

EARLY CAMBRIAN INTERGROWTHS OF ARCHAEOCYATHIDS, *RENALCIS*, AND PSEUDOSTROMATOLITES FROM SOUTH AUSTRALIA

by M. D. BRASIER

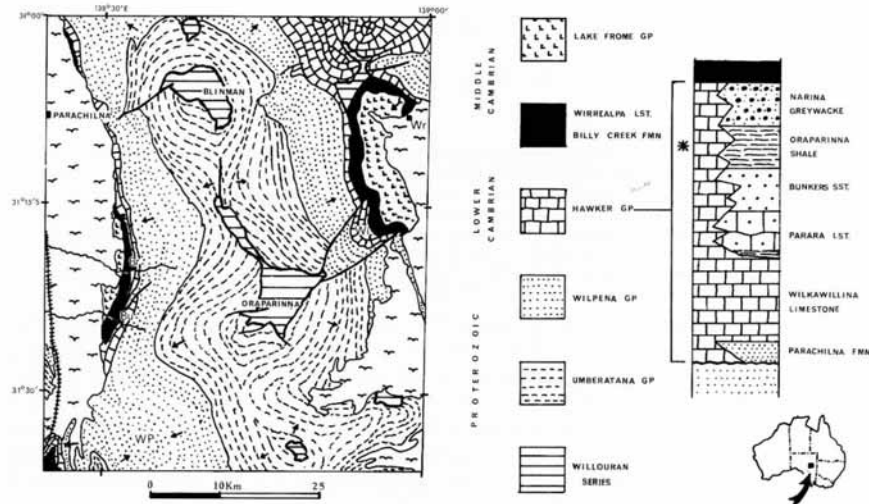
ABSTRACT. Lower Cambrian life and death assemblages of late Atdabanian-Botomian age are described from the Wilkawillina Limestone of South Australia. The biota, sedimentology, and diagenesis are analysed to reveal an ecological succession in which archaeocyathids grew one upon another, and were overgrown by the problematic organism *Renalcis*, with the cavities later filled by pseudostromatolites (coniatolites). A low-latitude, littoral habitat is inferred. Examination of the unusually well-preserved archaeocyathid intergrowths suggests that their individuality was strongly expressed, with an organization at least of sponge or coelenterate grade. Settlement and growth of archaeocyathid juveniles was apparently controlled by substrate type, space, and light. The life assemblage provides one of the oldest examples of competitive interreactions between animals.

THIS paper investigates some early Cambrian algal-archaeocyathid-*Renalcis* associations collected from the Wilkawillina Limestone of South Australia. During the early Cambrian these associations flourished widely and our present understanding of them owes much to the work of Russian geologists such as I. T. Zhuravleva and A. Yu. Rozanov (see Hill 1972). Nevertheless, for a proper understanding of both palaeoecology and biological affinities, more needs to be known about the growth relationships, microstructure, and diagenesis of the problematica involved and it is hoped that this study will stimulate discussion in these areas.

Archaeocyathids are generally associated with areas of carbonate sedimentation, whether as extensive blankets or as localized bioherms and biostromes within clastic strata. Although often quoted as the 'reef-builders' of the early Cambrian, they usually played a role subordinate to the lime-secreting and trapping algae with which they are commonly associated (Hill 1972). Few of these 'reefs' show any signs of wave-resistant structures or other attributes associated with that term and so the word 'bioherm' is preferred (Debrenne 1959). The Cambrian algae have been reviewed by Johnson (1966). The mound-building types are of uncertain affinities but are usually placed amongst either the Schizophyta or the Rhodophyta and include *Epiphyton* (possibly an arborescent red alga), *Girvanella* (possibly a tubular blue-green alga), and *Renalcis*. The algal affinities of *Renalcis* have been questioned by Riding and Brasier (1975) who suggest that it may have been an early form of calcareous foraminifer. Algal-archaeocyathid bioherms of the *Epiphyton-Renalcis* dominated type have been recorded from the early Cambrian of Siberia, southern Europe, Morocco, North America, Antarctica, and Australia (Debrenne 1959, 1964; Zhuravleva 1960, 1972, 1974; Hill 1972; Balsam 1973). The extensive archaeocyathid developments of South Australia have received little attention as yet but may also be largely algal (Professor D. Hill, written communication); they include *Epiphyton* and *Girvanella* (Walter 1967).

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In contrast, algal-archaeocyathid communities of stromatolitic type do not appear to have been so extensive. Debrenne (1964) has figured stromatolitic laminae enclosing possibly contemporaneous archaeocyathid cups from Morocco. More examples of 'stromatolite'-*Renalcis*-archaeocyathid intergrowths have been collected from the early Cambrian Wilkawillina Limestone of the Flinders Range, South Australia and are examined in this paper (text-fig. 1).



TEXT-FIG. 1. Geological map of the Parachilna to Wirrealpa area, Flinders Range, with detail of the Hawker Group succession. Br = Brachina Gorge; Bu = Bunyeroo Gorge; Wi = Wilkawillina Gorge; Wr = Wirrealpa; WP = Wilpena Pound. Based on Dalgarno and Johnson (1966).

Stratigraphy and palaeogeography

Much has yet to be learnt about the stratigraphic and palaeogeographic setting of the Cambrian in the Flinders Ranges. Goldring and Curnow (1967) and Wade (1970) have studied the conditions of deposition of the preceding Pound Quartzite which contains the soft-bodied Ediacara fauna. At that time the area formed part of a marine bay, with a north-south trending shoreline to the west, sheltered from the open sea to the east by shoals, possibly controlled by diapiric movements. The overlying sandstones and shales of the Uratanna and Parachilna Formations represent considerable transgressions over bioturbated, and in places much-eroded, surfaces. The trace fossils *Rusophycus* and *Curvolithus* are found in the Uratanna and *Diplocraterion*, *Plagiogmus*, and *Phycodes* in the Parachilna Formation. These may be taken to indicate a Cambrian age for the transgression (Glaessner 1969; Wade 1970; Webby 1973) and represent shallow-water conditions within the *Cruziana* facies.

On the western side of the anticlines about the Oraparinna and Blinman diapirs, at Brachina and Bunyeroo Gorge, the Parachilna Formation is succeeded conformably

by the Wilkawillina Limestone, but on the eastern side it appears to rest directly on the Pound Quartzite (Walter 1967). There, the Wilkawillina Limestone comprises a biohermal bank rich in archaeocyathids, which passes up into the more argillaceous Parara Limestone with fewer archaeocyathids, the Bunkers Sandstone with none, the Oraparinna Shale with some, and the Narina Greywacke with none. This succession is absent in the Brachina-Parachilna area to the west, where a continuation of the Wilkawillina Limestone forms a lateral, biohermal equivalent (Dalgarno 1964; Walter 1967). This lower Cambrian Hawker Group was succeeded by the middle Cambrian sandstones and tuffaceous shales of the Billy Creek Formation and the nodular Wirrealpa Limestone, both lacking archaeocyathids.

The pseudostromatolitic-archaeocyathid limestones of Brachina Gorge described in this paper occur also at Bunyerroo Gorge, about 8 km to the south (Walter 1967, pl. 7, fig. 5a). Both probably formed in a relatively sheltered bay devoid of terrigenous influx and subject only to periodic episodes of current or wave action. The biohermal banks and shoals to the east may have resembled barrier reefs, behind which were deposited these lime muds and *Renalcis*-archaeocyathid biomicrites. Collections by Walter from near the top of the Wilkawillina Limestone at Bunyerroo Gorge included *Robustocyathus* sp., *Spirillicyathus pigmentum* Bedford and Bedford, *Coscincyathus* sp., *Coscinoptycta* sp., *Flindersicyathus* sp., *Protopharetra*, and a colonial nochorocyathid. These Walter considered to be of middle early Cambrian age, as were those from the Ajax Limestone to the north-west of the range (Debrenne 1969), both workers arriving at their conclusions by comparison with the well-known successions of Siberia. A variety of early Cambrian trilobites, brachiopods, molluscs, hyolithids, sponge spicules, and tubular organisms have also been recorded from the Wilkawillina Limestone (Daily 1956). This paper updates the faunal list, the following archaeocyathid genera being identified in collections from near the top of the Wilkawillina Limestone at Brachina Gorge (asterisks denote a new record for Australia): '*Aldanocyathus**, *Ajacyathellus**, *Coscinoptycta*, *Dentatocyathus**, *Dokidocyathus*, *Erugatocyathus*, *Flindersicyathus*, *Gordonicyathus*, *Graphoscyphia**, *Mennericyathus*, *Metaldetes*, *Polycoscinus*, *Pretioyathus**, *Protopharetra*, *Robertocyathus**, and *Tumulocoscinus**. Other organisms include brachiopods, spicular structures, *Chancelloria* rosettes, and *Renalcis* sp. This fauna indicates a late Atdabanian (Kameshki) to early Lenian (Botomian) age for the Wilkawillina Limestone, as already suggested by Rozanov and Debrenne (1974).

