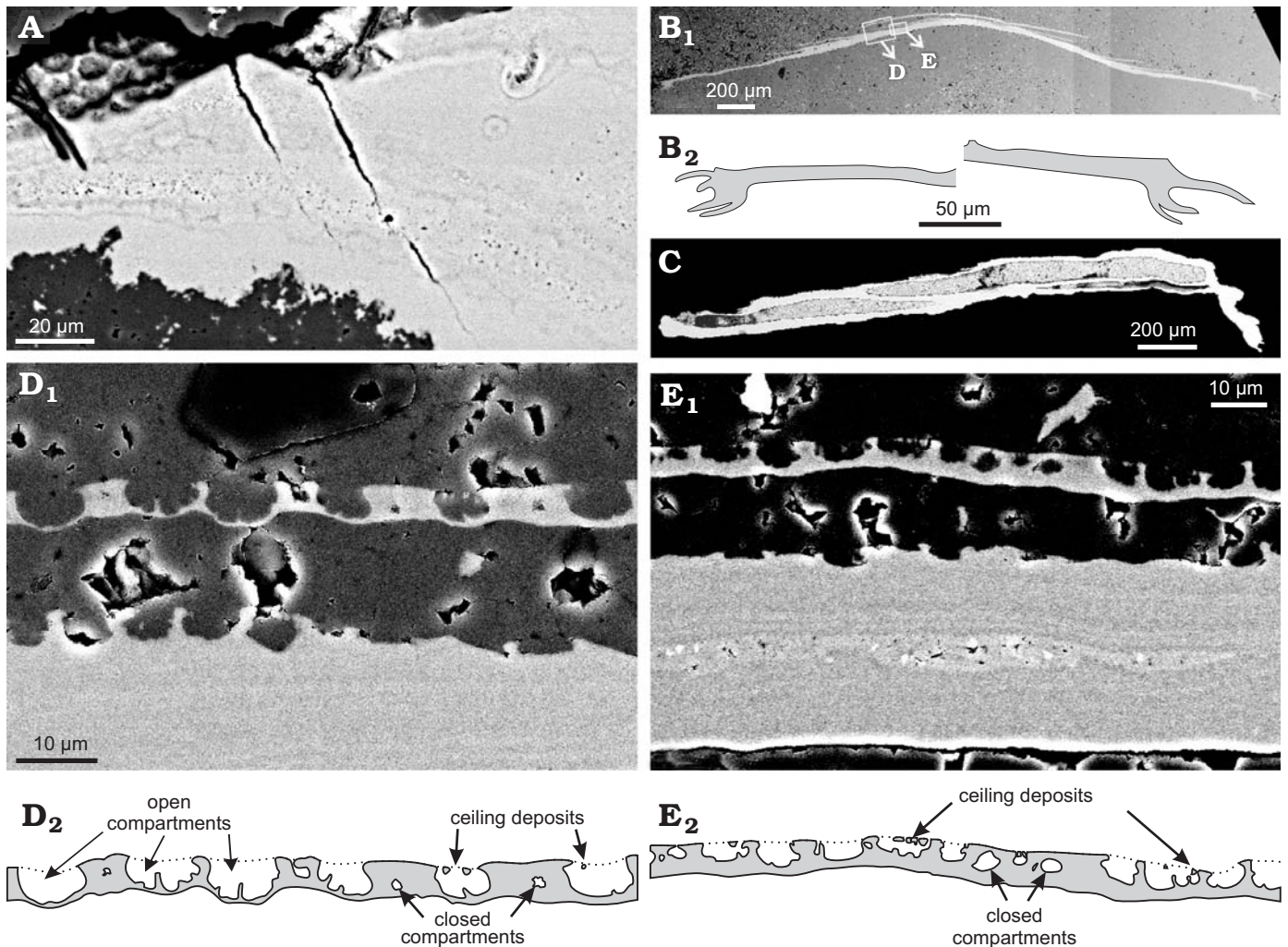
Fig. 6. Backscatter SEM images of polished cross-sections of Cambrian paterinate brachiopods, *Askepasma saproconcha* sp. nov. (A) and *Askepasma toddense* Laurie, 1986 (B–E). **A**. SAMP47096, Wilkawillina Limestone, Narina Road, showing polygonal ornament exposed along a crack (top left corner of image) and the traces of polygonal structures through the shell. **B**. SAMP43361, Wilkawillina Limestone, sample MMF0.0, in limestone matrix (B_1), transversal cross section showing thin fringes along the external shell surface; boxes show position of D and E; sketches of the lateral margins (B_2). Details of B showing the polygonal structures of the fringes along the external shell surface (D_1, E_1); labelled sketches (D_2, E_2) showing different stages of closure of polygonal compartments; dotted line indicates a hypothetic lamina that sealed the compartments and acted as surface for apatite along the top of the compartments (ceiling deposits). **C**. SAMP 43332, Wilkawillina Limestone, sample MMF0.0, longitudinal cross-section of a specimen that was isolated by acid maceration and embedded in resin.

