

Camenellan tomotiids from the Cambrian Series 2 of East Antarctica: Biostratigraphy, palaeobiogeography, and systematics

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Cambrian Series 2 shelly fossils from thick carbonate successions in East Antarctica have received limited systematic treatment through the 20th century. Described here are the East Antarctic camenellan tomotiids from the Shackleton Limestone in the Central Transantarctic Mountains and the Schneider Hills limestone in the Argentina Range. This material comes from both newly sampled collections and incompletely described material from older collections. The assemblage supports correlation to the *Dailyatia odyssei* Zone and *Pararaita janeae* Trilobite Zone of South Australia, with the newly examined specimens of *Dailyatia decobruta* from the Shackleton Limestone providing direct correlation to the Mernmerna Formation of the Ikara-Flinders Ranges and White Point Conglomerate of Kangaroo Island. These East Antarctic assemblages include five species referred to *Dailyatia*, in addition to an undetermined kennardiid species and fragments of the problematic *Shetlandia multiplicata*. The results further corroborate the notion that fossiliferous carbonate clasts found on King George Island were sourced from the same carbonate shelf as the Shackleton Limestone, with the taxon *S. multiplicata* found in both units. The Schneider Hills limestone in the Argentina Range has yielded sclerites of *Dailyatia icari* sp. nov., currently only known from this location.

Key words: Tomotiida, *Dailyatia*, biostratigraphy, palaeobiogeography, Cambrian, Central Transantarctic Mountains.

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Introduction

The distant reaches of Antarctica have proven a difficult to sample, yet important source of information on the palaeobiology and palaeobiogeography of problematic ani-

mals from the traditional “lower Cambrian”. Expeditions to sample the lower Cambrian Byrd Group in the Central Transantarctic Mountains during the 20th Century yielded trilobites (Palmer and Gatehouse 1972; Palmer and Rowell 1995), archaeocyaths (Debrenne and Kruse 1986), molluscs

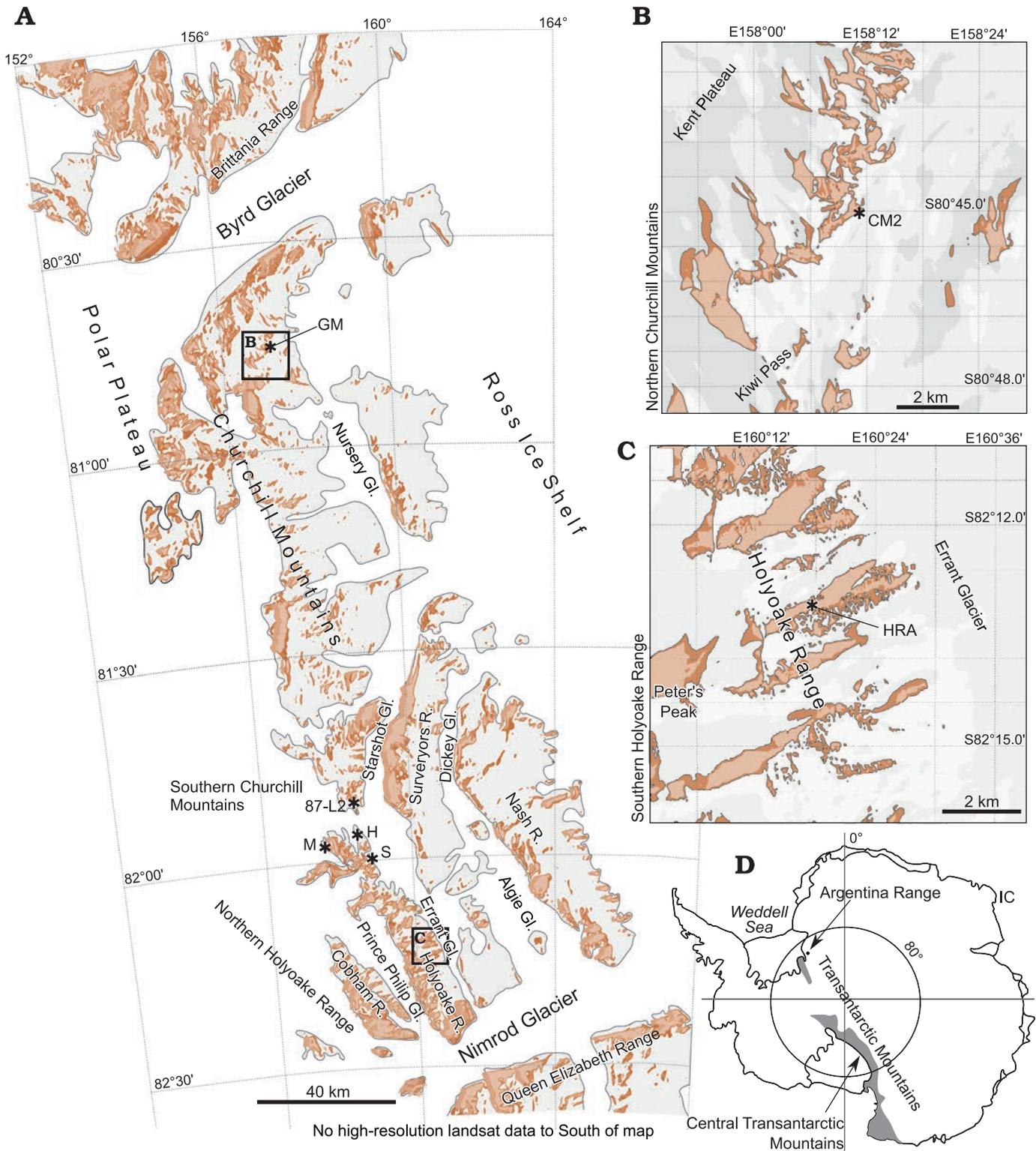


Fig. 1. **A.** Topographic map of the Central Transantarctic Mountains (adapted from the USGS 2008) with the main geographic features and the sites visited by the Kansas University expeditions (study areas marked by section names GM, 87-L2, M, H, S). The locality GM is the type locality for *Dailyatia braddocki*, which is close to the location of the CM2 section. The locality M is the type locality of *Dailyatia odyseii*. **B.** The area of the Churchill Mountains visited by the Swedish-Australian expedition, showing the location of the CM2 section. **C.** The area of the Holyoake Range visited by the Swedish-Australian expedition, showing the location of the HRA section. **D.** Overview of Antarctica showing the extent of the Transantarctic Mountains, including the the location of the Argentina Range, and IC (location on sections unknown) in the Schneider Hills (sampled by the Kansas Expeditions).

(Rowell et al. 1988; Evans 1992) and other shelly fossils (Rowell et al. 1988; Evans and Rowell 1990). These were mostly from spot-samples, hindering detailed analysis of biostratigraphic or palaeobiogeographic context. Following fieldwork in 2011, the first systematically sampled sections intersecting the Byrd Group from the Churchill Mountains and Holyoake Range (Fig. 1) yielded moderately diverse assemblages of molluscs (Claybourn et al. 2019) and brachiopods (Claybourn et al. 2020). The palaeobiogeographical resolution of East Antarctica has been improved on the back of new systematic descriptions, corroborating links to South Australia and demonstrating new similarities with the brachiopod fauna of North China (Pan et al. 2019; Claybourn et al. 2020) and the molluscan fauna of East Laurentia (Landing and Bartowski 1996; Landing et al. 2002; Skovsted 2004; Atkins and Peel 2004; Peel and Skovsted 2005; Claybourn et al. 2019). Additional systematic description of the tommotiids from East Antarctica further advance and refine the biostratigraphic correlation and palaeobiogeography of this region.

The tommotiids have proven a valuable tool for biostratigraphy, but only in recent years. They have been used in a new biostratigraphic scheme for South Australia, which includes the *Micrina etheridgei* Zone and *Dailyatia odyssei* Zone (Betts et al. 2016, 2017), the eponyms of which are both tommotiid taxa. *Dailyatia ajax* Bischoff, 1976, *Dailyatia macroptera* Skovsted, Betts, Topper, and Brock, 2015, *Dailyatia bacata* Skovsted, Betts, Topper, and Brock, 2015, and *Dailyatia helica* Skovsted, Betts, Topper, and Brock, 2015, are all found in South Australia, where they are important accessory taxa for defining the *M. etheridgei* Zone (Betts et al. 2016) which spans much of Stage 2 of the Terreneuvian Series and the regionally important *Parabadiella huoi* Trilobite Zone at the base of Series 2, Stage 3 (Betts et al. 2016, 2018). Many of these taxa also range down into the underlying *Kulparina rostrata* Zone (Betts et al. 2016). Skovsted et al. (2015) recognised that early descriptions of *Dailyatia ajax* from South Australia (Bischoff 1976; Demidenko in Gravestock et al. 2001) belonged to four different species, demonstrating the importance of thorough systematic treatment of scleritome animals known only from disarticulated sclerites (Bengtson et al. 1990; Bengtson 2004).

Thorough systematic treatment of the morphologically variable tommotiids is also vital for understanding their phylogenetic position. This enigmatic group of armoured bilaterians with an external scleritome forms an assemblage of plesions scattered around the base of the phoronid + brachiopod clade. The relationship of the tommotiids to the lophophorates has been the subject of much recent research, with different members postulated as stems to different crowns. In broad terms, tommotiids can be assigned to two main groups (Skovsted et al. 2009a; Larsson et al. 2014: fig. 22). The first group are the eccentrothecimorphs, some of which occupy a stem position to the linguliform brachiopods, including the tannulinids (Li and Xiao 2004; Holmer et al.

2008, 2011; Balthasar et al. 2009; Skovsted et al. 2014) and *Paterimitra* (Skovsted 2009b; Larsson et al. 2014). Another eccentrothecimorph taxon, *Eccentrotheca* has been interpreted to be in the phoronid stem group (Skovsted et al. 2008, 2011). The second group are the camenellan clade, including families Lapworthellidae, Tommotidae, and Kennardidae (Skovsted et al. 2009a). Camenellans share common features that unite them and distinguish them from those tommotiids that fall within the phoronid + brachiopod crown group. These include cone shaped sclerites (with a variable number of sclerites), a polygonal transverse section and growth series of comarginal ribs (Skovsted et al. 2009a, 2015; Devaere et al. 2014). The reconstruction of these scleritomes also illuminates dramatically different baupläne. The camenellans are reconstructed as having a worm- or slug-like appearance with the scleritome forming a dorsal armour (Evans and Rowell 1990: fig. 5; Skovsted et al. 2015: 100–103, fig. 79) and the sclerites of the eccentrothecimorphs have a variously modified tubular form (Holmer et al. 2008; Skovsted et al. 2011, Murdock et al. 2014).

Tommotiids from Cambrian Series 2 rocks of Antarctica were first published by Evans and Rowell (1990) from the Shackleton Limestone in the Central Transantarctic Mountains. They collected considerable numbers of *Dailyatia* sclerites and assigned them to two species: *Dailyatia braddocki* Evans and Rowell, 1990, and *Dailyatia odyssei* Evans and Rowell, 1990. The only other Antarctic tommotiid material discovered prior to the present study was limited to specimens from glacial erratics from the Miocene Cape Melville Formation of King George Island, north of the Antarctic Peninsula of West Antarctica (Wrona 1989, 2004). These include species of *Dailyatia* (which were assigned to *Dailyatia ajax* by Wrona 2004), rare sclerites of *Dailyatia* sp., the lapworthellid *Lapworthella fasciculata* Conway Morris in Bengtson et al., 1990 and fragments of the problematic *Shetlandia multiplicata* Wrona, 2004. As earlier stated, the use of abundant tommotiids from South Australia to form a regional chronostratigraphic scheme has demonstrated their utility as biostratigraphic tools after widespread and systematic sampling (Betts et al. 2016, 2017, 2018). However, the sparse data on tommotiids from East Antarctica has hindered their use in providing a biostratigraphic and palaeobiogeographic context to this region. The aim of this work is to rectify this by providing systematic descriptions on a wealth of new tommotiid data from East Antarctica.

Institutional abbreviations.—KUMIP, University of Kansas, Biodiversity Institute and Natural History Museum, Invertebrate Paleontology Collections, Lawrence, USA; NRM, Naturhistoriska riksmuseet (Swedish Museum of Natural History), Stockholm, Sweden.

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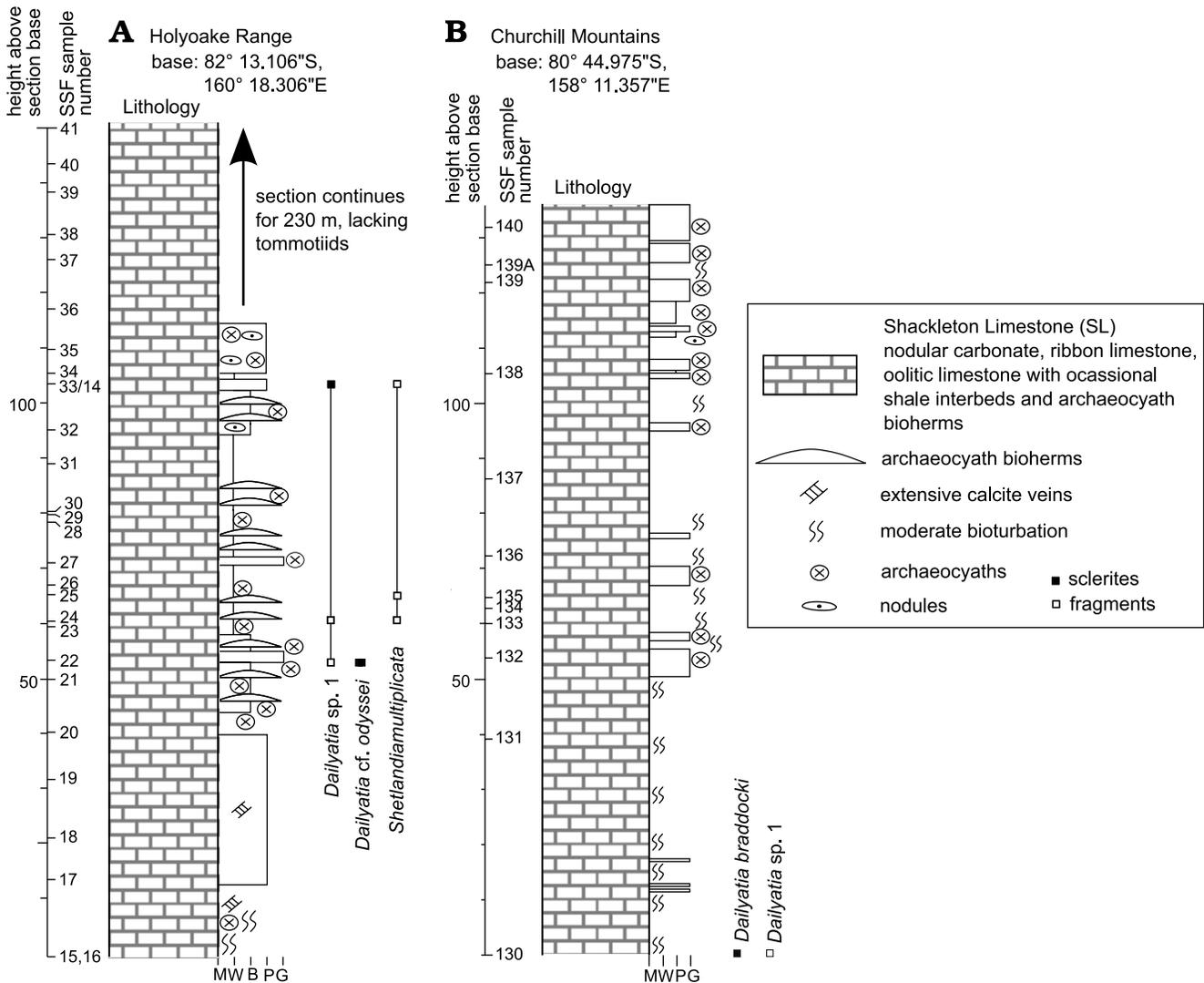


Fig. 2. Stratigraphic columns of the sampled sections in the Holyoake Range (HRA) and Churchill Mountains (CM2). Grain size: B, boundstone; G, grainstone; M, mudstone; P, packstone; W, wackestone.