Material and methods

The assemblages described below were collected as loose blocks from Brachina Gorge by Dr. R. Goldring during a study of the late Pre-Cambrian of the region. It was not possible at that time to determine their field relationships or precise stratigraphic horizon, but as this paper concentrates on organism interrelationships these problems are diminished. Two assemblages can be recognized in the collections: a life assemblage, or taphocoenosis and a death assemblage, or thanatocoenosis. The former consists of organisms preserved *in situ* (in growth position) and is represented by rock specimens Wilk. 1/1-1/30 and Wilk. 4 and 5, weighing altogether about 3½ lb. The death assemblage comprises organisms which have suffered uprooting, transport, abrasion, and breakage, presumably the result of current or wave action. This is represented by rock specimens Wilk. 2/1-2/3, of similar weight to the former. The rock specimens are deposited in the Geology Department of Reading University, whilst the thin sections are in the author's collection. The relatively complex intergrowths in the rocks were revealed by serial sectioning both normal to and co-axial with the predominant direction of archaeocyathid growth. In the life assemblage these

were made at measured intervals of about 10 mm. The slabs were then polished, etched, and stained ready for taking acetate peels using the technique of Davies and Till (1968). Additional thin sections were prepared for electron probe analysis and photography. Although archaeocyathids are invariably associated with bioherms or biostromes, their original life orientations have only rarely been preserved. The *in situ* life assemblage is therefore of particular interest because of the light it throws on the palaeobiology of these problematic organisms and their associates. Special issues relating to these problems are discussed in a later section.

DEATH ASSEMBLAGE

Biota. The bulk of the rock consists of broken and more-or-less prostrate adult archaeocyathids and less-damaged juvenile cups within a fibrous calcite matrix, interspersed with 'stromatolitic' structures of similar fabric (Pl. 35, figs. 1-5 and Pl. 37, figs. 1-2). The archaeocyathids include species (many undescribed) of the following genera: *Erugatocyathus*, *Mennericyathus*, *Gordonicyathus*, *Dokidocyathus*, *Dentatocyathus*, *Robertocyathus*, *Pretiocyathus*, *Tumulocoscinus*, *Graphoscyphia*, and *Protopharetra*. Their skeletal elements are usually preserved as dense, almost porcellaneous, microgranular calcite, often differentiated into lighter and dark layers. Some of this layering results from archaeocyathid 'secondary thickening' (see Hill 1972). The death assemblage also includes *Chancelloria* rosettes (Pl. 37, fig. 2) possibly part of the epidermal skeleton of an echinoderm (Goriansky 1973), together with indeterminate brachiopods, spicular structures, and other bioclastic debris. *Renalcis* concentrations occur rarely as overgrowths on the skeletal fragments or scattered through the matrix. All these broken skeletal elements indicate strong currents or turbulence at the time of deposition.

The origin of the 'stromatolites' in this assemblage (and in the life assemblage where they are similar) is not entirely clear. Laminae of fibrous calcite occur throughout as a matrix and in some places appear to have originated through recrystallization of lime mud. However, extensive 'stromatolite' structures also occur, many having

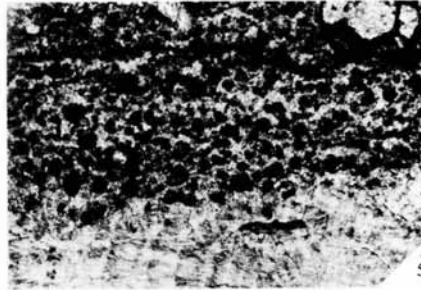
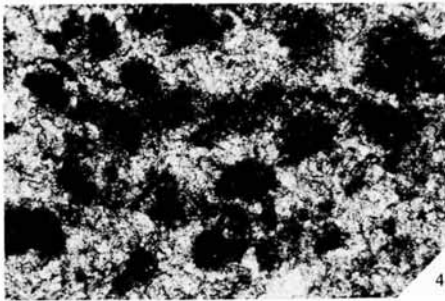
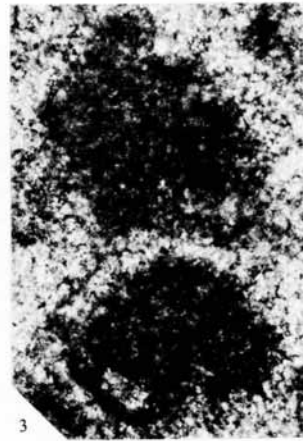
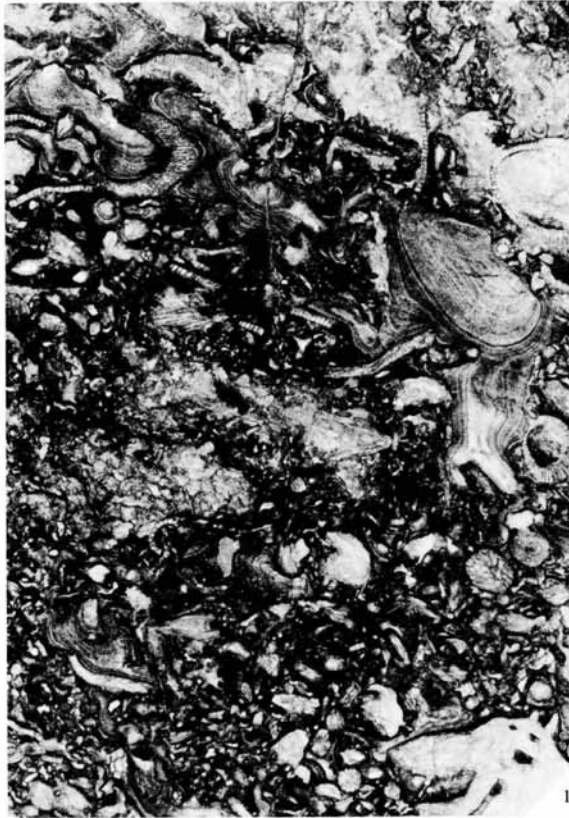


TEXT-FIG. 2. Mode of occurrence of the 'algal thalli' within the 'stromatolites'. A = micritic or equigranular calcite of outer layers; B = 'algal thallus'; C = dark lamella; D = drusy cavity, left by decomposed thalli?; E = radiaxial fibrous calcite lamella of inner laminae ($\times 10$).

the appearance of inverted *Conophyton* or oncolites. Despite the considerable diagenesis, possible organic structures can be discerned in the outermost laminae, represented by rows of discrete ovoid blebs (algal thalli?) composed of dark-grey or brown microgranular calcite. These either 'float' in a clearer calcite mosaic or are joined basally by a thin, dark lamella of similar microgranular composition (text-fig. 2 and Pl. 35, fig. 4). In several cases these 'thalli' are replaced by an equigranular brown dolomite

EXPLANATION OF PLATE 35

Figs. 1-5. Death assemblage. 1, weathered section through rock showing many broken cups and 'stromatolitic' intergrowths, $\times 1$. 2, side view of mammillated outer surface of a 'stromatolite'-coniatolite, $\times 1.6$. 3, detail of 'algal thalli' growing towards right, $\times 128$. 4, cluster of 'thalli', growing to bottom left, $\times 50.4$. 5, numerous 'thalli' underlain by fibrous calcite laminae, $\times 8$.



BRASIER, early Cambrian communities (archaeocyathids)

mosaic of larger crystal size than the surrounding matrix, or by voids, suggestive of organic decomposition.

The size of these 'thalli' ranges from less than 0.075×0.100 mm to at least 0.300×0.500 mm. The dark lamellae can be seen in places to pass from the outer layer into the core of the 'stromatolite', where they attenuate. Each dark lamella is usually less than one-quarter of the total laminar thickness (which varies from less than 0.2–1.0 mm or more) and is underlain by a lighter, thicker lamella of radiaxial fibrous calcite (Pl. 37, fig. 8). Towards the 'stromatolite' core these fibrous calcite crystals become larger and may cross the dark lamellar boundaries. X-ray analyses indicate these crystals to be largely low magnesium calcite, with $MgCO_3$ probably less than 1 mol %, together with subordinate quantities of dolomite. Stained peels and electron-probe analysis of similar laminae in the 'life assemblage' indicate that the dolomite was concentrated as minute crystals in the dark lamellae, as noted in many stromatolites. Discussion of the significance and interpretation of these 'stromatolites' follows in a later section.