moderately high. Notothyrium broad, closed entirely by a convex, triangular homeochilidium (Fig. $5E_3$). Post larval shell external ornament of well-developed, irregularly spaced, concentric growth lamellae bearing a micro-ornamentation of hexagonally close-packed, deep hemispherical pits, separated by high walls (Fig. 4J). Growth lamellae variably coarse and angular (Fig. 5E). Shell microstructure displays a rhythmic succession of alternating thin heavily mineralised compact laminae (around 5 μm thick; Fig. 7) and thicker less strongly mineralised laminae (Fig. 7) rarely with prominent elliptical cavities (Figs. 6C, 7D). Shell only partially mineralised with the degree of mineralisation decreasing towards the interior of the shell with the inner surface commonly lacking mineralisation (Fig. 7). Lateral margins thickened with thin lamellae extensions giving a frayed or hook-like appearance (Figs. 6B, 7D).

Fig. 7. Backscatter SEM images of polished limestone-hosted cross-sections of Cambrian paterinate brachiopods. *Askepasma saproconcha* sp. nov. (A–C) → and *Askepasma toddense* Laurie, 1986 (D). **A–C**. SAMP47096, Wilkawillina Limestone, Narina Road. **A**. Cross-section showing the typical features: a succession of well mineralized compact laminae (cl) and poorly mineralized originally organic-rich laminae (ol); note that the inner shell surface is not mineralized and that a distinct crack runs along the outer shell surface. **B**. Cross section showing ghost laminae along the outer shell margin (indicated by arrows). **C**. Cross-section showing the characteristic flaring out of laminae along the lateral shell margin; note also the elliptical cavities along the shell margin and the rudimentary fringes along the external shell surface (indicated by arrows). **D**. SAM P43361, Wilkawillina Limestone, sample MMF0.0, cross-section showing elliptical cavities, finely laminate layers and recrystallized layers (rc).
