

# Cyanobacterial–archaeocyathan–radiocyathan bioherms in the Wirrealpa Limestone of South Australia

PETER D. KRUSE

Northern Territory Geological Survey, P.O. Box 2901, Darwin, Northern Territory 0801, Australia

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The 140 m thick Wirrealpa Limestone of South Australia is an open-shelf marine deposit of Early–Middle Cambrian (Botomian or Toyonian) age. Bioherms preserved within this unit have a distinctive *Epiphyton* thrombolitic stromatolite framestone core colonized by a low-diversity archaeocyathan–radiocyathan biota of *Ajacyathus* sp., *Archaeocyathus abacus* n.sp., and *Girphanovella gondwana* n.sp., together with other skeletal invertebrates and macroborers. The largest bioherm, some 3 m in thickness and 36 m in length, is enclosed within an interval of thin-bedded to nodular silty bioclast limestone, but rests directly on a substrate of bioclast, intraclast, and onkoid packstone–floatstone–rudstone. The archaeocyathan–radiocyathan biota represents the youngest known Australian occurrence of these groups.

Le calcaire de Wirrealpa dans l'Australie du Sud, d'une épaisseur de 140 m, est un dépôt marin de plate-forme ouverte, d'âge cambrien précoce à moyen (Botomien ou Toyonien). Les biohermes préservés dans cette unité sont caractérisés par un cœur de type « framestone » formé du stromatolite thrombolitique *Epiphyton* et colonisé par un biote de *Ajacyathus* sp., *Archaeocyathus abacus* n.sp. et *Girphanovella gondwana* n.sp., en présence de d'autres restes d'invertébrés et de macroperforants. Le plus gros bioherme, quelque 3 m d'épaisseur et 36 m de longueur, occupe une intervalle de couches finement stratifiées et nodulaires d'un calcaire bioclastique silteux, et repose directement sur un substrat bioclastique et intraclastique de texture « packstone–floatstone–rudstone » oncoïde. Le biote à archaeocyathes–radiocyathes représente la plus jeune localité connue en Australie.

[Traduit par la rédaction]

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## Introduction

Archaeocyaths flourished worldwide throughout the Early Cambrian, but had essentially become extinct by early Middle Cambrian time. In the Australian context, the dénouement of the archaeocyaths and radiocyaths is represented by cyanobacterial–archaeocyathan–radiocyathan bioherms in the Wirrealpa Limestone of South Australia. These, together with archaeocyathan bioherms in Siberia, South China, and North America, mark the terminal development of metazoan-mediated bioconstructions in the Cambrian. Such bioconstructions did not reappear until the advent of spiculate sponge mounds in the Early Ordovician, about 40 Ma later.

The 140 m thick Wirrealpa Limestone of the Flinders Ranges (Fig. 1) is a transgressive–regressive unit of ooid and onkoid grainstone, peloid packstone, and bioclastic, intraclastic, stromatolitic, cryptalgal, fenestral, and nodular silty limestones. Deposition of the formation took place on a broad shelf in which ooid shoals at the seaward margin protected quieter open marine lagoons bordering an exposed mature land surface (Youngs 1977). Fluvial silts were episodically introduced to form generally thin interbeds among the carbonates generated on the shelf. Daily (1956) summarized the known biota of the formation: trilobite *Redlichia* aff. *nobilis* Walcott, brachiopods '*Obolella*' *wirrialpensis* Etheridge and *Eoorthis tatei* (Etheridge), mollusc *Helcionella* aff. *rugosa chinensis* Walcott, hyolith '*Biconulites*' aff. *hardmani* (Etheridge), alga *Girvanella*, stromatolites, sponge spicules, and archaeocyaths, which he designated Faunal Assemblage 10 and assigned to the early Middle Cambrian. The *Redlichia* was earlier determined as *Olenellus* sp. by Etheridge (1905).

Unlike their Atdabanian–Botomian predecessors in the Ajax and Wilkawillina limestones (Fig. 2), the Wirrealpa Limestone archaeocyaths and radiocyaths are neither diverse nor abundant, including only the archaeocyaths *Ajacyathus* sp. and *Archaeocyathus abacus* n.sp. and the radiocyath *Girphanovella gondwana* n.sp. The existence of such a low-diversity biota in a

favourable open marine carbonate setting is typical of the period of pronounced archaeocyathan decline represented in Siberian terms by the Toyonian stage. This stage is latest Early Cambrian in the Soviet conception but early Middle Cambrian in Australian terms. Jell (in Bengtson *et al.* 1990) records the trilobite *Redlichia guizhouensis* Zhou from the Wirrealpa Limestone, supporting correlation with the Lungwangmiao stage of China (approximately equivalent to the Toyonian stage). Associated acrothelid brachiopods (B. J. Cooper, personal communication, 1989) also point to a Toyonian or younger age. The occurrence of *Redlichia* and *Archaeocyathus* is consistent with a Toyonian age but could equally indicate an older, Botomian equivalence. *Ajacyathus* and *Girphanovella* have not been reported previously from Toyonian-age rocks and are otherwise Botomian.

## Systematic palaeontology

Specimens prefixed P31251–P31327 are deposited in the South Australian Museum, Adelaide.

PHYLUM	Archaeocyatha Bornemann 1884
CLASS	Regulares Vologdin 1936
ORDER	Ajacyathida Bedford and Bedford 1939
SUBORDER	Ajacyathina Bedford and Bedford 1939
FAMILY	Ajacyathidae Bedford and Bedford 1939
GENUS	<i>Ajacyathus</i> Bedford and Bedford 1939

## Type species

*Archaeocyathus ajax* Taylor 1910. Early Cambrian, Ajax Limestone, Ajax Mine, South Australia.

## Diagnosis

Outer wall simple, with or without false stirrup pores. Inner wall simple, with (true or false) stirrup pores and additional interseptal pore rows. Septa aporose to sparsely porous.

## Discussion

Debrenne (1974b) distinguished two subgenera of *Ajacyathus*: *A. (Ajacyathus)*, having true stirrup pores on the inner

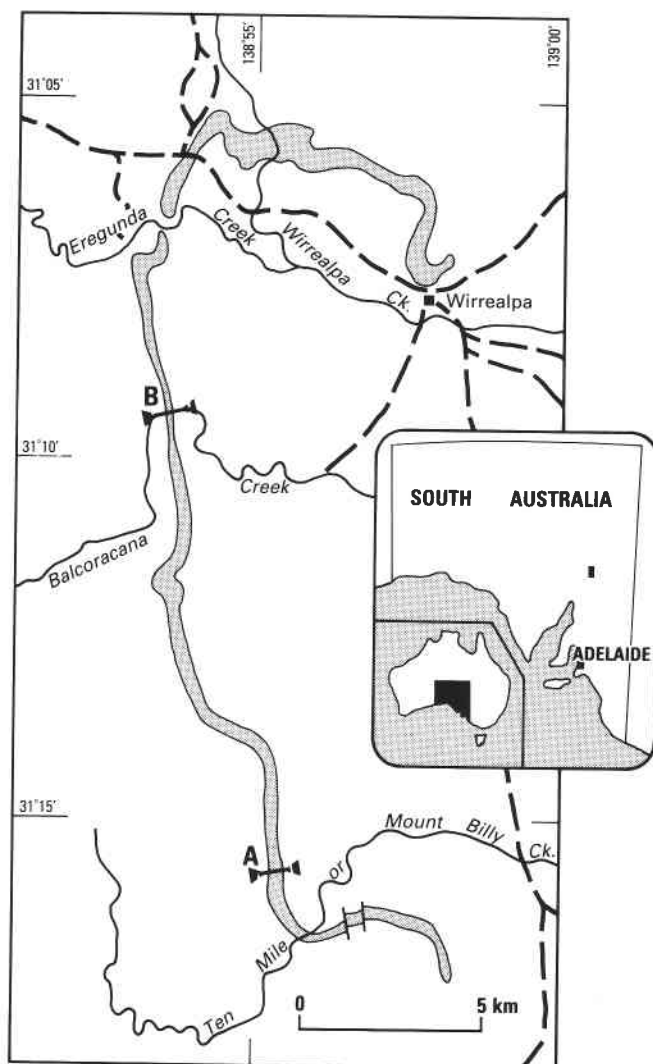


FIG. 1. Locality map. The shaded area indicates Wirrealpa Limestone outcrop; A and B: sections known to include cyanobacterial–archaeocyathan–radiocyathan bioherms.

wall, and *A. (Juricyathus)*, with false stirrup pores on the inner wall (and occasionally outer wall). The genus is otherwise known from the Botomian stage of Siberia and Mongolia and its equivalents in North America and Australia–Antarctica.

*Ajacicyathus* sp.  
(Fig. 3)

**Material**

One specimen P31266, Ten Mile or Mount Billy Creek section (= type section of Daily 1956 = section 19 of Youngs 1977), Flinders Ranges, South Australia.

**Description**

Specimen is a fragmentary arcuate transverse section with intervallum width 0.9 mm. Outer and inner walls with 3–5 rows of interseptal and stirrup pores (diameter 0.12 mm, lintels 0.11 mm, wall thickness 0.13 mm, porosity coefficient for both walls 1.1). Septa spaced 0.8–1.0 mm apart (intervallum coefficient = 1/1.0), aporose except for individual pores or a single pore row adjacent to “outer” wall.

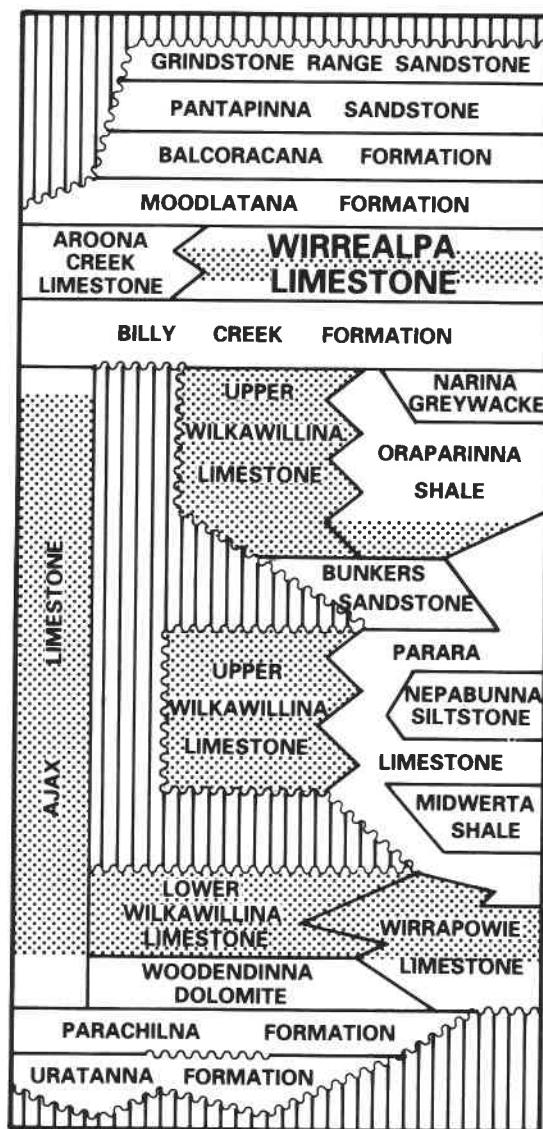


FIG. 2. Schematic stratigraphic column of Cambrian rocks in western and central Flinders Ranges. The stipple indicates archaeocyathan-bearing units.

