REEF-ASSOCIATED ARCHAEOCYATHANS FROM THE LOWER CAMBRIAN OF LABRADOR AND NEWFOUNDLAND

by FRANÇOISE DEBRENNE AND NOEL P. JAMES

ABSTRACT. The bioherms and biostromes of the Forteau Formation in southern Labrador and western Newfoundland are rich in archaeocyathans. The older bioherms contain five genera and six species while only three genera and three species are found in the younger biostromes. *Metaldetes profundus*, which constitutes up to 80% of the fauna in both horizons, exhibits a great variability in growth form, ranging from stick-like to cup-like to plate-like in shape. The other taxa present are ?*Metaldetes simpliporus* (sp. nov.), *Archaeocyathus atlanticus*, *Archaeosycon billingsi* and *Arrythmocricus kobluki* (gen. and sp. nov.). A new and enigmatic form *Retilamina amourensis* (gen. and sp. nov.) occurs as sheets and arched domes beneath which there is a diverse cavity-dwelling fauna of algae and invertebrates. The archaeocyathan fauna has many individuals yet few species. Such a distribution, in contrast to the relatively diverse fauna of other body and trace fossils associated with the bioherms and biostromes, is probably because Late Lower Cambrian time is well past the acme of archaeocyathan evolution and few genera are recorded anywhere in rocks of this age. Some aspect of the paleoenvironment (probably episodic nutrient supply) was especially conducive to archaeocyathan growth, allowing them to grow in large numbers in shallow water near the shoreline.

ARCHAEOCYATHANS, fossils composed of large, conical-shaped calcium carbonate skeletons, occur world-wide in rocks of Early Cambrian age. These fossils are the earliest known, large skeletal metazoa. They are also the most important fossils used for subdivision of Lower Cambrian strata and are the major skeletal components of the earliest metazoan reefs. They have particular reason to interest paleontologists, stratigraphers, and sedimentologists. The archaeocyathan fauna in the Forteau Formation along the Strait of Belle Isle (text-fig. 1), is a particularly significant one. The first archaeocyathan fossils were discovered in these strata in 1845. Although these classic fossils have been documented from scattered collections, they have never been thoroughly investigated in the field, nor has the taxonomy been revised in the light of modern classification. These archaeocyathans are also the primary skeletal elements of numerous bioherms that have the same attributes as other metazoan reefs which occur later in geologic time. The structure and sedimentology of these bioherms has been documented (James and Kobluk 1978) but the distribution of the various archaeocyathan genera and species within these structures has not been demonstrated. The purpose of this paper is (1) to describe and classify the reef-associated archaeocyathans in the Forteau Formation, and (2) to record the distribution of these archaeocyathans in the reefs and reef-derived sediments.

PREVIOUS STUDIES

The fossils were discovered along the eastern shores of Forteau Bay in southern Labrador by Captain H. W. Bayfield, a hydrographer, and later reported by him as corals (*Cyathophyllum*) (Bayfield 1845, p. 457). They attracted the attention of Sir William Logan, director of the Geological Survey of Canada, who dispatched J. Richardson to Labrador and Newfoundland to make a proper collection in 1860-1862. The resulting collection was unfortunately lost when the ship transporting them to

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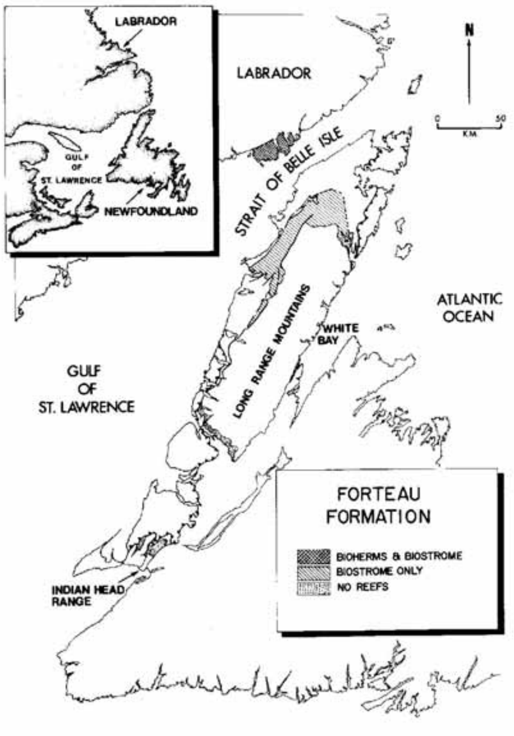
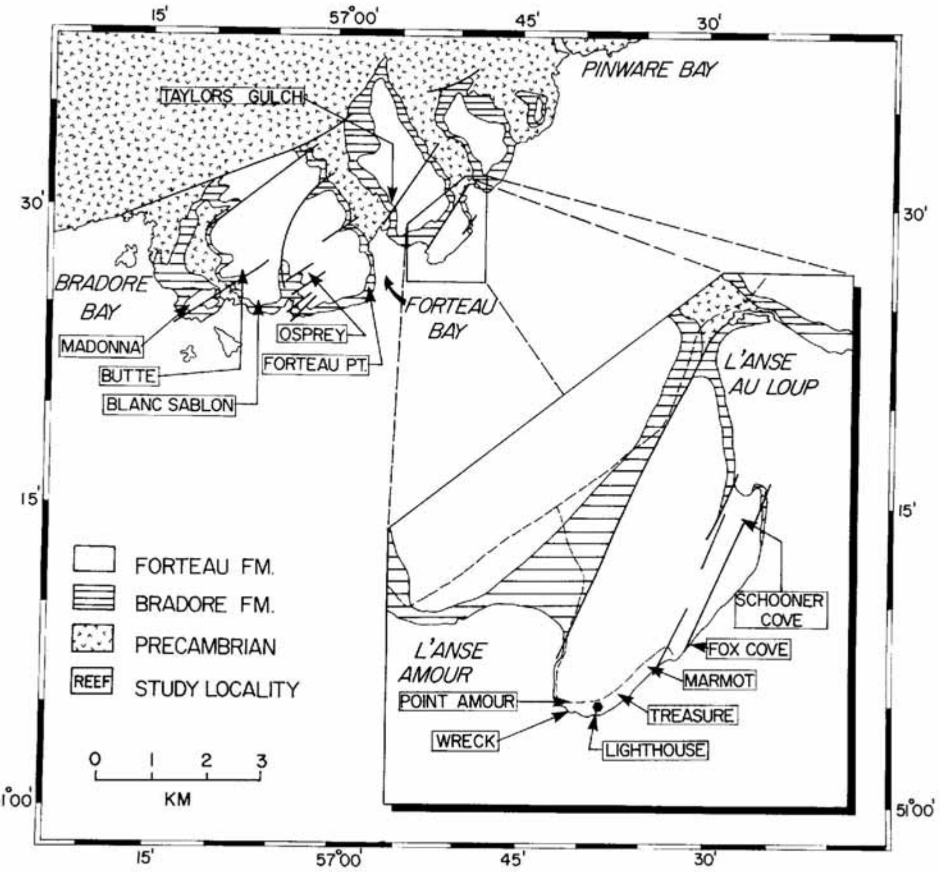


TEXT-FIG. 1. Location map illustrating the distribution of bioherms and biostromes in the Forteau Formation.

Montreal sank *en route* and only a few fragmentary specimens were submitted to Logan (1863). E. Billings, upon seeing the small samples, recognized them as unique, intermediate in structure between sponges and corals, and gave them the name *Archeocyathus* (Billings 1861) (emended to *Archaeocyathus* by Dawson in 1865). T. C. Weston was sent to recollect in 1872 and his samples were sent to C. D. Walcott for study, who in turn published his detailed descriptions of several specimens in 1886. C. Schuchert and W. H. Twenhofel from the Peabody Museum collected new specimens in 1910 and again sent the material to Walcott for identification. The results were published in a now classic memoir on the stratigraphy of western Newfoundland (Schuchert and Dunbar 1934). Further collections were made by C. O. Dunbar in 1920 and housed in the Peabody Museum. All of these collections were restudied by V. J. Okulitch who revised the systematics of the entire phylum (Okulitch 1940, 1943).

Since the last collections in 1920 and the last published descriptions of these collections in 1943, the only other taxonomic work has been done by C. C. K. Fong as an unpublished M.Sc. study (Memorial University 1967). Since this time the entire phylum has undergone complete taxonomic revision and the number of archaeocyathan taxa now known has increased dramatically, largely because of the extensive work in the U.S.S.R. Because the fauna from Labrador was the first to be described the fossils have priority in nomenclature and systematics. Taxa established from these original localities are for the most part wrongly identified outside Labrador (i.e. *Archaeocyathus*) and some identical forms are described under other names (i.e. *Metaldetes*, *Claruscyathus*).

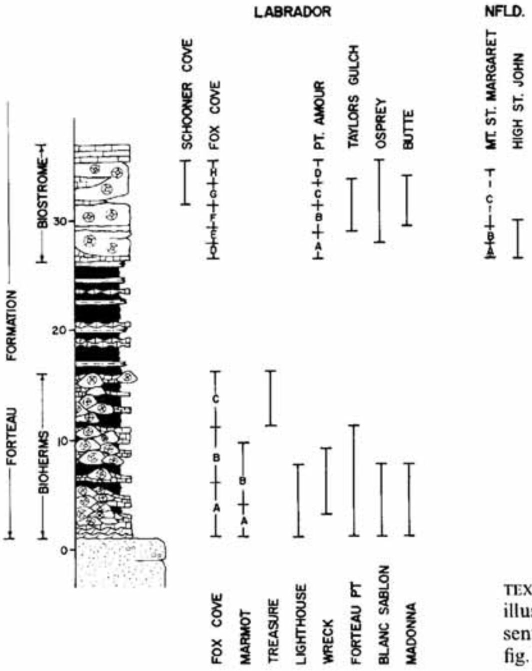


TEXT-FIG. 2. Location map of all the areas studied in Southern Labrador.

GEOLOGICAL SETTING

The Forteau Formation, which crops out in western Newfoundland and southern Labrador (text-figs. 1, 2) is part of the autochthonous sedimentary sequence of shallow-water strata that is found in and adjacent to the western margin of the Appalachian Orogen in eastern Canada (Williams and Stevens 1974). The Lower Cambrian part of the succession comprises a basal sandstone and conglomerate unit called in various places the Bradore Formation, the Bateau Formation or the Cloud Mountains Formation, which is overlain by a unit of limestones, siltstones, and shales (Forteau Formation), capped by a unit of sandstones and conglomerates termed the Hawke Bay Formation (Schuchert and Dunbar 1934; Betz 1939; Williams and Stevens 1969). Archaeocyathans occur only in the lower half of the Forteau Formation. The trilobite fauna in the Forteau Formation indicates a medial *Bonnia-Olenellus* Zone age in the Lower Cambrian (W. H. Fritz and A. R. Palmer, pers. comm.).

In southern Labrador only the lower half of the Forteau Formation is exposed, the remainder having been removed by erosion. The strata crop out in low but extensive sea cliffs, in a few of the river valleys and along the roadside in small quarries. Here the rocks can be broadly subdivided into three lithostratigraphic units (text-fig. 3); (1) a basal bioherm or patch-reef unit, (2) an intermediate series of well-bedded siltstones, shales, and limestones, and (3) an upper biostrome unit (James and Kobluk 1978). Well-bedded shales, siltstones, and some limestones also occur between the lower bioherms which tend to be isolated or clustered.



TEXT-FIG. 3. A stratigraphic column illustrating that part of the section represented at each of the localities in text-fig. 2.

Across the Strait of Belle Isle in Newfoundland the complete Forteau Formation (120 m) is exposed at several places in upthrust blocks along the western and northern flanks of the Long Range Mountains. The lower bioherm horizon grades south-eastward into shale and minor siltstone in western Newfoundland but the upper biostrome can be recognized at several localities adjacent to the Long Range Mountains (James and Fong 1976) (text-fig. 1). The eastern-most facies of the Forteau Formation are mainly shale and siltstone, with no bioherms or biostromes and only one archaeocyathan-rich unit at the base of the formation, with a completely different fauna.