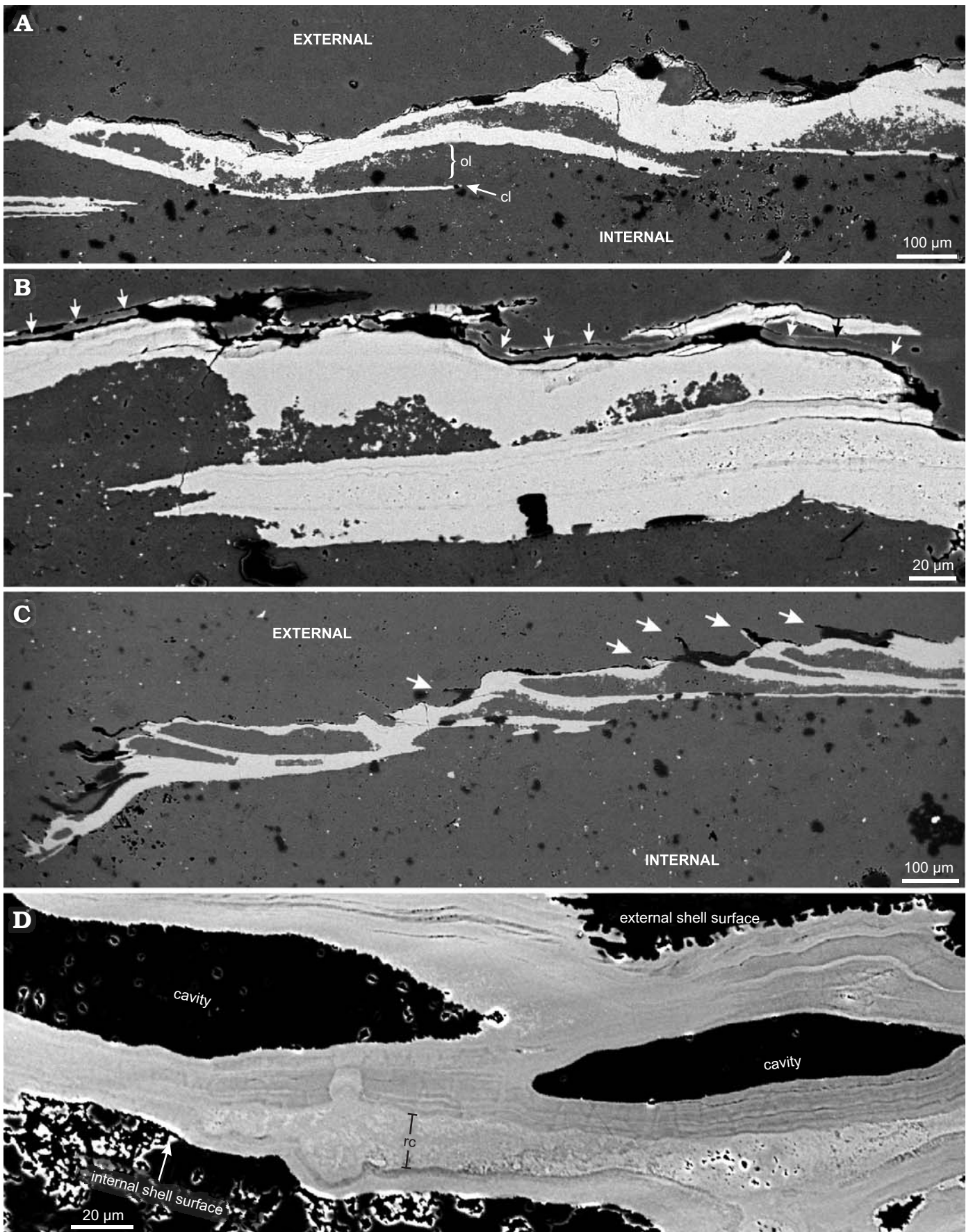
Remarks.—*Askepasma saproconcha* sp. nov. is based on approximately 30 specimens derived from the Wirrapowie and Wilkawillina limestones mainly recovered from the southern Arrowie Basin. The collection of *A. saproconcha* sp. nov. predominantly consists of crack-out macro-specimens with very few complete valves retrieved using acid-etching techniques. The large majority of acid-etched material is fragmentary as the shell of *A. saproconcha* sp. nov. is only weakly mineralised, a feature discussed below in the description of the shell microstructure. This species is considered the oldest known brachiopod from the lower Cambrian of South Australia and occurs as the sole brachiopod species in the lowermost Wilkawillina and Wirrapowie limestones. Many specimens of *A. saproconcha* sp. nov. have been collected from spot localities in the Arrowie Basin making correlation difficult, however, the lack of distinct *Abadiella huoi* Zone faunal constituents lends support to an early, pre-trilobitic occurrence of this species. This early occurrence of the species in South Australian Cambrian strata may prove useful for regional correlation in future studies. *Askepasma saproconcha* sp. nov. was first reported by Jago et al. (2006) as occurring in the basal part of the Wilkawillina Limestone type section in the Bunkers Graben and the Wirrapowie Limestone in the Chace Range. Jago et al. (2006: fig. 4A, B) illustrated a single specimen from the Chace Range and referred to it as simply *Askepasma* sp. A, specimen re-illustrated here (Fig. 4B).