Sedimentology and diagenesis. Within certain layers in the rock are patches of grey clotted micrite, commonly infilling brachiopods or other shells. These patches have indistinct margins, for they grade from micrite to silt-sized equigranular calcite to fibrous calcite. The stromatolitic laminae are also of fibrous calcite (see later), but differ in the possession of dark lamellae and distinct lamination. The micritic patches may represent less pure detritus, for small opaque minerals are present. Recrystallization may therefore have been inhibited by this lesser purity.

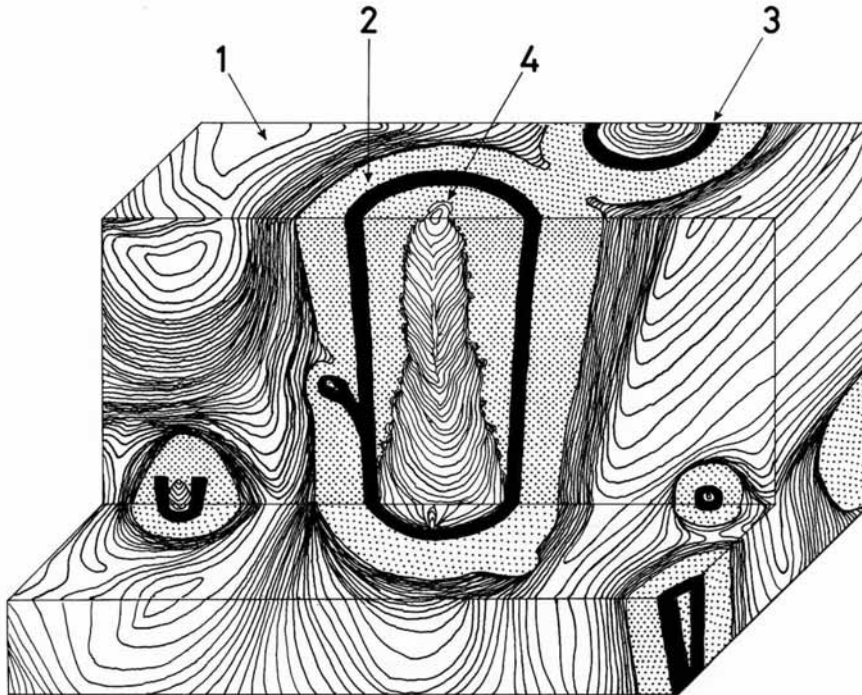
A mosaic of iron-stained quartz crystals occurs locally as a 'skin' at the contact between archaeocyathid outer walls and the peripheral layers of adjacent 'stromatolites'. The loculi are filled with a radiaxial fibrous calcite, which is probably a replacement of an acicular carbonate cavity infilling (Kendall and Tucker 1973).

LIFE ASSEMBLAGE

The constituents of this interesting assemblage are essentially the same as in the death assemblage. There are four major components (text-fig. 3) to be discussed: (a) archaeocyathid cups, (b) a 'perithecal' zone around the cups, containing *Renalcis*, (c) 'stromatolites' external to the archaeocyathid cups, and (d) 'stromatolites' within the central cavity of the archaeocyathid cups.

(a) *Archaeocyathid cups.* Most of the cups are Regulares, especially of the genera *Mennericyathus*, *Erugatocyathus*, *Robertocyathus*, *Coscinoptya*, *Ajacyathellus*, *?Polycoscinus*, and *'Aldanocyathus'*. The Irregulares are volumetrically less abundant but include *Protopharetra*, *?Flindersicyathus*, and *?Metaldetes*, the first being by far the commonest. Both classes of archaeocyathid have been preserved as dense, often layered microgranular calcite cups, with white radiaxial fibrous calcite or yellow ferruginous micritic calcite filling the intervallar spaces. Stylolites often occur along the walls, the skeletal elements having dissolved away locally.

It is significant that nearly all the Regulares share the same general growth direction



TEXT-FIG. 3. Cut-away diagram of the observed relationships of components in the life assemblage; 1 = 'stromatolites' external to archaeocyathid cups; 2 = perithecal zone; 3 = archaeocyathid cup; 4 = 'stromatolite' within archaeocyathid central cavity ($\times 2.5$).

and several reach heights of over 90 mm (see text-fig. 4). These cups often bear complex and delicate exothecal outgrowths (tersiae), invariably associated with the attachment of a regular juvenile or with the close growth of two or more 'adult' cups. None of the archaeocyathids examined throughout the 200 mm height of the rock specimen were attached initially to anything other than archaeocyathid cups. These factors rule out the possibility that the assemblage is allochthonous.

The small adherent *Protopharetra* are more common in the upper part of the specimen where they attach directly to regular cups without the prior development of tersiae or exothecal lamellae. All of these lack a central cavity and are largely non-porous, in contrast to the *Regulares*.

(b) 'Perithecal' zone. A 'perithecal' zone of micritic calcite occurs as a band of almost uniform width around each archaeocyathid, separating it from the various intergrowths of 'stromatolites' (text-fig. 5). This zone appears near-black in hand specimens (Pl. 36). A similar zone is seen marginal to the upper part of the central cavity,

again separating the archaeocyathid from the inner 'stromatolites'. In this case, however, the dark perithecal zone is not of uniform width but decreases down the central cavity until the 'stromatolite' comes directly into contact with the inner wall of the archaeocyathid cup. Thin sections and stained acetate peels reveal that the perithecal zone is packed with the small irregular chambers of *Renalcis*, probably *R. jacuticus* Korde, which is generally found rather earlier in Siberia (Zhuravleva, pers. comm. 1975). This organism appears to have attached to the outer and inner walls of the archaeocyathids and to have grown out from them at right angles, or nearly so. *Renalcis* appears to have grown freely, perhaps by settling on the mud of the perithecal zone, or growing attached to other individuals or pellets, as observed by Riding and Toomey (1972). Unfortunately, recrystallization of the rock is such that it is not possible to recognize any true pellets within the matrix. No *Epiphyton* has been recognized in these sections.

The areas between the chambers of *Renalcis* may consist of either clotted micrite, equigranular calcite mosaic, or radial fibrous calcite mosaic, the latter often adjacent to the fibrous calcite of the 'stromatolites'. Again, it is possible that these mosaics are diagenetic replacements of lime mud. Few biogenic components other than *Renalcis* occur in the perithecal zone, except near the top of the rock specimen, where the matrix is relatively shelly, with tubular organisms, sponge spicules, trilobite fragments, and inarticulate brachiopod valves. This more shelly material was presumably washed in from above at a period post-dating much of the *Renalcis*, for the material occurs as an infilling between clumps of the latter but never within the central cavity of the archaeocyathids.

(c) 'Stromatolites' external to the archaeocyathids. These 'stromatolite'-like structures comprise 50% or more by volume of the rock. In this assemblage the growth form consists of successive, usually vertical and convex-downwards, laminae reminiscent of stalactites (text-fig. 3). The laminae are interconnected throughout the rock in such a way that it might be thought to comprise a large, downward-growing overhang of a stromatolite, the structure being at least 185 mm long and 120 mm wide at the broadest point. Asymmetry of the growth form is marked, with laminae thinning and dying out in the vicinity of the perithecal zone. Thin sections reveal rows of ovoid 'thalli' and dark lamellae in the outer laminae, much as in the death assemblage. Each 'thallus' is separated from its neighbour by small hemispherical stacks of relatively thin laminae ('microstromatolites') which give the outer surface of the 'stromatolite' a mammillate appearance (Pl. 35, fig. 2). As in the death

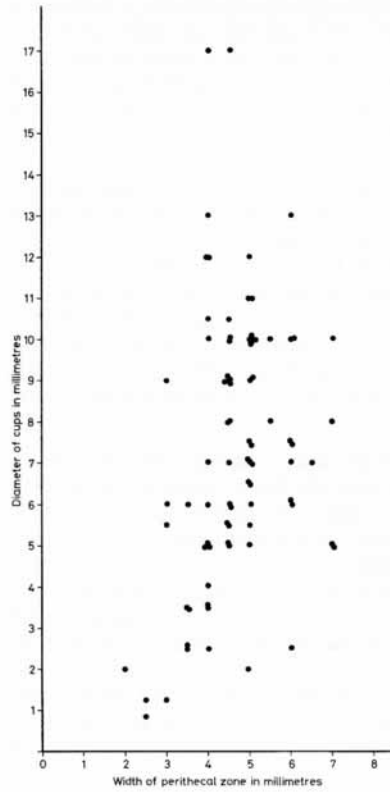
TEXT-FIG. 4. Archaeocyathid relationships in the life assemblage as revealed by serial sections. Horizontal distances between cups have been changed for graphic representation: O, X, and Q should be much closer, as should W and R.