STRATIGRAPHY AND COMPOSITION OF THE FAUNA

Methods

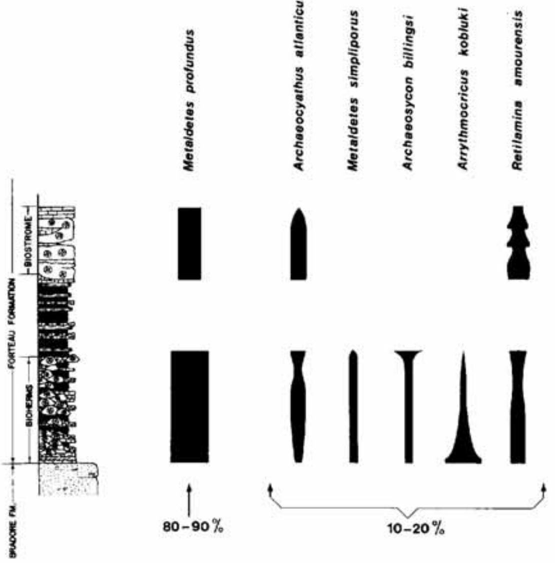
This study is part of a continuing synthesis of these well-exposed reef-associated sediments. During the initial phases of mapping by James in 1976 and 1977, the archaeocyathan-rich horizons were sampled extensively. The samples were examined by Debrenne who, by using a combination of thin-sections, ultra thin-sections, serial sections, and Scanning Electron Microscopy, classified and described the fauna. Results of this preliminary examination indicated that the fauna was one of low diversity, but high abundance. Luckily the different species possessed enough megascopic characteristics for differentiation in the field. In 1978 we visited almost all of the well-exposed archaeocyathan localities in the area together. The lower bioherm horizon was studied at eight localities in southern Labrador, while the upper biostrome horizon was studied at six localities in southern Labrador and at two localities in western Newfoundland. At each of these places we recorded the presence or absence of archaeocyathan species and morphotypes and their vertical and horizontal distribution in the outcrop. In addition we determined the relative abundance of each species in various parts of the bioherm or biostrome. Detailed tabulated data available from authors on request.

Faunal summary

Our field and laboratory analyses indicate that the archaeocyathan fauna consists of only six species: *Archaeocyathus atlanticus* (Billings 1861); *Metaldetes profundus* (Billings 1865); *?Metaldetes simpliporus* sp. nov.; *Archaeosycon billingsi* (Walcott 1886); *Arrythmocricus kobluki* gen. et sp. nov.; *Retilamina amourensis* gen. et sp. nov. Our findings are in contrast to those of Okulitch (1940, 1943), and Fong (unpublished M.Sc. thesis 1967), who have subdivided the archaeocyathan fauna into many more species.

Stratigraphic range and correlation

Stratigraphic distribution. Only in a few places is a complete section through both of the archaeocyathan-rich horizons present, and so all possible localities were visited in an attempt to confirm trends observed in the key-reference sections. The interval of section exposed at various places is outlined in text-fig. 3 while the data recorded at each are summarized in text-fig. 4. The most abundant archaeocyathan fauna, both in terms of taxa and individuals, occurs in the lower bioherm horizon; all of the forms are found here. *M. profundus*, *?M. simpliporus*, *A. atlanticus*, and *R. amourensis* occur in approximately the same relative proportion throughout this part of the section (text-fig. 4). *A. kobluki* is commonest in the lower 10 m and becomes progressively less abundant upwards, until, at the top of the unit, individuals are rare. In contrast, *A. billingsi* is rare



TEXT-FIG. 4. The relative abundance of archaeocyathan species with stratigraphic position in the lower part of the Forteau Formation. *M. profundus* comprises 80–90% of the fauna, with the remainder totalling 10–20%.

throughout the bulk of the section except in the upper 3 to 4 m, where its occurrence is coincident with many small bioherms. The fauna in the upper biostrome unit is greatly reduced, both in numbers and species. The only archaeocyathans found in this unit are the forms *M. profundus*, *A. atlanticus*, and *R. amourensis*. This restricted fauna is also found in the biostrome unit in western Newfoundland, supporting previous lithostratigraphic correlations (James and Fong, 1976), indicating the biostrome complex and associated ooid calcarenites can be traced over a distance of 110 km (north-west south-east), across the depositional strike.

The occurrence of *M. profundus* with or without dissepiments does not appear to have any stratigraphic significance, but rather those forms without dissepiments are commonest in pockets of lime mud, irrespective of the surrounding facies. Similarly, the outgrowths of skeletal material from the basic skeleton of *M. profundus*, corresponding to the form *Exocyathus canadensis* (Okulitch 1943), are common throughout. These elements have no separate stratigraphic importance, because we now consider this form as a true part of *M. profundus* and not as a separate species.

Correlation with other areas. The strata under study contain only Irregulares, most species of which characteristically have a long stratigraphic range. The commonest form, *M. profundus*, is not known elsewhere, but other species belonging to the genus are known from rocks equivalent to those of the Lenian Stage in the Sekwi Formation and Donald Formation in North America as well as in other localities in Australia and Antarctica. There is, however, no record of this genus from the U.S.S.R. or China. If *Archaeosycon*, *Claruscyathus*, and *Clarucoscinus* do prove to be synonymous, then the range of these forms will extend from the upper part of the Lenian Stage through the Elankian Stage, with their acme being in the Obruchev Horizon of the Elankian Stage. The age of the Forteau can perhaps be even more precisely defined on the basis of the occurrence of *Archaeocyathus*. Amongst the nineteen species of *Archaeocyathus* listed here eleven are found in the U.S.S.R. only in the Obruchev Horizon of the Elankian Stage, five are found in the Sekwi Formation of the N.W.T., Canada (*Bonnia-Olenellus* Zone), and three have a stratigraphic position unknown to the authors (in China or as dredgings). In summary, the range of the *Archaeocyathus* and *Archaeosycon* species allows us to correlate the Forteau Formation with the Elankian Stage and probably the Obruchev Horizon of the Siberian Platform. On the basis of trilobites, strata in this part of the Forteau Formation appear to be equivalent to rocks in the middle part of the *Bonnia-Olenellus* Zone (W. H. Fritz, A. R. Palmer, pers. comm.).

DISTRIBUTION OF ARCHAEOCYATHANS WITHIN THE REEFS

Bioherm Horizon (Text-Fig. 4)

The sedimentology and structure of these reefs, originally described by Balsam (1973), has recently been revised and documented in detail by James and Kobluk (1978). The bioherms are irregular masses of white to red resistant limestone surrounded by recessively weathering, well-bedded, green and red shales, siltstones, and some limestones (Pl. 48, fig. 1). Reefs occur either individually or in

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EXPLANATION OF PLATE 48

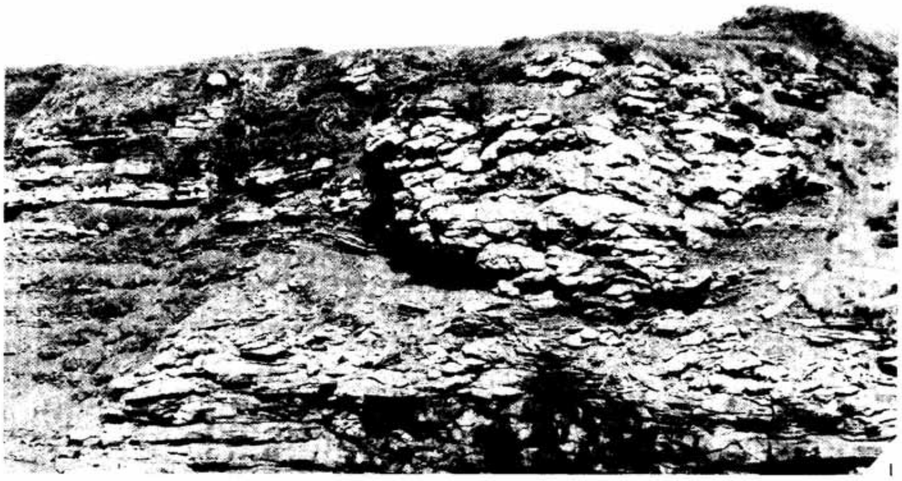
Fig. 1. Sea cliffs north of Fox Cove, Labrador, exposing a small patch reef about 8 m high (right) and bedded inter-reef strata (left).

Fig. 2. The cross-section of a small bioherm mound composed of many small, stick-shaped *Metaldetes profundus* skeletons with only scattered cups and bowl-shaped forms; scale in cm ×0·15.

Fig. 3. The upper surface of a small bioherm mound with many large, open cup and bowl-shaped *Metaldetes profundus* skeletons, ×0·12.

Fig. 4. The weathered top surface of part of the upper biostrome illustrating, in plan view, a cluster of *Archaeocyathus atlanticus*, scale in cm ×0·28.

Fig. 5. The weathered top surface of part of the biostrome illustrating the large, bowl-shaped *Metaldetes profundus* with thin, crenulated walls that are, in some cases, joined (at right), ×0·1.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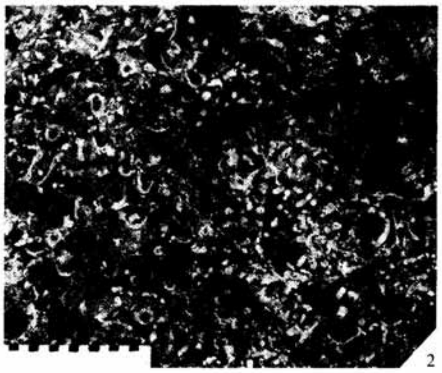
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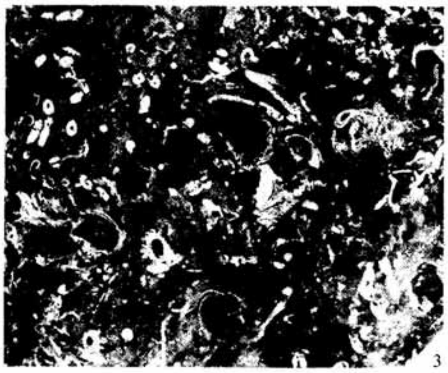
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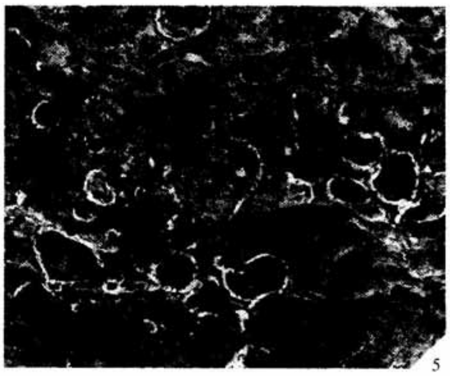
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DEBRENNE and JAMES, Archaeocyathan reefs groups and together with inter-reef calcarenites form large reef complexes. The basic structure of all bioherms is the same, a small pillow-shaped mound 0·2 to 1·0 m high and 1·0 to 2·0 m wide that is rich in archaeocyathans. These mounds occur singly, surrounded by skeletal calcarenite, or piled on top of one another to form bioherms. Individual bioherms may be as thick as 20 m and patch-reef complexes may be 200 m across. Bioherms are most abundant near the base and the top of the horizon but there are many complexes that span the entire thickness (15 m) of the unit.

Reef composition. Individual mounds are composed primarily of archaeocyathans, the calcareous algae *Renalcis*, and/or *Epiphyton* and lime mud (now microspar). Other accessory skeletal elements are hyolithid cones, trilobite carapaces, brachiopod shells, *Archaeotrypa* skeletons, echinoderm plates, sponge spicules, and *Chancelloria* remains. The archaeocyathans stand out as white skeletons in the red lime mudstone and most often comprise more than 60% of the rock (Pl. 48, figs. 2, 3). Calcarenites which surround the reefs are primarily skeletal grainstones, the commonest bioclasts being hyolithids, brachiopods, echinoderms, and trilobites. Archaeocyathan debris, as complete or fragmented skeletons, is common only around the reefs and is rare elsewhere.

Archaeocyathans. By far the commonest archaeocyath is *M. profundus*, comprising 80% to 90% of individuals in the reef mounds and between 20% and 50% of the rock volume. This species demonstrates a surprising plasticity in growth form, with skeletons varying from sticks (cylindo-conical with a diameter averaging 10 mm and a length averaging 190 mm) to cones (height = 190 mm, diam. = 80 mm), to cups (small rapidly widening cones with a U-shaped lower portion; stem—height = 80 mm, diam. = 10 mm, cup on top—height = 60 mm, diam. = 90 mm), to bowls (wide, open saucer-shaped forms with a maximum observed diameter of 250 mm). This polymorphism is illustrated only by *M. profundus*, all the other archaeocyathans have a stick-like shape and, except for *Arrythmocricus*, are larger than the stick-like forms of *M. profundus*.

?M. simpliporus is sparsely scattered throughout the complex. *Archaeosycon* is abundant in some layers, absent in others, and commonly upside-down. In contrast, *Archaeocyathus* and *Arrythmocricus* have a clustered distribution; they are absent from some areas of the reef yet they occur as groups of abundant, but separate, sticks in other areas.