Geological setting

The upper part of the Shackleton Limestone in the Holyoake Range consists of nodular carbonate, bedded limestone which is often highly bioturbated or oolitic and archaeocyath-microbiolite bioherms (Fig. 2). The Shackleton Limestone is overlain by the Holyoake Formation, an onlapping nodular siltstone, which in turn is overlain by the Starshot Formation. All three units are variably cross-cut by the Douglas Conglomerate. The transition from the Shackleton Limestone to Holyoake Formation probably represents the drowning of a carbonate platform (Rees et al. 1989; Myrow et al. 2002; Boger and Miller 2004) and change to deeper water facies associated with the Holyoake Formation (Goodge et al. 1993, 2004; Myrow et al. 2002). The Starshot Formation and Douglas Conglomerate are likely associated with the Ross Orogeny and mark the start of a collisional tectonic regime between East Antarctica and the palaeo-Pacific Plate (Rowell et al. 1988, 1992b; Myrow et al. 2002;

Squire and Wilson 2005; Foden et al. 2006; Paulsen et al. 2007).

The CM2 Section crosses 130 m of the Shackleton Limestone, with the top part of the section bounded by a severely deformed part of this unit (Fig. 2). The HRA section is 380 m and crosses 321.5 m of the uppermost Shackleton Limestone, although we only report findings from the lowest 150 m of this section, as the upper part of the Shackleton Limestone and younger units of the Byrd Group lack tomotiids. The remainder of this section is reported by Claybourn et al. (2019: fig. 2; 2020: fig. 2). In this unit, four horizons contain tomotiid fossils.

The tomotiid-bearing Shackleton Limestone reported by Evans and Rowell (1990) from both the northern margin of the Holyoake Range (sections M, H, S, Fig. 1) and the northern Churchill Mountains (section GM, Fig. 1) are from parts of the Shackleton Limestone that have undergone severe deformation so should be treated as isolated faunas (Evans and Rowell 1990: 692). The Shackleton Limestone from M, H, S

sections were described by Rees et al. (1989). The S and H sections contain a shallow-subtidal shelf association containing variable carbonates with biohermal reefs and bioturbation. Archaeocyathan-microbial reefs were reported from the H section (Rees et al. 1989: fig. 14). These sedimentological observations indicate a similar depositional environment between those sampled in the northern Holyoake Range and the new HRA section of the southern Holyoake Range.

A lesser known Cambrian Series 2 unit of East Antarctica, the informally named Schneider Hills limestone, crops out in the Schneider Hills of the southern Argentina Range (Fig. 1). The Schneider Hill limestone has an inadequately constrained biostratigraphy and may have been part of the same carbonate shelf that the Shackleton Limestone was deposited on (Rowell et al. 1992b). Rowell et al. (1992b) considered the Schneider Hills limestone as potentially a shallow-water equivalent of the deeper-water Hannah Ridge Formation (Rowell et al. 2001), which underlies the Drumian-aged Nelson Limestone (Rowell et al. 2001; Liebermann 2004; Bassett-Butt 2016), indicating a Series 2 or early Wuliuan age for these isolated outcrops. The archaeocyath fauna of the Schneider Hills limestone can be correlated with the Botoman Stage in the Siberian timescale (Debrenne and Kruse 1989).

The limited research that has been done on the outcrops in the Schneider Hills as well as other areas of the Argentina Range can give some clues to the age of this unit and relationship to other sedimentary packages of East Antarctica. The trilobite fauna collected from moraine boulders of unknown provenance at Mount Spann in the northern Argentina Range was described by Palmer and Gatehouse (1972). In-situ samples were not collected from Mount Spann, but an age can be estimated based on the rare non-endemic trilobites including *Xystridura* and *Redlichia*. *Xystridura* is known from Australia with two species collected at Mount Spann: *X. glacia* and *X. multilina* (Palmer and Gatehouse 1972). In Central and Northern Australia, the *Xystridura negrina/Redlichia forresti* Biozone covers the regional Ordian Stage (Laurie 2006), which lies within the upper part of Cambrian Series 2, Stage 4 (Sundberg et al. 2016), allowing for an approximate correlation based on this taxon. The upper range of *Xystridura* in the Northern Territory of Australia is not well constrained and has been recovered from the Tindall Limestone (Kruse 1990), Thornton Limestone and Arthur Creek Formation (Laurie 2012), where it ranges through the regional upper Ordian Stage into the Templetonian Stage (Laurie 2012; Smith et al. 2013), indicating *Xystridura* ranges into the Wuliuan Stage (Smith et al. 2013; Hally and Paterson 2014). *Solenopleura pruina* Palmer and Gatehouse, 1972, was also collected at Mount Spann, which has also been described from the Wuliuan-aged Nelson Limestone in the nearby Pensacola Mountains (Bassett-Butt 2016). These suggest that the succession in the Argentina Range spans Cambrian Stage 4 to the Wuliuan Stage, but it has not yet been thoroughly investigated biostratigraphically. Further systematic sampling of

fossils from the Schneider Hills limestone may constrain this, as previously the only systematically described fossil from this unit is the bradoriid arthropod *Bicarinella evansi* Rode, Liebermann, and Rowell, 2003 (Rode et al. 2003), known only from this location. The presence of tommotiid sclerites belonging to *Dailyatia* in the Schneider Hills limestone has been noted previously, but they were not described (Rowell et al. 1992a; Rode et al. 2003).

Material and methods

The fossils described in this paper come from two different collections. New material from the Holyoake Range and Churchill Mountains of the Central Transantarctic Mountains (Figs. 1, 2, sections HRA, CM2) was collected in the Austral summer of 2011 (by GAB, LEH, CBS). Bulk carbonate was processed by dilute 5–10% acetic acid maceration at Uppsala University and Macquarie University to extract phosphatic specimens following protocols outlined in Jeppsson et al. (1999).

The remaining material was sampled during field expeditions organised by personnel at Kansas University who collected material in the austral summers of 1984, 1985, 1987, and 1989. These samples were collected from unmeasured sections in the Holyoake Range (localities prefixed H, M, S), Churchill Mountains (GM and 87-L2) and Argentina Range (IC), shown in Fig. 1. Some tommotiid material has been described from these locations and are not re-described here (Evans and Rowell 1990).

Scanning electron microscope imaging was prepared using a Zeiss Supra 35 SEM at Uppsala University; a Hitachi S-4300 SEM at the Natural History Museum, Stockholm; and a Phenom XL benchtop SEM at Macquarie University. Material collected from the HRA and CM2 sections are deposited at the Swedish Museum of Natural History in Stockholm, Sweden (Naturhistoriska riksmuseet, NRM). Material collected by the Kansas University expeditions are deposited in the Kansas University Museum of Invertebrate Paleontology (KUMIP).

We follow the terminology of Skovsted et al. (2015: 11–16, figs. 5–7). For specimens in open nomenclature more general terminology is used when possible to avoid confusion over any implications of homology.

Results

In the HRA section, in the southern Holyoake Range (Figs. 1, 2), the tommotiids are represented by *Dailyatia* cf. *odyssei*, *Dailyatia* sp. 1, and *Shetlandia multiplicata*. They are clustered at four horizons in archaeocyath-rich biohermal limestone of the upper Shackleton Limestone, in the lower parts of the section (samples HRA/14, 22, 24, 25). In the CM2 section, in the northern Churchill Mountains (Figs. 1, 2), *Dailyatia braddocki* and *Dailyatia* sp. 1 are present only

Table 1. Sample localities for taxa described from new collections, taken from systematically sampled sections in the Southern Holyoake Range and Northern Churchill Mountains. Abbreviations: f, fragments.

Sclerite type	<i>Dailyatia</i> sp. 1			<i>Dailyatia braddocki</i>		<i>Dailyatia</i> cf. <i>odyssei</i>	<i>Shetlandia multiplicata</i>	
	f	A	C	f	C	f	C	f
Section HRA, southern Holyoake Range								
HRA/14	16	1	3					6
HRA/25								9
HRA/24	3							7
HRA/22	3					2	2	
Section CM2, northern Churchill Mountains								
CM2/130	33			9	8			

Table 2. Sample localities for taxa described from previously collected samples described in Evans and Rowell (1990) from the Holyoake Range, Churchill Mountains, and Argentina Range. Abbreviations: f, fragments.

Sclerite type	<i>Dailyatia icari</i> sp. nov.				<i>Dailyatia</i> sp. 1	<i>Dailyatia decobruta</i>		Kennardiidae indet.			
	f	A	C1	C2	f	f	C	f	1	2	3
Section H, northern Holyoake Range											
H84.2							1				
H84.6						1					
H84.17						1					
H84.20					1	7					
H84.25						9					
H84.26					1	15	2				
H85.25						2					
Section M, northern Holyoake Range											
M84.1							1	4			1
M84.2								3	1	1	5
M87.1											1
M87.3								1			
M87.4								5			
Section IC, Argentina Range											
IC84.2	2										
IC89.1	11		1								
IC89.2	50+	5	4	1							
IC3B	12		2	2							

at the collection locality marking the base of the section (samples CM2/130). The results are summarised in Table 1 and Fig. 2.

The H section (Fig. 1), in the northern Holyoake Range (Table 2) yielded predominantly sclerites of *Dailyatia decobruta* Betts in Betts et al., 2019 with rare fragments of *Dailyatia* sp. 1. The M section (Fig. 1) yielded almost exclusively sclerites from Kennardiidae indet., in addition to a single *D. decobruta* sclerite. The samples from the Argentina Range (section IC, Fig. 1) yield exclusively sclerites of *Dailyatia icari* sp. nov., which is known only from this area. The findings from the northern Holyoake Range and Argentina Range are summarised in Table 2.

Biostratigraphy

Cambrian Series 2 strata of East Antarctica are well exposed in the Churchill Mountains and Holyoake Range in the Central Transantarctic Mountains (Fig. 1), where the fossiliferous units of the Byrd Group are exposed. Combined data from newly described molluscs (Claybourn et al. 2019) and brachiopods (Claybourn et al. 2020) indicate a Cambrian Epoch 2, Age 4 for the upper part of the Byrd Group (upper Shackleton Limestone, Holyoake and Starshot formations), correlatable with the uppermost part of the *Dailyatia odyssei* Zone in South Australia (Betts et al. 2017). Previously collected *D. odyssei* from the northern Holyoake Range (sections M, H, S, Fig. 1; Evans and Rowell 1990) directly correlates this part of the Shackleton Limestone to the *D. odyssei* Zone of South Australia. Re-examined sclerites assigned in this work to *Dailyatia decobruta* from the northern Holyoake Range also provide correlation to the carbonate clasts of the White Point Conglomerate recovered from Kangaroo Island, South Australia (Betts et al. 2019) where it also occurs with *D. odyssei*. The assemblage of small shelly fossils recovered from the White Point Conglomerate clasts indicated an Epoch 2, Age 4 age, correlating to the *Pararaia janeae* Trilobite Zone and upper *D. odyssei* Zone (Jell in Bengtson et al. 1990; Betts et al. 2017). These fossils corroborated the original age designation of Jell in Bengtson et al. (1990) who recognised the trilobite assemblage of the White Point Conglomerate as part of their *P. janeae* Zone. *Dailyatia odyssei* from the Shackleton Limestone has only been recovered from the Churchill Mountains and northern Holyoake Range (Evans and Rowell 1990). Abundant *D. odyssei* sclerites reported by Evans and Rowell (1990) co-occurring with rarer *D. decobruta* enables correlation to the upper *D. odyssei* Zone and *P. janeae* Zone of the Mernmerna Formation (section NB; Betts et al. 2017: fig. 10). Species of *Dailyatia* which bear strong similarity to *Dailyatia decobruta* have also been recovered from the glacial erratics of King George Island (Wrona 2004), although reanalysis of this material is required to understand the taxonomic affinity of these specimens.

In the southern Holyoake Range (section HRA, Figs. 1, 2) an assemblage including *D. cf. odyssei*, *Dailyatia* sp. 1, and *Shetlandia multiplicata* is present. Biostratigraphic correlation is less clear based on these fossils alone, with no temporally constrained tommotioid fossils found in this section. The presence of *S. multiplicata* is the first example of this enigmatic taxon from autochthonous carbonates; it was previously only known from the glacial erratics of King George Island where it occurs with *Dailyatia* (Wrona 2004). The lack of *D. odyssei* may also indicate these fossils occur above the last appearance datum for this taxon (although specimens of *D. cf. odyssei* do occur here).

The tommotioid fauna from the Argentina Range consists exclusively of *Dailyatia icari* sp. nov., which is currently only known from this region. The Schneider Hills limestone remains biostratigraphically unconstrained with the discovery of this species.