Horizontal hatching = exothecal outgrowths; white 'cones' = Regulares; black shapes = Irregulares (mostly *Protopharetra*); question marks and dashed lines refer to uncertain origins or terminations.

Aldanocyathus sp. = cups C and R; *Ajacyathellus* sp. = cups D, H, U, X; *Memericcyathus* sp. = cups P, S, U, W, Z; *Robertocyathus* = cups G, O, Q; *Coscinoptycta* = cup N; *Polycoscinus* = cup T; *Erugato-*
cyathus = cup E; indet. coscinoocyathids = cups B, I, L; others uncertain or not represented. The cup letter symbols correspond with those used in the text and other figures.

C

assemblage the radiaxial fibrous calcite structure of the laminae becomes coarser and the crystals may cross the lamina boundaries. X-ray and electron-probe analyses revealed that the mineralogy is low magnesium calcite except in the region of the dark lamellae where higher MgO concentrations probably relate to small dolomite crystals. It is important to note that in no portion of the rock are the archaeocyathids and these external travertinous 'stromatolites' in contact. Instead, they appear to



TEXT-FIG. 5. Graph illustrating the relatively constant thickness of the perithecal zone.

the growth core is usually central. The interpretation of these curious growths is discussed later.

observe a mutual distance of separation which is remarkably constant (text-figs. 5 and 6A). This unusual relationship has not been described previously and its significance will be discussed in some detail later.

(d) 'Stromatolites' within the archaeocyathid central cavity. Almost without exception and regardless of size, the regular cups contain a 'stromatolite' growth within the central cavity, indistinguishable in microstructure from those surrounding the archaeocyathids in the death assemblages. Significantly, a few of them show signs of having originally been formed of clotted micrite, the radiaxial fibrous calcite forming diagenetically. There are two observable origins for these internal 'stromatolites'. Firstly, they can represent downgrowth into the central cavity from the surrounding, often overhanging, external 'stromatolite'. Alternatively, they may comprise completely independent growths which were apparently hanging in mid-water without an obvious origin (text-fig. 3 lower left). In all cases, however, the lower part of the central cavity is totally filled by the downward-curving laminae, frequently with the growth core to one side. These inner 'stromatolites' are the only instances in this assemblage where they and the archaeocyathid cups are demonstrably in contact. However, towards the upper part of the cups the algal laminae observe the mutual distance exhibited by the external 'stromatolites', and

SPECIAL ISSUES

The intergrowths described briefly in the foregoing assemblages prompt a number of questions concerning the biological affinities and palaeoecological relationships

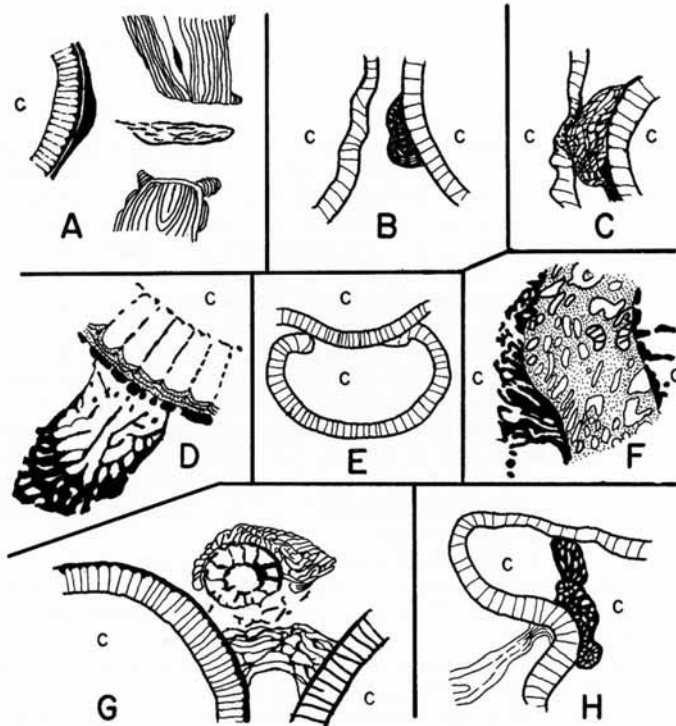
of the different organisms at such an early period in the fossil record. Points at issue dealt with below include archaeocyathid relationships, the nature of the 'stromatolites', and *Renalcis* and the nature of the perithecal zone.

Archaeocyathid relationships

Growth relationships. As mentioned previously, all the archaeocyathids in the life assemblage appear to be in their positions of growth. The relative sizes of the individuals and their relationships are plotted in text-fig. 4. This illustrates that all growth stages are present and intimately interconnected, some cups reaching heights of almost 150 mm. Several trends can be elucidated from these data. Firstly at the top of the sequence (150 mm+) where the 'stromatolitic' growth is virtually lacking, the cups appear to have grown more haphazardly, suggesting that 'stromatolites' were exercising some control over their growth further down. Conversely, in the lower part, several 'adult' cups (E/B and U/Z) have been squashed together because of overcrowding or accidental dislodgement. This resulted in growth distortion along with the production of tersiae (calcified exothecal tissue?). In cup B, for example, the skeletal elements appear to have been disrupted adjacent to the tersiae produced from cup E (text-fig. 6B, C, and F). Likewise in cup Z, the intervallum is missing adjacent to cup U (text-fig. 6E). Both U and Z and E and B are different genera so that no sexual interaction can be inferred. In cup O localized distortion of septa and walls is seen in association with tersiae.

Another case of distortion occurs in cup W. This was apparently due to the settlement of juveniles on both outer and inner walls (text-fig. 6H). The distortion is again associated with the formation of tersiae but it is not clear whether these were produced by the host (cup W) or the juveniles. However, these and several other cases are indicative of the sensitivity of the growth form of archaeocyathids. It would seem to indicate the existence of initially non-calcified soft parts in the region of growth, presumably at the top of the cup. The remarkable tersiae surrounding cup O appear to have been produced by that organism and may have served some function of support. Again they are most pronounced where other cups are close but not usually in contact. Here also, the interreaction took place between cups of different genera. Some kind of sensory mechanism might therefore be indicated.

The attachment of juveniles by tersiae or exothecal lamellae was predominantly to the outer wall of larger cups. There is no significant correlation between the taxa of juvenile and host. Many of these juveniles were apparently prevented from growing to a large size because of confined conditions. For example, those which settled on cups which were growing close to the external 'stromatolites' rarely reached adult size (e.g. cups A, D, J, O, and B). Others, especially those which grew laterally or low down on the host cup were impeded by the outer wall of adjacent cups (e.g. λ). Conversely, juveniles which settled either near the top of an old (dead?) cup (e.g. X, H, and O) or on the inner wall or a relatively wide cup (e.g. L, V) were able to thrive because there was plenty of room for growth. It is interesting to note here that settlement on the inner wall was rare, unless the cup was wide. Those on the inner wall of G appear to lack tersiae and arise directly from the wall but close inspection shows that pressure solution has cut out the contact between them. Even so none of these reached lengths of more than a few millimetres.



TEXT-FIG. 6. Camera-lucida drawings of some growth relationships from the life assemblage.

A, mutual distance observed between 'stromatolic laminae' (top and bottom) and cup O with tersia, $\times 4$; B, tersiae from the cup on the right (cup E), with mirrored distortion in the cup on the left (cup B), $\times 3$; C, a later stage of the above, with disruption of septa and walls in cup B, $\times 3$; D, tersiae and secondary thickening in *Robertocyathus* sp. (cup O), $\times 12$; E, breakdown of skeleton of cup Z adjacent to wall of cup U, $\times 2$; F, detail of C, showing distortion of the skeletal elements (black) adjacent to tersiae (stippled), $\times 11$; G, tersiae produced by a juvenile (cup X) attaching to two larger cups (O and G), $\times 4$; H, distortion of walls of larger cup (W) in region of juvenile attachment to outer wall (bottom left). Tersiae in black. c = side of central cavity.