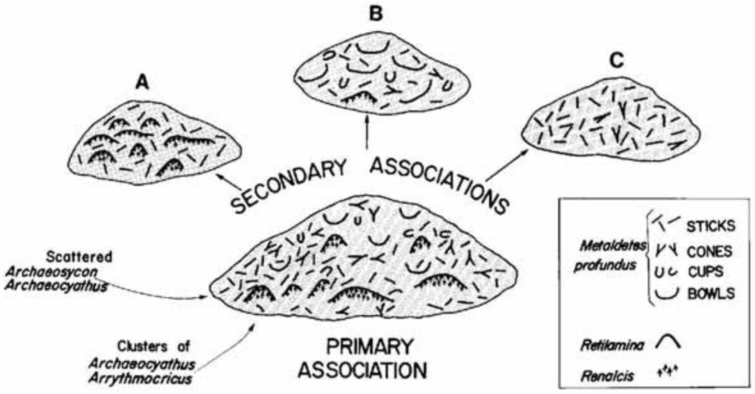
R. amourensis is commonest as a thin, sheet-like skeleton exhibiting a limpet-like shape whose maximum height is less than 3 cm. In many cases these skeletons are flattened with a relief of less than 1 cm. The undersides of these forms are almost always encrusted with *Renalcis* and/or *Epiphyton* and other microflora and microfauna (Kobluk and James 1979). The remainder of each shelter cavity is floored with internal sediment and occluded with cement.

Primary association. The distribution of various archaeocyathan taxa as well as of the different morphotypes of *M. profundus* varies greatly from reef to reef and even from mound to mound within any one reef. This variation has no obvious trend, large numbers of mounds may be similar in composition yet adjacent mounds in the same reef may be quite different. There is, however, an association of archaeocyathans that recurs most commonly, which we have termed the primary association (*sensu* Scott 1976). This primary association (text-fig. 5) includes a high density of *M. profundus* stick and cone-shaped skeletons with few bowl-shaped and cup-shaped growth forms (Pl. 48, fig. 2). *Retilamina* and associated *Renalcis* occur scattered throughout the rock but are commonest at the base of any one mound or group of mounds. Single sticks of *Archaeocyathus* and *Archaeosycon* are ubiquitous components of this association. In some areas clusters of *Archaeocyathus* and/or *Arrythmocricus* occur together with the more prevalent species.

Secondary association. Three other associations which are less common but readily identifiable, occur within the reefs (text-fig. 5).

(A) The lower or central parts of large reefs are often composed almost entirely of *Retilamina* with a few stick-like archaeocyathans. Because of the shape of *Retilamina* these zones contain the most spectacular cavities and associated structures.

(B) The upper parts of reefs or mounds often have a relatively large number of bowl-shaped *M. profundus* (Pl. 48, fig. 3). Particularly noticeable at these levels are the exothecal outgrowths of skeletal material on all archaeocyathans.



TEXT-FIG. 5. A sketch illustrating the various spatial relationships of different archaeocyathans in the mounds that make up the bioherms. The primary association is the most commonly observed distribution, with secondary associations less common, but recurring.

(C) Within some reefs, mounds, or groups of mounds, the limestone is composed entirely of stick-like archaeocyathans, with only rare cone-shaped and bowl-shaped forms. The most important component of this association is *M. profundus*, but in these high-density occurrences the sticks are generally smaller, 6–10 mm in diameter as opposed to 10–15 mm in diameter in the primary association. Associated with these are sticks of *Archaeocyathus* and *Arrythmocricus*, often in clusters.

Biostrome Horizon (Text-fig. 4)

In the middle of the Forteau Formation (the uppermost exposed strata in Labrador) is a remarkably persistent limestone unit composed of laterally equivalent lithotypes, a thin- to thick-bedded sequence of ooid-rich lime grainstones and an intercalated succession of archaeocyathan-rich lime mudstones, lime grainstones, and minor siltstones or shales. The archaeocyathan-rich lithotype is the biostrome unit (James and Fong 1976). The oolite is commoner in the west and the biostrome commoner in the east. The biostrome consists of a series of distinct, tabular to wedge-shaped subunits that grade laterally into skeletal calcarenite. Individual subunits are often vertically separated from one another by calcarenites. Each of the archaeocyathan units is from 2 to 6 m thick and individual units can be recognized in succession in outcrops 6 km apart (Hughes 1979). At any one locality the biostrome is composed of three to five separate subunits.

Biostrome composition. The limestones are commonly green-grey in colour with occasional units variegated green and red. In outcrop the limestones are characteristically nodular and contrast with the evenly bedded calcarenites. The nodules are caused by extensive stylolitization. These stylolites bound small pods and lenses that are composed of (1) green finely crystalline, iron-rich dolomite, that weathers brown, (2) brachiopod-trilobite grainstones, and (3) lime-mudstone rich in archaeocyathans, and *Renalcis* or *Epiphyton* with occasional *Archaeotypa*, *Chancelloria*, and an enigmatic multi-tabulate organism *Labyrinthus soraufi* (Kobluk 1979). The lack of colour contrast between archaeocyathans and matrix as well as the ubiquitous lichen and weathering crust make outcrops of the biostrome difficult to study.

Archaeocyathans. The relative abundance of archaeocyathans within each subunit of the biostrome is much less that in the bioherms below. This is in part because most of the skeletons are the larger cup- and bowl-shaped forms, all belonging to the species *M. profundus*, leaving less room for smaller forms. *M. profundus* comprises 80% to 90% or more of the total archaeocyathan fauna, except in specific zones described below, where *Archaeocyathus* and *Retilamina* are abundant. The most diverse archaeocyathan association is found in the basal parts of individual subunits. Here the fauna includes almost equal proportions of *M. profundus* (in all growth forms), clumps of colonial *Archaeocyathus*, and/or sheets of *Retilamina*. Individual colonies of *Archaeocyathus* (Pl. 48, fig. 4) are up to 20 cm across and 32 cm high. *Retilamina* occurs as sheet-like, yet arching skeletons that form small cavities which support colonies of *Renalcis*. These sheets commonly occur piled on top of one another.

Above these basal layers the bulk of each subunit is almost monospecific, mostly *M. profundus*, with only scattered *Retilamina*. Almost all of these skeletons are upright, few are toppled. The green-grey horizons are characterized by cup-shaped, bowl-shaped, and plate-shaped and a few stick-shaped skeletons of *M. profundus*. Some of the cups are straight-sided and as long as 19 cm. Individual plates may be as large as 15 cm in diameter. Bowls are occasionally nested with two or three bowls on top of one another. The stick-shaped forms are only one-fifth as abundant as in the lower bioherm horizon, but are larger, with the average diameter being 15 mm in contrast to 6 mm in the lower horizon. These sticks are generally found lying horizontally.

Red-coloured, intensively stylolitized layers are characterized by numerous large, convoluted bowls, with a very thin intervallum (Pl. 48, fig. 5). In the upper parts of many units cups and sticks of *M. profundus* are often bound together with exothecal skeletons to form small clumps of individuals.

DISCUSSION

The reef-associated fauna of high numbers yet low diversity is in contrast to reef faunas in most other parts of the geologic record. Because we do not know the biological affinities of the Archaeocyatha with certainty, we cannot compare these fossils to any living organisms. As a result, we have chosen to analyse the two non-biological criteria available: (1) the paleoenvironment as represented by the sedimentary record, and (2) the specific time period in which the organisms lived, to see if the distribution can be explained, in part, by these factors.

Paleoenvironment

The Bradore and Forteau Formations are the basal part of the Sauk Sequence (Sloss 1963) which records the gradual inundation of the North American craton in Lower Paleozoic time. On the basis of palaeomagnetic determinations southern Labrador was equatorial during late Lower Cambrian time, lying between 10 and 20 degrees south latitude (Pearce, Kobluk and James 1978).

Bradore Formation. The sequence of sandstones stratigraphically below the reefs of the Bradore Formation is predominantly clean, well-washed, cross-bedded quartz and arkosic arenite. The lower half of the formation is a trough cross-bedded arkosic arenite with quartz pebble conglomerates near the base where it rests on Precambrian crystallines. These rocks, with sedimentary structures similar to other Lower Paleozoic sandstones recognized as fluvial sediments (Shumm 1968), are interpreted to be braided stream deposits. These streams flowed across a Precambrian terrain which had been extensively weathered, and had local relief of at least 50 m. The abundance of fresh orthoclase in these relatively mature, coarse-grained sandstones suggests an arid climate (Folk 1974). The upper half of the Bradore Formation is a more evenly bedded, massive arkosic arenite to quartz arenite. The trace fossil *Skolithos linearis* is abundant throughout, with large-scale cross-stratification and a more diverse ichnofossil assemblage (*Monocraterion*, *Dolopichnus*, and *Lingulichnus*) near the top. These rocks probably represent a tidal sand-shoal to barrier island complex.

Forteau Formation. The part of the Forteau Formation under study is a sequence of bioherms and surrounding bedded siltstones, shales, and limestones. The bioherms are locii of prolific carbonate production. They are either isolated small mounds or a succession of mounds that grew one upon the other through a stratigraphic interval of up to 20 m. There appear to be few major breaks in reef growth save numerous small bored hardgrounds at the top of individual mounds within the bioherms

(James and Kobluk 1978). Reef growth was continuous, while occasional bursts of carbonate production resulted in expansion of the reefs and the skeletal calcarenite beds that surround them.

The more subtle characteristics of the environment are recorded in the inter-reef sediments, deposited in response to the interplay between siliciclastic and carbonate sedimentation. These bedded sediments are characteristically cyclic (Pl. 48, fig. 1) and individual cycles can be traced laterally over an area of several square kilometers. Each cycle is coarsening-upward in style, beginning with a sharp basal contact overlain by fissile shale, in turn grading up into bioturbated shale and nodular limestones, and terminating at the top with calcareous siltstone or bioturbated silty limestone. Individual cycles vary from 0.4 to 2.0 m in thickness with various units in each cycle ranging from a few centimetres to a meter thick. The shales are fissile mudrocks with a relatively high silt-size fraction and low clay-size fraction. The silt-size grains are mainly quartz and microcline (similar to the underlying sandstones) while the clay-size fraction is mainly illite micas and minor chlorite. All of the carbonates are fossiliferous, containing trilobites, echinoderm debris, hyolithellids, hyolithids, *Chancelloria* remains, *Stenathecoides*, sponge spicules, and calcareous and phosphatic brachiopods (A. R. Palmer, pers. comm.). The details of this fauna are as yet unknown. The more terrigenous parts of the cycles contain a wide variety of trace fossils including *Anemonichnus*, *Chondrites*, *Cruziana*, *Monocraterion*, *Monomorphichnus*, *Paleophycus*, *Planolites*, *Rusophycus*, *Skolithos*, *Stipsellus*, and *Teichichnus* (Pemberton, James and Kobluk 1979). The evidence of currents and waves is meagre. The carbonates are sometimes rippled, mostly in the form of small-scale rhomboid and symmetrical bed forms. The biostratinomy of reef-derived sedimentary particles suggests sorting by weak tidal currents (Poynter 1978).

Interpretation. Applying Walthiers Law of Facies (Middleton 1973) this vertical succession records a series of laterally equivalent facies, deposited under tropical conditions, that migrated westward on to the craton. The adjacent facies at any one time graded eastward from a fluvial braided stream (Lower Bradore) environment in the west, to a strandline (Upper Bradore) environment to a shallow marine, open shelf (Forteau) environment. Bioherms developed immediately adjacent to the strandline. The rivers which drained the (possibly) arid landscape were likely fast and ephemeral, and emptied directly on to the strandline complex. The coarse-grained sediments were caught on the strandline whereas the fine grained, K-rich silts and clays bypassed and were deposited offshore. The carbonate-shale cycles suggest periodic disturbances that brought large amounts of terrigenous mud offshore, on to the shelf. These events appear to have been followed by periods of quiescence and clear-water, carbonate sedimentation. This suggests that reef growth was in a shallow, predominantly tranquil, near shore, brackish to normal marine setting. The style of cyclicity implies disturbances that were not catastrophic. Nutrients would be in good supply in such a setting but might be introduced episodically.

Diversity. One of the cornerstones of modern ecology and paleoecology is the stability/time hypothesis (Sanders 1968, 1969; Bretsky and Lorenz 1969, 1970; Valentine 1971, 1972). Briefly, it states that stressed and/or young environments will have fewer species than non-stressed and/or old environments. This theory has recently been questioned in terms of the data upon which it is based and its applicability to specific modern and ancient environments which do not display the predicted results (Abele and Walters 1979). There are numerous examples, for instance, of low diversity communities in stable environments or high diversity communities in severe, unpredictable, or unstable environments (Huston 1979). Finally, it has been suggested that the whole theory as originally stated is tautological (Peters 1976). One of the basic assumptions of this and other current theories is that communities tend towards competitive equilibrium and that those communities at equilibrium exhibit the greatest variety of species. There is, however, growing evidence that many natural systems are not at equilibrium, yet exhibit high species diversity, and that if competitive equilibrium *is* ever reached it is expressed by the increase and eventual dominance of one competitor, with a concomitant decrease in the others (Connell 1978; Huston 1979). Those communities with a high diversity of species appear to be prevented from reaching equilibrium by periodic population reductions and environmental fluctuations. Connell (1978) proposed that it is the frequency at which disturbances occur which is critical. At low frequencies of disturbance equilibrium is reached and so low diversity results. At intermediate frequencies of disturbance equilibrium is never achieved and so high diversity is maintained. At high frequencies of disturbance low diversity is the norm because the community never has a chance to recover between catastrophies. Huston (1979) has extended this concept to include such factors as population growth rate. At low to intermediate frequencies of disturbance, low growth rates allow maintenance of diversity by slowing the approach to equilibrium, while high growth rates lead to rapid dominance by one species and so low diversity. This in turn can be related to nutrient supply. If basic nutrient supply is low (as opposed to extreme deficiency or toxicity) growth rates are reduced and therefore diversity is high; if nutrient supply is high then diversity is reduced.