The new species displays many similarities with the other early Cambrian South Australian paterinate, *Askepasma toddense*, such as a subquadrate shell shape, apsacline ventral interarea, low, hypercline dorsal interarea and the distinctive polygonal pitting micro-ornament. *Askepasma saproconcha* sp. nov. can be discriminated by the presence of a well-developed, pronounced chevron-shaped fold and deep sulcus (Fig. 4F) and a wider delthyrium (compare Fig. 2D–F with Fig. $4B_2$). The width of delthyrium in the type species is approximately 1.5 to 1.92 times that of the delthyrium height with a delthyrial angle between 75 and 88° (e.g., Fig. $2D_1$, F_1, H). *Askepasma saproconcha* sp. nov. displays a delthyrium with width that is 3 to 3.2 times that of its height and with a delthyrial angle of 114–115° (e.g., Fig. $4B_2$). *Askepasma toddense* is also invariably plicate, however, the degree and development of the fold and sulcus in the two species is strikingly different. The fold in the dorsal valve of *A. toddense*, if present, is relatively shallow (Fig. $3B_2$, F_1) compared to the well-defined, pronounced, very sharp fold displayed in the dorsal valves of *Askepasma saproconcha* sp. nov. (Fig. 5A, B, D_3). The shell microstructure also differs between the species with *A. saproconcha* being much less strongly mineralised. The combination of morphological characteristics possessed by *Askepasma saproconcha* sp. nov. is unique and readily distinguishes the taxon from other species of *Askepasma*.

The shell of *Askepasma saproconcha* sp. nov. is additionally perforated by a type of hollow, phosphatic tubular canals (see Holmer et al. 2006). These canals are invariably oriented subparallel to the shell lamination and were originally docu-

mented by Holmer et al. (2006) in specimens recovered from the Wirrapowie Limestone, south of Hawker, near the ruins of Kanyaka Station. However, these canals are only sporadically preserved and it seems that their presence is reliant on the degree of phosphatisation at that particular locality. The specimens documented by Holmer et al. (2006) from the Wirrapowie Limestone for example, are heavily phosphatised in comparison with etched shells from other localities that are invariably fragmentary and even partly dissolved during the acid preparation stage. The reoccurring pattern of shell-penetrative setal canals in brachiopod-like problematic fossils, such as *Micrina*, *Heliomedusa*, and *Mickwitzia* (Holmer et al. 2002; Williams and Holmer 2002; Balthasar 2004) suggests that shell-penetrative setae are a character trait that may be deeply rooted within the brachiopod stem-group (Holmer et al. 2002, 2008; Holmer and Popov 2007). Canal-like structures, however, have subsequently been found in other Cambro-Ordovician taxa including the probable stem group linguliformean, *Setatella* (Skovsted et al. 2010) and Ordovician orthoid brachiopods (Jin et al. 2007; Jin and Zhan 2008) as well as in Ordovician siphonotretids (Popov et al. 2009). The canaliform shell structure observed in *Askepasma saproconcha* sp. nov. is not a characteristic morphological feature of the genus having not been reported from specimens of *A. toddense*. The presence of setal canals in unrelated forms and their absence in related forms (e.g., present in *A. saproconcha* and absent in *A. toddense*) may indicate that this is a plesiomorphic feature having been developed and subsequently lost multiple times, proving unhelpful for phylogenetic studies.

Stratigraphic and geographic range.—Lower Cambrian (lower–middle Atdabanian, Terreneuvian, Stage 2, Cambrian Series 2, Stage 3?), basal part of the Wilkawillina Limestone, Wilkawillina Limestone type section, Bunkers Graben. Wirrapowie Limestone, Chace Range and Kanyaka area, Southern Arrowie Basin, South Australia.