The scarcity of settlements on the inner walls may be explained in a number of ways. The strong upward water currents presumed to have been set up in the central cavity (Balsam and Vogel 1973) might have prevented settlement there, even after the death of the host, if the currents were passive as these authors have suggested. However, as already noted, *Renalcis* settled at some stage in the central cavity. If the inner 'stromatolites' developed during the life of the archaeocyathid then the central cavity would have been unattractive or impossible for post-mortem settlement of juveniles. More likely is the possibility that the development of juveniles

was relatively substrate-specific and required well-lit, well-circulated conditions which the narrow central cavities would not have provided. Similar phenomena are observed with respect to the small adherent irregular archaeocyathids, mostly species of *Protopharetra*. There is a tendency for these to be larger and more abundant away from the lower part of a cup, again perhaps due to the less confined conditions. Although they may attach to *tersiae* they do not appear to form any of their own, growing directly on to the outer or inner wall of the host cup. Their generally upward growth expansion does not seem consistent with a parasitic mode of life and is perhaps more reminiscent of the habit adopted by recent coral-encrusting foraminifera such as *Homotrema*, i.e. suspension or deposit feeding. It seems likely from these observations that the settlement of both regular and irregular archaeocyathids upon other cups did not take place until those cups were dead, with the possible exception of γ upon W, for they would otherwise have been more uniformly colonized. This may imply either that these colonizations took place in cycles, or perhaps more likely, that the living archaeocyathids had some means of preventing the settlement of epibionts. The existence of a thin 'ectoplasmic' layer (like that of the perforate foraminifera), which was ciliate, flagellate, or pseudopodial, or the cleaning activities of mobile symbionts around the outer wall (as with the imperforate foraminifera, see Loeblich and Tappan 1964, p. C70) might be inferred.

The terminations of most of the larger cups have been simplified in text-fig. 4. In many cases the top of the cup is not normal to the growth axis (as illustrated) but at an angle of up to 45 degrees. The reason for this appears to be inhibition of growth due to close proximity of 'stromatolites' or other archaeocyathids. The skeletal elements of the upper parts of the cup also exhibit greater diagenesis, with much solution of calcite. Stained peels reveal a change there from normal to ferruginous calcite. Why these effects should have been localized to the top of the cup is not clear. It may be that downward percolations after burial preferentially affected the relatively open upper regions of the intervallum, there being no closure observed in these cups.

Biological implications of growth relationships. The affinities of the archaeocyathids may eventually be evinced by studies of their palaeobiology. Zhuravleva, in her definitive study of the group (1960), regarded them as multicellular organisms consisting of uniform, largely undifferentiated cells which filled the intervallar loculi. Feeding currents were considered to pass through the pores of the outer wall to those of the inner wall and thence up the central cavity (1960), or down the central cavity and out through the outer wall and terminal region of the intervallum (1974). She concludes that archaeocyathids possess a degree of differentiation higher than that of the Protozoa but lower than that of the Porifera, inferring that Archaeocyatha were representatives of the first Metazoa and ancestral to all others (1970). A new kingdom, the Archaeata, has even been suggested for archaeocyathids, aphrosalpingoids, soanitids, and receptaculitids (Zhuravleva 1974).

There are, nevertheless, grounds for believing that the archaeocyathids were at least of sponge grade and possibly higher. Their separation from the calcisponges has recently been contested by Ziegler and Rietschel (1970) on the grounds that they share a similar skeletal morphology, a criterion which has always been central to the debate. They do not mention, however, that the skeletal elements of many

archaeocyathids have such a strong symmetry that measurements like intervallum or interseptal width, pore size, pore spacing, and the number of septa relative to cup size are used as viable specific and generic characters. This regular symmetry infers regular and well-coordinated mitoses of the calcifying cells, a degree of somatic integration at least equivalent to, if not greater than, that found in the Porifera.

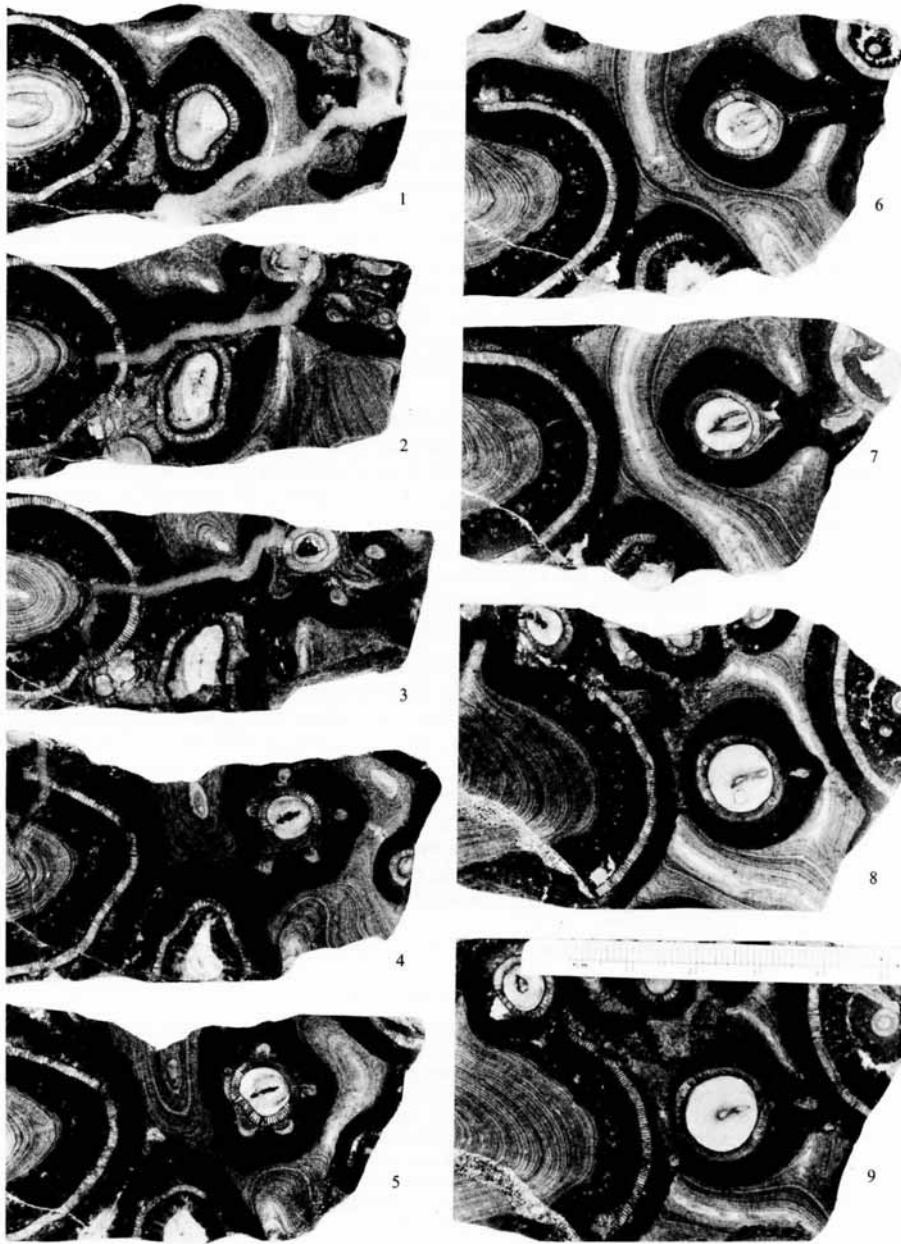
Tissue restoration. The biological affinities of any group may be evinced by their observable faculties of tissue restoration subsequent to injury and by their tissue compatibility with organisms of the same or different species. In the sponges, for instance, Korotkova (1970) has shown that the more highly integrated unioscular sponges (which have relatively distinct body symmetry) restore their injuries by regeneration proper, so that the lost parts are completely and harmoniously replaced. The less well-integrated multioscular sponges, however (which have an irregular body outline), tend to develop whole new organisms at the injury site, the former tissues being completely reorganized. In these there is a resultant change in growth polarity. It is important to note that observations on the restoration of damage in archaeocyathid cups (Zhuravleva 1960) resemble those of the more highly organized unioscular sponges, so that the group cannot fairly be regarded as having been more lowly than the Porifera.

The ability of living sponges to redevelop from aggregates of cells or fragments of the body is well known and has often been cited as evidence that sponges are colonies rather than individuals. Despite the many observations on archaeocyathids, though, there is little to suggest that they were capable of these faculties of regeneration. One might expect to find, for instance, new cups arising from broken fragments if they were of such lowly organization. The evidence from the assemblages studied here suggests rather that archaeocyathid tissues were not very plastic. Overcrowding with other cups resulted not so much in dramatic changes of symmetry, or the budding of individuals, as in the cessation of growth in the trauma region, so far as can be ascertained.