**Remarks**

It is not possible from this single transverse section to determine whether the observed stirrup pores are of the true or false variety. Hence attribution to one or another of the subgenera recognized by Debrenne (1974b) cannot be made.

CLASS	Irregulares Vologdin 1936
ORDER	Archaeocyathida Okulitch 1935
SUBORDER	Archaeocyathina Okulitch 1935
FAMILY	Archaeocyathidae Hinde 1889
GENUS	<i>Archaeocyathus</i> Billings 1861

**Type species**

*Archaeocyathus atlanticus* Billings 1861. Early Cambrian (Bonnia–Olenellus Zone), Forteau Formation, Forteau Bay, Labrador, Canada.

**Diagnosis**

Conical cup displaying some irregularly developed smooth



FIG. 3. *Ajacicyathus* sp.; Ten Mile or Mount Billy Creek bioherm. Transverse section P31266.  $\times 10$ . "Outer" wall uppermost. The curvilinear structure in the second locus from the left is not a tabula; it is probably a burrow.

transverse expansions and constrictions of outer wall. Outer wall compound. Inner wall with one pore row per intertaenia, each pore supporting a more- or less-developed short pore tube. Intervallum with undulating, sometimes bifurcating taeniae of netlike porosity, and synapticulae.

#### Discussion

Because of its inconsistent development between and even within specimens, the laminated secondary calcification (stereoplasm) investing the primary skeleton can be discounted for taxonomic purposes.

Possible synonyms of *Archaeocyathus* are *Pycnoidocyathus* Taylor 1910, *Retecyathus* Vologdin 1932, and *Flindersicyathus* Bedford and Bedford 1937.

As in type *Archaeocyathus*, *Flindersicyathus* typically shows irregular, low expansions and constrictions of the outer wall; the intervalum bears undulose taeniae with synapticulae linking each interpore node, and distinctive, long, upwardly angled pore tubes project from the inner wall pores. *Pycnoidocyathus* cups show pronounced periodic transverse annulations of the outer wall and, in the intervalum, straight pseudosepta with fewer synapticulae. *Archaeocyathus*, *Pycnoidocyathus*, *Retecyathus* and *Flindersicyathus* have been variously synonymized in the past (e.g., Zhuravleva 1960; Hill 1972; Debrenne 1974a; Palmer and Rozanov 1976); *Sanxiacyathus* Yuan and Zhang 1977 and *Retecyathus* (*Pararetecycyathus*) Yuan and Zhang 1978 will undoubtedly be synonyms of one or more of these.

*Archaeocyathus abacus* n.sp.  
(Figs. 4, 14A; Table 1)

#### Name

From Latin *abacus* (masc.) = a square board; alluding to the checkerboard pattern formed by taeniae and synapticulae within the intervalum.

#### Material

Thirty-eight specimens. Holotype P31258; paratypes P31254, 31261–31263, 31269, 31274, 31276–31278, 31280, 31283; additional material P31251–31253, 31255–31257, 31259–31260, 31264–31268, 31270–31273, 31275, 31279, 31281, 31282, 31284–31288, Ten Mile or Mount Billy Creek section (= type section of Daily 1956 = section 19 of Youngs 1977); additional material P31319–31321, Balcoracana Creek section (= section 1 of Youngs 1977), Flinders Ranges, South Australia.

#### Diagnosis

Inner wall pore tubes of length up to 0.45 mm, inclined at up to 45° to wall surface. Taeniae with up to 12 pore rows across intervalum, a synapticula at each interpore node.

#### Description

Cup narrowly conical, diameter up to 36 mm, with intervalum up to 11 mm in width. Outer wall compound with 2–3 irregular pores per intersept (diameter 0.17–0.25 mm, lintels 0.06–0.09 mm, porosity coefficient 1.2–1.3, wall thickness 0.1 mm). Adjacent pores may amalgamate at their margins. Microporous sheath of 3–5 rounded micropores per framework pore (micropore diameter 0.09–0.11 mm, lintels 0.05–0.06 mm). Outer wall shows irregular low expansions and constrictions.

Inner wall pores rounded, arranged in longitudinal rows, one per intersept, and in near-horizontal files (diameter 0.32–0.43 mm, lintels 0.08–0.13 mm, porosity coefficient 2.9–5.2, wall thickness 0.11 mm). Vertical lintels (length 0.25–0.45 mm) are inclined at up to 45° to wall surface, forming incipient pore tubes covering lower half of each inner wall pore.

Taeniae undulating, sometimes bifurcating toward outer wall, with 5–6 rows of rounded to subquadrate pores in cups of diameter about 7 mm, increasing to about 12 rows in cups of diameter around 22 mm. Pore rows inclined steeply upward and outward toward outer wall, where they are associated with slight transverse annulations of that wall. A synapticula is present at each interpore node, linking adjacent taeniae. Sporadic pseudotabulae, surmounting local expansions of outer wall, are inclined upward and inward toward inner wall (pore diameter 0.10 mm, lintels 0.07 mm in holotype).

#### Remarks

The irregular outer wall undulations and presence of synapticulae at each interpore node in the intervalum of the new species recall *Flindersicyathus* Bedford and Bedford, but in that genus the inner wall pore tubes are much more strongly developed. From illustrated examples (Debrenne and James 1981) it appears that type *Archaeocyathus* also has linking synapticulae at each taenial interpore node, or nearly so.

Among existing named species, only *Spirocyathus irregularis* Taylor 1910 from the underlying Ajax Limestone is morphologically similar to *A. abacus*, but Gravestock (1984) has transferred *irregularis* to *Auliscocyathus* Debrenne 1974a on the basis of the rudimentary outer wall preserved in the holotype.

PHYLUM	incertae sedis
CLASS	Radiocyatha Debrenne, Termier and Termier 1970
FAMILY	Girphanovellidae Debrenne, Termier and Termier 1971
GENUS	<i>Girphanovella</i> Zhuravleva in Zhuravleva et al. 1967

#### Type species

*Girphanovella girphanovae* Zhuravleva in Zhuravleva et al. 1967. Early Cambrian (Botomian stage), River Shivelig-Khem, Tuva, USSR.

#### Diagnosis

Two-walled solitary or colonial skeletons of spherical, pyriform, or conical shape. Walls composed of nesasters (stellate units consisting of rays radiating from a central locus or disc, rays more or less confined to one plane). Outer wall with nesasters of two sizes, the smaller interstitial to the larger: on inner surface of wall, 6–12 basic rays radiate from a locus; on outer surface of wall, basic rays may bifurcate to generate up to

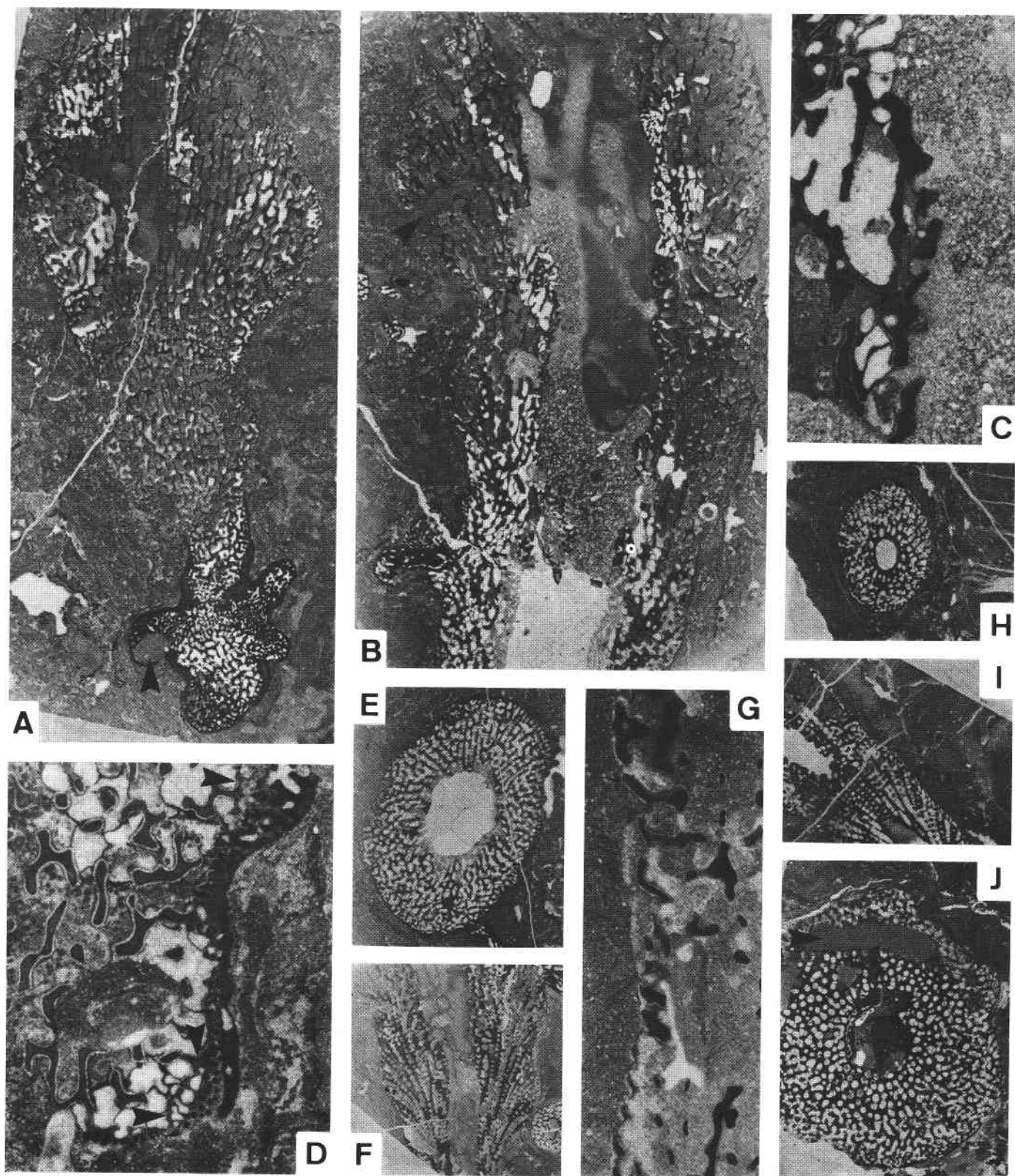


FIG. 4. *Archaeocyathus abacus* n.sp.; Ten Mile or Mount Billy Creek bioherm. (A–E) Holotype P31258. (A, B) Longitudinal sections. Note macroborings (arrowheads).  $\times 2.5$ . (C) Detail of inner wall in longitudinal section, showing pore tubes (central cavity to right).  $\times 12$ . (D) Detail of outer wall in tangential section, showing outer wall pores (arrowheads) and external micropores.  $\times 12$ . (E) Transverse section.  $\times 4.5$ . (F) Paratype P31277; longitudinal section showing septal porosity.  $\times 4.5$ . (G) Paratype P31269; detail of inner wall in longitudinal section showing pore tubes (central cavity to left).  $\times 12$ . (H, I) Paratype P31262. (H) Transverse section.  $\times 4.5$ . (I) Longitudinal section showing inner wall pores.  $\times 4.5$ . (J) Specimen P31266; transverse section. Note macroborings (arrowhead).  $\times 4.5$ .