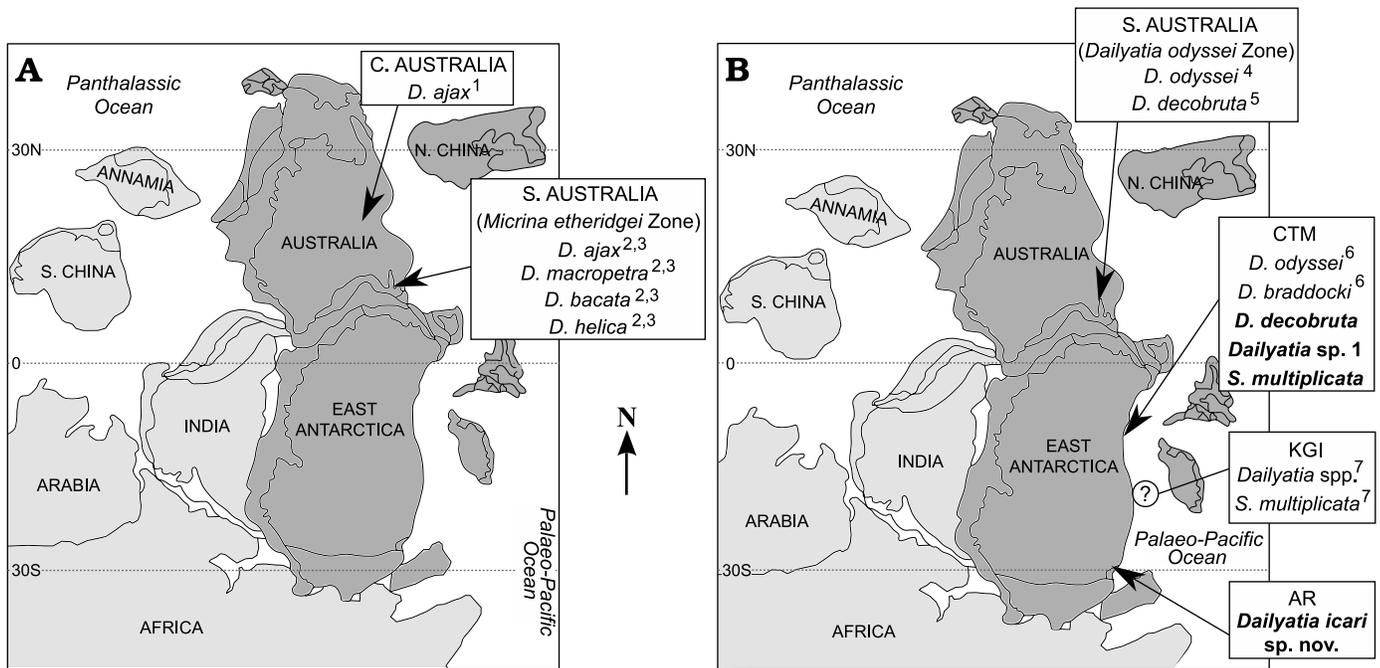


Fig. 3. Palaeobiogeographic maps of the distribution of *Dailiyatia* and other camenellan tommotiids from East Gondwana (dark grey). New occurrences described in this paper in bold. Maps show the Cambrian (A) Terreneuvian Series to basal Series 2, Stage 3 (i.e., upper range of the *Micrina etheridgei* Zone for South Australia, Betts et al. 2016, 2017) and (B) Series 2 (from the base of the *Dailiyatia odysssei* Zone for South Australia, Betts et al. 2016, 2017). Data for previous occurrences: ¹ Laurie 1986; ² Skovsted et al. 2015; ³ Betts et al. 2016; ⁴ Betts et al. 2017; ⁵ Betts et al. 2019; ⁶ Evans and Rowell 1990; ⁷ Wrona 2004. Abbreviations: CTM, Central Transantarctic Mountains; KGI, King George Island; AR, Argentina Range. Map adapted from Torsvik and Cocks (2013) and Yang et al. (2015).

Palaeobiogeography

Within Antarctica.—Original descriptions of *Dailiyatia* from Antarctica were made by Evans and Rowell (1990) from collection sites in the northern Holyoake Range and southern and northern areas of the Churchill Mountains (Fig. 1; Evans and Rowell 1990: fig. 1). The endemic *Dailiyatia braddocki* was only recovered from the northern Churchill Mountains (locality GM87.1 of the GM section, Fig. 1; Evans and Rowell 1990: fig. 1, table 1). In our investigation, this species was also recovered from the CM2 section (Fig. 2), in the same region of the Churchill Mountains (Fig. 1). Within Antarctica, previously described *Dailiyatia odysssei* is also known from the northern and southern parts of the Churchill Mountains and the northern Holyoake Range in the Central Transantarctic Mountains (Fig. 1, localities GM, 87-L2, H, M, S; Evans and Rowell 1990: fig. 1, table 1). New material comparable to *D. odysssei* from the Holyoake Range, include only poorly preserved C sclerites of *Dailiyatia* cf. *odysssei* in the southern Holyoake Range (section HRA, Figs. 1, 2).

The Shackleton Limestone of the southern Holyoake Range (section HRA, Figs. 1, 2) contains a faunule including three tommotiids: *Dailiyatia* sp. 1, *Dailiyatia* cf. *odysssei*, and *Shetlandia multiplicata*. The Shackleton Limestone in the northern Holyoake Range has a different assemblage of tommotiids, including *Dailiyatia* sp. 1, *Dailiyatia decobruta*, and Kennardiidae indet. originally described by Evans and Rowell (1990) and identified here as *Dailiyatia odysssei*. The

northern Holyoake Range also hosts the type locality for *Dailiyatia odysssei* (locality M84.2; Evans and Rowell 1990). As such *Dailiyatia* sp. 1 is the only tommotiid species that occurs in both the northern and southern regions in the Holyoake Range, although it is known only from two sclerite fragments in the northern Holyoake Range (Table 1). In the northern Churchill Mountains (sections CM2 and GM, Figs. 1, 2), *D. odysssei* co-occurs with *Dailiyatia braddocki* (Evans and Rowell 1990: table 1), making *D. odysssei* the only faunal link between the northern Holyoake Range and the northern Churchill Mountains.

These taxa also provide evidence for the provenance of glacial erratics recovered from the Miocene glaciomarine Cape Melville Formation of King George Island. These erratics yielded *Shetlandia multiplicata* which also occurs in the autochthonous carbonates of East Antarctica (Fig. 3; Wrona 2004). *Shetlandia multiplicata* is known from the Shackleton Limestone of the southern part of the Holyoake Range (section HRA, Figs. 1, 2, Table 1). The Shackleton Limestone is a likely source for these erratics, as suggested by Wrona (2004), as they also contain the camenellan tommotiid *Lapworthella fasciculata* (Wrona 2004) and similar assemblages of brachiopods (Holmer et al. 1996) and bradoriids (Wrona 2009) not currently known from the autochthonous rocks of the Shackleton Limestone. The Argentina Range yields sclerites of *Dailiyatia icari* sp. nov. (Fig. 3). This species is currently only known from disarticulated sclerites of the temporally unconstrained Schneider Hills limestone.

East Gondwana.—Of the seven previously named species of *Dailyatia*, which all occur in the Cambrian Series 2 of East Gondwana, only *Dailyatia odyssei* and *Dailyatia decobruta* occur in both East Antarctica and South Australia (Fig. 3). *Dailyatia braddocki* (Shackleton Limestone, Churchill Mountains), the newly described *Dailyatia icari* sp. nov. (Argentina Range), *Dailyatia* sp. 1, and Kennardiidae indet. (Shackleton Limestone, Holyoake Range), and the problematic *Shetlandia multiplicata* (Shackleton Limestone, Holyoake Range and the King George Island erratics) are apparently endemic to East Antarctica (Fig. 3). In East Antarctica, *Dailyatia decobruta* has been recovered from the Shackleton Limestone, with the majority of South Australian specimens collected from the allochthonous limestone clasts of the White Point Conglomerate of Kangaroo Island. The carbonate clasts of the White Point Conglomerate have uncertain provenance but bear faunal similarities to shelly fossil assemblages from the Koolywartie Limestone Member of the Parara Limestone of the Yorke Peninsula, South Australia (Paterson et al. 2007; Betts et al. 2019). Rare sclerites of *D. decobruta* are also found in the Mernmerna Formation of the Arrowie Basin (“*Dailyatia* sp. A” of Skovsted et al. 2015; Betts et al. 2017).

Dailyatia odyssei is also present in both East Antarctica and South Australia. Sclerites were reported from the Shackleton Limestone by Evans and Rowell (1990), where they were found widespread in the rocks sampled in the northern Churchill Mountains and northern Holyoake Range (Fig. 2). In the southern Holyoake Range, the new HRA section yielded no unambiguous *D. odyssei* sclerites, with only a few poorly preserved sclerites tentatively referred to *D. cf. odyssei*. In South Australia, *D. odyssei* is widespread in its eponymous *D. odyssei* Zone of both the Arrowie and

Stansbury basins (Gravestock et al. 2001; Skovsted et al. 2015; Betts et al. 2017).

Systematic palaeontology

Lophophorata Hyman, 1959

Class Incertae sedis

Order Tommotiida Missarzhevsky, 1970

Family Kennardiidae Laurie, 1986

Dailyatia Bischoff, 1976

Type species: *Dailyatia ajax* Bischoff, 1976, lower Cambrian, Ajax Limestone, Mt. Scott Range, northern Flinders Ranges, South Australia.

Dailyatia icari sp. nov.

Figs. 4–6.

ZooBank LSID: urn:lsid:zoobank.org:act:33673DE4-7750-48D8-BC9C-7DCBE8198C7A

Etymology: From Latin *Icarus* (latinized genitive derivation of the Greek *Ikaros*), the legendary Greek character who flew to close to the sun; in reference to the radial plicae resembling rays of the sun.

Type material: Holotype: KUMIP 585059, C1 sclerite from locality IC3B (Fig. 5A). Paratypes: KUMIP 585054, A sclerite from locality IC89.2 (Fig. 4A); KUMIP 585070, C2 sclerite from locality IC3B (Fig. 6C).

Type locality: Sample locality IC3B of the Schneider Hills limestone, Argentina Range, East Antarctica.

Type horizon: Unknown horizon in Cambrian Series 2.

Material.—Six A sclerites from sample IC89.2 (KUMIP 585054–585058, 5 figured), six C1 sclerites from sample IC3B (KUMIP 585059, 585060, 2 figured), one C1 scler-

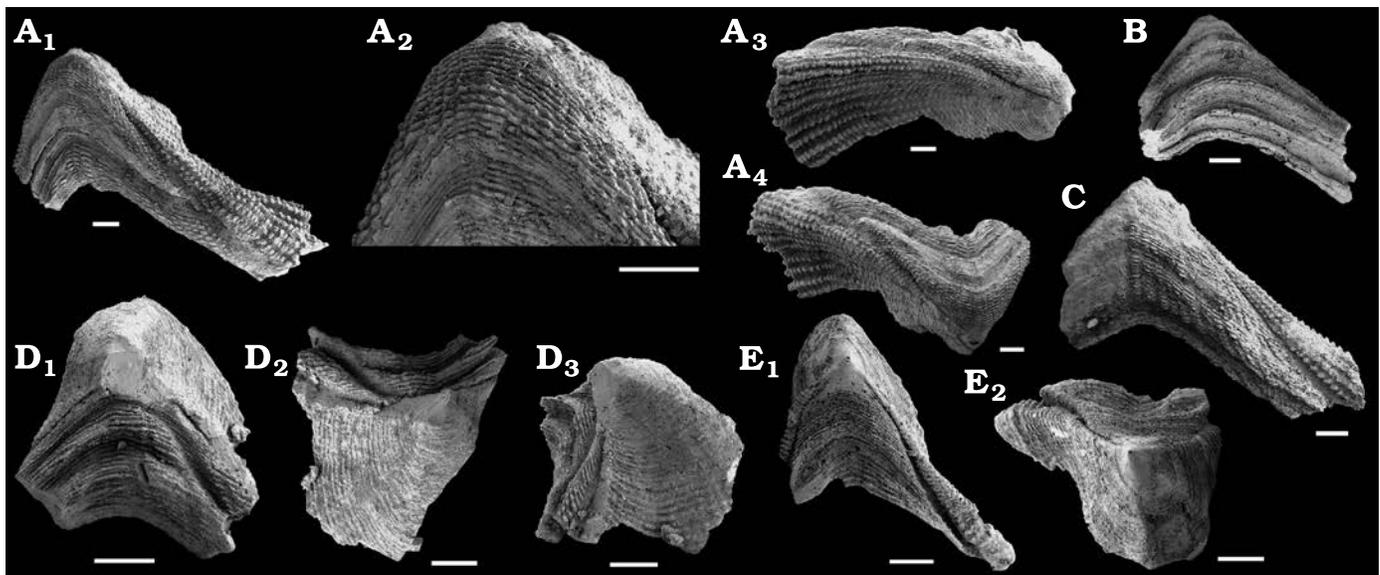


Fig. 4. The camenellan tommotiid *Dailyatia icari* sp. nov. A sclerites from the lower Cambrian Schneider Hills limestone, Schneider Hills, Argentina Range, Antarctica. A. KUMIP 585054, view of anterior field (A₁), enlarged view of the anterior apical area (A₂), oblique view of the lateral field (A₃), apical view with anterior to the top (A₄). B. KUMIP 585055, anterior field of broken sclerite. C. KUMIP 585056 anterior field of broken sclerite. D. KUMIP 585057, view of anterior field (D₁), apical view with anterior to the top (D₂), lateral view (D₃). E. KUMIP 585058, view of anterior field (E₁), apical view with anterior to the top (E₂). Scale bars 200 μm.