Taken in total, the community of organisms, both body fossils and ichnofossils, in the reef and reef-associated sediments of the Forteau Formation is a relatively diverse one for early Cambrian time. The environment in which these organisms lived was relatively tranquil, yet subject to periodic disturbances shown by the cyclicity of the inter-reef sediments. The correlation between a periodically disturbed environment and diverse fauna is consistent with some current ecological thinking. The lack of extensive sheets of reef debris swept off the mounds and broken skeletons suggests that these disturbances, while widespread, were not catastrophic, perhaps more in the form of periodic influxes of mud from land as the result of rainstorms and floods than large cyclonic oceanic storms that churned up the whole bottom. Because we cannot gauge the time involved we cannot say how frequent these events were.

In contrast to the distribution of other organisms, however, the archaeocyathan community appears to have responded to other environmental factors. The large number of individuals and small number of species, together with the almost complete dominance of the fauna by one form, suggests a community that had reached dynamic equilibrium. A possible explanation (Huston 1979) is that the archaeocyathans, in contrast to the other benthic organisms, had a very high population growth rate. As a result the archaeocyathans recovered from any disturbances much more rapidly than the other taxa and quickly returned to equilibrium. This in turn implies that the archaeocyathans were especially well-adapted to this environment and able to utilize the available trophic resources exceptionally well. We can at this stage only speculate as to which of the trophic resources was the most critical but it is tempting to call upon food supply in such an obviously nutrient-rich setting.

Geological Age. To assess the diversity of the archaeocyathan fauna in this area in terms of its geological age we have plotted the variation in the number of archaeocyathan genera with time for all documented localities which we know of in text-fig. 6. In the oldest strata of the Tommotian Stage, a total of fifteen families are known, all from the Siberian Platform (U.S.S.R.). A marked increase in diversity is recorded in the Atdabanian Stage, coincident with the first appearance of trilobites. Differences in the faunas from area to area at this stage are likely due to radiation out from a centre of

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EXPLANATION OF PLATE 49

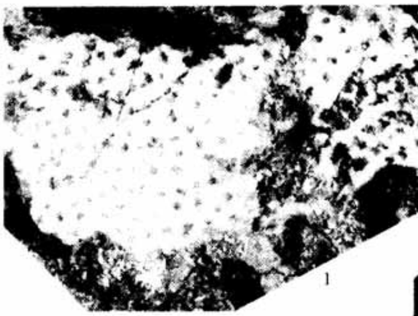
Field Exposures.

Fig. 1. *Retilamina amourensis* sp. nov. × 1, Treasure Reef (Bioherm), upper wall with holes.

Figs. 2, 5, 6. *Metaldetes profundus* (Billings). 2, × 0·5, Fox Cove; a cylindrical cup with well marked external bulges. 5, × 1, Treasure Reef (Bioherm horizon); a narrow cup surrounded by several rings of exostructures ('*Exocyathus*' *canadensis* Okulitch). 6, × 0·5, Fox Cove; a conical expanding cup (plate-like form).

Fig. 3. *Archaeocyathus atlanticus* Billings, × 1·5, Fox Cove, Bioherm horizon.

Fig. 4. *Archaeosycon billingsi* (Walcott), × 1, Treasure Reef; a longitudinal section with the tabulae well exposed.



1

2

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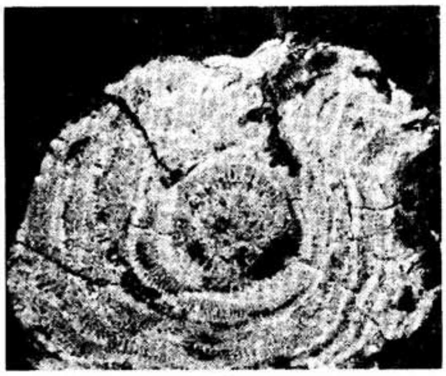
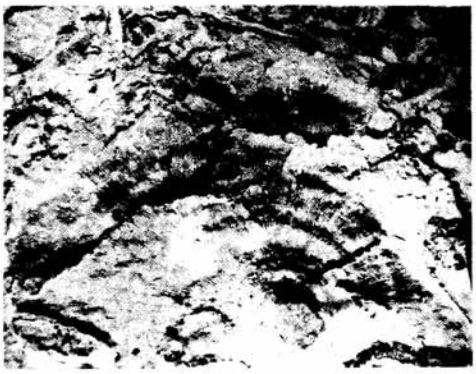
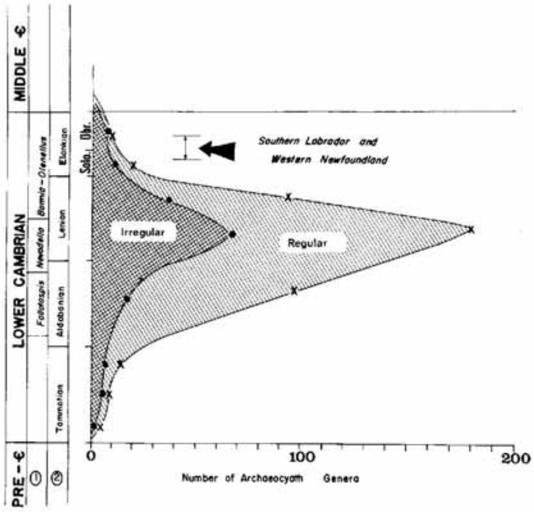


5



6

DEBRENNE and JAMES, Archaeocyathid reefs



TEXT-FIG. 6. A plot of the number of archaeocyathan genera against time for the Lower Cambrian (data from Debrenne, pers. obs.), with the time interval represented by the Forteau Formation superimposed. Stages at left: (1) North American trilobite zonation of Fritz (1972), (2) Lower Cambrian stages of the Siberian Platform, U.S.S.R. from Rozanov and Debrenne (1974); correlation from Palmer and Rozanov (1976) (Solo = Solontzy horizon; Obr = Obruchev horizon.)

dispersion, which was probably somewhere in the Altai-Sayan region of the western U.S.S.R. During the Lenian (Botomian of some authors), archaeocyathans achieve their greatest geographic extent and widest diversity, coincident with the rapid expansion of trilobite genera (Rozanov and Debrenne 1974). At this time differences in faunas between areas are strongly marked. There is a stock of taxa distributed world-wide as well as some well-defined endemic forms. Towards the close of the succeeding Elankian Stage (Lenian of some authors) there is a dramatic decrease in the numbers of taxa as well as of individual archaeocyathans. The remaining fauna evolved in place from the already diversified stock, probably in areas which were isolated, and so provincialism is the rule. On the basis of this analysis it is evident that the archaeocyathan fauna we have described here flourished at a time well past the acme of archaeocyathan evolution and just prior to the extinction of the phylum. In this respect the number of species and genera is similar to other archaeocyathan occurrences of this age elsewhere and so is not unusual.

SYSTEMATIC PALAEONTOLOGY

Archaeocyathans were some of the first animals to develop a calcium carbonate skeleton. The basic skeleton is relatively simple, composed of an individual 'cup' comprising two coaxial, inverted porous cones (the walls) which are connected by various, more or less radial and sometimes horizontal, skeletal elements (Hill 1972). The two main groups (classes) of archaeocyathans, Regulares and Irregulares, are defined by their ontogenetic evolution (Zhuravleva 1960). The archaeocyathans described in this report all belong to the class Irregulares. Generally speaking, most of the Irregulares have a central cavity and an inner wall, which, in the early stages of development are not differentiated. The radial partitions (pseudosepta) in the intervallum (the area between walls), when present, are seldom as uniform or evenly spaced as in the Regulares. The porosity of the walls is never as complicated as in the Regulares and the number of types of pores is less important. Vesicular tissue (dissepiments), secondary thickening (stereoplasma), and exostructures (outgrowths) are frequent and well developed in the Irregulares whereas they are uncommon amongst Regulares.

All samples figured in this study are retained at the Geological Survey of Canada, Ottawa (GSC); other samples are retained in the Muséum National D'Histoire Naturelle, Paris (MNHN).

Family ARCHAEOCYATHIDAE Hinde, 1889
Genus ARCHAEOCYATHUS Billings, 1861

1861 *Archeocyathus* Billings, p. 4.
1865 *Archaeocyathus* Dawson, p. 51.
1868 *Archeocyathus* Billings; Meek, p. 62.
1878 *Archaeocyathus* Billings; Roemer, p. 369.
1886 *Archaeocyathus* Billings; Walcott, p. 75 (type-species *atlanticus*).
1889 *Spirocyathus* Hinde, p. 136 (type-species *atlanticus*)
1932 *Retecyathus* Vologdin, p. 20 (type-species *laqueus* Vologdin, lecotype chosen by Simon 1939, p. 36)
1940 *Archaeocyathus* Billings; Okulitch, p. 77 (type-species *atlanticus*)

Type-species. *A. atlanticus* Billings 1861, subsequent designation by Walcott 1886. The choice of *profundus* by Hinde (1889) as the type species is incorrect according to the rules of zoological nomenclature because *profundus* was not described together with the first documentation of the genus *Archaeocyathus* in 1861 (Okulitch 1937). The original spelling *Archeocyathus* used by Billings (1861–1865) and Meek (1868) was emended to *Archaeocyathus* by Dawson (1865) and has since passed into general use, even though it is not a valid emendation. Hill (1965), in the interest of stability, submitted this case to the ICZN, and the spelling *Archaeocyathus* is now the only officially accepted form.

Diagnosis. Conical cup displaying a few smooth transverse constrictions. Outer wall with many fairly regular small pores; inner wall with one pore per intertaenial space; intervallum made of pseudosepta (or taeniae) undulating and sometimes bifurcating. Few synapticulae and dissepiments. Most of the primary elements of the skeleton, and notably the inner wall and the inner part of the intervallum adjacent to the central cavity, are surrounded by secondary laminations which can be three or four times thicker than the initial skeleton. Outgrowths, although not as important as in *Metaldetes*, are present mainly as buds of limited size.

Discussion. The development of successive layers considerably changes the aspect of the skeletal structures and leads to the formation of 'narrow loculi often closed at their end' and of 'internal canals' (Hinde 1889, p. 134). Hinde (1889) was the first to recognize these secondary layers describing 'a primary central layer enclosed by successive secondary layers of a minute granular carbonate of lime'. Because of this additional skeletal material the nature of the inner wall is difficult to describe. Where there are many secondary layers of stereoplasma then the original single oval pores in each intertaenial space are transformed into 'canals'. It appears that the wall was not originally composed of these canals because, despite the rarity of examples, there are specimens in which there is an initial bare skeleton (Pl. 50, fig. 1). Thus it seems that the secondary laminations, whose cause or origin we do not know, are not of high taxonomic importance, especially since their occurrence is not consistent in the interior of even a single individual.

Although the microcrystalline nature of the *A. atlanticus* skeleton has been known since the work of Hinde (1889) only recently have the fine crystallites in the non-thickened skeletal material been examined (Lafuste and Debrenne 1977). The nature of the secondary tissue remains unresolved. Using ultra-thin sections (using the technique developed by Lafuste 1974) and scanning electron microscope (Camebax, Institut de Paleontologie, technician S. Laroche) the composition of the optically clear zone that surrounds the initial skeleton has been determined. In thin section the zone is composed of prismatic crystals of calcite, elongated and aligned with their c-axes perpendicular to the original skeletal walls. The size of these crystallites is 0·75 μm × 2·0 μm while the diameter of the crystallites that comprise the tubercules and main elements of the skeleton are always less than 0·75 μm (Pl. 55, fig. 2). The crystallites of successive sheets have the same shape as those of the skeleton with a slightly smaller average size (0·50 μm). Between each of the secondary laminations or sheets are palisades of larger crystals, somewhat less distinct compared with those between the original skeleton and the beginning of the stereoplasma (Pl. 55, fig. 2). The last layer is formed by small crystallites whose diameter approximates that of the vesicular tissue (Lafuste and Debrenne 1977).

On the basis of these and other observations it appears that the formation of the skeleton, precipitation of secondary laminations and finally the formation of dissepiments occurs in many different stages. The ability of the organism to produce different skeletal structures at different times has been noted before (Lafuste and Debrenne 1977) but in the case of *A. atlanticus* it is even more complex than previously supposed. The biological reasons for these secondary skeletal elements are at present completely unknown. It is certain, however, that for whatever reasons (e.g. ecological, seasonal, pathological, defensive) the archaeocyathan reinforced its skeleton several times, with or without interruptions of paling tissue, secreting elements of microscopic composition comparable to those of the primary skeleton.