TABLE 1. *Archaeocyathus abacus* n.sp

	Specimen					
	P31258 <sup>a</sup>	P31261	P31262	P31276	P31277	P31278
Cup						
<i>D</i>	20.0	16.2	6.9	22.0	15.7	12.9
Int	7.0	5.1	2.3	6.7	4.9	4.6
IC	1:11.8	1:9.7	1:4.8	—	1:10.3	—
RK	4.5	—	4.8	—	4.1	—
GPC	1.3	1.2	—	—	1.2	—
Outer wall						
<i>n</i>	~2	2-3	—	—	~2	~2
$\phi$	0.17	~0.2	—	—	~0.2	0.25
<i>l</i>	0.06	0.08	—	—	0.07	0.09
$\phi/l$	2.8	2.5	—	—	2.9	2.8
<i>e</i>	0.08	—	—	—	—	—
Inner wall						
<i>n</i>	1	1	1	1	1	—
$\phi$	0.37	0.38	0.38	0.43	0.32	—
<i>l</i>	0.11	0.13	0.09	0.08	0.10	—
$\phi/l$	3.5	2.9	4.2	5.2	3.3	—
<i>e</i>	—	0.11	—	—	0.11	—
Septa						
<i>n</i>	~10	7-8	5-6	~12	8-10	—
$\phi$	0.45	0.42	0.29	0.49	0.33	—
<i>l</i>	0.11	0.16	0.10	0.14	0.12	—
$\phi/l$	4.1	2.7	3.0	3.4	2.8	—
<i>e</i>	0.10	0.10	0.08	0.10	0.10	—

NOTES: All measurements in mm. Abbreviations: *D*, cup diameter; Int, intervalum width; IC, intervalum coefficient = ratio of sides of intervalar loculi in transverse section; RK, radial coefficient = number of septa/cup diameter; GPC, general porosity coefficient = porosity coefficient for inner wall/porosity coefficient for outer wall; *n*, number of vertical pore rows (per intersept for walls, across intervalum for septa);  $\phi$ , pore diameter; *l*, lintels (distance between adjacent rims of neighbouring pores);  $\phi/l$ , porosity coefficient; *e*, wall or septum thickness.

<sup>a</sup>Holotype.

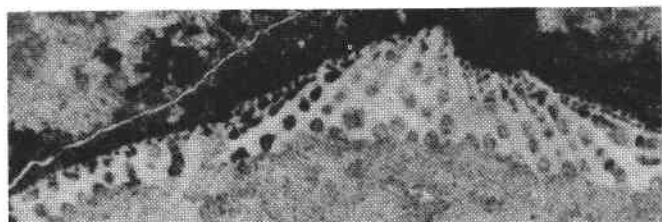


FIG. 5. *Radiocyathus minor* (Bedford and Bedford 1934), upper Wilkawillina Limestone, Old Wirrealpa Mine. Transverse section of outer wall, showing microporous sheath on outer wall nesasters.  $\times 9$ .

about 20 rays, with or without connecting bars, ray tips uniting to form an irregular perforate net. Inner wall with uniformly sized nesasters, their rays not confined to plane of wall, ray tips uniting to form loose meshwork. Intervalum traversed by radial rods linking nesaster loci of inner wall to loci of larger outer wall nesasters.

#### Discussion

The terms aster (Kruse and West 1980) and rosette (Zhuravlev 1986) are synonymous with nesaster as introduced by Debrenne *et al.* (1971) and used here.

*Girphanovella* is from the Botomian and possibly late Atabanian of Tuva and Transbaykal (Zhuravleva *et al.* 1964, 1967), Mongolia, Canada (Zhuravlev and Sayutina 1985), and perhaps Morocco (Debrenne 1977). Zhuravlev and Sayutina (1985) synonymized the type species with the earlier *Dokidocyathina georgensis* Rozanov (in Zhuravleva *et al.* 1964).

The only other conical-pyriform two-walled radiocyath genus is *Radiocyathus* Okulitch 1937, described originally from the Botomian of South Australia. The type and only known species *Radiocyathus minor* (Bedford and Bedford 1934) was described on the basis of silicified material from the Ajax Limestone at the Ajax Mine. Neither the original description and subsequent revisions (Debrenne *et al.* 1970) nor additional reports from the Amadeus Basin of central Australia (Nitecki and Debrenne 1979; Kruse and West 1980, also from silicified material) make mention of a microporous sheath on the outer wall. However, a small collection of unsilicified *R. minor* from the coeval upper Wilkawillina Limestone at Old Wirrealpa Mine shows that the species possesses a continuous microporous sheath covering the outer surface of the outer wall, with about four micropores per interstitial perforation of the nesaster ray net (Fig. 5). This sheath is a more significant distinction between *Radiocyathus* and *Girphanovella* than the variation in



TABLE 2. *Girphanovella gondwana* n.sp.

	Specimen					
	P31289	P31291	P31292	P31294	P31296	P31298 <sup>a</sup>
Cup						
<i>D</i>	13	23	17	28	36	23
Int	3	5	4	5	6	6
Rod <i>t</i>	0.1–0.3	0.1–0.3	0.1–0.4	0.3–0.6	0.2–0.5	0.1–0.3
Outer wall						
<i>d</i>	1.0–2.0	1.5–2.0	2.0	2.0–2.5	2.0–4.5	1.5–3.0
<i>nn</i>	6–7	6–9	~8	6–8	>6	6–7
<i>rt</i>	0.6	0.7	0.6	0.6	1.1	0.6
<i>e</i>	~0.5	~0.4	~0.5	~0.7	~0.8	~0.6
Inner wall						
<i>d</i>	~1.0	1.5–2.0	~1.5	~1.5	1.5–2.5	0.5–1.5
<i>nn</i>	~6	6–9	~6	6–7	~6	6–7
<i>rt</i>	0.2	0.2	0.3	0.3	0.4	0.2
<i>e</i>	~0.2	~0.3	~0.2	~0.4	~0.4	~0.2

NOTES: All measurements in mm. Abbreviations: Rod *t*, rod thickness; *d*, distance between centres of nesasters; *nn*, number of rays per nesaster; *rt*, maximum ray thickness; other abbreviations as in Table 1.

<sup>a</sup>Holotype.

outer wall nesaster size proposed by Zhuravlev and Sayutina (1985).

*Girphanovella gondwana* n.sp.  
(Figs. 6, 12; Table 2)

1986 *Radiocyathus*; Zhuravlev, p. 42.

1989 *Radiocyathus* sp.; Kruse and Debrenne, fig. 5.

**Name**

From Sanskrit *gondwana* = land of the Gonds; the first species named from a Gondwana continent.

**Material**

Twelve specimens. Holotype P31298; paratypes P31289–P31297, Ten Mile or Mount Billy Creek section (= type section of Daily 1956 = section 19 of Youngs 1977); additional material P31326, questionably P31327, Balcoracana Creek section (= section 1 of Youngs 1977), Flinders Ranges, South Australia.

**Diagnosis**

Outer wall thicker than inner wall. Nesasters with 6–9 rays, loci spaced 1.0–4.5 mm apart on outer wall and 0.5–2.5 mm apart on inner wall.

**Description**

Cup conical–pyriform, diameter up to 60 mm, with intervalum 10 mm or more in width. Outer wall 0.4–0.8 mm thick, constructed of nesasters having about 6 basic rays on inner surface and 6–9 rays on outer surface (maximum ray thickness 0.6–1.1 mm). Rays on inner surface unite with neighbours; rays

of adjacent nesasters on outer surface are united and linked by bars to form an irregular net perforated by interstices. Interstices rounded, polygonal (diameter generally 0.2–0.6 mm), or elongate (length up to 1.5 mm). Loci of nesasters generally thicker than rays, giving uneven outer surface. Nesasters spaced 1.0–4.5 mm apart. Unevenly distributed, isolated or tufted spines (length up to 0.2 mm) project from outer surface.

Inner wall 0.2–0.4 mm thick, constructed of smaller nesasters with 6–9 rays each. Rays not strictly confined to plane of wall, hence forming a loose meshwork (maximum ray thickness 0.2–0.4 mm). Nesasters spaced 0.5–2.5 mm apart. Unevenly distributed spines or knobs of diameter up to 0.3 mm (generally 0.05–0.1 mm) project into central cavity from inner wall.