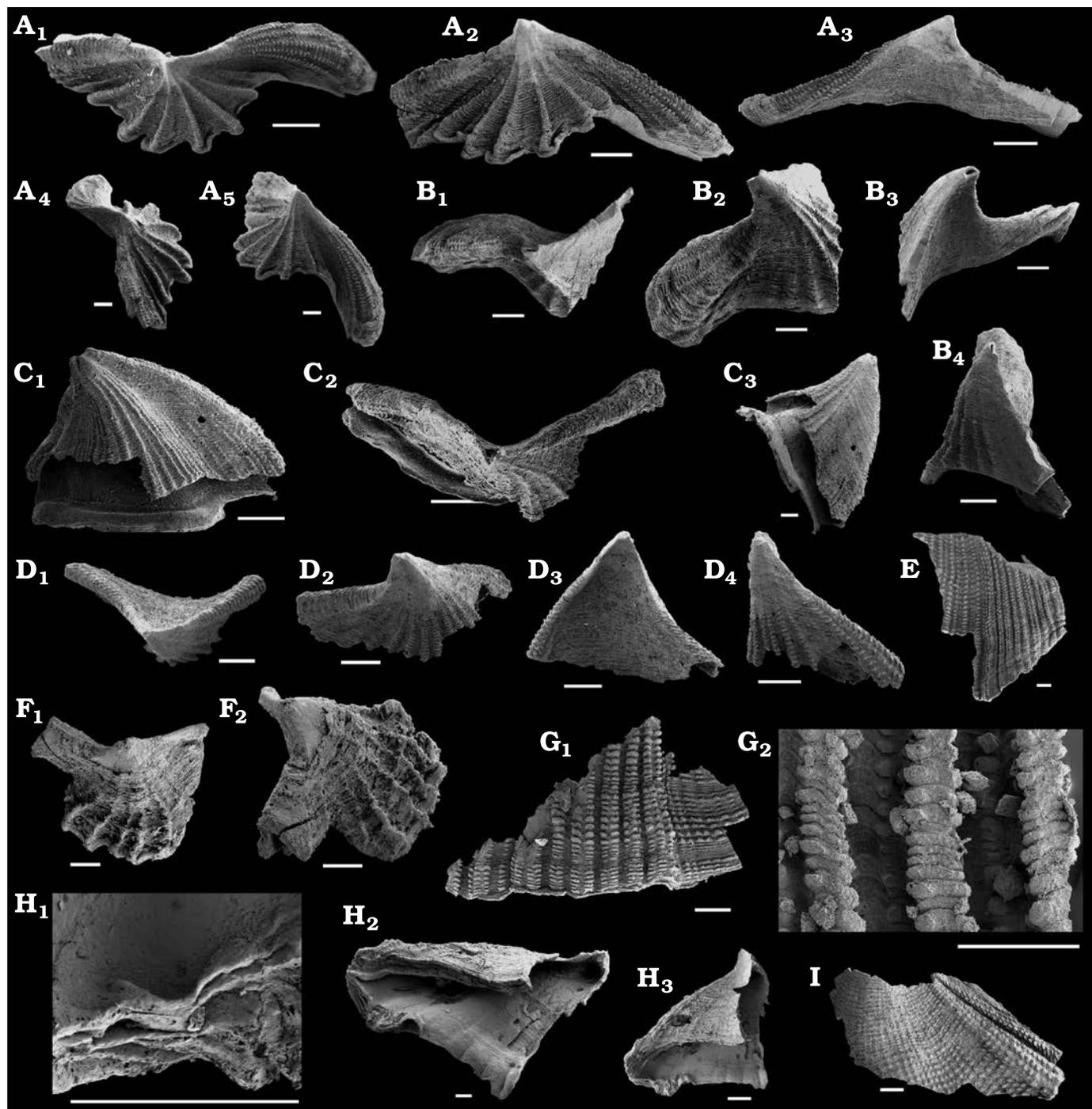


Fig. 5. The camenellan tommotioid *Dailyatia icari* sp. nov. C1 sclerites and sclerite fragments from the lower Cambrian Schneider Hills limestone, Schneider Hills, Argentina Range, East Antarctica. **A.** Dextral sclerite, KUMIP 585059, apical view (A₁), view of dorsal (A₂) and ventral (A₃) surfaces, view of distal (A₄) and proximal (A₅) edges. **B.** Sinistral sclerite, KUMIP 585060, apical view (B₁), oblique view of proximal edge and dorsal surface (B₂), oblique view of distal edge and ventral surface (B₃), view of distal edge (B₄). **C.** Dextral sclerite, KUMIP 585061, dorsal (C₁), apical (C₂), and oblique dextral (C₃) views. **D.** Dextral sclerite, KUMIP 585062, apical (D₁), apical-dorsal (D₂), ventral (D₃), and lateral (D₄) views. **E.** Large fragment from unknown sclerite type, KUMIP 585063. **F.** Sclerite of unknown chirality, KUMIP 585064, apical (F₁) and lateral (F₂) views. **G.** Sclerite fragment from unknown sclerite type, KUMIP 585065, detail showing distinctive pseudoplicae (G₁), general view (G₂). **H.** Sclerite of unknown chirality, KUMIP 585066, detail of apertural margin (H₁), oblique views of the aperture (H₂, H₃). **I.** Fragment of unknown sclerite type showing pseudoplicae, KUMIP 585067. Scale bars 200 μ m.

ite from sample IC89.1 (KUMIP 585061), four C1 sclerites from IC89.2 (KUMIP 585062, 585064, 585066, 3 figured), one C2 sclerite from sample IC89.2 (KUMIP 585068), two C2 sclerites from sample IC3B (KUMIP 585069, 585070).

Numerous fragments from sample IC84.2, IC89.1, IC89.2 (KUMIP 585063, 585065, 585067, 3 figured) and IC3B, listed in Table 2. Cambrian Series 2, Schneider Hills limestone, Argentina Range, East Antarctica.

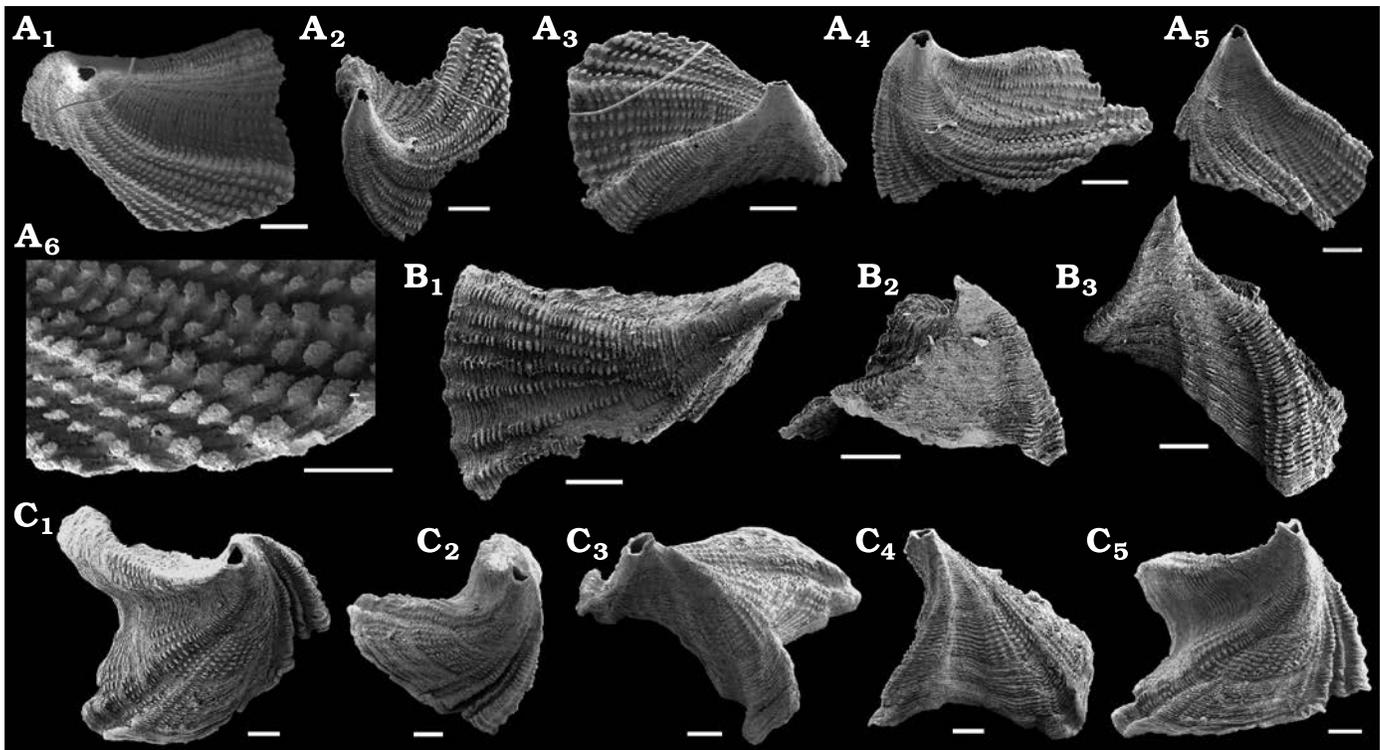


Fig. 6. The camenellan tommotiid *Dailyatia icari* sp. nov. C2 sclerites from the lower Cambrian Schneider Hills limestone, Schneider Hills, Argentina Range, East Antarctica. A. KUMIP 585068, apical (A₁), oblique lateral (A₂), ventral (A₃), lateral (A₄), and dorsal (A₅) views, detail of pustulose ornament on the central surface of A₁ (A₆). B. KUMIP 585069, apical (B₁), lateral (B₂), and ventral (B₃) views. C. KUMIP 585070, apical (C₁), lateral-dorsal (C₂), ventral (C₃), lateral (C₄), and dorsal (C₅) views. Scale bars 200 μ m, except A₆, 100 μ m.

Diagnosis.—Species of *Dailyatia* with distinctive ornament of pseudoplicae formed by pustules in a single or double-row. Ornament of densely set, narrow concentric ribs. Sclerite subtypes C1 and C2 recognised, no subtypes recognised for A sclerites. A sclerites pyramidal, triangular or pentagonal in transverse section. No plicae present on concave anterior field. Apex slightly coiled anteriorly. C1 sclerites slightly coiled over ventral side with array of well-developed and regular radial plicae on dorsal side. Dorsal and proximal edges with pseudoplicae, ventral side concave with comarginal ribs and lacking pseudoplicae. C2 sclerites strongly torted, triangular in transverse section and coiled ventrally. Ventral field concave, with weakly developed pseudoplicae. Dorsal field with broad central surface bounded by broad furrows separating the central plicae from the distal and marginal edges.

Description.—Sclerites pyramidal with two sclerite types identifiable (A and C) and two C sclerite subtypes identifiable: C1 and C2. C1 sclerites dorso-ventrally compressed (Fig. 5A₁, A₄, B₁, C₂, D₁, H₂, H₃), C2 sclerites conical and torted (Fig. 6A₁, C₁).

A sclerites conical and bilaterally symmetrical. Comarginal ribs are dense and cover sclerites with larger specimens with closely packed rows of pseudoplicae formed by rounded pustules (Fig. 4A). Pseudoplicae are only weakly developed on smaller specimens (Fig. 4D, E). Anterior field is concave and lacking plicae (Fig. 4A₁, A₃, B, C, D₁, D₂, E₁, E₂). Growth disturbances are present on the anterior surface in the form

of comarginal depressions (Fig. 4A₁, B, C, D₁). The anterior field is separated from the lateral fields by a deep furrow and an anterolateral plication (Fig. 4A₁, A₃, A₄, C, D₁–D₃, E₁, E₂). The lateral field is concave, with dense pseudoplicae (Fig. 4A₃) or lacking pseudoplicae (Fig. 4E₂). The posterior field is partially preserved in part on two sclerites where they are separated from the lateral field by a weakly developed posterolateral plication (Fig. 4D₂, E₂). A deltoid cannot be clearly delineated on the posterior field.

C1 sclerites all have dorsoventral compression and a broad V-shape when viewed apically (Fig. 5A₁, B₁, C₂, D₁). The central part of the ventral side lacks plicae and pseudoplicae but has 1–3 weakly developed pseudoplicae at the proximal edge (Fig. 5A₃, B₁, D₃). Pseudoplicae are lacking on the central surface of the dorsal side but are present on the proximal edge (2–5 pseudoplicae, Fig. 5A₁, A₅, B₂, C₂, D₁) and distal edge (1–3 pseudoplicae, Fig. 5A₁, A₄, B₂, C₂, D₁). The central surface of the dorsal side is dominated by 7–8 strongly developed radiating plicae which dominate the entire field forming an evenly curved central surface (Fig. 5A₁, A₂, B₁, B₂, C₁, C₂, D₁, C₂, F₁, F₂). The plications start at the smooth, unornamented apex and radiate towards the aperture of the sclerite (Fig. 5A₁, B₂, D₂). One sinistral C1 sclerite is slightly torted, with the apex overhanging the proximal edge (Fig. 5B).

C2 sclerites are strongly torted, pyramidal and triangular in transverse section (Fig. 6A₁, B₁, C₁). The ventral field is concave and lacks plicae but has 2–7 weakly developed

pseudoplicae and is separated from the proximal and distal edges by furrows (Fig. 6A₃, B₃, C₃). The dorsal field has a broad central surface, covered by densely set pseudoplicae formed by rounded pustules (Fig. 6A₄, A₅, B₁, C₂, C₄, C₅). The central area is bounded proximally by a plication, with a broad furrow separating the central surface from the proximal edge (Fig. 6A₂, C₁, C₄). A narrow furrow with three plicae separating the central surface from the distal edge is present in one specimen (Fig. 6C₁, C₂, C₅).

The comarginal ribs are ubiquitously distributed across all persevered sclerites, except at the smooth apex of the C1 sclerite (Fig. 5A₁, B₂, D₂) and some A sclerites (Fig. 5E) and are separated by narrow inter-rib grooves. The pseudoplicae are typically unevenly spaced and are delineated by a series of broad pustules (Fig. 5E, G, I), separated by furrows (Fig. 5G). On one C2 sclerite the pseudoplicae are variably developed on the dorsal fields with well-developed pustules developed in a central band, with only comarginal ribs towards the apex and weakly developed, intermittent bands of pustules towards the base (Fig. 6C). Some sclerite fragments have pseudoplicae formed by paired radial rows of pustules (Figs. 5E, G, I, 6A₆). This arrangement develops out of a single radial row of pustules and splits into a paired radial row towards the base, the pairs forming single pseudoplicae (Fig. 5E–G). These paired pustules are arranged along comarginal ribs in the same manner as other specimens' pseudoplicae with single columns of pustules (Fig. 5E–G, compare *Dailyatia bacata*, Skovsted et al. 2015: fig. 34). Reticulate micro-ornament seen in other *Dailyatia* species is not present on most specimens, but a poorly preserved example may be seen on one (Fig. 6A₆).

Remarks.—The few available specimens of *Dailyatia icari* sp. nov. from the Schneider Hills limestone in the Argentina Range have a distinct morphology and ornament clearly delineating them from other species of *Dailyatia*. The A sclerites of *D. icari* are not well preserved, with the posterior part of the sclerite typically broken. A distinguishing feature of the A sclerites of *D. icari* is the well-developed furrow at the lateral edges of the anterior field bounding the well-developed anterolateral plication, which is not found on other species of *Dailyatia*. The distinctive radially plicate dorsal side of the C1 sclerites is also unique amongst species of *Dailyatia*. Other species, like *Dailyatia ajax* (Skovsted et al. 2015: figs. 16C, L, N, P, 17Q) and *D. helica* (Skovsted et al. 2015: fig. 39A–F, K–T, W, X) share a well-developed series of plicae on the dorsal side of C1 sclerites. However, the C1 sclerites of *D. ajax* are conical and taller than they are wide (Skovsted et al. 2015: figs. 15–17), unlike the squat C1 sclerites of *D. icari*, which are typically wider than they are tall (Fig. 5A₁, A₂, C₁, C₂). The C sclerites of *D. helica* have a dorsally elongated central surface which forms a deep recession between the central surface and the distal edge (Skovsted et al. 2015: fig. 39), a feature not present in *D. icari* sp. nov. The C1 sclerites of *D. icari* sp. nov. are dorsoventrally flattened and have a broad V-shape when viewed apically (Fig. 5A₁, C₂, D₁, F₁). This is similar to the C sclerites of *Dailyatia*

braddocki (Evans and Rowell 1990: figs. 6.8, 6.14). *Dailyatia icari* is easily distinguished from *D. braddocki* as the C sclerites of *D. braddocki* lacks radial plicae and pseudoplicae (Evans and Rowell 1990: figs. 6.7–6.14).

The C2 sclerites of *D. icari* sp. nov. can be distinguished from those of other species by the broad central surface. For example, the C2 sclerites of *Dailyatia odyssei* have a comparable degree of torsion, but have a well-defined central plication (Skovsted et al. 2015: fig. 49A–H). The C2 sclerites of *Dailyatia macroptera* are also strongly torted, but these have a dorsal surface with a deep concave surface (Skovsted et al. 2015: fig. 25A–I, M–S), easily distinguishing them from the convex central surface on the dorsal field of C2 sclerites of *D. icari*.