Tissue compatibility. The interreactions observed between archaeocyathids are also relevant to an understanding of their biological status. It is now known that immunity or compatibility reactions between cells of different individuals become more sophisticated as one ascends the animal kingdom. In sponges, mixtures of cells from two different species will aggregate to form mixed clumps which only separate out with time (Humphreys 1970). There are no reports of cell damage or killing of incompatible cells in sponge interreactions (Hildemann 1974), attesting to the loose organization of the Porifera. Nevertheless, fusion between incompatible sponge colonies does not take place (Ivker 1972). In the coelenterates, incompatibility between allogeneic individuals is more the rule, for example contact between incompatible colonies of the same or different species of *Acropora* (staghorn coral) results in a zone of destruction of the soft tissues (Hildemann 1974), and allogeneic colonies

EXPLANATION OF PLATE 36

Figs. 1-9. Horizontal serial sections through a portion of the life assemblage showing the archaeocyathids, perithecal zone (dark), and 'stromatolites' (laminated or white infillings of cups), $\times 1$.



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of the hydroid *Hydractinia echinata* fail to fuse when grown in contact, with hyperplastic growth rather than tissue destruction taking place at the contact zone (Ivker 1972). In this species a hierarchy of incompatibility exists between different colonies. The stronger strains produce dense fringes of intertwined stolons by hyperplastic growth which serve to smother some of the weaker strains.

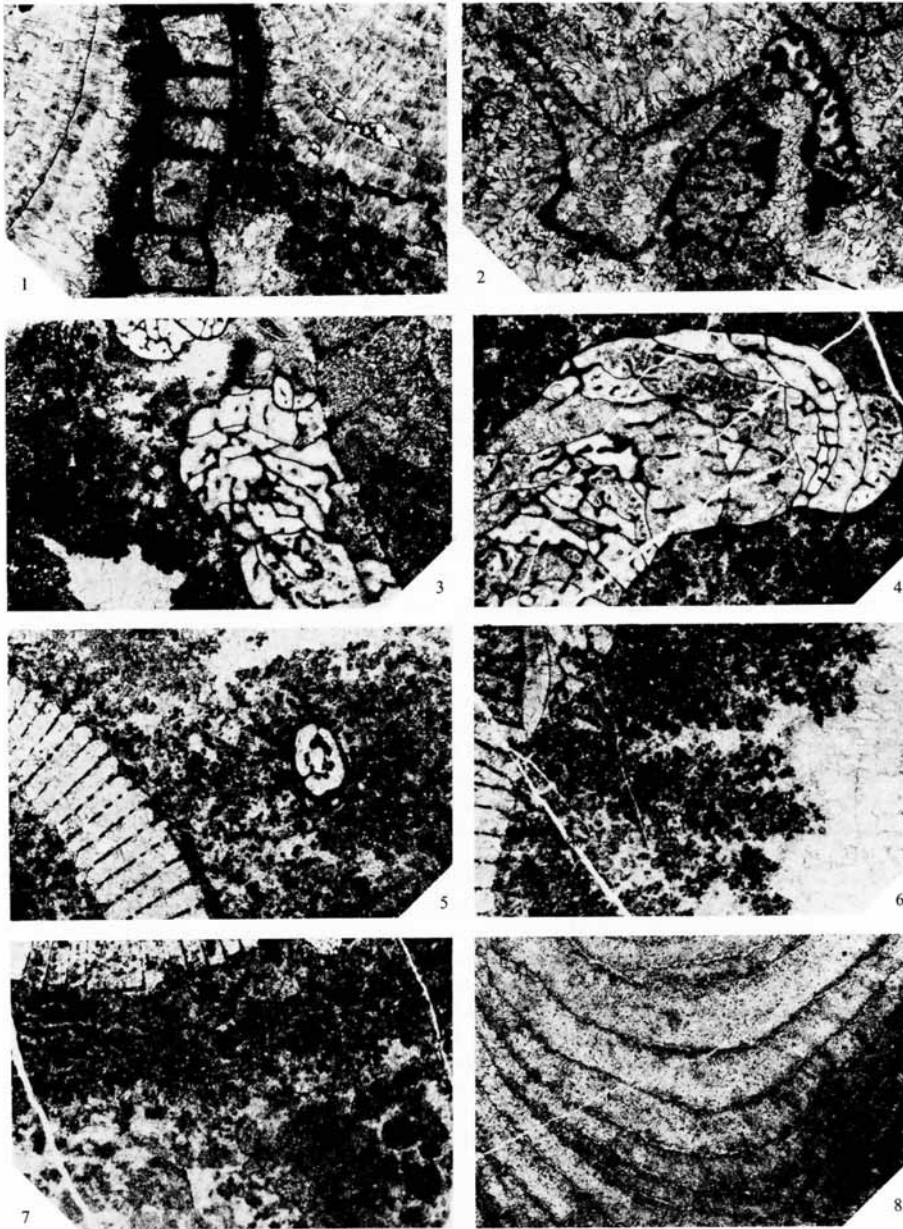
The observed archaeocyathid interreactions are similar to the above. The exothecal outgrowths produced by proximity or contact of two individuals of the same or different species may be analogous to the hyperplastic growth of hydroids. That is, it represented a proliferative response of ectodermal cells to contact with foreign-cell surfaces. In some instances (e.g. text-fig. 6c and f) the skeletal elements of the recipient were distorted by tersiae from a neighbouring cup. The fact that in nearly every case only one individual seems to have produced tersiae in an encounter is in accord with the observations on hydroids, and likewise indicates a hierarchy of incompatibility.

There is, furthermore, no evidence of any harmonious fusion of elements between apparently compatible archaeocyathids such as one might expect from primordial metazoans. The recorded lack of tersiae in Irregulares and certain Regulares could be considered the result of a lesser porosity of the outer wall, providing protection from external interference. The phenomenon of secondary thickening sometimes observed on the inner surfaces of the outer wall (see text-fig. 6b) is frequently associated with exothecal outgrowths and may likewise have been a defensive mechanism. One concludes that the individuality of these archaeocyathids was strongly expressed. If it was general then it is suggestive of an organization higher than sponges.

Feeding. Although it has long been recognized that archaeocyathids were filter feeders, it has recently been suggested by Balsam and Vogel (1973) that the filter-feeding currents were not actively pumped, but rather, set in motion passively by the conical perforate structure of the cup. But it is unlikely that those which lacked a central cavity operated in this manner; furthermore, in those with feebly porous to non-porous walls, the low ratio of pore to wall-surface area would have caused the establishment of vertically successive vortices within the central cavity in the absence of a pumping mechanism. Such vortices would have limited the exchange of nutrients on which the organism would have passively depended. In addition, it is not clear why Balsam and Vogel consider that early Metazoa had lost the ability

EXPLANATION OF PLATE 37

Figs. 1-2. Death assemblage. 1, 'stromatolitic' laminae and 'algal thalli' abutting against an archaeocyathid (centre), $\times 8$. 2, *Chancelloria* rosette, with adherent *Protopharetra* in recrystallized micrite, $\times 8$.
 Figs. 3-8. Life assemblage. 3, *Protopharetra* adhering to regular archaeocyathid wall, overgrown by *Renalcis*. Horizontal section, $\times 8$. 4, *Protopharetra* with fibrous and equigranular cavity-fill cement, overgrown by *Renalcis*. Vertical section, $\times 8$. 5, regular archaeocyathids overgrown by *Renalcis*. Horizontal section, $\times 8$. 6, inner wall of cup O with adherent *Renalcis* and *Protopharetra*. Laminae of inner 'stromatolite' (coniatolite) visible in central cavity to the right, $\times 8$. 7, outer wall of cup O (top) encrusted by *Renalcis*. ? 'algal thalli' (bottom) surrounded by rims of fibrous calcite, on the margins of a 'stromatolite'. Horizontal section, $\times 8$. 8, 'stromatolitic' laminae of coniatolite with dark dolomitic and paler fibrous calcite lamellae. Horizontal peel, $\times 20$.



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to move water actively, arising as they probably did from ciliate or flagellate ancestors, especially when such a faculty would have had strong selective advantages.

Zhuravleva (1974) justifiably pointed out that the diversity of skeletal structure found in archaeocyathid genera does not permit a single, cogent explanation of current flow. However, she speculated that flowage in cup-like forms was active, coming in through the central cavity and out via the outer wall or intervallar terminations or vice versa. This pattern would contradict Balsam and Vogel's flume experiments and it is difficult to envisage active currents developing in opposition to the natural, passive tendencies. The suggestion that these animals fed on bacteria and dissolved organic matter (Balsam 1973) is reasonable. However, the feeding mode of the non-porous *Protopharetra* must have been different. Apart from their degenerate appearance there is nothing else to suggest that they were parasitic on the Regulares. Whether they were sessile microcarnivores, bacteriophages, or general suspension feeders is as yet uncertain. Debrenne (1975) suggests that placement of archaeocyathids in a distinct Kingdom may be premature. More work is required on microstructure, on exothecal outgrowth, and on analogies with other organisms before any statement about affinities can be upheld.