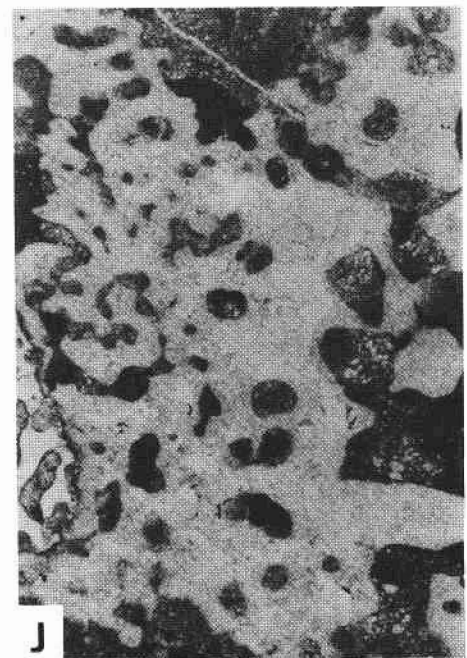
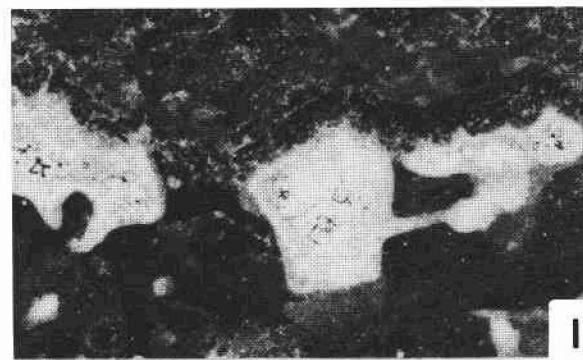
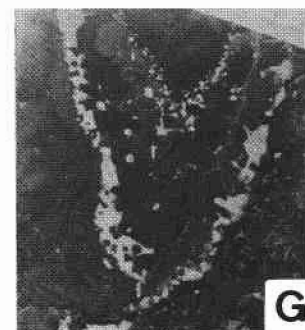
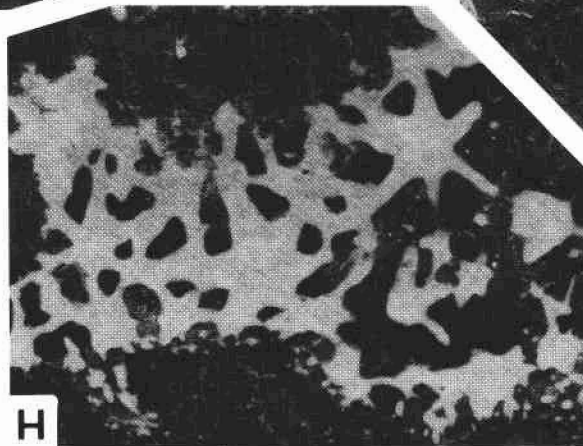
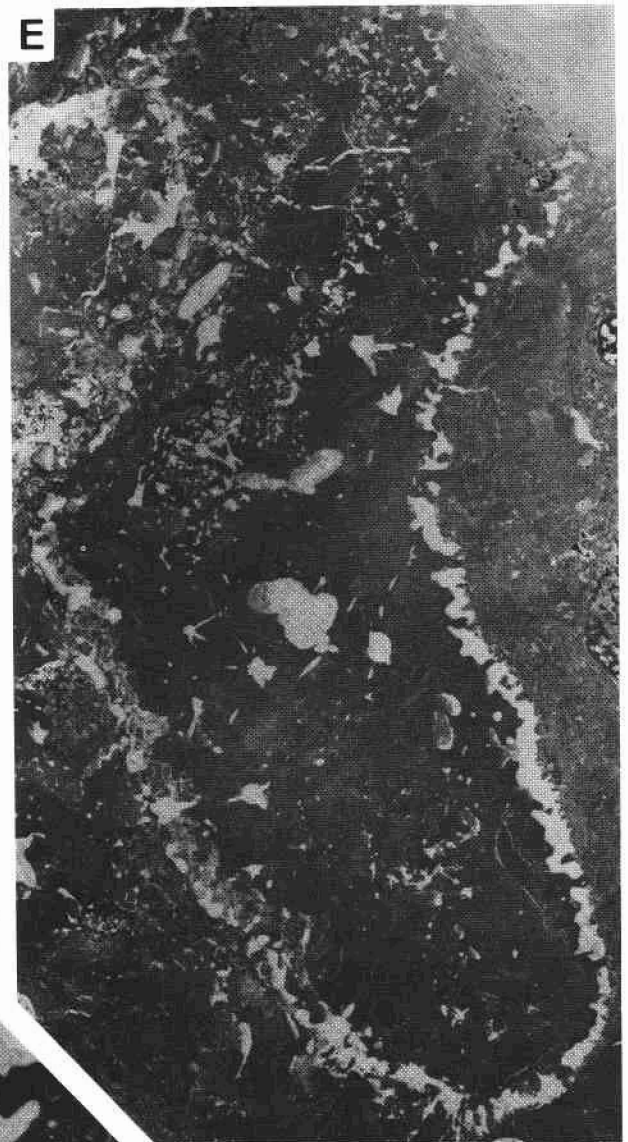
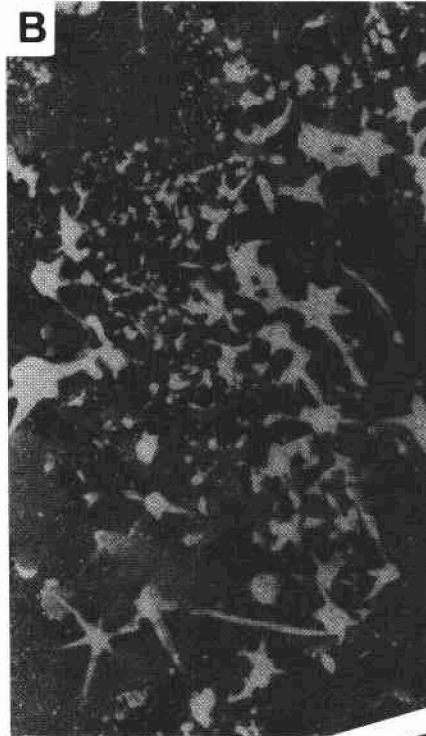
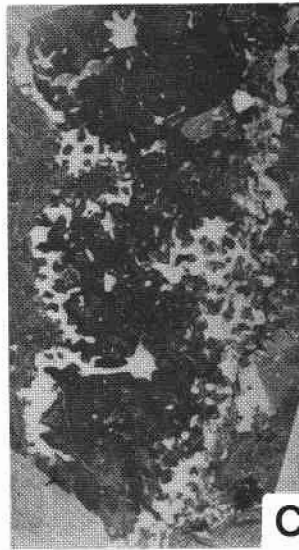
Intervallum with radial rods linking opposite nesaster loci, rods seemingly thickening toward outer wall (thickness 0.1–0.6 mm). Scattered nesasters up to 6 mm diameter in intervallum.

**Remarks**

Paratype P31296 (Fig. 6J) displays the most convincing outer wall “sheath” in the collection, but even in this specimen there is a continuous size gradation between larger and smaller perforations (diameter 0.1–0.9 mm) and no clear spatial demarcation into sheath and framework. The “sheath” of this example is apparently associated with secondary thickening of the outer wall, and perhaps also with exothecal structures. *Girphanovella gondwana* n.sp. does not possess a true microporous sheath as in *Radiocyathus*.

The size range of outer wall nesasters seems not to be as pronounced in *G. gondwana* as in the type species. Large nesasters in the latter attain 6.0 mm diameter, with up to 20 rays on the outer surface (Zhuravlev and Sayutina 1985); as well, the

FIG. 6. *Girphanovella gondwana* n.sp.; Ten Mile or Mount Billy Creek bioherm. (A–E) Holotype P31298. (A) Transverse section.  $\times 4.5$ . (B) Detail of inner wall in tangential section.  $\times 7.5$ . (C, D) Tangential sections of outer wall.  $\times 4.5$ . (E) Longitudinal section. Note macroborings.  $\times 2.5$ . (F, G) Paratype P31292. (F) Transverse section.  $\times 4.5$ . (G) Longitudinal section.  $\times 4.5$ . (H) Paratype P31297, detail of outer wall in tangential section.  $\times 7.5$ . (I) Paratype P31290, detail of outer wall in longitudinal section (intervallum below), showing spines on outer surface.  $\times 12$ . (J) Paratype P31296; detail of outer wall in tangential section.  $\times 12$ .



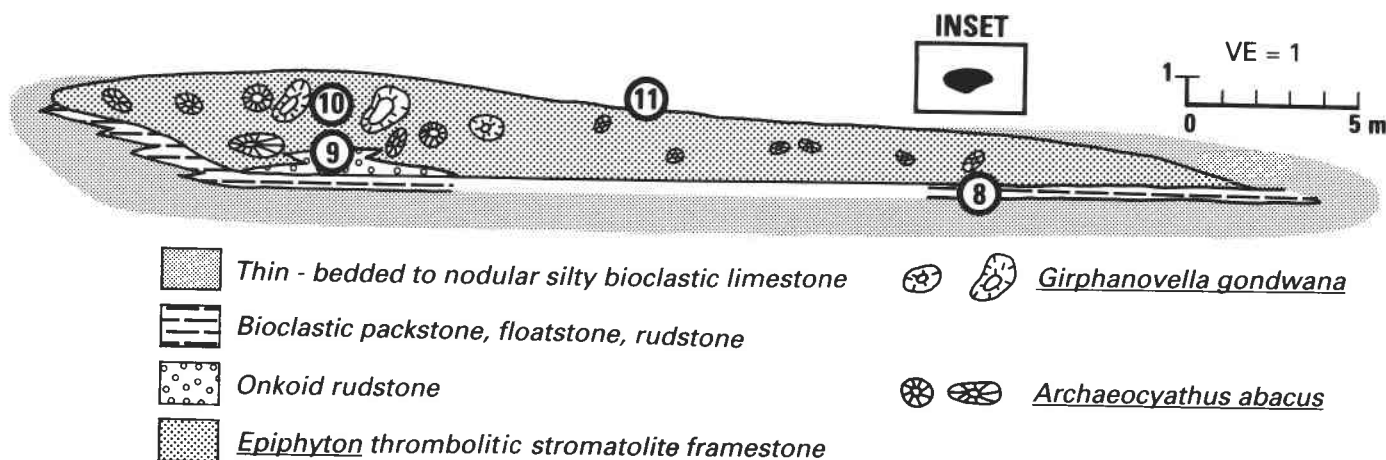


FIG. 7. Schematic section through cyanobacterial–archaeocyathan–radiocyathan bioherm, Ten Mile or Mount Billy Creek section. Circled numbers refer to figures in this paper. Inset: studied bioherm of Balcoracana Creek section at same scale (see Fig. 13).

inner wall is much thicker (up to 1.1 mm), and neither wall has projecting knobs or spines.

### Bioherms

Bioherms in the Wirrealpa Limestone were examined at two sections: Ten Mile or Mount Billy Creek (the type section of Daily 1956 = section 19 of Youngs 1977) and Balcoracana Creek (section 1 of Youngs 1977). Other stromatolitic or thrombolitic bioherms in the formation have been briefly described by Youngs (1977): small, subrounded bioherms up to 1 m in size and larger, columnar types up to 8 m high. These apparently lack archaeocyaths or radiocyaths and are not considered further here.

Optical petrographic distinction of cementation and recrystallization fabrics is hampered by a pervasive neomorphism in the Wirrealpa Limestone. The microstructure of all bioclasts except trilobites, calcareous algae, and (in general) archaeocyaths has been transformed to a fine to coarse equant spar, which in some cases diminishes in size toward the margins. These latter cases suggest that the present spar may be derived from a precursor cement occluding leached bioclast moulds, but this is uncertain. Spar occluding larger fenestrae, obvious shelter porosity, and borings with geopetal micrite fillings is assumed to represent original cements. This apart, petrographic features and relationships are readily observable.

#### Ten Mile or Mount Billy Creek

In this section, bioherms attain their greatest development in the Wirrealpa Limestone between 77 and 81 m from the base of the unit, here 134 m in thickness. The best-exposed bioherm, described below, outcrops on the south bank of the small tributary creek denoting the line of section. An additional bioherm on the slope above the opposite bank is poorly exposed but includes small archaeocyaths, presumably *A. abacus*, up to 1.5 cm diameter in a cyanobacterial framestone.