Dailyatia icari sp. nov. have pseudoplicae formed by radial rows of pustules. Similar pseudoplicae are found in other species, most notably *Dailyatia decobruta* (Betts et al. 2019: fig. 17G–I) and *Dailyatia bacata* (Skovsted et al. 2015: fig. 34), however, the pseudoplicae of *D. bacata* have crenulated walls between them which are not present in *D. icari* sp. nov. *Dailyatia bacata* also lacks the pseudoplicae formed by paired pustules that occurs in some specimens of *D. icari* sp. nov. The pustules of *D. bacata* also protrude further from the main body of the sclerite than those of *D. icari* (Skovsted et al. 2015: fig. 34B, H), and have a reticulate ornamentation both on the pustules and the depressions between their pseudoplicae (Skovsted et al. 2015: fig. 34C, H), whereas *D. icari* sp. nov. lacks such micro-ornamentation.

Dailyatia decobruta, known from both the Cambrian Series 2, Stage 4 carbonate clasts of the White Point Conglomerate, Kangaroo Island, and the Mernmerna Formation in the Flinders Ranges, South Australia (Betts et al. 2019: figs. 15–18) and the Shackleton Limestone of the northern Holyoake Range (Fig. 7C–F) also has dense pustules arranged in pseudoplicae (Betts et al. 2019: fig. 17G–I). The C sclerites of *D. decobruta* are easily distinguishable from C sclerites of *D. icari* as they lack radiating central plicae on their dorsal side (Betts et al. 2019: figs. 16D, E, H–J, 17A, B). The C2 sclerites of *D. decobruta* are similarly torted to the C2 sclerites of *D. icari*. However, the strong dorsoventral compression of the C2 sclerites of *D. decobruta* (Betts et al. 2019: fig. 17D–F) clearly distinguish these species, as the C2 sclerites of *D. icari* are pyramidal in shape (Fig. 6A₁, C₁).

Another East Antarctic endemic, *Dailyatia* sp. 1, from the Shackleton Limestone in the Holyoake Range, has an arrangement of chaotically distributed plicae with small rows of crests with a reticulated ornament rather than pustules (Fig. 9F₂). These often form oblique rows that join the main sequence of concentric ribs at irregular intervals (Fig. 8A₁, 9F, G). This ornamentation distinguishes these fragments from *D. icari* sp. nov. which exhibits single or paired pustulose pseudoplicae.

A broken *D. icari* sp. nov. specimen shows the typically continuous growth laminations of *Dailyatia* (Fig. 5H). Small pits are visible at the apertural margin at the base of

the sclerite may be the imprints of epithelial cell moulds (Fig. 5H₁).

Stratigraphic and geographic range.—Unknown horizon in Cambrian Series 2, Schneider Hills limestone, Argentina Range, East Antarctica (Table 2).

Dailyatia braddocki Evans and Rowell, 1990

Fig. 7A, B.

1988 *Dailyatia* spp.; Rowell et al. 1988: figs. J, K, M.

1990 *Dailyatia braddocki* n. sp.; Evans and Rowell 1990: 696, figs. 6.1–6.17.

2015 *Dailyatia braddocki*: Skovsted et al. 2015: fig. 9A–F.

Material.—Eight broken C sclerites from the CM2/130 sample (NRM X10001, X10002, 2 figured) (Table 1, Fig. 2). Cambrian Series 2, Stages 3, 4, Shackleton Limestone of the Northern Churchill Mountains, East Antarctica.

Description.—C sclerites with strong dorso-ventral compression. A single well-developed plica is preserved on proximal edge of ventral side, projecting slightly away from the edge, partially covering a small furrow on the ventral side (Fig. 7A₂, B₁). On the ventral side, the distal edge is separated from a plica by a furrow (Fig. 7A). Sclerites with stepped concentric ribs and ornament of small pustules arranged along the ribs but do not form pseudoplicae (Fig. 7A₂, B₂).

Remarks.—The sclerites found in the CM2 section in the Churchill Mountains are both broken but fall within the diagnosis for *Dailyatia braddocki* (Evans and Rowell 1990: 696). *Dailyatia braddocki* was originally only found at one locality in the northern Churchill Mountains (GM87.1, Fig. 1; Evans and Rowell 1990: table 1), close to the CM2 locality (Fig. 1) reported herein. The broad-shaped profile of the sclerites with single radial plica on the ventral side at the proximal edge are the same as those from the original collections of Evans and Rowell (1990: figs. 6.7, 7–10, 13, 14). The weakly developed pustules of *D. braddocki* were not described or figured by Evans and Rowell (1990) but re-imaging material from their GM87.1 locality (Fig. 1) shows this ornamentation is present (Fig. 9H, I; Skovsted et al. 2015: fig. 9A–E).

Stratigraphic and geographic range.—Cambrian Series 2, Stages 3, 4, Shackleton Limestone of the Northern Churchill Mountains, Central Transantarctic Mountains, East Antarctica (Table 1, Evans and Rowell 1990).

Dailyatia decobruta Betts in Betts et al., 2019

Fig. 7C–F.

cf. 2004 *Dailyatia ajax*; Wrona 2004: figs. 9A–D, 11A, B, 12A.

2015 *Dailyatia* sp. A; Skovsted et al. 2015: fig. 51.

2019 *Dailyatia decobruta* sp. nov.; Betts et al. 2019: 514–515, figs. 15–18.

Material.—Four C1 sclerites, one from H.84.2, two from H.84.26, and one from M84.1 (KUMIP 585071–585074, all figured) (Fig. 1, Table 2; Evans and Rowell 1990). Fragmentary material found through the H and M sections

of Evans and Rowell (1990), listed in Table 2. Cambrian Series 2, Stage 4(?) of the Shackleton Limestone in northern Holyoake Range, East Antarctica.

Description.—The specimens fit within the diagnosis (Betts et al. 2019: 513–515) for C1 sclerites. They are triangular in cross section (Fig. 7C₂, D₁) with the apex slightly coiled over the concave ventral field. Dense pustulose ornamentation forms pseudoplicae on the convex dorsal field (Fig. 7C₁, C₃). The pustules and troughs between the pseudoplicae are covered in a fine reticulate micro-ornamentation (Fig. 7C₁, C₃).

Plicae are generally poorly developed, but a broad central radial plication on the dorsal field is present in two specimens (Fig. 7C₂, D₁, F) and a single plica is present on the dorsal field adjacent to the proximal edge in one specimen (Fig. 7E₁). The ventral field lacks plicae. The distal and proximal edges are variable, with broad rounded edges in two specimens (Fig. 7C₂, D₁) and narrow edges in two (Fig. 7E₁, F₂). The apertural margins of the sclerites from the Shackleton Limestone are broken, so information on the complete size and shape of the aperture is missing. A single minute oval perforation is present on the apices of all specimens (Fig. 7C₂, D₁, E₂, F₂) with a width of 31–69 µm and a length of 15–30 µm (n = 3). The apical part is smooth in all but one specimen (Fig. 7E).

Remarks.—Ornament consisting of pustules arranged into regular rows (pseudoplicae) and covered by reticulate micro-ornament is a key characteristic of this species. The three specimens from the Shackleton Limestone exhibit this ornamentation and are overall very closely similar to those recently described from the White Point Conglomerate (Betts et al. 2019: 513–515), though they vary in some non-diagnostic characteristics. For example, the Antarctic specimens lack the torsion seen in the C2 and C2a sclerites from the White Point Conglomerate (Betts et al. 2019: fig. 18). The extent of the pustulose ornament also differs slightly, which covers the entire sclerite surface, including the apex in specimens from the White Point Conglomerate (Betts et al. 2019: fig. 17A–C), but is not present on the apical area in specimens from the Shackleton Limestone, which is smooth. The ventral surface of two C1 sclerites from the Shackleton Limestone are also slightly less dorsoventrally compressed than those figured by Betts et al. (2019: fig. 16). The specimens of *D. decobruta* from the White Point Conglomerate also have an apex that overhangs the ventral part of the aperture when viewed apically (Betts et al. 2019: fig. 16D₂, E, I₂), whereas the apertural margin in specimens from the Shackleton Limestone extend out beyond the apex, increasing the size of the internal cavity (Fig. 7C₂, D₁, D₂, E₁).

Dailyatia decobruta co-occurs with two fragments of *Dailyatia* sp. 1 in the Shackleton Limestone in the northern Holyoake Range (samples H84.20 and H84.26, Table 2). These taxa can be easily distinguished as *Dailyatia* sp. 1 lacks the densely set pseudoplicae of *D. decobruta*, and

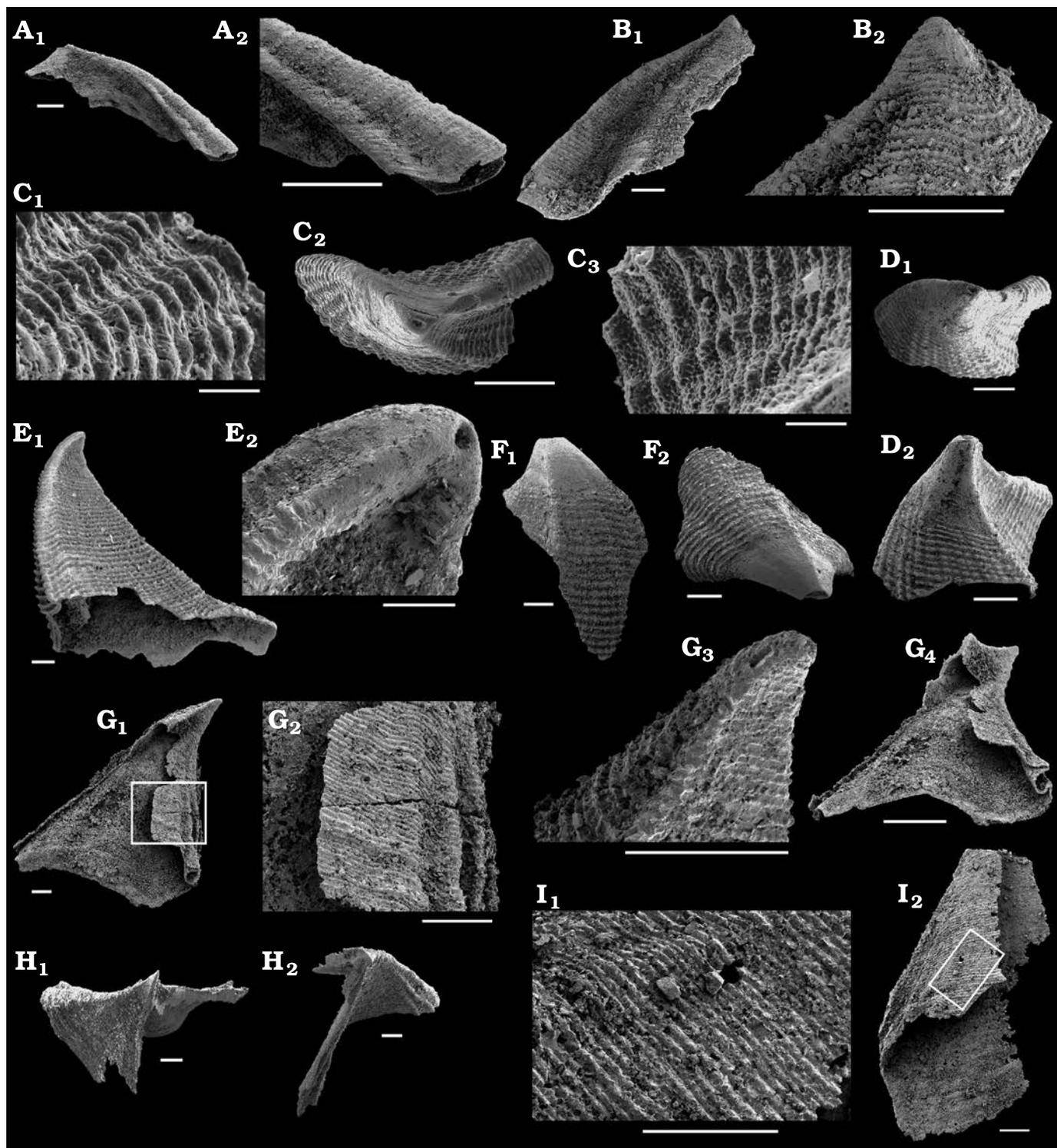


Fig. 7. The camenellan tommotiids from from the Cambrian Series 2, Stages 3, 4, Shackleton Limestone, Transantarctic Mountains, East Antarctica. *Dailiyatia braddocki* Evans and Rowell, 1990, Churchill Mountains (A, B), *Dailiyatia decobruta* Betts in Betts et al., 2019, Holyoake Range (C–F), and *Dailiyatia* cf. *odyssei*, Holyoake Range (G–I). A. C sclerite, NRM X10001, ventral view (A₁), detail showing fold in the margin of the ventral field (A₂). B. Sclerite of unknown chirality, NRM X10002, dorsal view (B₁), detail showing apex (B₂). C. Dextral C sclerite, KUMIP 585071, details showing micro-ornament on the anterior-lateral (C₁) and the posterior (C₃) fields, apical view (C₂). D. Dextral C sclerite, KUMIP 585072, apical view (D₁), view of proximal edge and dorsal field (D₂). E. Sclerite of unknown chirality, KUMIP 585073, oblique view of ventral field (E₁), view of apical area showing perforated apex (E₂). F. Sclerite of unknown chirality, KUMIP 585074, dorsal (F₁) and oblique apical (F₂) views. G. Dextral C sclerite, NRM X10003, view of broken dorsal field (G₁), detail showing fine growth series (G₂), apex (G₃), oblique basal view showing plicae at distal edge (G₄). H. Sinistral C sclerite, NRM X10004, apical view (H₁), oblique view of distal edge and part of ventral field (H₂). I. Unknown sclerite type, NRM X10005, ventral view (I₁), detail showing fine growth series (I₂). Scale bars 200 μ m, except E₂, 50 μ m.

bears distinctive, strongly developed pseudoplicae formed from aligned crenulated projections. The sclerites of *D. decobruta* from the Shackleton Limestone bear similarity to specimens assigned to *Dailyatia ajax* from the glacial erratics from King George Island in West Antarctica (Wrona 2004). As mentioned by Betts et al. (2019) those from King George Island do not develop the densely arranged pseudoplicae characteristic of *D. decobruta*, although they share similar gross morphology.

Stratigraphic and geographic range.—Cambrian Series 2, Stage 4(?) of the Shackleton Limestone in northern Holyoake Range, Central Transantarctic Mountains, East Antarctica (Table 2); Cambrian Series 2, Stage 4 (upper *Dailyatia odyseii* Zone, *Pararaia janeae* Zone) of the Mernmerna Formation (NB section) in the eastern Flinders Ranges (Skovsted et al. 2015; Betts et al. 2017) and carbonate clasts recovered from the White Point Conglomerate of Kangaroo Island, South Australia (Betts et al. 2019).