If the presence of stereoplasma is considered a secondary phenomenon so that its systematic significance is only at the specific or intraspecific level, then the genus *Archaeocyathus* is close to the genus *Protopharetra*, which differs only in the irregularity and density of its taeniae, more or less organized in well-defined radial pseudosepta or alveoles, remaining at the stage of amoeboid plates (Debrenne 1964, p. 30). On the other hand, the genus *Flindersicyathus* Bedford (actually considered as a recent synonym of *Pycnoidocyathus* Taylor) has been frequently interpreted as a junior synonym of *Archaeocyathus* (Zhuravleva 1960; Rozanov 1977). *Flindersicyathus* differs from *Archaeocyathus*, however, mainly in the composition of its inner wall, which contains oblique canals in the shape of a very long S, the opening leading toward the top of the central cavity.

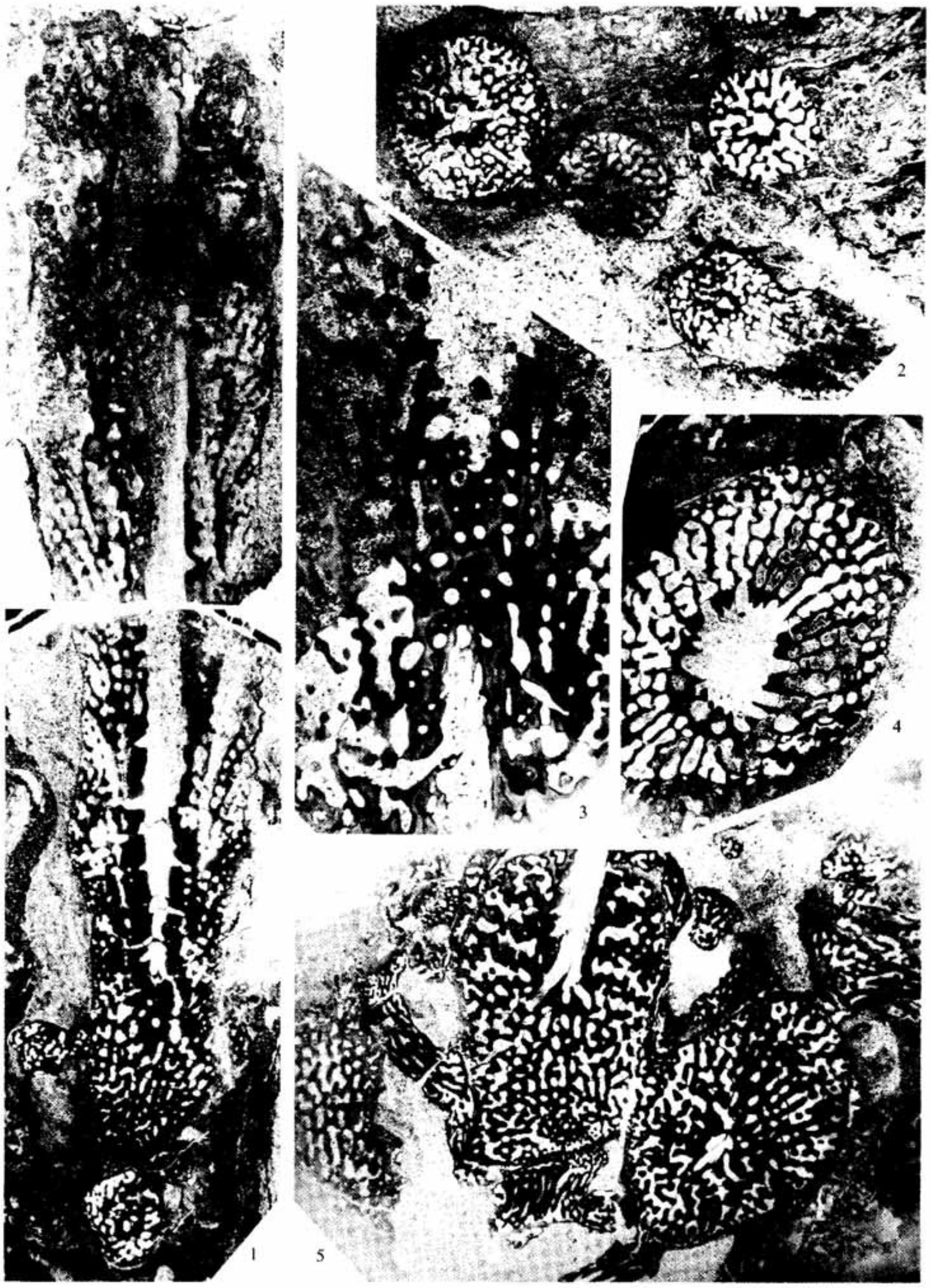
Geographic and stratigraphic distribution. This may change by revision of species according to the above observations. Labrador, Antarctica, U.S.S.R., Mongolia, China, Spain, Elankian Stage.

Included species. altaicus Vologdin 1932 (formerly *Metaldetes*) *arborensis* Okulitch 1954 (*Archaeocyathus*), *borealis* Okulitch 1955 (*Archaeocyathus*), *camptophragma* Vologdin 1937 (formerly *Retecyathus*), *constrictus* Raymond 1931 (formerly *Spirocyathus*), *grandis* Yaroshevich 1966 (*Archaeocyathus*), *hupehensis* Chi 1940 (formerly *Spirocyathus*), *kusmini* Vologdin 1932 (formerly *Retecyathus*), *laqueus* Vologdin 1937 (formerly *Retecyathus*), *loculiformis* Okulitch 1955 (*Archaeocyathus*), *microporosus* Chernysheva 1960 (*Archaeocyathus*), *operosus* Zhuravleva 1955 (formerly *Retecyathus*), *regularis* Krasnopeeva 1960 (*Archaeocyathus*), *seliverstovae* Yazmir *et al.* 1975 (formerly *Retecyathus*), *shixiqiaoensis* Zhang 1974 (formerly *Retecyathus*), *subradiatus* Vologdin 1931 (formerly *Spirocyathus*), *tenuis* Vologdin 1940 (formerly *Spirocyathus*), *yavorskii* Vologdin 1931 (formerly *Retecyathus*).

EXPLANATION OF PLATE 50

Figs. 1–5. *Archaeocyathus atlanticus* Billings, 1861. 1, GSC 62106, × 3, lower and upper parts of the same longitudinal section. Variations in dissepimentation and development of stereoplasma from the initial part of the top, Mount St. Margaret, Newfoundland. 2, GSC 62107, × 3, three juvenile cups, with a different development of stereoplasma, Mount St. Margaret, Newfoundland. 3, GSC 62108, × 5, tangential section of the inner wall: skeleton light grey, stereoplasma dark, Fox Cove, Labrador. 4, GSC 62109, × 3, upper transverse section. The secondary layers are developed on the inner side of the initial wall, Fox Cove, Labrador. 5, GSC 62110, × 3, a cluster of colonial cups with buds, Fox Cove, Labrador.

PLATE 50



DEBRENNE and JAMES, *Archaeocyathus*

Archaeocyathus atlanticus Billings, 1861

Plate 48, fig. 4; Plate 50, figs. 1–5; Plate 54, fig. 4; Plate 55, fig. 2

1861 *Archeocyathus atlanticus* Billings, pp. 5–6, fig. 5
1866 *Archeocyathus atlanticus* Billings; Walcott, pp. 73–74, pl. III, figs. 1–2.
1887 *Archaeocyathus atlanticus* Billings; Bornemann, p. 42, pl. 33, fig. 5.
1940 *Archaeocyathus atlanticus* Billings; Okulitch, pp. 77–78, pl. I, figs. 1–3.
1943 *Archaeocyathus atlanticus* Billings; Okulitch, p. 68, pl. 5, fig. 102, pl. 18*c*.
?1948 *Archaeocyathus atlanticus* Billings; Okulitch, p. 344, pl. 54, figs. 1–2.
?1954 *Archaeocyathus atlanticus* Billings; Okulitch, p. 295, pl. 28, figs. 1–2.
?1955 *Archaeocyathus atlanticus* Billings; Okulitch, p. III, fig. 1.
1959 *Archaeocyathus atlanticus* Billings; Greggs, p. 67, pl. 12, figs. 7–9; pl. 14, fig. 4.

Material. Holotype, GSC 369; other material: GSC 62106, 62107, 62108, 62109, 62110; MNHN L83 001, L83 005, L83 008, L83 039, L83 045, L83 049, L83 050.

Diagnosis. Cylindro-conical cups, fairly narrow central cavity often limited by the development of the stereoplasma. The maximum diameter of the forms studied is 20 mm. Most of the samples have a diameter of 10 mm, an intervallum of 3·5 to 4·0 mm and a central cavity of 3·5 to 2·0 mm. When the stereoplasma is well developed around the inner wall, the size of the intertaenial spaces varies with the secondary development of the skeletal tissue; it ranges from 0·3 to 0·5 mm with diameter of 9–10 mm. The outer wall has fairly regularly distributed small pores, with a diameter of 0·05 mm, separated by lintels of the same size. It is often encased on the outside by a pellicle of dissepimental tissue. The openings of the pores of the inner wall vary with the nature of the secondary laminations; small rounded openings indicate the presence of thin canals across the stereoplasma. The central cavity is generally empty, except for some vesicular bridges. It can be very narrow (0·8 mm).

Discussion. The holotype (GSC 369) is a single, large, cylindrical fragment 27 to 30 mm in diameter. Although most of the samples collected from Labrador are smaller, some rare cups are as large as the holotype and so precise identification and definition of the specific variability is possible. Amongst the species presently listed in the genus, some are too poorly preserved or inadequately described to permit precise comparison (e.g. *altaicus* Vologdin, *constrictus* Raymond, *loculiformis* Okulitch.) The North American species *arborensis* Okulitch and *borealis* Okulitch have a comparatively thinner primary skeleton (disregarding the development of stereoplasma) and the intervallum elements are closer together. The species formerly belonging to *Retecyathus* have more twisted taeniae, less radial pseudosepta, and more abundant synapticulae.

Geographic and stratigraphic distribution. Specimens from British Columbia are poorly preserved making a precise determination impossible; in the absence of new material the presence of *A. atlanticus* in British Columbia is doubtful. The species from Antarctica (Gordon 1920, p. 6, pl. III, fig. 32; pl. IV, figs. 37–42) are probably closer to *Archaeocyathus ksmini* Vologdin and Siberian species than to *A. atlanticus*. The specimen described as *Spirocyathus atlanticus* (Billings) by Ting (1937, pp. 368–369, pl. XIII, figs. 1–4) should be identified as the *?Pycnoidocyathus irregularis* (Taylor). *A. atlanticus* Billings seems to be confined to Labrador.

Family METACYATHIDAE Bedford and Bedford, 1934

Genus METALDETES Taylor, 1910

1910 *Metaldetes* Taylor, p. 151.
1934 *Metacyathus* R. and W. R. Bedford, p. 5.
1937 *Cambrocyathus* Okulitch, p. 251.
1943 *Metethmophyllum* Okulitch, p. 79.
1957 *Bedfordcyathus* Vologdin, pp. 182–209.
?1959 *Schiderticyathus* Krasnopeeva, pp. 3–4.
1965 *Ladaecyathus* Zhuravleva 1960, Hill, pars, p. 84.
1971 *Ladaecyathus* Zhuravleva 1960; Handfield, pars, p. 53.
1973 *Praefungia* Debrenne, p. 228.

Type Species. Metaldetes cylindricus Taylor 1910, University of Adelaide (S.A.). *Holotype*. T 1592A.

Diagnosis. Single or colonial cups. The outer wall has an initial covering with more or less regular small pores, covered on the outside by a second layer connected to the first by spines (pores in 'trident' in Taylor's original diagnosis). Spines project into the central cavity from the inner wall and support a microporous sheath. When there are endothecal structures inside the central cavity the microporous sheath is replaced by a membrane of vesicular tissue. The inner wall develops late in ontogeny. The apical part with no central cavity is full of skeletal elements without distinct radial direction, but with many tangential links between them. Later, after the individualization of the inner wall, the central cavity clears itself more or less completely (the presence of an endothecal structure is common when the exothecal structure is well developed); at this stage the skeletal elements in the intervallum are organized into radial pseudosepta which may be connected by dissepiments or sometimes by synapticulae.