The studied bioherm (Fig. 7) is entirely enclosed within thin-bedded to nodular silty bioclastic limestone, termed biosparite by Youngs (1977). Flexure of beds adjacent to the bioherm (as exposed in the creek bed) is due to the draping of peribiohermal sediments against the bioherm margin (confirming original topographic relief) and their later differential compaction.

The bioherm substrate is a 1 m thick interval of bioclast packstone, floatstone, and rudstone (Embry and Klovan 1971)

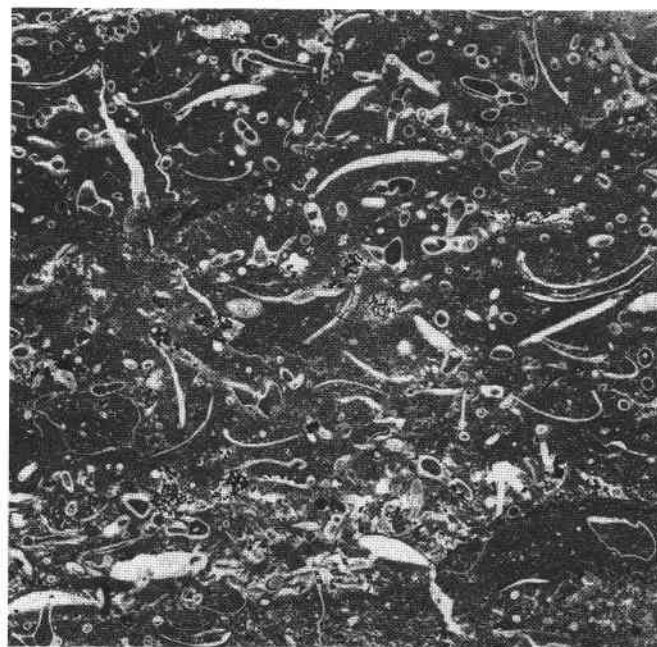


FIG. 8. Bioclastic packstone–floatstone–rudstone substrate to Ten Mile or Mount Billy Creek bioherm. P31302.  $\times 2.5$ .

within which individual beds may attain a thickness of 10 cm (Fig. 8). Bioclasts include fragments of cancelloriids, trilobites, hyoliths, brachiopods, molluscs, echinoderms, radiocyaths, and archaeocyaths, the larger examples often showing associated shelter porosity. Peloids and sparry or micritic intraclasts may also be locally present.

Beneath the thickest part of the bioherm is a small area of onkoid rudstone (Embry and Klovan 1971): flattened *Girvanella*-rich intraclasts and onkoids 2–10 mm thick and several centimetres across probably represent recycled crusts (Fig. 9). Onkoid nuclei include brachiopod, cancelloriide and trilobite fragments. Cortices consist of abundant 10–20  $\mu\text{m}$  wide *Girvanella* tubules with baffled or adherent interstitial micrite; tubules in combination form crusts, tussocks, and minicolumns. In the minicolumns, essentially prostrate *Girvanella* tubules form linked columns 0.2–0.5 mm in diameter, oriented normal to the onkoid surface (Fig. 9C). Cortices are often selectively



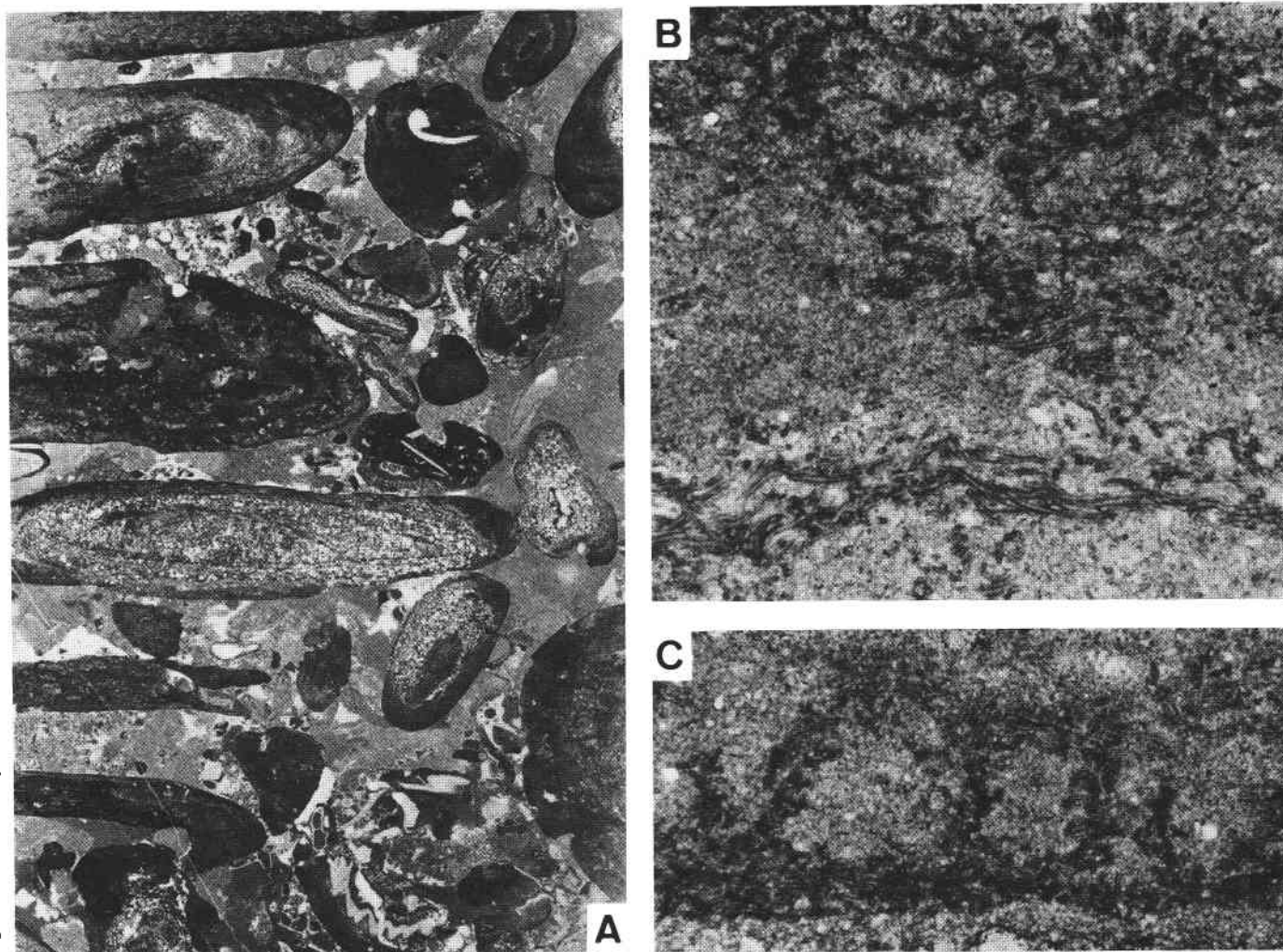


FIG. 9. Onkoid rudstone; substrate to thickest part of Ten Mile or Mount Billy Creek bioherm. (A) General view.  $\times 2.5$ . (B) Detail of A showing *Girvanella* crust (below) and open network (above) in onkoid cortex.  $\times 55$ . (C) Detail of A showing *Girvanella* minicolumns in onkoid cortex.  $\times 55$ .

dolomitized. Matrix to the onkoids is a sediment rich in *Epiphyton* clots as well as fragmentary chancelloriids, trilobites, hyoliths, brachiopods, and echinoderms, the latter showing syntaxial overgrowths.

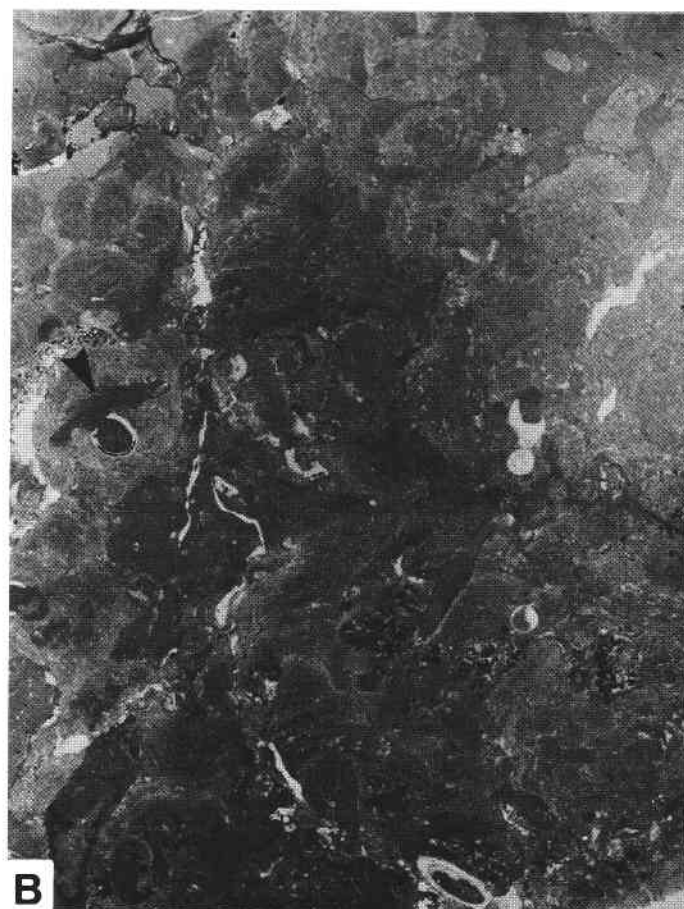
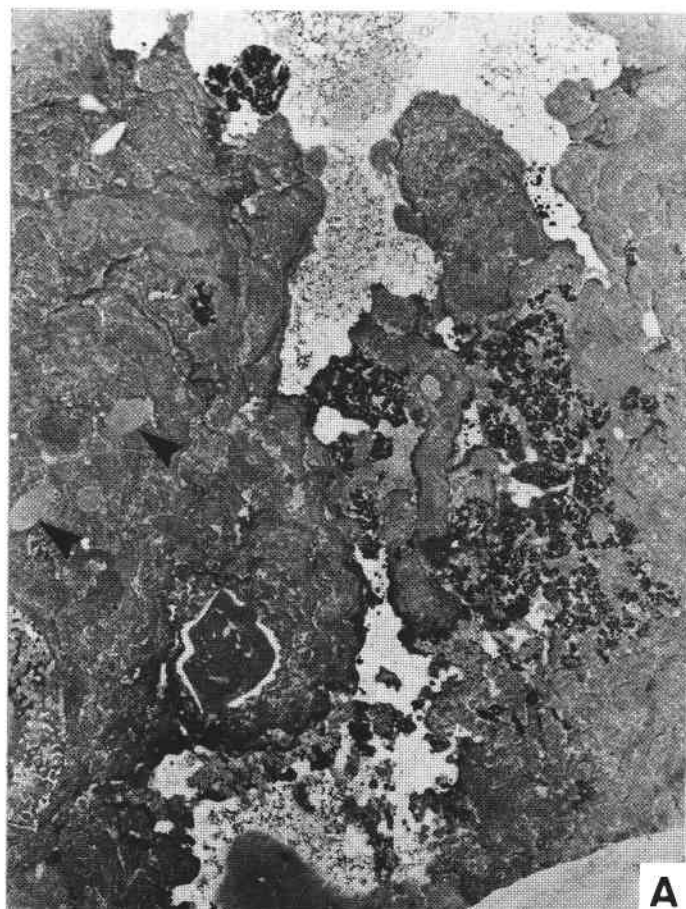
The bioherm itself is essentially a thrombolitic stromatolite framework colonized by a limited noncyanobacterial biota of archaeocyaths, radiocyaths, brachiopods, hyoliths, and macroborers. Narrowly conical *Archaeocyathus* and conical-pyri-form *Girphanovella* cups attain their greatest size at the northern end of the bioherm, where it is a maximum 3 m thick. The bioherm tapers to the south, reaching a total length of 36 m.