Dailyatia cf. odyseii (Evans and Rowell, 1990)

Fig. 7G–I.

Material.—Two C sclerites of uncertain subtype, one of unknown type and a single fragment from the sample HRA/22 (NRM X10003–X10005, 3 figured) (Fig. 1, Table 1). Southern Holyoake Range, Cambrian Series 2.

Description.—Two C sclerites and one sclerite of uncertain type, triangular in transverse section with slight compression (Fig. 7H), slightly recurved at the apex, which overhangs the ventral side (Fig. 7H) and lacking torsion. Dorsal field convex, ventral field concave. Sclerite ornament is densely packed with concentric ribs which are lacking pustules (Fig. 7G₂, I₁). Micro-ornament not preserved. Dorsal side with single preserved plication in the central surface (Fig. 7G₁, H₁). In one specimen, the ventral side close to both the proximal and distal edges has two weakly developed plicae (Fig 7G).

Remarks.—The few sclerites of this species from the Shackleton Limestone of the Holyoake Range are too few in number and too poorly preserved to make a positive species-level assignment. They bear closest resemblance to *Dailyatia odyseii* C1 sclerites from the type locality in the Shackleton Limestone (Evans and Rowell 1990: figs. 7.1–7.8) and Series 2 carbonates of the Arrowie and Stansbury Basins, South Australia (Skovsted et al. 2015: figs. 44–50). Material from the type locality in the northern Holyoake Range (M84.2; Fig. 1) have the same densely set comarginal ribs (Fig. 7G₂, I₁) as those from the Southern Holyoake Range, and overall pyramidal shape and triangular transverse section (Evans and Rowell 1990: figs. 7.4, 7.5).

Weakly developed plicae are present at both the distal and proximal edges of the ventral side of *D. cf. odyseii*, a feature not present in *D. odyseii sensu stricto*, which has plicae developed regularly across the ventral surface in some specimens (Skovsted et al. 2015: fig. 48S, U). The gross morphology of *D. cf. odyseii* from the Shackleton Limestone

and the C1 sclerites from South Australia are similar, with overall pyramidal shape, triangular transverse cross section, concave ventral fields and slightly recurved apex (Skovsted et al. 2015: fig. 48B–J, X–AA). *Dailyatia cf. odyseii* cannot be definitively assigned to *D. odyseii* as certain important characteristics are not present or have not been preserved. These include the reticulate micro-ornament and pustules on sclerites of *D. odyseii* (Skovsted et al. 2015: fig. 50). In addition, only a single radial plication is preserved on the dorsal side of *D. cf. odyseii*, whereas *D. odyseii* C1 sclerites typically have two. The central surface forms a concave furrow between the central radial plication and distal edge on the dorsal side of the C1 sclerites of *D. odyseii* (Skovsted et al. 2015: fig. 48) which is not present in *D. cf. odyseii*. In contrast, *D. cf. odyseii* from the Shackleton Limestone has a flat central region of the dorsal surface. The sclerites from the Shackleton Limestone are also dissimilar to C2 sclerites of *D. odyseii* from the Mernmerna Formation in the Flinders Ranges, South Australia, which typically have a much more recurved apex and are torted (Skovsted et al. 2015: fig. 49). The single dorsal radial plication in C2 sclerites of *D. odyseii* is separated from both the proximal and distal edges by broad concave fields.

The specimens can be easily distinguished from *Dailyatia ajax* which has tall, conical sclerites with abundant radial plications (Skovsted et al. 2015: figs. 16, 17). C sclerites of *D. cf. odyseii* are harder to distinguish from the C1 sclerites of *Dailyatia macroptera*, as they both have plicated distal and proximal edges on the ventral surface (Skovsted et al. 2015: fig. 24O, S) and dense concentric ribs (Skovsted et al. 2015: fig. 26). However, the C1 sclerites of *D. macroptera* are more dorso-ventrally compressed than in *D. cf. odyseii* and have a reduced, flat central surface on the dorsal side, separated by two plicae (Skovsted et al. 2015: fig. 24D, G–I, J, Y–X, AC). *Dailyatia cf. odyseii* can also be distinguished from *Dailyatia bacata* as it lacks the diagnostic rounded pustules ornamenting the concentric ribs (Skovsted et al. 2015: fig. 34). Compared to *Dailyatia helica*, the C1 sclerites of *D. cf. odyseii* lack the distinctive plicate central surface of C sclerite subtypes. The C2a sclerites of *D. helica* are strongly coiled, unlike the slightly overhanging apex of *D. cf. odyseii*.

Dailyatia sp. 1

Figs. 8, 9A–G.

Material.—One A sclerite and numerous A sclerite fragments (NRM X10006–X10012, 7 figured), three C sclerites (NRM X10013–X10015), and numerous indeterminate fragments (NRM X10016–X10019, 4 figured) from sample HRA/14, southern Holyoake Range (Figs. 1, 2, Table 1). Fragmentary material also found in samples H84.20 and H84.26, northern Holyoake Range (Fig. 1, Table 2; Evans and Rowell 1990) and sample CM2/130, northern Churchill Mountains (Figs. 1, 2, Table 1). Cambrian Series 2, Stages 3, 4.

Description.—Two sclerite types identifiable (A and C). Pyramidal sclerites with distinctive irregular arrangement

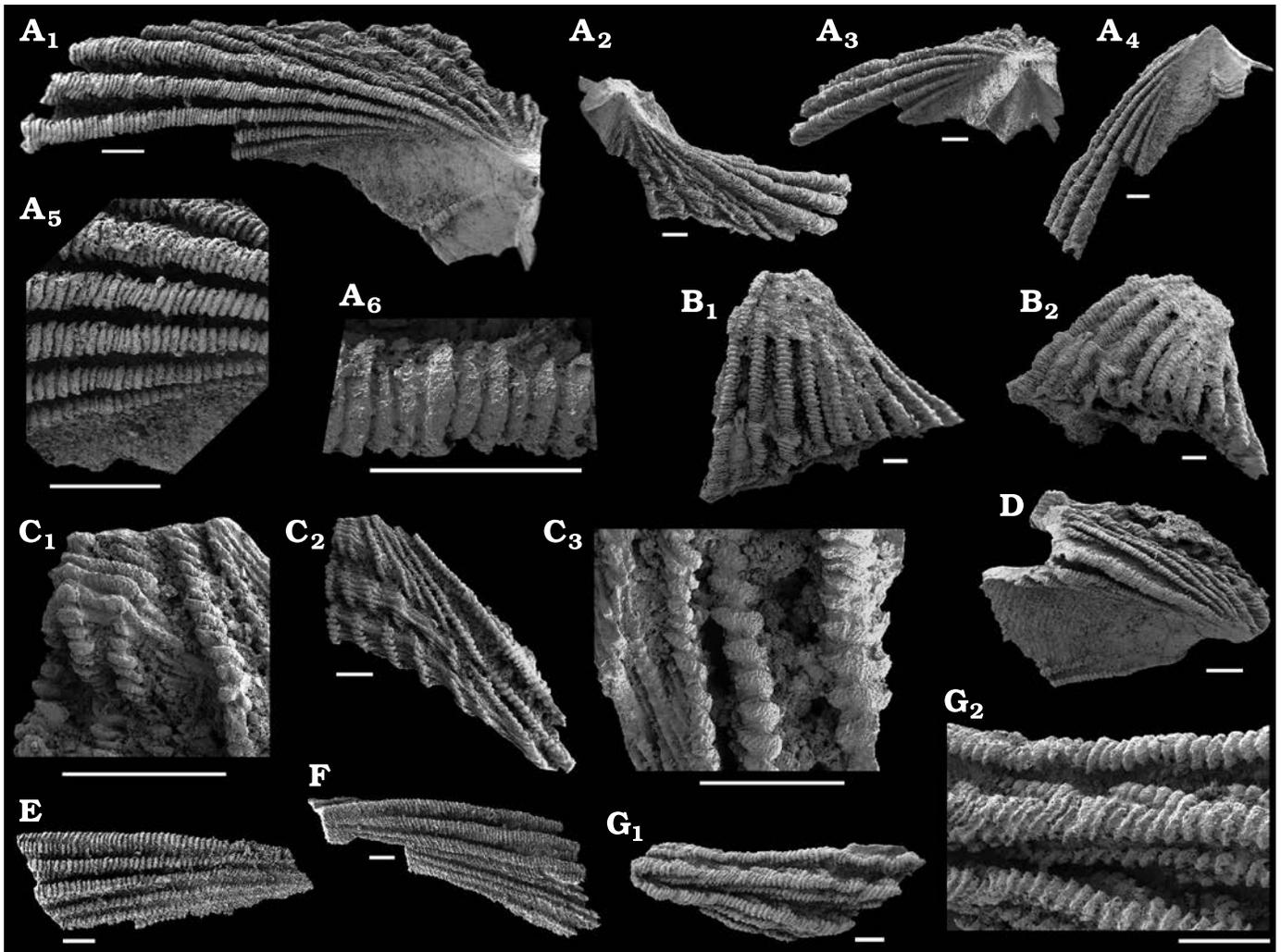


Fig. 8. The camenellan tommotiid *Dailyatia* sp. 1 A sclerites and fragments from the Cambrian Series 2, Stages 3, 4, Shackleton Limestone, Holyoake Range, Transantarctic Mountains, East Antarctica. A. A sclerite, NRM X10006, apical (A₁), anterior (A₂), oblique posterior (A₃), and posterior (A₄) views, magnification of radial plicae on the lateral field (A₅), magnification of single plica showing the densely stacked growth series of the radial plicae (A₆). B. Fragment of A sclerite anterior field, NRM X10007, general view (B₁), oblique view showing cross section of plicae (B₂). C. Fragment of A sclerite anterior field, NRM X10008, top of specimen (C₁), general view (C₂), detail showing plicae (C₃). D. Fragment of A sclerite with partial lateral and anterior field, NRM X10009. E. Fragment of sclerite lateral field, NRM X10010. F. Fragment of A sclerite lateral field, NRM X10011. G. Fragment of unknown sclerite type, with chaotically distributed plicae, NRM X10012, general view (G₁), detail (G₂). Scale bars 200 μ m.

of widely spaced out plicae. Plicae have densely set comarginal ribs with reticulate ornamentation preserved on their crests (Fig. 9E₁, E₂, F).

A single, large A sclerite fragment partially preserving the anterior, lateral and posterior fields was recovered from the HRA section (Fig. 8A). This fragment is low and uncoiled with a blunt apex. Smaller fragments of the anterior and lateral fields of A sclerites are also identifiable (Fig. 8B–G). Antero-lateral plication is well-developed (Fig. 8A₁–A₄). Postero-lateral plication present, but truncated by a break in the sclerite close to the apex (Fig. 8A₁). The anterior field and anteriormost part of the lateral field are dominated by large plicae, themselves coated by thick and well-developed comarginal ribs with broad, expanded crenulations which obscure the furrows (Fig. 8A₁–A₅). The plicae on the anterior field are chaotically spaced and devel-

oped, and bifurcate towards the apertural margin (Fig. 8A₂, B, C). On the antero-lateral region, plicae are more regular, and have sets of small rows of pustules that develop from near the base of the furrows between the plicae and merge with the plicae towards the aperture (Fig. 8A₁, A₅, B₂, G). The lateral trough is concave and smooth close to the apex and have dense comarginal ribs towards the aperture, without any ornamentation (Fig. 8A₁, A₃, A₄, D).

Three C sclerites are preserved. It is not possible to identify subtypes due to the low numbers of sclerites. The sclerites are pyramidal and triangular or rectangular in transverse section lacking torsion (Fig. 9A₁, B₃, C₁), with one sclerite slightly coiled towards the ventral side (Fig. 9A₁, A₃). The posterior field is concave with a variable number and distribution of plicae (Fig. 9A₅, B₂). One specimen has three regular plicae bordering or intersecting the proximal

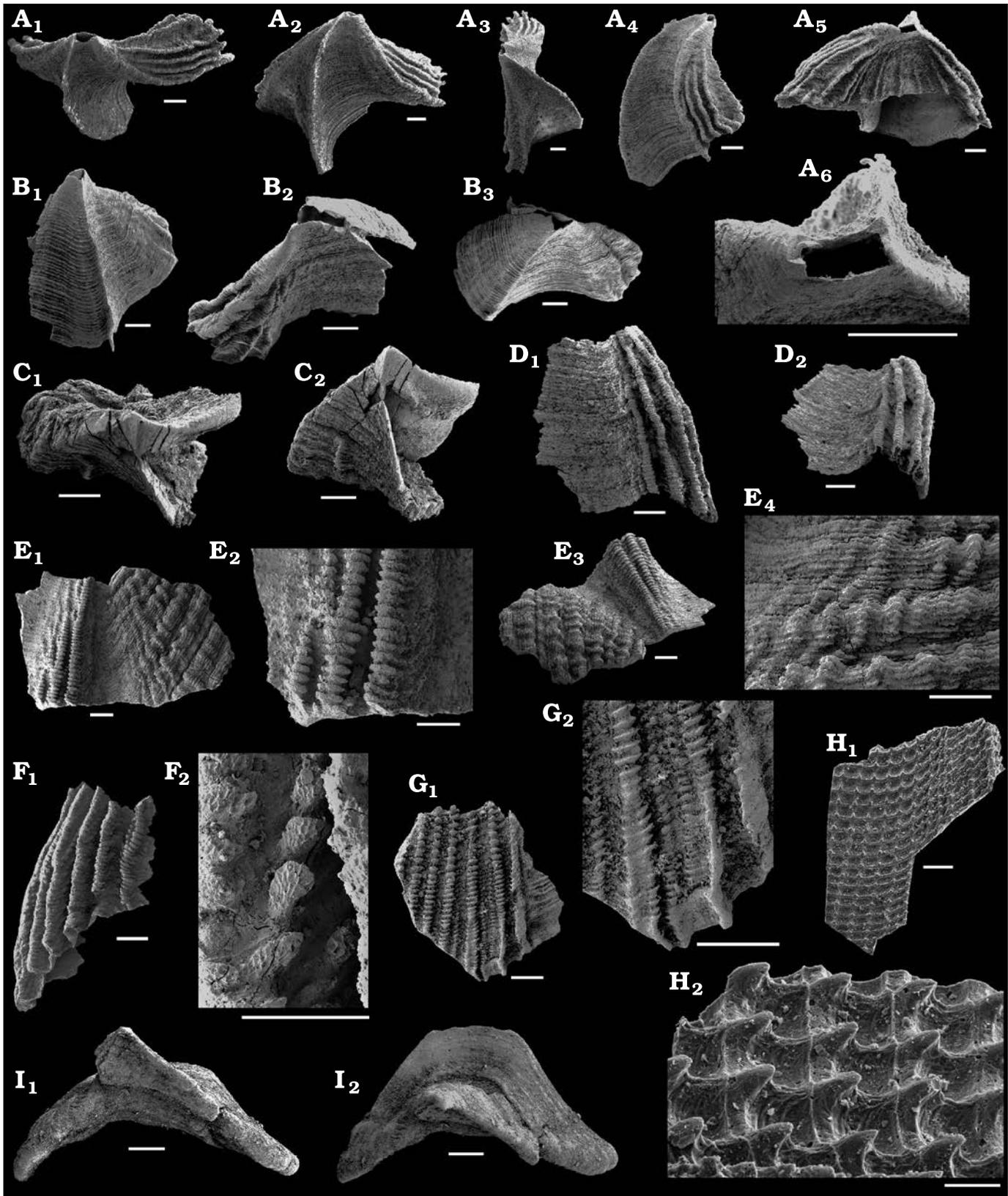


Fig. 9. The camenellan tommotiid from the Cambrian Series 2, Stages 3, 4, Shackleton Limestone, Transantarctic Mountains, East Antarctica. *Dailyatia* sp. 1, C sclerites and indeterminate fragments, Holyoake Range and Churchill Mountains (A–G) and *Dailyatia braddocki* Evans and Rowell, 1990, Churchill Mountains (H, I). A. Dextral C sclerite, NRM X10013, apical view (A₁), dorsal field (A₂), proximal edge (A₄), distal edge (A₃), ventral field (A₅), detail showing broken apex (A₆). B. Dextral C sclerite, NRM X10014, oblique view of distal edge and dorsal field (B₁), oblique view of proximal edge and ventral field (B₂), and apical view (B₃). C. Sinistral C sclerite, NRM X10015, apical view (C₁), oblique view of proximal edge and dorsal →

edge and ten plicae irregularly developed across the ventral field (Fig. 9A₄, A₅). Another has two plicae at the distal edge and a tangled arrangement of plicae adjacent to the proximal edge on the ventral field (Fig. 9B₂). A single large plication in the centre of the dorsal surface separates two concave fields bordered by the proximal edge and distal edge. (Fig. 9A₂, B₁, C₂). These concave fields generally lack plicae or pseudoplicae except for 1–2 weakly developed plicae close to the distal edge (Fig. 9A₂, B₁, B₃).