Discussion. The revision of Bedford's and Taylor's collections indicates that the more or less complete, prolific development of vesicular tissue and the almost complete evolution of the taeniae into radial pseudosepta are not generic characteristics (Debrenne 1969, p. 355; 1973, p. 219). The genera *Metacyathus* Bedford and *Bedfordcyathus* Vologdin appear to be recent synonyms of *Metaldetes*. A comparison with *Cambrocyathus* Okulitch has already been proposed, notwithstanding the separation of *Metaldetes* and *Cambrocyathus* on the basis of a more complete acquisition of regular radial pseudosepta in *Cambrocyathus*. The large number of '*Cambrocyathus*' examined in the material from Labrador indicate intra-specific rather than inter-specific variations in skeletal structure. Likewise the genus *Praefungia* Debrenne (1973), which was provisionally erected to encompass all the species without dissepiments, falls into synonymy with *Metaldetes*, all the transitional forms having been found in the material from Labrador. These observations also lead us to doubt the validity of attributing the species *fortiseptatus* Hill (1965) and *fischeri* Handfield (1971) to the regular genus *Ladaecyathus* Zhuravleva (1960). Examination of the holotypes (British Museum (Natural History) and GSC) leads us to include them in the revised genus *Metaldetes*. The inconsistent character of the double inner wall suggests a possible synonymy of the genus *Schiderticyathus* Krasnopeeva (1959) with *Metaldetes*. We were not able to examine this material ourselves and so for the present, we reserve a definitive opinion on this genus.

Okulitch (1943) erected the genus *Metethmophyllum* for *Ethmophyllum meeki* Walcott (1889). He pointed out the strong similarities between this new genus and *Cambrocyathus*, the only difference being the lack of synapticulae in *Metethmophyllum*. As synapticulae are not a characteristic feature for *Cambrocyathus* (now *Metaldetes*) there is no reason to maintain *Metethmophyllum* as an independent genus.

Species included. cylindricus Taylor 1910, *dissepimentalis* Taylor 1910 (gathering the species *conicus* Bedford R. and W. R. 1934, *irregularis* Bedford R. and W. R. 1934, *taylori* Bedford R. and W. R. 1936, all of which are considered junior synonyms by Debrenne 1974, p. 221), *dispersa* Debrenne 1974, *meeki* Walcott 1891 (formerly *Metethmophyllum* Okulitch 1943), *resseri* Okulitch 1943 (formerly *Metethmophyllum* Okulitch 1943), *plicatus* Gordon 1920, *profundus* Billings 1865 (formerly *Cambrocyathus* Okulitch 1937—gathering the species *amourensis* Okulitch 1943, *dissepimentalis* Okulitch 1943, *loupensis* Okulitch 1940, *labradorensis* Okulitch 1943, *Metethmophyllum fisheri* Handfield 1971—previously *Ladeacyathus* Zhuravleva 1960, all of which are here considered junior synonyms of *profundus*), *superbus* Bedford R. and W. R. 1936 (formerly *Praefungia* Debrenne, 1974). The following species, *caribouensis* Handfield 1971, *lairdi* Hill 1965, *simpliporus* nov. sp., and *ramulosus* Bedford R. and J. 1937, all of which have some untypical characteristics, and the species *donaldi* Okulitch 1948 and *septimus* Okulitch 1948, which are poorly preserved, are tentatively included in the genus *Metaldetes*.

Geographic and stratigraphic distribution. Australia, Antarctica, British Columbia, Yukon, Virginia, Labrador, Newfoundland. Middle and Upper part of the Lower Cambrian. Not known in the Soviet Union and China.

Metaldetes profundus (Billings 1865)

Plate 48, figs. 2, 3, 5; Plate 49, figs. 2, 5, 6; Plate 51, figs. 1–5; Plate 53, fig. 1; Plate 55, fig. 3

1865 *Archeocyathus profundus* Billings, pp. 4–5, figs. 1–4.
1886 *Ethmophyllum profundum* (Billings); Walcott, p. 84, pl. I, figs. 1*a–d*; pl. II, fig. 3; pl. IV, fig. 3; pl. VIII, fig. 3.
non 1887 *Archaeocyathus profundus* Billings; Bornemann, p. 41, pl. 32, figs. 1–2.
1889 *Archaeocyathus profundus* Billings; Hinde, p. 136, pl. V, figs. 1–2.
1937 *Cambrocyathus profundus* (Billings); Okulitch, p. 251.
?1940 *Cambrocyathus loupensis* Okulitch, pp. 82–83, pl. 1, fig. 4.
1943 *Cambrocyathus profundus* (Billings); Okulitch, p. 72, pl. 6, fig. 7; pl. 7, figs. 1–2; pl. 8, figs. 1–5; pl. 9, fig. 3; pl. 18*a*.
1943 *Cambrocyathus amourensis* Okulitch, p. 76, pl. 9, fig. 3; pl. 10, fig. 3; pl. II, figs. 1–3; pl. 18, fig. 1*b*.
1943 *Cambrocyathus dissepimentalis* Okulitch, p. 77, pl. II, fig. 4.
?1943 *Methethmophyllum labradorensis* Okulitch, p. 80, pl. 13, fig. 14.
1946 *Cambrocyathus profundus* (Billings); Okulitch, p. 85, pl. IV; pl. VIII, fig. 1A.
1946 *Cambrocyathus amourensis* Okulitch, p. 85, pl. I, fig. A, B; pl. II; pl. III; pl. VI, figs. 4, 6, 7; pl. VII, figs. 1B, 2, 4.
?1955 *Pycnoidocyathus amourensis* (Okulitch), p. 58, pl. II, figs. 5–8.
?1957 *Pycnoidocyathus amourensis* (Okulitch); Kawase and Okulitch, p. 925, pl. 112, fig. 1.
?1957 *Cambrocyathus dissepimentalis* Okulitch; Kawase and Okulitch, p. 925, pl. 112, fig. 7.
?1959 *Pycnoidocyathus amourensis* (Okulitch); Greggs, p. 76, pl. 13, figs. 9–10.
1964 *Cambrocyathus profundus* (Billings); Debrenne, p. 100, pl. 44, figs. 3–4.
1964 *Cambrocyathus amourensis* Okulitch; Debrenne, p. 100, pl. 44, figs. 2–5.
1971 *Ladaecyathus fischeri* Handfield, p. 54, pl. VIII, figs. 3*a–e*; pl. IX, figs. 1*a–b*.

The species with ? correspond to poorly preserved specimens, known only from unprepared samples. It is impossible therefore to be sure of their specific characteristics.

Material. Lectotype, selected: Okulitch, 1943, p. 96, pl. 7, figs. 1–2, GSC 341; other material: GSC 62111, 62112, 62113, 62114, 62115; MNHN L83 003, L83 006, L83 009, L83 014, L83 017, L83 022, L83 026, L83 028, L83 046, L83 051.

Description. Cup of variable external form: cylindrical with a height of 40–50 mm and constant diameter (average 10 mm)—sticks; cylindro-conical with external bulging (height 190 mm, diameter 80 mm); bell-shaped cones (bowls) to saucers with a variable height (reaching a maximum observed diameter of 250 mm) (pl. 49, figs. 5, 6). The size of the intervallum is generally wider for small cups (2·10 mm for a diameter of 10 mm) than for the larger ones (1·9 mm for a diameter of 40 mm) and it also varies because of the transverse annular bulges most often related to development of exothecal structures (Okulitch 1943, pl. 48, fig. 1). Cups linked to one another by exothecal tissue (which possibly plays the role of coenenchyme), may be regarded as colonial (pl. 51, figs. 1, 3). The walls are complex. The outer wall has a fairly thick skeleton (0·10 mm) with two to four pores per intertaenial space, often developed into funnels protected by spines. These spines form a second covering and support a membrane or give rise to exothecal structures (pl. 55, fig. 3). These structures are also found, although not as commonly, in the inner wall (two to three pores per intertaenial space). The spines, acting as an additional

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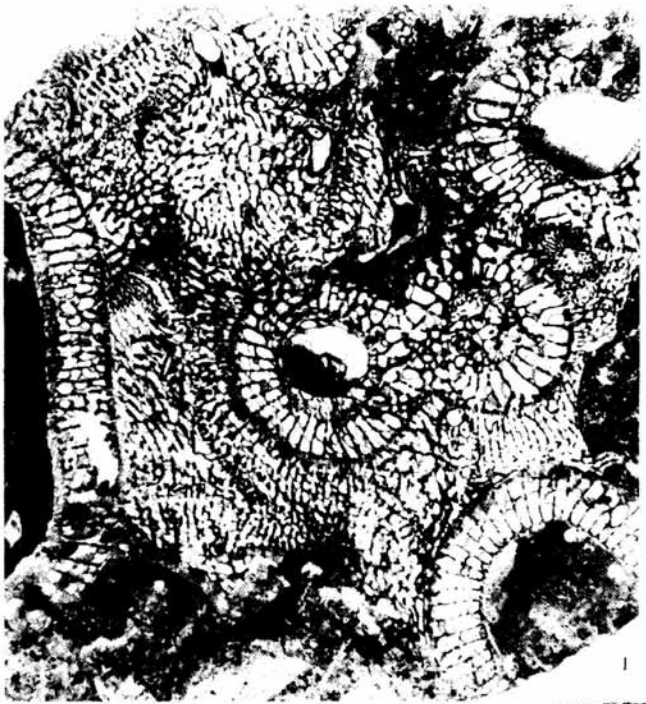
EXPLANATION OF PLATE 51

Figs. 1–5. *Metaldetes profundus* (Billings, 1865). 1, GSC 62111, ×3, colonial cups and development of exostructure building a massive colony, Schooner Cove, Labrador. 2*a*, *b*, GSC 62112, ×3, longitudinal section of the lower part (stick-like portion) of an expanding cup (Bowl), Mount St. Margaret, Newfoundland. 3, GSC 62113, ×3, adult cups with exostructures and a narrow zone of endostructure, Fox Cove, Labrador. 4, GSC 62114, ×3, intraspecific variation: a specimen without dissepiments, similar to '*Ladaecyathus*' *fischeri* Handfield, Mount St. Margaret, Newfoundland. GSC 62115, ×3, intraspecific variations: diminution in the number of septa and increase in the width of intervallum, Forteau Point, Labrador.

PLATE 51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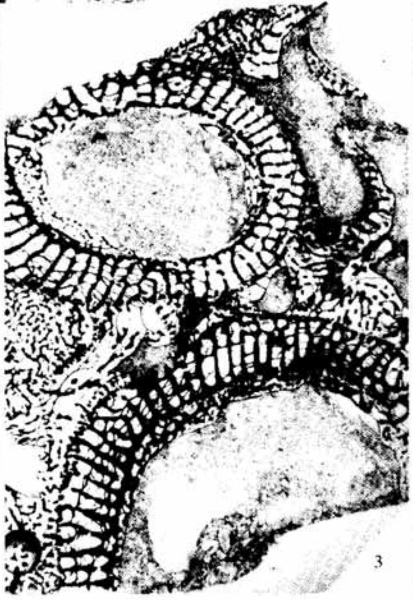
2a


2b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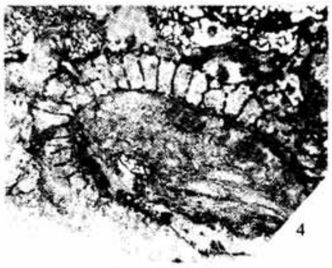
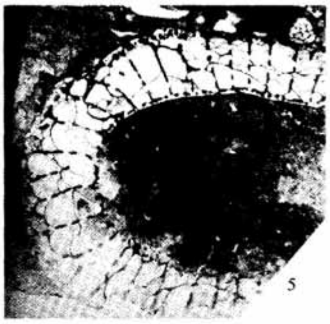

4


5

DEBRENNE and JAMES, *Metaldetes*

defence, may support protecting membranes and/or endothecal structures. Nevertheless, they are not as consistent as in the outer wall. It is not possible to use these elements as specific criteria because all the examples can be present in a single individual.

The parietal coefficient (RK) would be more useful in speciation but it is difficult to establish here because of the very irregular nature of the bowl-shaped forms. Nevertheless, after serial sectioning and numerous measurements on forty individuals, the main characteristics for a basic diameter of 20 mm are as follows: in the lower patch reefs the intervallum varies from 2·10 to 3·0 mm in width and the interseptum distance from 0·6 to 0·8 mm whereas in the upper biostrome the intervallum varies from 1·6 to 2·0 mm in width with an interseptum distance of 0·5–0·6 mm. Because of the small differences in the numerical data, a much larger sample base is needed for both reef complexes to statistically differentiate these two apparent groups into species.

Discussion. The great variability of the external shape (pl. 48, fig. 3), size of the intervallum, and distribution of the parieties and dissepiments (pl. 51, figs. 2, 4, 5) prevent us from defining taxonomic categories at the species level. We presently consider all these variations as intraspecific, within the species *profundus* Billings. Further studies based on population systematics are needed to establish if the variations observed fall into a single species or not. The wide specific variability is also present in material from Australia and most of the species described have been gathered into a limited number of taxa (see Debrenne 1974). The species *dissepimentalis* Taylor from Australia differs from *profundus* by the presence of a comparatively large intervallum and a massive cylindrical body (up to 95 mm high with a diameter of 40 mm and an intervallum of 10 mm). Direct comparison with the other species listed above is difficult because none of them has been studied from the viewpoint of specific variability. *M. cylindricus* Taylor and *M. plicatus* Gordon appear to be very similar to *M. profundus*.