By far the most common lithology constituting the biohermal core is *Epiphyton* thrombolitic stromatolite framestone (Kennard and James 1986), in which abundant *Epiphyton* and rare *Renalcis* constitute the principal mesoclots (Fig. 10). The component columnar stromatolites (columns 2–10 cm in diameter) have a laminoid fabric with elements of the lenticular laminoid and laminoid fenestral types of Monty (1976): cyanobacterial cushions and mats are irregularly superimposed, and there is some alignment of elongate fenestrae within columns. Larger fenestrae may be occluded by coarse equant spar. The laminar appearance is enhanced by scattered mats of darker, well-preserved *Epiphyton* mesoclots and, rarely, *Girvanella* mantling individual cushions. Discrete cushions and

larger, more irregular areas of well-preserved *Epiphyton* mesoclots are also present. Column microstructure is clotted, probably derived from the disintegration and recrystallization of *Epiphyton* thalli to microspar (cf. Coniglio and James 1985). There is gradation from areas that can be more confidently related to *Epiphyton* thalli in terms of size, spacing and arrangement of clots (Figs. 10A, 10C) through to areas of discrete 0.03–0.05 mm sized peloids, with lamination in part due to differential packing and (or) cementation of these (Fig. 10D). Possibly, clots generated by the disintegration of *Epiphyton* bushes were incorporated into accreting stromatolitic laminae by a co-occurring noncalcified sediment-trapping and (or) carbonate-precipitating, filament-dominated microbial community (Kennard and James 1986, p. 494).

The intercolumn matrix is micrite with occasional hyolith and brachiopod debris, and, locally, scattered quartz silt. Detrital micrite in troughs between cyanobacterial cushions within stromatolite columns suggests that column growth was episodic.

*Archaeocyathus* and *Girphanovella* cups are rarely, if ever, preserved in growth position. Overwhelmingly, cups are toppled and incorporated into the thrombolitic stromatolite framestone by providing hard substrates for cyanobacterial growth. *Girvanella* may partially encrust cups. Large cups (diameter up to 6 cm) thrived only in a small area some 2–3 m



wide in the thickest portion of the mound; only scattered small cups about 1 cm in diameter are found elsewhere. This size variation in archaeocyathan and radiocyathan cups is the only evident vertical variation within the biohermal core.

Subspherical to ellipsoidal detrital peloids 0.05–0.3 mm in diameter (i.e., larger than the thickness of branches in *Epiphyton* thalli) are present within the micrite infilling the central cavities of some *A. abacus* cups.

Macroborings 1–3 mm in diameter are locally common within the thrombolitic stromatolite framestone, particularly associated with *A. abacus* cups, but also penetrate stromatolites, well-preserved *Epiphyton*, bioclasts, and micrite. Most are completely infilled with micrite, but a few have partial geopetal micrite infills occluded by prismatic fine spar. Rare examples totally occluded by clear prismatic spar display cloudy spar rims possibly representative of a now-recrystallized initial cement. Such macroborings, together with fenestrae in the stromatolite columns, constitute the few cavities preserved in the bioherm. No cryptobionts have been recognized within these.

The upper surface of the bioherm is diffuse, passing upward into the enclosing nodular bioclastic limestone with diminution in the degree of thrombolitic binding relative to stromatolitic. There is some reworking, evidenced by fragments and chunks of stromatolite columns and archaeocyath cups (Fig. 11).

#### Balcoracana Creek

Archaeocyaths and radiocyaths were collected from two levels in this well-exposed Wirrealpa Limestone section totaling 139 m in thickness. Poorly preserved probable *G. gondwana* are rare in an interval of well-developed domal stromatolites 77–79 m above the formation base. This bed is in part a bioclast-oid-onkoid wackestone-packstone including a variety of coated grains with cancelloride, trilobite, echinoderm, or ooid nuclei and radial-concentric to concentric cortices (Fig. 12). Some cortices have *Girvanella* laminae. Many of the ooids are dolomitized and the remainder neomorphosed to prismatic spar.

At a higher stratigraphic level, *A. abacus* occurs in one of a number of cyanobacterial mounds 86–90 m above the formation base. The relevant mound is about 1.5 m long and 1 m high, with the archaeocyaths restricted to a small central area, about 10 cm across, of thrombolitic stromatolite like that comprising the core of the Ten Mile or Mount Billy Creek bioherm (Figs. 13, 14A). This small area is enveloped by patchy or lenticular micrite and unlaminated (thrombolitic) material of the "clotted-peloidal" type (above) (Fig. 14B). Burrows or borings 0.3–1.5 mm in diameter and fenestrae are common. A marginal onkoid-echinoderm-micritic and clotted cyanobacterial intra-clast rudstone (Fig. 14C) may represent substrate. The perimound sediments are not exposed.

#### Depositional environment

Youngs (1977) proposed a depositional model in which the Wirrealpa Limestone represents a single marine transgressive-regressive cycle across that portion of the stable Cambrian shelf



FIG. 11. Upper surface of bioherm, Ten Mile or Mount Billy Creek section. Thrombolitic stromatolite framestone with intercolumn micrite (now dolomitized) passing upward into laminated stromatolitic framestone. P31316.  $\times 2.5$ .

now identified as the Arrowie Basin. From local correlations depicted in her Fig. 5, the bioherms under discussion fall within a single interval in the middle part of the formation, which was deposited at or near the height of the transgression. Youngs (1977) recognized two broad depositional regimes in the formation: a more offshore Ooid Bank Megafacies, a shallow, higher energy zone characterized by a network of intertonguing ooid shoals; and a more protected Lagoonal Megafacies, a shallow but low-energy zone retaining direct communication with the open sea.

Silty nodular bioclastic limestones, of the type enveloping the Ten Mile or Mount Billy Creek bioherm, formed over wide areas of the shelf in both megafacies, in the shallow, quiet waters of the lagoon and the more protected parts of intershoal

FIG. 10. *Epiphyton* thrombolitic stromatolite framestone; Ten Mile or Mount Billy Creek bioherm. Arrowheads denote macroborings.  $\times 2.5$ . (A) P31300; clearly delineated columns; dolomitized "cavity" at top is presumed to represent original micrite by analogy with partially dolomitized intercolumn micrite at bottom; note well-preserved bushy *Epiphyton* at centre right, ?orthide brachiopod at lower left, and partially recrystallized *A. abacus* at extreme lower left. (B) P31299; hyolith conchs and *Epiphyton* bushes enveloped by thrombolitic stromatolite framestone; note intercolumn micrite. (C) P31307; more clotted portion of framestone with common *Epiphyton* bushes; *A. abacus* at bottom left; note intercolumn micrite. (D) P31308; *A. abacus* and hyolith conchs enveloped by thrombolitic stromatolite framestone.



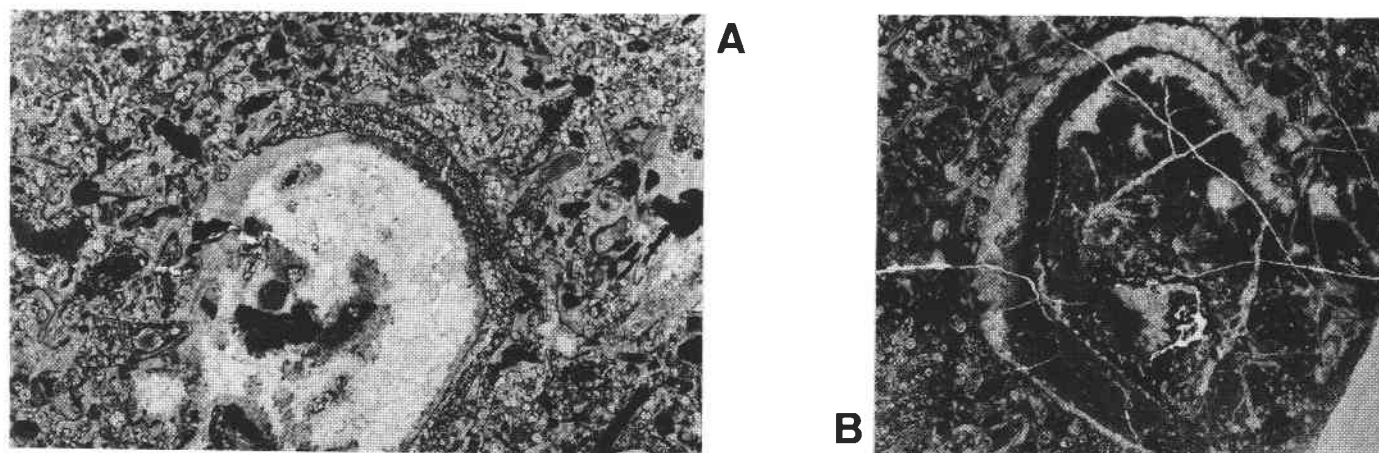


FIG. 12. *Girphanovella gondwana* n.sp.; from 77–79 m interval, Balcoracana Creek section. (A) Transverse section of probable specimen in dolomitized packstone; P31327.  $\times 2.5$ . (B) Transverse section of specimen in undolomitized wackestone–packstone  $\times 2.5$ .