Shell structure

Being among the oldest known brachiopods, *Askepasma* holds a crucial position in understanding the transition in shell microstructure from tommotiids to crown group brachiopods (Balthasar et al. 2009). While sharing many important features, *A. toddense* and *A. saproconcha* differ with respect to the degree of mineralisation with the latter being less strongly mineralised.

Both species show the rhythmic succession typical of crown-group linguliformean brachiopods which is characterised by alternating thin heavily mineralised compact laminae (around 5 μm thick; Fig. 7) and thicker less strongly mineralised laminae (Fig. 7) (see also Balthasar et al. 2009: fig. 2E). In extant organophosphatic brachiopods this shell succession results from the cyclic deposition of apatite, polysaccharides, and chitin or collagen (Williams et al. 1992, 1994) and by analogy, we assume that the thicker but less strongly miner-

alised laminae of *Askepasma* originally were organic-rich. In the poorly mineralised *A. saproconcha* the organic-rich laminae commonly appear as recessive units between prominent compact laminae and usually exhibit a patchy distribution of apatite. The degree of mineralisation in *A. saproconcha* gradually decreases towards the interior of the shell with the inner surface commonly lacking mineralization (Fig. 7). *Askepasma toddense*, by contrast, shows no gradient in the degree of mineralization and the internal surface is mineralized (Figs. 6A, B, 7D). In both species of *Askepasma* the thicker organic-rich laminae are often recrystallized (Fig. 7D), which is a common feature of originally organic-rich organophosphatic laminae and is probably due to the redistribution of apatite during the decomposition of labile organic compounds (Balthasar 2007).

The prominent elliptical cavities that are common in shells of *A. toddense* (Figs. 6C, 7D) and, more rarely, *A. saproconcha* (Fig. 7C) are an integral parts of the shell structure as they are defined by detaching shell layers (Fig. 7D). These cavities are usually entirely devoid of apatite and in the rare cases in which apatite occurs within, it forms cement along the cavity wall (Fig. 7D: lower right corner) thus showing that the cavity was empty at the time of cement formation. The cavities were probably formed by the local detachment of the shell-secreting epithelium from the upper laminae. This would explain the undisturbed laminar nature of the shell layers immediately above and below the cavities. This would imply that the cavities were empty during the life time of the organisms.

Both species of *Askepasma* possess a characteristic polygonal surface ornament that penetrates the entire shell (Fig. 6A, D, E; for *A. toddense* see also Balthasar et al. 2009). Individual polygons are up to 10 μm in diameter with about 5 μm high lateral walls and range from box to bowl shaped in cross-section (Fig. 6D, E). Virtually identical shell-penetrating polygonal networks are known from the sclerites of the tommotiids *Eccentrotheca*, *Paterimitra*, tannuolinids (Balthasar et al. 2009), and the paterinid *Salanygolina* (Holmer et al. 2009) whereas they are currently unknown from unquestionable crown-group brachiopods. Etched material of *A. toddense* (Fig. 2C$_2$) and *A. saproconcha* (Holmer et al. 2006: fig. 2H) show that the polygonal compartments that form the external ornament of *Askepasma* are filled with distinct granules. Cross sections of *A. toddense* show that these granules appear as spicular ingrowths of the compartment walls (Fig. 6D). The infill of these polygonal compartments of the surface layer ranges from a few minute and isolated granules less than a micron in size to solidly filled compartments with a small but distinct hollow gap in their centre (Fig. 6E) suggesting that the open spaces were filled from the margins inwards. By comparison, polygonal compartments within the shell do not exhibit comparable ingrowths but commonly show a fine-scale (sub-micron) lamination (Balthasar et al. 2009: fig. 1I), thus suggesting a different mode of deposition between the outermost and interior polygonal laminae. Furthermore, the occurrence of small apatite deposits along the ceiling of the polygonal compartments