Geographic and stratigraphic distribution. Confined to Labrador and Newfoundland, the upper part of the Lower Cambrian.

Metaldetes? simpliporus Debrenne and James sp. nov.

Plate 53, fig. 5

Material. Holotype, GSC 62124; other material: MNHN L83 015, L83 018, L83 023, L83 030, L83 032.

Diagnosis. Cylindrical cup with double outer wall, inner wall poorly defined, and central activity partially filled with skeletal elements which are different from the endothecal structures present in the other species and are probably from spines of the inner wall. The intervallum is large and filled with loosened pseudosepta and vesicular tissue.

Discussion. We do not know exactly which of the large diameter cone-shaped forms might correspond to these sticks; probably they are incompatible because of the width of the intervallum. The diameter of the cylindrical cup can reach 40 mm, with an intervallum of 4·6 mm and partitions 0·8 mm apart. The outer wall supports a second layer although the inner wall is simple (one or two pores). It is difficult to discern whether the elements of the central cavity (pl. 53, fig. 5) which are fastened to this wall can be considered equivalent to the spines and the protective zone of the *Metaldetes* types. The central cavity frees itself later than in the other species of *Metaldetes*; it is included in the genus (with some reservations) because the young stages of *Metaldetes* have no definite inner wall and no central cavity (*M. cylindricus* Taylor 1910, fig. 88). The development of exothecal structures in concentric zones is fairly constantly associated with these cups (pl. 53, fig. 5). These large diameter sticks with a well-defined central cavity recall *Protopharetra radiata* Bornemann, but the outer wall is more complex in *simpliporus*. In North America *Metaldetes caribouensis* Handfield is extremely similar (based on the examination of unpublished figures) but because it does not exceed 8 mm in diameter it is extremely difficult to unite these forms. Okulitch (1943, pl. 12, figs. 4, 5) described and figured a form named *dunbari* from the Forteau Formation. This stick-like form, which does not have a central cavity, may be related to *caribouensis* but unfortunately the outer wall of the specimen is weathered away and so it cannot be compared with *simpliporus*.

Family ARCHAEOSYCONIDAE Zhuravleva, 1960
Genus ARCHAEOSYCON Taylor, 1910

Type-species. Archaeosycon billingsi Walcott, 1886

Diagnosis. Cylindrical cups, solitary or in colonial association, with a wide intervallum in which are developed successive porous, domed tabulae connected by longitudinal rods, perpendicular to the tabulae, arranged in radial highly porous pseudosepta. Outer wall formed by the down-turned edges of tabulae, inner wall delineated by the taeniae and tabulae and screened by an independent microporous sheath. Stereoplasma occurs as a rule at the level of the inner wall and may thicken other skeletal elements as well. Dissepiments *sensu stricto* and exostructures often present. No synapticulae.

Discussion. The presence of abundant material in Labrador has allowed us to accurately describe the skeletal elements and their interconnections; a microporous inner wall has never been described before but in these samples it is always present, regardless of whether the skeleton displays secondary thickening or not. The exact structure of the radial elements has been determined: the oblique upward and outward alignment of rods suggest that pseudosepta are present and that rods are not scattered haphazardly. They form coarsely porous thin radial pseudosepta, well illustrated in transverse sections (pl. 52, fig. 5). At the junction with tabulae the rods are flattened and nearly fuse to form thin radial alignments. Between tabulae these rods are thinner and the radial alignment is more difficult to determine, especially in longitudinal section because the section has to be cut exactly through a septa 0·09 mm thick, perforated by pores of 0·5 to 1·0 mm diameter. The early stages have an internal space filled by twisted taeniae. The inner wall and the central cavity are defined later in ontogeny. Secondary thickenings (stereoplasma) may change during the growth of the same cup. Exostructures occur as buds, generally developed at the base of the cups. *Archaeosycon* always has a cylindrical habit (sticks) and often occurs in clusters. These latter features are similar to those observed in the genus *Archaeocyathus*.

Claruscyathus Vologdin, 1932 and *Clarucoscinus* Handfield, 1971 could both be junior synonyms of *Archaeosycon* Taylor, 1910; unfortunately, in both cases, the exact structure of radial elements is not sufficiently known, and the presence of an inner microporous wall could not be either proven or disproven from the description or figures available at the present time. Study of the type material is now needed. *Archaeosycon* Taylor and the Irregulares with pseudotabulae (*Flindersicoscinus* Debrenne, 1970, *Dictyocoscinus* Bedford, 1936, *Metacoscinus* Bedford, 1934) have two different structural plans: in *Archaeosycon* the main intervallum structures are the arched tabulae while vertical radial rods are connecting elements; in the other species, septa are the main elements and tabulae are only present as horizontal sporadic structures built as sieves on a synapticulae system. The structure of *Archaeosycon* is much closer to *Paracoscinus* Bedford, 1936 and *Pycnoidocoscinus* Bedford, 1936, particularly as far as the inner wall pattern is concerned. But in these two genera, septa are solid and sparsely porous skeletal elements do not form a delicate framework of rods. *Tabulacyathus* Vologdin, 1932, *Abakanicyathus* Konyushkov, 1964, and specially *Tabulacyathellus* Missarzhevskiy, 1964 have a strong resemblance to *Archaeosycon*. The wall structure as well as the scarcity and slenderness of vertical rods, however, prevent complete identification.

Stratigraphical and geographical distribution. Until the case of *Claruscyathus* is solved, *Archaeosycon* is restricted to North America: Yukon, Alaska, Labrador.

Archaeosycon billingsi (Walcott 1886)

Plate 49, figs. 3, 4; Plate 52, figs. 1–5; Plate 53, fig. 2; Plate 55, fig. 4

1866 *Archaeocyathus billingsi* Walcott, p. 74, pl. III, figs. 3–3*a–c*.
1889 *Coscinocyathus billingsi* Walcott, p. 600; pl. 51, figs. 2, 2*a*, 2*b*.
1910 *Archaeosycon billingsi* (Walcott); Taylor, p. 111, text-fig. 50.
1943 *Archaeosycon billingsi* (Walcott); Okulitch, p. 83, pl. 14, figs. 2, 3, 4.
1943 *Archaeosycon vesiculosum* Okulitch, p. 82, pl. 15, figs. 1, 2.

Material. Holotype, USNM 15302; other material: GSC 62116, 62117, 62118, 62119, 62120; MNHN L83 040, L83 042, L83 044, L83 048.

Description. Conical cups, solitary, connected by external coenchyme or coenchyme-like tissue, or colonial by budding (clusters of *Archaeosycon*). The maximum diameter observed is 38 mm for a length of 195 mm. The tapering of the cone is restricted to the first 30 mm; in this case the diameter increases only from 30 mm to 38 mm for a length of 160 mm. Concomitantly the central cavity increases from 7·5 to 15 mm, the intervallum remaining nearly constant (9–12 mm). Tabulae are, on the average, 1·5 mm apart. Most of the specimens, in particular the holotype, are smaller than that described above. Dimensions: diameter 16 mm; intervallum 4·5 mm; intertabulum 1·0–1·2 mm; interseptum 0·6–0·7 mm; pores of tabulae and outer wall 0·10–0·20 mm; thickness of skeletal elements (taeniae, rods, tabulae, and lintel without stereoplasma) 0·05–0·09 mm; inner wall: openings 4 mm, micropores 0·5 mm sometimes subdivided by thinner partition to 0·05 mm.

Discussion. *A. vesiculosum* was described for the forms having 'cystose' tissue, i.e. stereoplasma. As in the case of *Archaeocyathus* and *Metaldetes* species, this feature is not a species characteristic and all intermediate forms may be present within a single specimen. Known only from Labrador.

Family PROTOCYCLOCYATHELLIDAE Vologdin, 1956
Genus ARRYTHMOCRICUS Debrenne and James, gen. nov.

Type-species. *A. kobluki* sp. nov.

Derivation of name. arrythmos = irregular, cricos = ring.

Diagnosis. Solitary or colonial cups. The outer wall is finely and regularly porous. The intervallum is composed of thin undulating taeniae, whose crests are bound by synapticulae and dissepiments; the ensemble forms a loose web, which contracts in regular meshes toward the periphery covered by the outer wall which acts as a secondary perforated layer. The inner wall has regular ring structures formed by the lower margins welded into an S-curve, with one canal per intersept (pseudo-annuli). The inner margin of the links can sometimes carry fine spikes. The initial stages do not have a central cavity; the skeletal elements are scattered and connected by dissepiments; the outer wall is compact, the inner wall has incomplete rings.

Discussion. The presence of the pseudo-annular inner wall is restricted among the Irregulares to the genera *Protocyclocyathus* Vologdin 1955 and *Fenestrocyathus* Handfield 1971. The form studied here differs from *Fenestrocyathus* Handfield in the architecture of the intervallum elements; in that latter genus, the pseudosepta and the synapticulae form a regular cubic mesh network. The case of *Protocyclocyathus* Vologdin is more difficult. This genus is known only from the figure of the type-species *Cyclocyathus irregularis* Vologdin, 1940, itself represented by a single thin section, now lost (Zhuravleva, personal communication). It is not possible to use the written description and the single figure to validate the genus. Consequently we propose to establish a new taxon. If a detailed revision of the genus *Protocyclocyathus*, including choice of a neotype, should happen in the future and it

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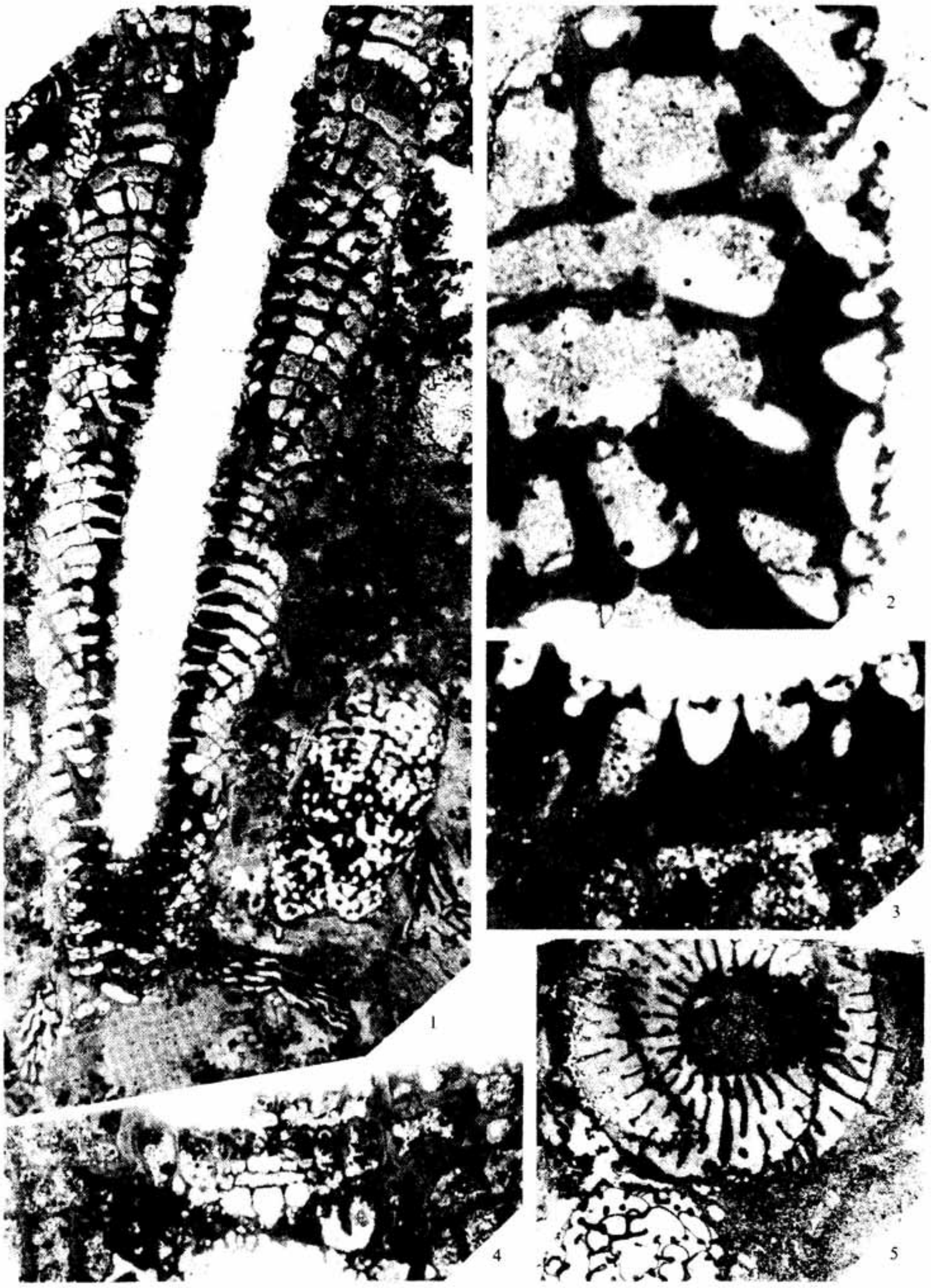
EXPLANATION OF PLATE 52

Figs. 1–5. *Archaeosycon billingsi* Walcott, 1886. 1, GSC 62116, × 4, longitudinal section with lateral buds, an association of vertical rods forming crude septa, dissepimentation and secondary thickening of the inner wall, Treasure Reef, Labrador. 2, GSC 62117, × 20, an enlargement of the inner part of the intervallum with arched tabulae and vertical rods, inner openings to the central cavity screened by a microporous sheath (dotted line)—central cavity to the left, Fox Cove, Labrador. 3, GSC 62118, × 20, details of a transverse section—central cavity at the top—tangential section of a tabulae, inner wall and microporous sheath, Treasure Reef, Labrador. 4, GSC 62119, × 10, tangential view of the microporous secondary inner wall, Treasure Reef, Labrador. 5, GSC 62120, × 10, transverse section with radial elements (traces of the junction of pseudosepta and tabulae) and tabulae in tangential view, Fox Cove, Labrador.