THE 'STROMATOLITES'

The 'stromatolitic' structures described from both assemblages are unusual both in their mode of growth and preservation. Their interpretation affects interpretation and inferences about the other organisms and hence it is necessary to examine the origin of these structures. Four origins are plausible: (i) stromatolite, (ii) sediment recrystallization, (iii) rim-cement cavity fill, and (iv) tufa cavity fill ('coniatolite').

(i) *Stromatolitic origin.* The outer layers of the 'stromatolites' frequently bear ovoid thallus-like structures with 'microstromatolitic' laminae between them (text-fig. 2) giving the outer surface a mammillate appearance (Pl. 35, fig. 2). These 'thalli' resemble recent clumps of Chroococcales cells which are known to form non-laminated clotted fabrics on the lateral (often vertical) selvages of stromatolites (Gebelein 1974). The occurrence of 'thalli' in clotted, unlaminated patches in both assemblages could confirm this analogy. However, the laminae are defined by thin dark lamellae and these would more resemble those produced by recent thin sheathed Oscillatoria, which can construct vertical and overhanging structures in association with Chroococcales (ibid.). A fibrous calcite, travertine-like appearance may result from recrystallization of trapped or precipitated CaCO_3 material, perhaps the result of the activities of denitrifying bacteria. The latter often concentrate below the surface of algal mats, leading to the crystallization of fibrous high magnesium calcite or aragonite (Milliman 1974, pp. 49-50 and 188) which may in turn convert to radial fibrous low magnesium calcite (Kendall and Tucker 1973). Such sub-surface bacterial diagenesis would, for instance, account for the progressive loss of the 'organic' structures towards the centres of the 'stromatolites'. Similar fabric is known in the Cambrian stromatolite *Actinophycus* Korde from Siberia. However, the 'thalli' more closely resemble those of the stromatolitic alga *Stereophycus* Korde (Zhuravleva, pers. comm. 1975). Despite these similarities there are a number of important objections to the stromatolitic hypothesis. The downward and outward

growth of nearly all laminae has been mentioned, as has the observed connection between certain internal and external 'stromatolites'. Even accepting this, it is difficult to envisage how stromatolitic algae could grow downwards into the central cavity, bounded on all sides by archaeocyathid walls or *Renalcis* encrustations. Some of these internal structures formed after the central cavity was totally 'roofed over' by *Renalcis*. Another objection is that the gross growth structures are totally unlike those of any described stromatolites, with many thin 'tubes', 'limbs', and isolated 'eyes' developed by largely encapsulating laminae. Such structures could hardly have been self-supporting in space. Furthermore, there are no indications of the desiccation structures which characterize many true stromatolites.

(ii) *Sediment recrystallization origin*. Cullis (1904) and Orme and Brown (1963) have described the development of acicular carbonate from lime mud. Certainly, transitions from lime mud, through silt-sized equant grains to elongate calcite fibres have been observed in the Wilkawillina Limestone. However, the large multilaminar structures formed in these 'stromatolites' are far removed from the small rims or irregular patches noted elsewhere and by the above authors. Successive generations of fibrous calcite with straight crystal boundaries, and of more or less uniform size are more typical of cavity-fill cements (Wolf 1965). It is therefore unlikely that the complex structures arose from simple recrystallization of a micrite matrix.

(iii) *Rim cement-cavity fill origin*. Such cements form around the rims of cavities (e.g. skeletal structures, sheet cracks, etc.) as early diagenetic inward-growing fibrous sparite layers and are typical of reef-associated sediments (Wolf 1965). They are usually associated with drusy or granular calcite infilling of the cavity, internal sediment layers, and other geopetal structures such as stromatactis. None of these is seen in the 'stromatolites'. A further objection to this hypothesis is the over-all complexity of the outward-growing mammillate structures. These are much more consistent with the following origin.

(iv) *Tufa ('Coniatolite')-cavity fill origin*. In all respects other than in the presence of organic (?) thalli, the 'stromatolites' resemble tufa (e.g. stalactites), especially with regard to the distal drip-tips seen in those forms within archaeocyathid central cavities (text-fig. 3). Aragonitic travertines, known as 'coniatolites', are found forming today in the intertidal and supratidal regions of the Persian Gulf (Purser and Loreau 1973). These are usually found on beach rock or other hard surfaces, and may develop stalactitic form at overhangs or in cavities. Whilst coniatolites may morphologically resemble stromatolites, they differ from them in their dripstone micro-morphology (superimposed laminae of honey-coloured fibrous calcite), their downward growth around the edges, their lack of desiccation features, or bird's-eye structures and scarcity or lack of detrital sediment. All these features correspond with the 'stromatolites' discussed above.

Discussion. The structures are interpreted as coniatolites formed by downward dripping of marine brines into cavities, during a period of subaerial exposure (tidal?), as in the recent Persian Gulf and the Bathonian limestones of Bourgogne. The *Renalcis* encrustations helped to bind the archaeocyathid cups together, leaving cavities between or within. In the death assemblages, cavities were left by the sudden

deposition of large cups and coarse biogenic detritus and these were infilled by the tufas. Early diagenetic alteration of the aragonite to calcite, without evidence of leaching, may indicate an arid environment.

If one accepts the marine tufa (coniatolite) origin, then the algal 'thalli' and lamellae must be explained. There are several possibilities. Firstly, the most distinctive 'thalli' are seen only in the outer laminae and in few sections. These may have grown on or within the tufa at a late stage, where there was sufficient light. Secondly, the cruder blebs more commonly seen could represent diagenetic alteration of *Renalcis* and pelletoids of the perithecal zone into which the tufa has grown. Thirdly, the organic structures may be those of bacteria, blue-green algae or fungi responsible for, or associated with, the formation of tufas. Similar downgrowing 'cryptalgal' mats and heads have been described from the undersides of sheet cracks in the late Palaeozoic of Algeria (Bertrand-Sarfati and Fabre 1972), whilst others have been seen by the writer in the Triassic of Glamorganshire. In both cases fibrous calcite has developed in the downgrowing laminae under lagoonal conditions. As flexibacteria can form siliceous stromatolites in the absence of light (Brock 1969) it is possible that similar organisms may be involved in the formation of tufas in such unlit spaces (e.g. see Krumbein 1968).

RENALCIS AND THE PERITHECAL ZONE

The 'mutual distance' observed between archaeocyathids and the 'stromatolites' relates to a more or less constant thickness of *Renalcis* encrustations around the outer walls. Similar perithecal zones of *Renalcis* have been observed by the writer in other assemblages from the Wilkawillina Limestone and from elsewhere around the world. These overgrowths will form the subject of a later study but several points are worth noting here. Firstly, the absence of *Renalcis* from the intervallum and lower central cavity requires explanation. Whilst the intervallum may have been closed off by an organic membrane or filled with tissue, the central cavity almost certainly was not. The *Renalcis* zone gets thicker as the central cavity widens, which could suggest that a dependence upon light or well-circulated water kept the organism out of the lower central cavity.

A second point concerns the role played by *Renalcis* as a binding organism strong enough to prevent the disruption of a delicate archaeocyathid community in a littoral habitat. This kind of encrusting-binding habit seems generally inconsistent with blue-green affinities, as are certain other points about the organism (Riding and Brasier 1975).

CONCLUSIONS

1. The archaeocyathids were growing in warm, shallow sublittoral waters in a geographic setting resembling a wide backreef lagoon. Their faunal associates included trilobites, brachiopods, echinoderms, hyolithids, *Chancelloria*, and various problematica.

2. Juvenile archaeocyathids mostly attached to the upper, outer wall of an older, probably dead cup. Inner-wall settlements took place only where the central cavity

was wide. *Regulares* commonly formed exothecal outgrowths at the attachment site whilst *Irregulares* attached directly. Those juveniles which grew upright from near the top of the host cups attained a larger size than those which grew laterally and lower down on a cup, for the latter were overcrowded by other individuals.

3. Growth distortions occurred where two archaeocyathid cups came into contact, indicating the existence of non- or poorly calcified parts in the region of growth at the top of the cup. Exothecal outgrowths are associated with these overcrowding phenomena and may have represented a proliferative response of the ectoderm to the presence of foreign cells. They also served for adherence. Considerations of the level of cellular integration indicated by archaeocyathid skeletal structure, especially consequent to damage or contact with other individuals, suggest that they had an organization as high and possibly higher than that of the Porifera.

4. In the life assemblage the outer walls of the cups were encrusted by colonies of the calcareous-chambered organism *Renalcis*. These encrustations were probably post-mortem and were substantial enough to bind the delicate archaeocyathid intergrowths together. *Renalcis* is usually lacking from the lower part of the central cavity and all of the intervallum of the archaeocyathid hosts. In the death assemblage, the cups were mostly uprooted and transported before *Renalcis* encrustation was able to take place.