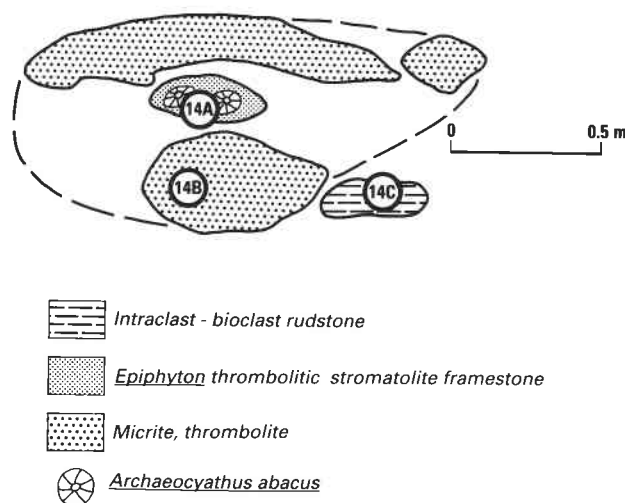


FIG. 13. Schematic section through studied cyanobacterial–archaeocyathan bioherm, Balcoracana Creek section. Circled numbers refer to figures in this paper.

areas within the ooid bank. The Ooid Bank Megafacies attained its greatest extent at the height of the transgression, and at that time the cyanobacterial–archaeocyathan–radiocyathan bioherms can be envisaged developing in subtidal, open marine but calm and shallow waters, on the impure bioclastic carbonate mud and silt between and flanking ooid shoals.

The Ten Mile or Mount Billy Creek bioherm has definite topographic relief (as evidenced by drape of flanking beds) and a pervasive organic (cyanobacterial) framework. The lack of any evident fissure filling, talus, or capping grainstone (Wilson 1975, pp. 366–369) is consonant with the postulated calm environment. Equally, there is no direct association with oolite or tidal channels, as in Botomian cyanobacterial–archaeocyathan reefs in the Poleta Formation of western United States (Rowland 1984).

### Some comparisons

Of Toyonian cyanobacterial–archaeocyathan bioconstructions, only those in the Forteau Formation of Labrador have been rigorously studied. Siberian examples of this age are small, with only small regular archaeocyath cups (Siberian Platform), or elsewhere, extensive bioherm complexes with

mainly large, irregular archaeocyaths, these organisms accounting for only some 5–10% of the bioherm volume (Zhuravleva, cited in James and Debrenne 1980). Coeval buildups in the Tianheban Formation of South China have not been documented sedimentologically.

In the Forteau Formation of Labrador, biconvex buildups, variously termed bioherms or patch reefs (James and Kobluk 1978; Debrenne and James 1981), consist of loaf- or pillow-shaped mounds, 1–2 m wide and up to 1 m high. Mounds occur singly or collectively, in some cases forming complexes up to 20 m high and 200 m long. As in the Wirrealpa Limestone, peribiohermal sediment is generally a skeletal calcarenite, with or without nodular-interbedded shales. Archaeocyaths (here, six irregular species) are common only in bioherms and immediately adjacent peribiohermal sediments. The biohermal core differs from the Wirrealpa Limestone examples in being composed simply of archaeocyath cups, *Renalcis*, and cement in a red lime mud matrix – an archaeocyath floatstone (Embry and Klován 1971). Nevertheless, borings and truncated archaeocyath cups on upper surfaces indicate that at least some bioherms were lithified prior to deposition of the overlying skeletal sand. Characteristically geostrophic encrustation of archaeocyath cups by *Renalcis* was an important constructional process, these organisms accounting for some 30% of the bioherm volume; however, these organisms never produced the laminoid thrombolitic stromatolites integral to the Wirrealpa Limestone bioherms. Forteau Formation bioherms also exhibit a suite of reef cavities, including shelter cavities beneath *Retilamina* cups and dissolution cavities. Bioherms in both formations were affected by macroborers; in the Forteau Formation bioherms these penetrate archaeocyaths, matrix, and the first-stage cement.

Older archaeocyathan bioconstructions are far more widespread, with a virtually worldwide distribution in the Botomian (e.g., Read 1980; Rowland 1984; Rowland and Gangloff 1988; Debrenne *et al.* 1989; Rees *et al.* 1989; James and Gravestock 1990). Like the Forteau Formation bioherms, they typically comprise cyanobacteria, archaeocyaths, lime mud, and cement in varying proportions.

Hence the thrombolitic stromatolite framestone core of the Wirrealpa Limestone bioherms remains distinctive.

A slightly younger (late Middle Cambrian) bioherm in the Petit Jardin Formation of Newfoundland records a shallow



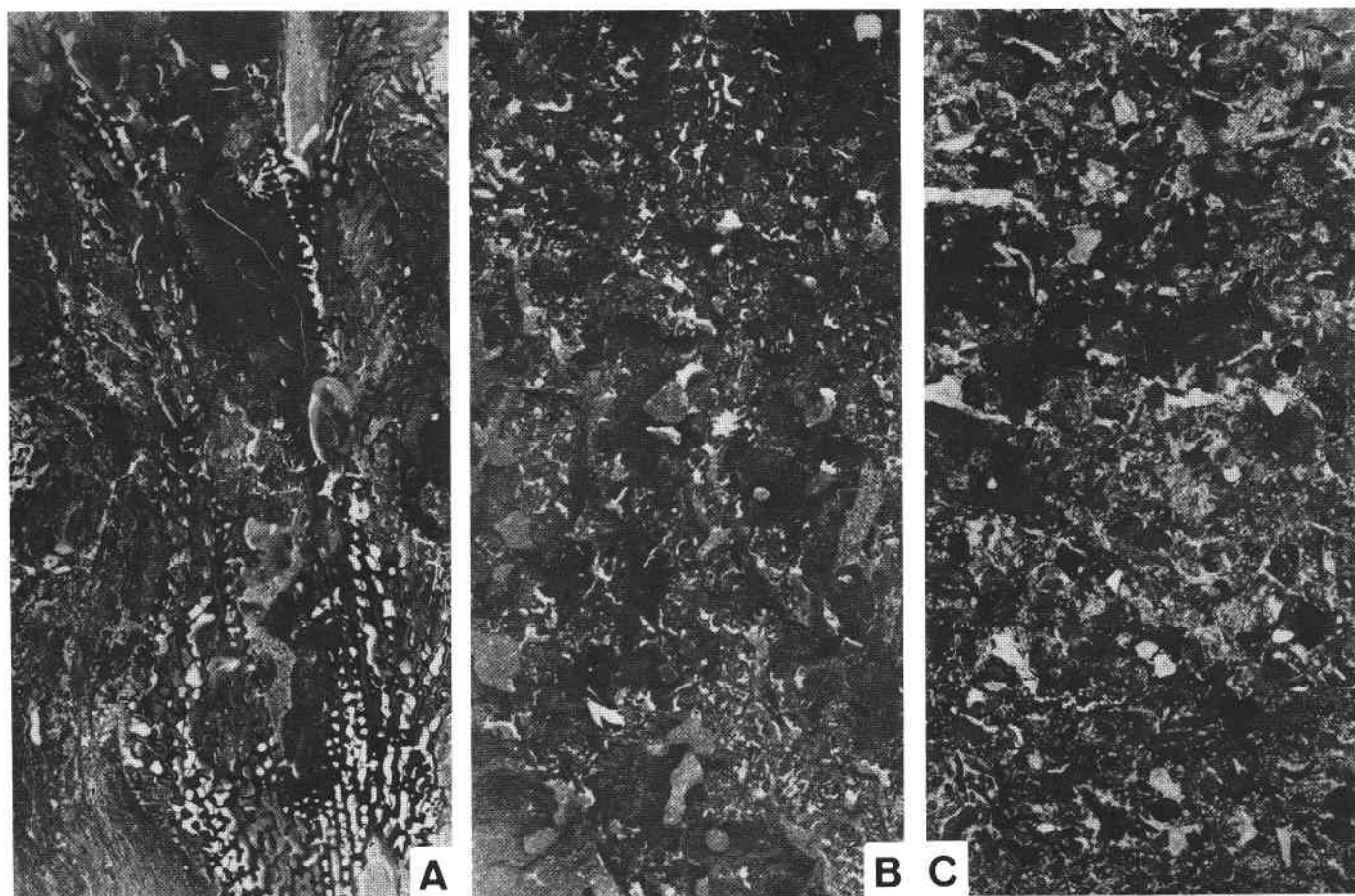


FIG. 14. Cyanobacterial-archaeocyathan bioherm, Balcoracana Creek section.  $\times 2.5$ . (A) P31319; *A. abacus* in thrombolitic stromatolite framestone. Note macroboring at inner wall. (B) P31323; micrite and unlaminated (thrombolitic) limestone; note fenestrae with geopetal micrite infills. (C) P31324; intraclast-bioclast rudstone, possibly representing bioherm substrate.

subtidal to intertidal shoaling event, commencing with basal thrombolitic pedestals and passing upward through composite stromatolitic thrombolites into capping planar stromatolites (Kennard *et al.* 1989). Although this example is too young to include archaeocyaths, its depositional setting is analogous to that of the Wirrealpa Limestone: the bioherm is enclosed by nodular to ribbon limestone, shale, and pebble conglomerate representing a low-energy siliciclastic-carbonate shelf rimmed by a peritidal ooid shoal complex. The laminated stromatolitic framestone capping the Ten Mile or Mount Billy Creek bioherm possibly denotes a similar upward shoaling.

### Summary

Cyanobacteria and archaeocyaths were the only common Cambrian organisms with frame-building capacity. Hence, Cambrian bioconstructions can be cast as three basic types: purely cyanobacterial, essentially cyanobacterially constructed but with associated archaeocyaths and (or) radiocyaths, and archaeocyathan-poriferan (mud mounds). The Wirrealpa Limestone bioherms described above are of the second type.

These Botomian- or Toyonian-age Wirrealpa Limestone bioherms display a distinctive *Epiphyton* thrombolitic stromatolite framework. Some of these bioherms were colonized by the archaeocyaths *Ajaciccyathus* sp. and *A. abacus*, the radiocyath *G. gondwana*, and macroborers. The largest known bioherm was established on a moderate-energy subtidal substrate. The association of large archaeocyaths and radiocyaths immediately

above coarse onkoid rudstone suggests that the development of large *Girvanella*-bearing onkoid clasts may have provided the crucial impetus for the establishment of bioherm development, perhaps by providing a stable substrate for *Epiphyton* attachment and growth during periods of relative calm. In any case, once established, *Epiphyton* was able to extend laterally by constructing columnar thrombolitic stromatolites of laminoid fabric. The coincidence of optimal conditions for thrombolitic stromatolite development and for archaeocyathan and radiocyathan growth is noteworthy: the largest archaeocyath and radiocyath cups are in the thickest part of the bioherm. Conversely, the biohermal milieu was inimical to most other skeletal invertebrates: these are more common in peribiohermal sediments. The action of macroborers testifies to a rapid calcification of the thrombolitic stromatolite columns as rigid structures, potentially wave resistant but seemingly not subject to excessively high energy conditions; no talus has been recognized. The archaeocyaths and radiocyaths in these bioherms are the youngest Australian representatives of their respective groups.