of the surface layer (Fig. 6D, E) indicates the presence of a lamina that sealed the top of the outermost polygons. No such surface layer was preserved in any of the studied specimens, but limestone-hosted specimens of *A. saproconcha* exhibit a distinct outermost ghost layer, ca. 5 μm thick and composed of calcite that is lined by a very thin (sub-micron) veneer of apatite (Fig. 7B). This ghost layer was observed in several specimens of limestone-hosted and articulated *A. saproconcha* and tends to grade into a distinct gap along the outer shell surface (Fig. 7B: upper left corner). In the absence of a ghost layer, a distinct crack has been observed in all limestone-hosted specimens of *A. saproconcha* (e.g., Fig. 7A, B).

Based on these observations it is likely that the outermost polygonal surface layer of *Askepasma*, and possibly other taxa possessing the polygonal shell structure, was covered by an additional lamina of low preservation potential. Preservation and the relative timing of diagenesis provide some insights into the original composition of this layer. Although, now calcitic in some specimens, an original calcareous composition is unlikely as such a layer would be preserved much more commonly. An organic surface layer, at least in position similar to a periostracum, is more likely. In order for this organic surface layer to be replaced by a crack, the surrounding limestone matrix must have been lithified at the time that this outermost layer disappeared. This suggests a relatively recalcitrant organic composition, possibly chitin or collagen, both of which are common in the shells of modern organophosphatic shells (Williams et al. 1992, 1994). Such a chitinous or collagenous surface layer probably represents the precursor of the periostracum of the brachiopod crown-group which is composed of far less durable organic compounds (Williams 1997).

In addition to the unique outer shell layer and the tendency to reduce the degree of apatite mineralisation, the lateral shell margins of both species of *Askepasma* are different from known crown-group brachiopods. In limestone-hosted cross-sections the lateral margin swells in thickness due to the local thickening of organic-rich laminae (Figs. 6B, 7D). Thin lamellae extend out along the thickened margin giving it a frayed expression in some specimens while others develop finger to hook-like extensions (Figs. 6B, 7D). Similar thin extensions are common along the entire external shell surface where they form distinct fringes (Figs. 6B$_1$, D, E; see also Balthasar et al. 2009: fig. 1H). These fringes are composed of the polygonal outside layer with a varying degree of a mineralised basal support (Fig. 6B$_1$, D, E), probably homologous to the compact laminae of the rest of the shell. The fringes along the lateral margin and external shell surface were probably formed by the repeated retraction of the marginal shell-secreting outer epithelium.

Although paterinids assume a basal position of the subphylum Linguliformea in the higher-level taxonomy that was adapted for the Treatise of Invertebrate Paleontology (Williams et al. 1996; 2000), paterinids have always been seen as being at odds with all the other brachiopods owing to their

organophosphatic composition linking them to linguliform brachiopods whereas their general shell morphology has more in common with rhynchonelliform brachiopods. Recent work has shown that paterinid shells possess a characteristic network of polygonal cells that is otherwise only known from tommotiids (Balthasar et al. 2009; Holmer et al. 2009).

Elliptical cavities, for example, occur in a number of tommotiid taxa including *Paterimitra* (UB, unpublished data) and *Eccentrotheca* (Balthasar et al. 2009: figs. 1G, 2A) and the strong reduction in shell mineralisation along the organic-rich laminae described here for *A. saproconcha* can also be seen in tannuolinids (Balthasar et al. 2009, Data Repository item 2009281). Also the marginal swelling up of laminae are known from tommotiids (e.g., *Camenella*, Skovsted et al. 2009a) and irregular hook-like lateral margins are found in *Eccentrotheca* (Balthasar et al. 2009: fig. 2A) and *Paterimitra* (UB, unpublished data) and probably aided the fusion of sclerites. As none of these shell structural characters are known from crown-group brachiopods they probably represent plesiomorphic features that were lost before the emergence of the crown group. Many of the features described here of the shell of *Askepasma* strengthen the view that *Askepasma* and probably paterinids in general might better be interpreted as occupying a position in the proximal stem group to all brachiopods.

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