5. Structures resembling stromatolites surround the archaeocyathids in many places. These are interpreted as early post-mortem tufas ('coniatolites'), formed by brines percolating downwards into cavities, perhaps during low tides. These tufas encouraged the recrystallization of some lime mud matrix into radiaxial fibrous carbonates.

Much further work needs to be done on the sedimentological relationships and the mode of preservation of these problematic early Cambrian organisms before their palaeoecology and palaeobiology will come to light. With the above and many other studies one hopes eventually to build up a clearer picture of one of the most important periods in the history of life, the Cryptozoic-Phanerozoic transition.

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REFERENCES

- BALSAM, W. L. 1973. *Ecological interactions in an early Cambrian archaeocyathid reef community*. Ph.D. dissertation, Brown University, 152 pp. University Microfilm, Ann Arbor, Michigan.
- and VOGEL, S. 1973. Water movement in archaeocyathids: evidence and implications of passive flow in models. *J. Paleont.* **47**, 979-984.
- BERTRAND-SARFATI, J. and FABRE, J. 1972. Les stromatolites des formations lacustres post-moscoviennes du Sahara septentrional (Algérie). *24th Int. geol. Congr. Montreal*, **7**, 458-470.
- BROCK, T. D. 1969. Vertical zonation in hot spring algal mats. *Phycologia*, **8**, 201-205.

- CULLIS, C. G. 1904. The mineralogical changes observed in the cores of the Funafuti Boring. In *Coral Reef Report, The Atoll of Funafuti*. Sect. XIV, Royal Society, London. Pp. 392-420.
- DAILY, B. 1956. The Cambrian in South Australia. *El Sistema Cambrico*, 20th Int. geol. Congr. Mexico, Pt. 2, 91-147.
- DALGARNO, C. R. 1964. Report on the Lower Cambrian stratigraphy of the Flinders Ranges, South Australia. *Trans. R. Soc. S. Austr.* **88**, 129-144.
- and JOHNSON, J. E. 1966. Parachilina. Geol. Atlas 1:250,000 ser. *Geol. Surv. S. Austr.* sheet H54-13.
- DAVIES, P. J. and TILL, R. 1968. Stained dry cellulose peels of ancient and recent impregnated carbonate sediments. *J. sed. Petrol.* **38**, 234-237.
- DEBRENNE, F. 1959. Recifs, biohermes ou bancs fossilifères d'Archaeocyatha. *Bull. Soc. geol. France*, 7th series, **1**, 393-395.
- 1964. Archaeocyatha. Contribution a l'étude des faunes cambriennes du Maroc, de Sardaigne et de France. *Serv. Min. Carte Géol. Maroc. Notes & Mém.* no. 179, **1**, 265 pp.
- 1969. Lower Cambrian Archaeocyatha from the Ajax Mine, Beltana, South Australia. *Bull. Brit. Mus. nat. Hist. (Geol.)*, **17**, 295-376.
- 1975. Analyse de l'article de I. T. Zhuravleva sur la 'Biologie des Archaeocyathes'. *Cnidaires Fossiles*, vol. 1974, no. 2, 47-51.
- GEBELEIN, C. D. 1974. Biologic control of stromatolite microstructure: implications for Precambrian stratigraphy. *Am. J. Sci.* **274**, 575-598.
- GLAESSNER, M. F. 1969. Trace fossils from the Precambrian and basal Cambrian. *Lethaia*, **2**, 369-393.
- GOLDRING, R. and CURNOW, C. N. 1967. The stratigraphy and facies of the Late Precambrian at Ediacara, South Australia. *J. geol. Soc. Austr.* **14**, 195-214.
- GORIANSKY, W. 1973. On the necessity of excluding *Chancelloria* from the sponges. In *Problemy Paleontologii i biostratigraphii nizhnego Kembrija sibirii dal' nego vostoka*. Izdat. Nauka Sib. Otdel. 39-44.
- HILDEMAN, W. H. 1974. Some new concepts in immunological phylogeny. *Nature*, **250**, 116-120.
- HILL, D. 1972. Archaeocyatha. In TEICHERT, C. (ed.). *Treatise on Invertebrate Paleontology, Part E*, 1. Geol. Soc. Am. and Univ. Kansas Press, 158 pp.
- HUMPHREYS, T. 1970. Biochemical analysis of sponge cell aggregation. *Symp. zool. Soc. Lond.* **25**, 325-334.
- IVKER, F. E. 1972. A hierarchy of histo-incompatibility in *Hydractinia echinata*. *Bull. Biol.* **143**, 162-174.
- JOHNSON, J. H. 1966. A Review of the Cambrian Algae. *Q. Col. Sch. Mines*, **61**, 162 pp.
- KENDALL, A. C. and TUCKER, M. E. 1973. Radial fibrous calcite: a replacement after acicular carbonate. *Sedimentology*, **20**, 363-390.
- KOROTKOVA, G. P. 1970. Regeneration and somatic embryogenesis in sponges. *Symp. zool. Soc. Lond.* **25**, 423-436.
- KRUMBEIN, W. F. 1968. Geomicrobiology and Geochemistry of the 'Nari-Lime-Crust' (Israel). In MULLER, G. and FRIEDMAN, G. M. (eds.). *Recent Developments in Carbonate Sedimentology in Central Europe*. Springer-Verlag, Berlin, 138-147.
- LOEBLICH, A. R. and TAPPAN, H. 1964. Protista 2; Sarcodina, chiefly 'Thecamoebians' and Foraminiferida (2 vols.). In MOORE, R. C. (ed.). *Treatise on Invertebrate Paleontology, Part C*. Geol. Soc. Am. and Univ. Kansas Press, 900 pp.
- MILLIMAN, J. D. 1974. *Marine Carbonates*. Springer-Verlag, Berlin, 375 pp.
- ORME, G. R. and BROWN, W. W. M. 1963. Diagenetic fabrics in the Avonian Limestones of Derbyshire and North Wales. *Proc. Yorks. geol. Soc.* **34**, 51-66.
- PURSER, B. H. and LOREAU, J.-P. 1973. Aragonitic, supratidal Encrustations on the Trucial Coast, Persian Gulf. In PURSER, B. H. (ed.). *The Persian Gulf*. Springer-Verlag, Berlin, 343-376.
- RIDING, R. 1972. Calcareous algae and some associated microfossils from Ancient Wall Reef Complex (Upper Devonian), Alberta. *Bull. Am. Assoc. petrol. Geol.* **56**, 648.
- and TOOMEY, D. F. 1972. The sedimentological role of *Epiphyton* and *Renalcis* in Lower Ordovician Mounds, Southern Oklahoma. *J. Paleont.* **46**, 509-519.
- and BRASIER, M. D. 1975. The earliest calcareous foraminifera. *Nature*, **257**, 208-210.
- ROSANOV, A. Y. and DEBRENNE, F. 1974. Age of archaeocyathid assemblages. *Am. J. Sci.* **274**, 833-848.
- WADE, M. 1970. The stratigraphic distribution of the Ediacara Fauna in Australia. *Trans. R. Soc. S. Austr.* **94**, 87-104.
- WALTER, M. R. 1967. Archaeocyatha and the biostratigraphy of the Lower Cambrian Hawker Group, South Australia. *J. geol. Soc. Austr.* **14**, 139-152.

- WEBBY, B. D. 1973. Trace fossils from the Lintiss Vale Formation of New South Wales: a late Precambrian fauna. *Search*, **4**, 494-496.
- WOLF, K. H. 1965. Littoral environment indicated by open space structures in algal limestones. *Palaeogeog. Palaeoclim. Palaeocol.* **1**, 183-223.
- ZHURAVLEVA, I. T. 1960. *Arkheotsiaty Sibirskoy platformy*. Akad. Nauk. SSSR, Moscow, 344 pp.
- 1970. Porifera, Sphinctozoa, Archaeocyathi—their connections. *Symp. zool. Soc. Lond.* **25**, 41-59.
- 1972. Archaeocyathids of the Lower Cambrian facies complex, pp. 31-109. In *Problemy Biostratigraphy i Paleontology nizhnego kembriya Sibiri Tzdar*. Nauka, Moscow, 248 pp. [In Russian.]
- 1974. Biology of Archaeocyatha. In *Stratigraphical studies, Jubilee Book in honour of Academician B. S. Sokolov*. Izdat, Nauka, Moscow, 107-129. [In Russian.]
- ZIEGLER, B. and RIETSCHER, S. 1970. Phylogenetic relationships of fossil calcisponges. *Symp. zool. Soc. Lond.* **25**, 23-40.

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