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- Canada) commented on aspects of the manuscript. The material was initially studied during tenure of a French Government Scientific and Professional Scholarship at the Muséum national d'histoire naturelle, Paris, in 1982. Christine Kennedy typed the manuscript. Garry Evans drafted the line drawings. Barry Ledwidge printed the photographs from negatives prepared with the assistance of Bob Davis. This paper is published with the approval of the Secretary, Northern Territory Department of Mines and Energy.
- BEDFORD, R., and BEDFORD, J. 1937. Further notes on Archaeos (Pleosporgia) from the Lower Cambrian of South Australia. *Memoirs of the Kyancutta Museum*, **4**: 27–38, Pls. 27–41.
- . 1939. Development and classification of Archaeos (Pleosporgia). *Memoirs of the Kyancutta Museum*, **6**: 67–82, Pls. 42–52.
- BEDFORD, R., and BEDFORD, W. R. 1934. New species of Archaeocyathinae and other organisms from the Lower Cambrian of Beltana, South Australia. *Memoirs of the Kyancutta Museum*, **1**: 1–7, Pls. 1–6.
- BENGSTON, S., CONWAY MORRIS, S., COOPER, B. J., JELL, P. A., and RUNNEGAR, B. N. 1990. Early Cambrian fossils from South Australia. *Association of Australasian Palaeontologists, Memoir 9*.
- BILLINGS, E. 1861. New species of Lower Silurian fossils: on some new or little known species of Lower Silurian fossils from the Potsdam Group (Primordial zone). *Geological Survey of Canada, Montréal*.
- BORNEMANN, J. G. 1884. Bericht über die Fortsetzung seiner Untersuchungen cambrischer *Archaeocyathus*-Formen und verwandter Organismen von der Insel Sardinien. *Zeitschrift der Deutschen Geologischen Gesellschaft*, **36**: 702–706.
- CHI, Y. S. 1940. Cambrian Archaeocyathina from the gorge district of the Yangtze. *Bulletin of the Geological Society of China*, **20**: 121–147.
- CONIGLIO, M., and JAMES, N. P. 1985. Calcified algae as sediment contributors to Early Paleozoic limestones: evidence from deep-water sediments of the Cow Head Group, western Newfoundland. *Journal of Sedimentary Petrology*, **55**: 746–754.
- DAILY, B. 1956. The Cambrian in South Australia. 20th International Geological Congress, Mexico, vol 2, pp. 91–147.
- DEBRENNE, F. 1974a. Les archéocyathes irréguliers d'Ajax Mine (Cambrien inférieur, Australie du Sud). *Bulletin du Muséum national d'histoire naturelle, Sciences de la Terre*, **33**: 185–258.
- . 1974b. Anatomie et systématique des archéocyathes réguliers sans plancher d'Ajax Mine (Cambrien inférieur, Australie du Sud). *Géobios*, **7**: 91–138, Pls. 19–28.
- . 1977. Archéocyathes du Jbel Irhoud (Jebilet-Maroc). *Bulletin de la Société Géologique et Minéralogique de Bretagne, sér. C*, **7**: 93–136.
- DEBRENNE, F., and JAMES, N. P. 1981. Reef-associated archaeocyathans from the Lower Cambrian of Labrador and Newfoundland. *Palaeontology*, **24**: 343–378.
- DEBRENNE, F., TERMIER, H., and TERMIER, G. 1970. Radiocyatha. Une nouvelle classe d'organismes primitifs du Cambrien inférieur. *Bulletin de la Société géologique de France*, **12**: 120–125, Pls. 4–6.
- . 1971. Sur de nouveaux représentants de la classe des Radiocyatha. Essai sur l'évolution des Métazoaires primitifs. *Bulletin de la Société géologique de France*, **13**: 439–444, Pls. 29–30.
- DEBRENNE, F., GANDIN, A., and ROWLAND, S. M. 1989. Lower Cambrian bioconstructions in northwestern Mexico (Sonora). Depositional setting, paleoecology and systematics of archaeocyaths. *Géobios*, **22**: 137–195.
- EMBRY, A. F., and KLOVAN, J. E. 1971. A Late Devonian reef tract on northeastern Banks Island, N.W.T. *Bulletin of Canadian Petroleum Geology*, **19**: 730–781.
- ETHERIDGE, R., JR 1905. Additions to the Cambrian fauna of South Australia. *Transactions and Proceedings of the Royal Society of South Australia*, **29**: 246–251, Pl. 25.
- GRAVESTOCK, D. I. 1984. Archaeocyatha from lower parts of the Lower Cambrian carbonate sequence in South Australia. *Association of Australasian Palaeontologists, Memoir 2*.
- HILL, D. 1972. Archaeocyatha. In *Treatise on invertebrate paleontology. Part E. Vol. 1. Edited by C. Teichert*. Geological Society of America, Boulder, CO, and University of Kansas, Lawrence, KS.
- HINDE, G. J. 1889. On *Archaeocyathus*, Billings, and on other genera, allied to or associated with it, from the Cambrian strata of North America, Spain, Sardinia, and Scotland. *Quarterly Journal of the Geological Society of London*, **45**: 125–148.
- JAMES, N. P., and DEBRENNE, F. 1980. Lower Cambrian bioherms: pioneer reefs of the Phanerozoic. *Acta Palaeontologica Polonica*, **25**: 655–668.
- JAMES, N. P., and GRAVESTOCK, D. I. 1990. Lower Cambrian shelf and shelf margin buildups, Flinders Ranges, South Australia. *Sedimentology*, **37**: 455–480.
- JAMES, N. P., and KOBLUK, D. R. 1978. Lower Cambrian patch reefs and associated sediments: southern Labrador, Canada. *Sedimentology*, **25**: 1–35.
- KENNARD, J. M., and JAMES, N. P. 1986. Thrombolites and stromatolites: two distinct types of microbial structures. *Palaaios*, **1**: 492–503.
- KENNARD, J. M., CHOW, N., and JAMES, N. P. 1989. Thrombolite-stromatolite bioherm, Middle Cambrian, Port au Port Peninsula, western Newfoundland. In *Reefs in Canada and adjacent areas. Edited by H. H. J. Geldsetzer, N. P. James, and G. E. Tebbutt*. Canadian Society of Petroleum Geologists, Memoir 13, pp. 151–155.
- KRUSE, P. D., and DEBRENNE, F. 1989. Review of archaeocyath microstructure. *Association of Australasian Palaeontologists, Memoir 8*, pp. 133–141.
- KRUSE, P. D., and WEST, P. W. 1980. Archaeocyatha of the Amadeus and Georgina Basins. *BMR Journal of Australian Geology and Geophysics*, **5**: 165–181.
- MONTY, C. L. V. 1976. The origin and development of cryptalgal fabrics. In *Stromatolites. Edited by M. R. Walter*. Elsevier, Amsterdam, pp. 193–249.
- NITECKI, M. H., and DEBRENNE, F. 1979. The nature of radiocyathids and their relationship to receptaculitids and archaeocyathids. *Géobios*, **12**: 5–27.
- OKULITCH, V. J. 1935. Cyathospongia—a new class of Porifera to include the Archaeocyathinae. *Transactions of the Royal Society of Canada, section 4*, **29**: 75–106, Pls. 1–2.
- . 1937. Some changes in nomenclature of Archaeocyathi (Cyathospongia). *Journal of Palaeontology*, **11**: 251–252.
- PALMER, A. R., and ROZANOV, A. YU. 1976. Archaeocyatha from New Jersey: evidence for an intra-Cambrian unconformity in the north-central Appalachians. *Geology*, **4**: 773–774.
- READ, B. C. 1980. Lower Cambrian archaeocyathid buildups, Pelly Mountains, Yukon. *Geological Survey of Canada, Paper 78–18*.
- REES, M. N., PRATT, B. R., and ROWELL, A. J. 1989. Early Cambrian reefs, reef complexes, and associated lithofacies of the Shackleton Limestone, Transantarctic Mountains. *Sedimentology*, **36**: 341–361.
- ROWLAND, S. M. 1984. Were there framework reefs in the Cambrian? *Geology*, **12**: 181–183.
- ROWLAND, S. M., and GANGLOFF, R. A. 1988. Structure and paleoecology of Lower Cambrian reefs. *Palaaios*, **3**: 111–135.
- TAYLOR, T. G. 1910. The Archaeocyathinae from the Cambrian of South Australia, with an account of the morphology and affinities of the whole class. *Memoirs of the Royal Society of South Australia*, **2**: 55–188.
- VOLOGDIN, A. G. 1932. Arkheotsiaty Sibiri, vyp. 2. Fauna kembriyskikh izvestnyakov Altaya [in Russian]. (Archaeocyatha of Siberia, vol. 2. Fauna of the Cambrian limestones of the Altay). Gosudarstvennoe Nauchno-tekhnicheskoe Geologo-razvedochnoe Izdatel'stvo, Moscow, Leningrad.
- . 1936. Istoriya issledovaniya, morfologiya i stratigraficheskoe znachenie arkheotsiat [in Russian]. (History of investigation, mor-

- phology and stratigraphic significance of archaeocyaths.) *Problemy Sovetskoi Geologii*, **10**: 917–918.
- WILSON, J. L. 1975. Carbonate facies in geologic history. Springer-Verlag, Berlin.
- YOUNGS, B. C. 1977. The sedimentology of the Cambrian Wirrealpa and Aroona Creek Limestones. Geological Survey of South Australia, Bulletin 47.
- ZHURAVLEV, A. YU. 1986. Radiocyathids. *In* Problematic fossil taxa. Edited by A. Hoffman and M. H. Nitecki. Oxford University Press, New York, pp. 35–44.
- ZHURAVLEV, A. YU., and SAYUTINA, T. A. 1985. Radiotsiaty Mongolii. K revizii "klassa" Radiocyatha [in Russian]. (Radiocyaths of Mongolia. On the revision of the "class" Radiocyatha). *Trudy Instituta Geologii i Geofiziki, Sibirskoe Otdelenie*, **632**: 52–62, Pls. 22–24.
- ZHURAVLEVA, I. T. 1960. Arkheotsiaty Sibirskoy Platformy [in Russian]. (Archaeocyaths of the Siberian Platform). Akademiya Nauk SSSR, Moscow.
- ZHURAVLEVA, I. T., KONYUSHKOV, K. N., and ROZANOV, A. YU. 1964. Arkheotsiaty Sibiri. Dvustennye arkheotsiaty [in Russian]. (Archaeocyaths of Siberia. Two-walled archaeocyaths). Nauka, Moscow.
- ZHURAVLEVA, I. T., ZADOROZHNYAYA, N. M., OSADCHAYA, D. V., POKROVSKAYA, N. V., RODIONOVA, N. M., and FONIN, V. D. 1967. Fauna nizhnego kembriya Tuvy (opornyy razrez R. Shivelig-Khem) [in Russian]. (Lower Cambrian fauna of Tuva (R. Shivelig-Khem reference section)). Nauka, Moscow.