The plicae are erratic in their shape and distribution, sometimes degenerating into a chaotic and tangled arrangement (Figs. 8A₂, B, C, G, 9F). They are defined by densely set, rounded and broad crenulations (Figs. 8A₅, A₆, C₃, E, F, G₂, 9E₂, F, G). Between well-developed plicae multiple, irregularly-spaced sets of pustules develop in the furrows forming pseudoplicae that grow towards the crest of each plica and merge with them aperturally (Figs. 8A₁, G, 9E₁, E₂, G). In some fragments, plicae also bifurcate or have whole new plicae develop within the furrows of older growth sets (Figs. 8E–G, 9G). On the anterior field of an A sclerite fragment, the plicae are truncated by thickened comarginal bands which are raised across the furrows, with a new growth series continuing basally but laterally offset from the previous series (Fig. 8C). One fragment from an unknown sclerite type (Fig. 9E) also has three distinct types of ornament: First is a weakly developed field of comarginal ribs and minute pustules. This merges laterally with a second type of ornament which consists of a set of three plicae which are bounded by a furrow lacking any form of ornament preserved (Fig. 9E₂). A third type is a dense growth series of pseudoplicae which are crossed by comarginal troughs which interrupt the pseudoplicae (Fig. 9E₄). A reticulate micro-ornament is present on the wide, densely set crests of plicae and pseudoplicae (Figs. 8A₆, C₁, C₃, 9F₂). The furrows are typically smooth, lacking any micro-ornament (Fig. 9E₁, E₂, F).

Remarks.—The external ornament of *Dailyatia* sp. 1 is most comparable to the densely plicate *Dailyatia ajax*. The plicae of *Dailyatia* sp. 1 are more densely set where present (Fig. 8A₅, G₂), compared to the more widely distributed but slightly less densely set plicae in *D. ajax* (Skovsted et al. 2015: figs. 11–17). Overall, the morphology of *Dailyatia* sp. 1 sclerites are easily distinguished from *D. ajax* which has distinctly tall and conical sclerites, whereas the sclerites of *Dailyatia* sp. 1 are low. The A sclerite of *Dailyatia* sp. 1 has dense and parallel radial plications similar to the A1 sclerites of *Dailyatia macroptera* (Skovsted et al. 2015: fig. 21), especially the plicate variety (Skovsted et al. 2015: fig. 27A, B). The low, pyramidal sclerites of *Dailyatia bacata* are also similar in gross form to *Dailyatia* sp. 1. However, the devel-

opment of radial plicae on *Dailyatia* sp. 1 distinguishes it from *D. bacata*, which lacks the dense plicae on the ventral side of the C sclerites and the irregular, dense plicae on the anterior side of the A sclerite seen in *Dailyatia* sp. 1. The extreme coiling of *Dailyatia helica* sclerites is also not observed in any *Dailyatia* sp. 1 sclerites.

The C sclerites of *Dailyatia* sp. 1 also have some similarities to C1 sclerites of *Dailyatia odyssei* in overall pyramidal shape. However, the dorsal radial plications on the C1 sclerites and ventral radial plications on the C2 sclerites of *Dailyatia* sp. 1 are typically absent from the C1 and C2 sclerites of *D. odyssei*. Only in larger C1 (Skovsted et al. 2015: fig. 48S, U) and C2 sclerites (Skovsted et al. 2015: fig. 49C) of *D. odyssei* do plicae form on the ventral field.

The ornamentation of *Dailyatia* sp. 1 is distinctive and indicate a consistent novel development of plicae. The emergence of new plicae from furrows is known from *Dailyatia odyssei*, but is generally uncommon (e.g., Skovsted et al. 2015: fig. 50H). The most common example of such irregularity in the development of *Dailyatia* sclerites occurs in damaged or gerontic specimens. Interruption of the development of growth series is marked by comarginal troughs and is known from most other species, including *Dailyatia ajax* (Skovsted et al. 2015: figs. 71, 73G, H), *Dailyatia macroptera* (Skovsted et al. 2015: figs. 72C–F, 73A–C, 74A–E) *Dailyatia bacata* (Skovsted et al. 2015: fig. 73D–F), *Dailyatia helica* (Skovsted et al. 2015: fig. 73I, J), *Dailyatia odyssei* (Skovsted et al. 2015: figs. 50G, 74F, G) and *Dailyatia braddocki* from the Shackleton Limestone (Fig. 9I). *Dailyatia* sp. 1 develops similar interruptions in plicae development, with plicae laterally offset from the previous growth series (Fig. 8A₂, B, C), a growth pattern is also seen in damaged or gerontic specimens of *Dailyatia* (Skovsted et al. 2015: figs. 71–73). However, growth interruptions in *Dailyatia* sp. 1 are unlikely to be gerontic features as the interruptions appear in the earliest stages of the anterior field of A sclerites, differentiating it from typical gerontic growth disturbance in *Dailyatia* that typically start closer to the aperture (e.g., Skovsted et al. 2015: fig. 73). An example of gerontic disturbance of a *Dailyatia braddocki* C sclerite from the Shackleton Limestone, Churchill Mountains (sample GM87.1, Fig. 1) is shown in Fig. 9I.

The irregular arrangement of radial plications on the anterior field of *Dailyatia* sp. 1 is also similar to a large, potentially gerontic *D. macroptera* from the Mernmerna Formation (Skovsted et al. 2015: figs. 21F–H, 71F, G). Strongly plicate sclerite varieties of *Dailyatia macroptera* (Skovsted et al. 2015: fig. 27) and *Dailyatia helica* (Skovsted et al. 2015: fig. 43) are uncommon but do occur in South Australia. Hence, while *Dailyatia* sp. 1 can be distinguished from *D. macroptera*

field (C₂). **D.** Fragment of unknown sclerite type, NRM X10016. Showing fragment surface (D₁) and oblique view (D₂) showing plicae cross-section. **E.** Fragment of unknown sclerite type, NRM X10017, various views of multiple ornament types (E₁–E₄). **F.** Fragment of unknown sclerite type, NRM X10018, general view (F₁), detail showing pseudoplicae emerging from furrows between the radial plicae (F₂). **G.** Fragment of unknown sclerite type, NRM X10019, general view (G₁), detail showing plicae bifurcation (G₂). **H.** Fragment of unknown sclerite type, KUMIP 585075, general view (H₁), detail of surface showing raised pustules forming the pseudoplicae (H₂). **I.** Dextral C sclerite with band of disturbed growth, KUMIP 585076, view of ventral field (I₁), apical view (I₂). Scale bars 200 µm, except F₂, 100 µm; H₂, 50 µm.

tera and *D. odyssei* based on gross morphology, there is a possibility that *Dailyatia* sp. 1 is a “plicate variant” of these or another *Dailyatia* species.

Kennardiidae indet.

Fig. 10.

1990 *Kennardia* sp. A; Evans and Rowell 1990: 699, fig. 7.9.

1990 *Kennardia* sp. B; Evans and Rowell 1990: 699, figs. 7.10–7.12.

Material.—One symmetrical first sclerite type (KUMIP 585077, 1 figured), one symmetrical second sclerite type (KUMIP 585082, 1 figured) and seven asymmetrical third sclerite types (KUMIP 233002, 585078–585081, 585083, 585084, 6 figured) from M section, northern Holyoake Range (Fig. 1, Table 2; Evans and Rowell 1990). Numerous fragments were also recovered from this section (Table 2). Cambrian Series 2, Stages 3–4.

Description.—Three identifiable sclerite types. First sclerite type symmetrical, low, curved over the ventral field and quadrangular in transverse section (Fig. 10A). Second sclerite type coniform, symmetrical, tall, straight and hexagonal in transverse section (Fig. 10G). Third sclerite type coniform, asymmetrical, tall, coiled over the ventral field, and triangular in transverse section (Fig. 10B–F, H, I). Sclerites with a distinctive growth set of wide, wall-like comarginal ribs and inter-rib grooves.

The first sclerite type symmetrical with dorsal field lacking plicae and with no clear distinction from the lateral fields (Fig. 10A₁) which have a single, weakly developed plica bound by furrows (Fig. 10A₃). Ventral field is flat and straight, lacking plicae (Fig. 10A₂). The sclerite is coiled only at the apex where it overhangs the ventral field (Fig. 10A₂). Growth series forming wall-like comarginal ribs, well-developed and present on entire sclerite surface, following the transverse profile of the sclerite.

The second sclerite type known from single, poorly preserved sclerite. The anterior field is gently curved laterally with two weakly developed plicae (Fig. 10G₁). Lateral fields triangular in shape, flat and straight, lacking plicae (Fig. 10G₁, G₃). Posterior field side triangular and straight, lacking plicae (Fig. 10G₂). Growth sets developed on the entire sclerite surface and follow the transverse profile of the sclerite on the dorsal side and lateral fields. The growth sets on the ventral side curve upwards into broad inverted U-shape (Fig. 10G₂).

The third sclerite type is tall, triangular, asymmetrical with a concave ventral surface and convex dorsal surface in smaller specimens, but curves back towards the dorsal side in larger specimens (Fig. 10E₁, H₁). The ventral side has a series (3–7) of well-developed radial plicae with the outmost bordering the proximal and distal edges (Fig. 10C₂, D₁, E₃, E₄, F₁, H₁). The proximal edge is shorter than the distal edge. The dorsal side has a single, large and broad plication in larger specimens (Fig. 10C₁, D₂, H₂, H₃). The fields bounded by the central plication and the proximal edge is flat or slightly concave (Fig. 10D₂, H₁). The field bounded

by the central plication and distal edge is convex (Fig. 10C₁, H₃). The dorsal side lacks pseudoplicae on all but the largest specimen, where they are formed by lateral irregularly spaced series of weakly developed pustules (Fig. 10E₁, E₂). In one small specimen, the dorsal side lacks any plication and forms a single evenly convex field (Fig. 10B).

Remarks.—Specimens of Kennardiidae indet. from the Shackleton Limestone of the Holyoake Range have a mosaic of kennardiid features. They are united by wall-like comarginal ribs on their growth sets similar to those found in *Kennardia* (Laurie 1986: fig. 7). They also fit the diagnostic criteria for Kennardiidae in having three distinct sclerite types with ubiquitous growth sets, but potentially have two symmetrical forms instead of one. No reticulate micro-ornamentation is present on the sclerites, but this is similar to other specimens recovered from the same samples (e.g., *Dailyatia odyssei* from samples M84.1, M84.2, recovered by Evans and Rowell 1990, see Fig. 1), and hence may be preservational.

Evans and Rowell (1990: 699, figs. 7.9–7.12) described specimens of Kennardiidae indet. from the same localities and referred them to two species in open nomenclature: “*Kennardia* sp. A” and “*Kennardia* sp. B” on the basis of the coarse concentric ribs similar to those in *Kennardia*. “*Kennardia* sp. B” was considered by Skovsted et al. (2015: 22, 31) to potentially represent *Dailyatia ajax* C1 sclerites, as they share a tall, conical shape, triangular transverse section with well-developed radial plicae and comarginal ribs. Evans and Rowell’s (1990) specimens were split into two species based on “*Kennardia* sp. B” being much larger and with pustules forming pseudoplicae. These criteria are not sufficient to delineate these species based on the limited number of sclerites originally described. Size is unsuitable in this case as it can be a product of different ontogenetic stages and ornamentation of kennardiid sclerites is variable within and across sclerite types.

The symmetrical first sclerite form of Kennardiidae indet. is similar to the symmetrical Form A of the monospecific genus *Kennardia* Laurie, 1986, which was described from the Todd River Dolostone of the Amadeus Basin, Northern Territory, Australia (Laurie 1986: fig. 8A). They can be clearly delineated by the lack of reticulate micro-ornament on Kennardiidae indet., which is a ubiquitous character of *Kennardia*, along with the more strongly developed comarginal ribs (Laurie 1986: fig. 8F–H). There may be a difference in transverse section, with the single symmetrical Kennardiidae sclerite more triangular at the apex and subcircular towards the base, and *Kennardia* Form A sclerites described as subrectangular (Laurie 1986: 439), although this is not figured clearly by Laurie (1986) and based on a single sclerite of Kennardiidae indet. An A sclerite of *Kennardia* sp. from the Mt Scott Range of South Australia (Skovsted et al. 2015: fig. 8) is also similar to the first sclerite form of Kennardiidae indet. The dorsal side of this sclerite is also gently curved laterally with no clear delineation from the lateral fields and the apex overhangs

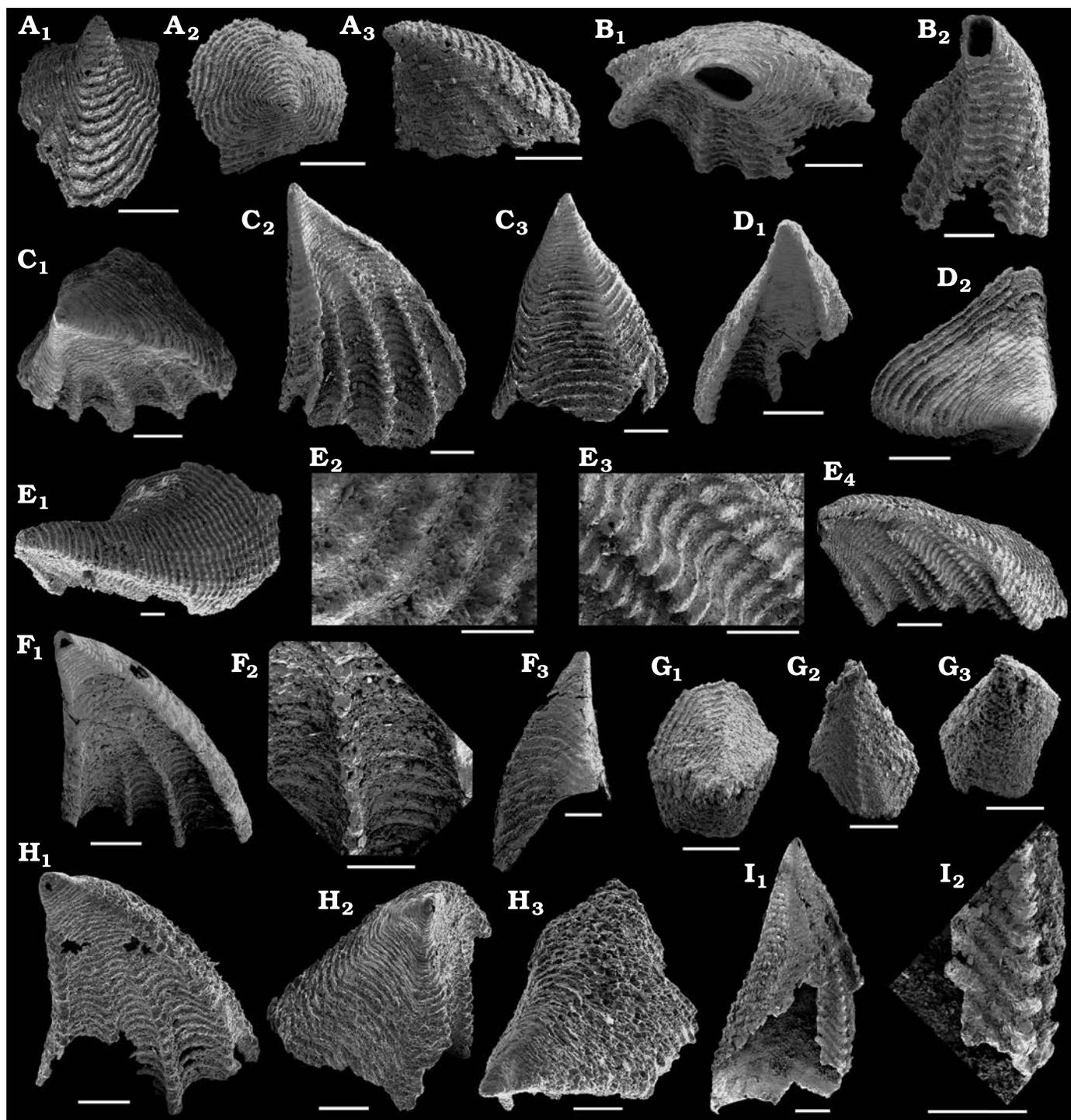


Fig. 10. The tomotioid Kennardiidae indet. from the Cambrian Series 2, Stages 3, 4, Shackleton Limestone, Holyoake Range, Transantarctic Mountains, East Antarctica. **A.** Symmetrical first sclerite type, KUMIP 585077, apical view (A₁), oblique view of posterior field (A₂), lateral field (A₃). **B.** Third sclerite type, KUMIP 585078, apical (B₁) and lateral (B₂) views. **C.** Third sclerite type, KUMIP 585079, apical view (C₁), ventral side (C₂), dorsal side (C₃). **D.** Third sclerite type, KUMIP 585080, ventral side (D₁), apical view (D₂). **E.** Third sclerite type, KUMIP 233002, apical view (E₁), detail of dorsal side (E₂), detail of ventral side (E₃), ventral side (E₄). **F.** Third type of sclerite, KUMIP 585081, ventral side (F₁), detail showing plicae on ventral surface (F₂), distal edge (F₃). **G.** Second type of sclerite, KUMIP 585082, apical view (G₁), oblique view of posterior field (G₂), lateral field (G₃). **H.** Third type of sclerite, KUMIP 585083, posterior side (H₁), distal edge (H₂), apical view (H₃). **I.** Third type of sclerite, KUMIP 585084, ventral side (I₁), detail showing plicae on the ventral surface (I₂). Scale bars 200 μ m, except E₂, E₃, I₂, 100 μ m.

the posterior field (Skovsted et al. 2015: fig. 8A, B). The posterior field is concave in *Kennardia* sp., whereas it is flat in Kennardiidae indet.

The symmetrical second sclerite type is similar to the symmetrical sclerite of Tommotiid gen. et sp. nov. from the Koolyurtie Limestone Member of the Parara Limestone of

the Stansbury Basin, South Australia (Paterson et al. 2007: fig. 4A–C). This sclerite is also tall and conical and has the same hexagonal transverse section. However, the symmetrical sclerite of Tommotiid gen. et sp. nov. is slightly curved over the ventral field, unlike Kennardiidae indet. and the comarginal ribs curve towards the apex on the lateral fields of Tommotiid gen. et sp. nov., whereas they are straight in Kennardiidae indet.

Radial plicae have been considered as a diagnostic character of *Dailyatia* (Skovsted et al. 2015: 18) and are also present on the ventral surface of the third, symmetrical sclerite type of Kennardiidae indet. These sclerites of Kennardiidae indet. are similar to C sclerites of some forms of *Dailyatia*, for example the C1 sclerites of *Dailyatia ajax*. The C1 sclerites of *D. ajax* in particular have a similar tall and pyramidal form to the third sclerite type of Kennardiidae indet. (Fig. 10C₁, C₂, F₃, H, I₁; Skovsted et al. 2015: fig. 16L–Q). However, the dorsal side of the C1 sclerite of *D. ajax* has plicae (Skovsted et al. 2015: fig. 16L–Q), a feature which is only present on the ventral side of Kennardiidae indet. (Fig. 10C₂, E₄, F₁, H₁). Plicae are also present on the dorsal side of C2 sclerites of *D. ajax* (Skovsted et al. 2015: figs. 10N, 17Q).

Kennardiidae indet. can be excluded from both *Kennardia* and *Dailyatia* as it has two symmetrical sclerite types and single asymmetrical type, in contrast to a single symmetrical sclerite type and two asymmetrical types in *Kennardia* and *Dailyatia*. They can also be distinguished from *Kennardia* as Kennardiidae indet. has radial plicae, a feature which is diagnostic of *Dailyatia*. The wall-like ribs present on Kennardiidae indet. are similar to the wall-like ribs of *Canadiella* (Skovsted et al. 2020: figs. 5, 6), but lacks the pustulose ornamentation of this genus (Skovsted et al. 2020: figs. 5M, 6M, N)

Family uncertain

Shetlandia Wrona, 2004

Type species: Shetlandia multiplicata Wrona, 2004; Lower Cambrian clasts from the Miocene Cape Melville Formation, King George Island, South Shetland Islands, Antarctica.

Shetlandia multiplicata Wrona, 2004

Fig. 11.

2004 *Shetlandia multiplicata* sp. nov.; Wrona 2004: 34, figs. 14, 15A–E, H–J, 16.

Material.—Exclusively fragmentary material, with 22 fragments recovered from samples HRA/24, HRA/25, and HRA/14 (NRM X10020–X10024, 5 figured), southern Holyoake Range (Figs. 1, 2, Table 1). Cambrian Series 2, Stages 3, 4.

Description.—Fragments preserve flat to gently curved sclerite fields; no large plications or apices are preserved. No micro-ornament is preserved. Two distinct arrangements of plicae occur on the fragments. Firstly, rows of closely stacked, overlapping arches delineate tall, prominent

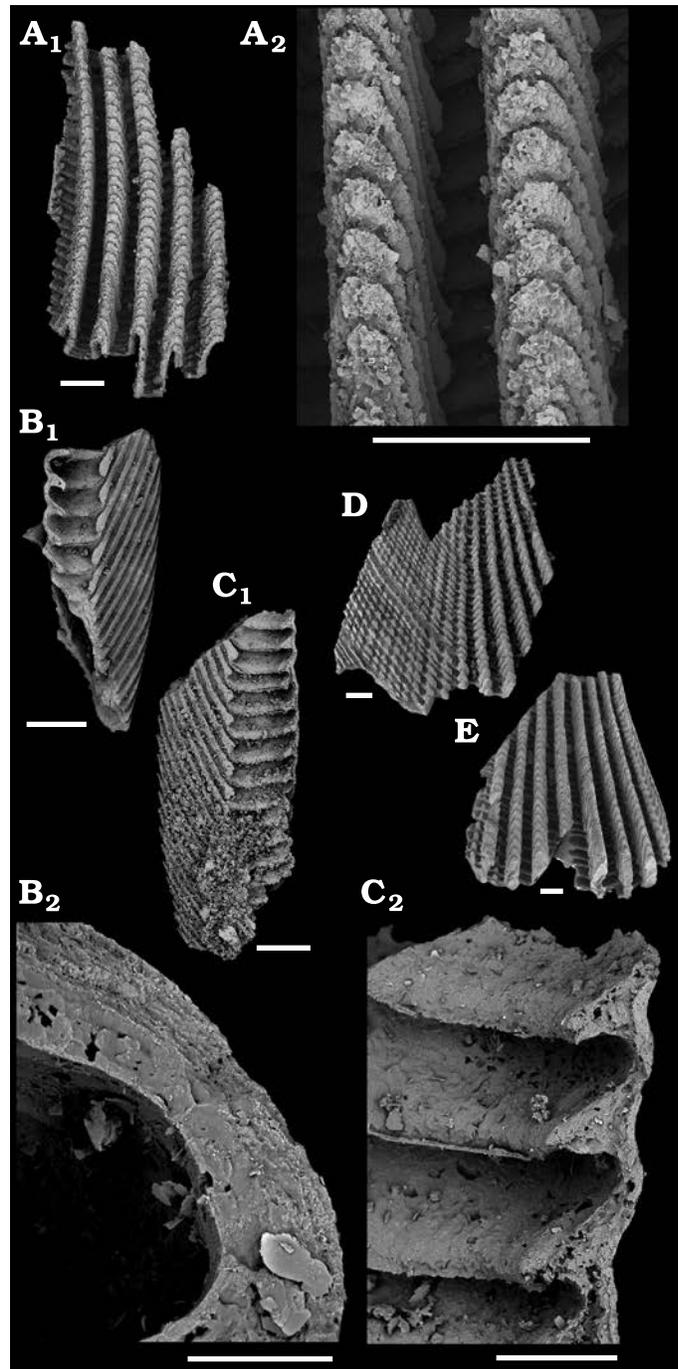


Fig. 11. The tomotiid *Shetlandia multiplicata* Wrona, 2004, unknown type sclerite fragments from the Cambrian Series 2, Stages 3, 4, Shackleton Limestone, Holyoake Range, Transantarctic Mountains, East Antarctica. A. NRM X10020, general view (A₁), detail showing arched growth series (A₂). B. NRM X10021, general view (B₁), detail of broken margin (B₂). C. NRM X10022, general view (C₁), detail of comarginal ribs and broken edge (C₂). D. NRM X10023. E. NRM X10024. Scale bars 200 μ m, except B₂, 100 μ m. A–C taken with backscattered electron detector.

radial plicae which extend from the top of the plicae to the groove (Fig. 11A). The arches increase in size towards the base of the sclerite. These plicae are separated by grooves with concentrically oriented ribs at their base. These ribs do not contact the base of the arches (Fig. 11A₂) but are part

of the same growth series. The second type of ornament (found on only one sclerite fragment) is weakly developed pseudoplicae formed by a series of pustules in concentric rows (Fig. 11D). A markedly different type of ornament also occurs and consists not of plicae but of densely packed concentric, wall-like ribs which are also present on one fragment (Fig. 11B₁, C).

Remarks.—*Shetlandia multiplicata* was previously known only from glacial erratics recovered from the glaciomarine Miocene Cape Melville Formation, King George Island, South Shetland Islands of West Antarctica and is generally poorly understood (Wrona 1989, 2004). However, despite the fragmentary nature of the holotype, it has unique ornamentation and plication that is unknown from any other tomotioid genus.

The few fragments from the Shackleton Limestone in the Holyoake Range can be confidently assigned to *Shetlandia multiplicata* Wrona, 2004, due the unique morphology of the dense plicae. The densely packed arches that make up these plicae are identical in morphology to those originally described from King George Island (Wrona 2004: fig. 14M–T). Pustules arranged into pseudoplicae are also found on some sclerite fragments from King George Island (Wrona 2004: fig. 15H, I). The third ornament of concentric wall-like ribs is also found on both sets of fragmentary material.

Stratigraphic and geographic range.—Cambrian Series 2, Stages 3, 4, of the Shackleton Limestone in southern Holyoake Range, Central Transantarctic Mountains, East Antarctica; carbonate clasts (Cambrian Series 2, Stage 4?) from the Miocene Cape Melville Formation, King George Island, West Antarctica (Wrona 2004).

Conclusions

Seven tomotioid taxa from Antarctica are described. From the Argentina Range, the apparently endemic *Dailyatia icari* sp. nov. is the first tomotioid described from this region of East Antarctica. From new sections through the Shackleton Limestone in the Holyoake Range, *Dailyatia* cf. *D. odyseii*, *Dailyatia* sp. 1, and *Shetlandia multiplicata* are described. A new section in the Churchill Mountains yielded sclerites of *Dailyatia braddocki*. From previously collected material in the Holyoake Range, *Dailyatia decobruta* and Kennardiidae indet. are described.

The tomotioid fauna of East Antarctica provides new data for biostratigraphic correlation and relative dating of the Shackleton Limestone. *Dailyatia decobruta*, occurring alongside *Dailyatia odyseii* in the northern Holyoake Range provides a new platform for age designation. These co-occurring species correlate this part of the Shackleton Limestone to the Cambrian Series 2, Stage 4 (South Australian upper *Dailyatia odyseii* Zone and *Pararaia janeae* Zone) White Point Conglomerate (Betts et al. 2019) and upper Mernmerna Formation (Betts et al. 2017) in South Australia.

The material described tells a more complex story of endemism in Cambrian Series 2 tomotioids. Discovery of *D. decobruta* from the Holyoake Range is only the second species of *Dailyatia* found in autochthonous rocks of East Antarctica and South Australia, after *D. odyseii*. The two remaining named species: *Dailyatia braddocki* and *Dailyatia icari* sp. nov. are known only from their type localities in the Churchill Mountains and Argentina Range, respectively. Unnamed species *Dailyatia* sp. 1 and tomotioids *Shetlandia multiplicata* and Kennardiidae indet. from autochthonous rocks are known only from East Antarctica.

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