DEBRENNE and JAMES, *Archaeosycon*

corresponds to *Arrythmocricus*, then this new genus would be its junior synonym. For the present, species with taeniae and synapticulae possessing a simple outer wall and a pseudo-annular inner wall are regrouped under the genus *Arrythmocricus*.

Arrythmocricus kobluki Debrenne and James gen. et sp. nov.

Plate 53, figs. 1–4

Material. Holotype, GSC 62123; other material: GSC 62121, 62133; MNHN L83 016, L83 019, L83 024, L83 033, L83 038, L83 047.

Name. After Dr. D. R. Kobluk.

Diagnosis. Cylindrical cups, whose diameter is 8 mm for an intervallum of 2·1 to 2·4 mm at the adult stage. Colonies expand by lateral budding. The intervallum is full of undulating taeniae, with a thickness of less than 0·06 mm. Taeniae are connected by synapticulae, 0·25–0·30 mm apart forming a pseudohexagonal network. The meshes contract, close up, and become more regular at the periphery (0·16–0·20 mm). The outer wall covers the alveolar zone with a finely porous sheet possessing four pores per alveolar cell (diameter 0·04 mm, lintel 0·02 mm, thickness of the sheet (8·04). The inner wall is formed by a succession of annulae, 0·21 mm apart, the thickness of the sheet is less than 0·05 mm. The free edges of the annulae are spiked and can cover the whole surface facing the central cavity. The vesicular tissue is abundant and is most often limited to the subhorizontal sheets which traverse the intervallum and also the central cavity, to some variable space. These vesicular bridges which extend out from the inner wall support skeletal elements and contain spikes. A few isolated bars occur in more of these elements between the vesicular sheet and the elements of the inner wall (Pl. 53, fig. 3). The succession of sheets-to-bars-to-elements of the inner wall occurs repeatedly.

Development of the cups. The cups begin as a compact outer envelope with skeletal elements dispersed in the inner cavity, and at this stage there is neither inner wall, nor central cavity. The inner wall develops slowly (between 3 and 5 mm in diameter), first as a simple sheet with one pore per intersept, then as angled canals. Finally, the annulae are formed by fusion of the lateral margins of the intervening canals. At the same time the central cavity becomes free of skeletal elements, except for the vesicular bridges.

Budding and exothecal structures. From a simple cylindrical cup, a colonial form can develop through lateral budding. Very often, the base is enlarged and flattened when it is stuck on the wall of another species (Pl. 53, figs. 1, 2).

Discussion. This species is very near '*Flindersicyathus*' *macdamensis* Handfield, 1971. Examination of the type material, loaned by the Geological Survey of Canada, did not reveal the presence of complete rings. It seems that, in the case of *F. macdamensis*, the inner wall is made of bracts linked in incomplete annular shelves. More complete material would allow us to determine if this is an intraspecific variation or not. As a result of this difficulty we think it necessary to establish, provisionally, a new species.

EXPLANATION OF PLATE 53

Figs. 1–4. *Arrythmocricus kobluki* gen. et sp. nov. 1, GSC 62121, Paratype, × 5, transverse section of colonies by lateral budding and exothecal interstitial tissue. Associated *Metaldetes profundus* cups, Fox Cove, Labrador. 2, GSC 62122, Paratype, × 5, longitudinal section with tangential view of the annular inner wall and tangential view of the mesh-like outer wall. Exostructures anchoring the cup to an *Archaeosycon billingsi* Walcott (to the right). Surrounding patches of *Renalcis*, Treasure Reef, Labrador. 3, GSC 62123, Holotype, × 5, longitudinal section the S-shape of the annuli is visible; vesicular bridges are developed horizontally and carry some migrated elements from the inner wall, Fox Cove, Labrador. 4, GSC 62123, Holotype, × 5, tangential view of the annular inner wall at its junction with the septa, Fox Cove, Labrador.

Fig. 5. *Metaldetes ?simpliporus* sp. nov. GSC 62124, holotype, × 3, oblique longitudinal section: alveolar structures of the central cavity, with no define inner wall—successive layers of exostructures, Fox Cove, Labrador.

PLATE 53

DEBRENNE and JAMES, Archaeocyathans

Order UNCERTAIN
Family UNCERTAIN
Genus *Retilamina* Debrenne and James gen. nov.

Type-species. Retilamina amourensis sp. nov.

Derivation of name. rete = net, lamina = sheet.

Diagnosis. Large thin sheets, broadly undulating, often convex or patelliform, composed of skeletal elements which form a dictyonal-type network. One of the faces is open; the other is a compact wall, with occasional openings, carrying regularly distributed vesicules of various shapes. The ends of the skeleton are closed by the downward incurving of this wall. The wall may be thickened by secondary tissue of stereoplasma type. These thickenings may occur continuously in some individuals, but with a variable thickness. When there are openings and/or vesicles, there is no more skeletal thickening (Pl. 54, fig. 1). This stereoplasm also occurs at the contact between *Retilamina* and other organisms, or between two *Retilamina*. Few dissepiments are observed throughout the sheet. This dome-like habit commonly forms the roof of a cavity. The dictyonal network supports associated fauna (*Protophareta*-like buds and stolons issued from the exostructures of *Metaldetes*) and flora described in the reef cavities (James and Kobluk 1978; Kobluk and James 1979).

Retilamina amourensis Debrenne and James sp. nov.

Plate 49, fig. 1; Plate 54, figs. 1–5; Plate 55, fig. 1

Material. Holotype, GSC 62128; other material: GSC 62125, 26126, 26127, 62129; MNHN L83 003, L83 010, L83 012, L83 013, L83 020, L83 025, L83 027, L83 029, L83 034, L83 036, L83 041, L83 052.

Name. After Point Amour, Labrador.

Diagnosis. Retilamina occurs as small, gently convex domes in the form of an inverted, very shallow bowl, often resembling a large limpet. The skeleton is irregularly undulating and several individuals may be stacked irregularly on top of one another. The thickness of the inverted 'saucer' corresponds to the width of the skeletal network. A series of field observations indicates that the convex part with the compact wall bearing the vesicles is always uppermost, with the open network supporting attached bunches of renalcids and/or *Epiphyton*, *Archaeotrypa* or *Protopharetra*-like buds and stolons (Pl. 54, figs. 1–2), facing downward.

The skeletal elements combine to form a scaffolding of flattened bars, going in three directions (dictyonal network). The average width of the network is 1·5 to 2·0 mm, the thickness of a skeletal element 0·05 to 0·08 mm, the distance between them varying from 0·2 to 0·3 mm. The skeleton itself is composed of slightly interlocking calcite crystallites, small crystallites (1·8 mm) forming the margins of the skeletal elements, the larger crystallites (3 μm) associated with a few persistent small crystallites

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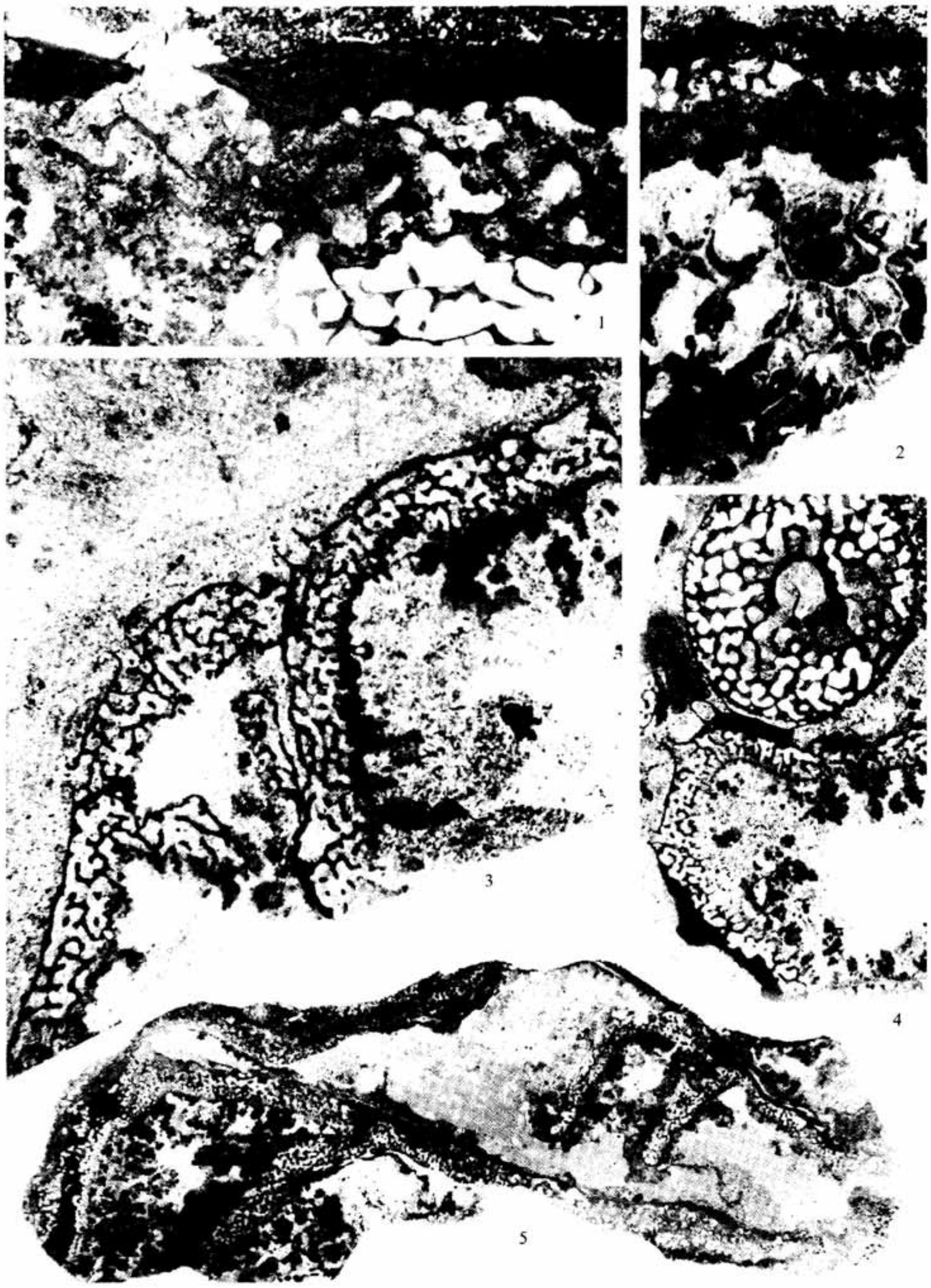
EXPLANATION OF PLATE 54

Figs. 1–5. *Retilamina amourensis* gen. et sp. nov. 1, GSC 62125, Paratype, × 15, close up of stereo-plasma development with reduction in thickness at the level of an external aperture. Detail of dictyonal network, Lighthouse Reef, Labrador. 2, GSC 62126, Paratype, × 10, cross-section of *Retilamina* illustrating the open-mesh network on the underside, attached *Renalcis* and a skeleton of *Archaeotrypa* Fritz, 1947 (polygonal pores), Osprey Reef, Labrador. 3, GSC 62127, Paratype, × 7·5, two associated limpet-like skeletons of *Retilamina*. Upper wall with vesicules of various shape, Mount St. Margaret, Newfoundland. 4, GSC 62128, Holotype, × 5, vesicules of various shape and development of stereoplasma in contact with an *Archaeocyathus atlanticus* Billings cup, Mount St. Margaret, Newfoundland. 5, GSC 62129, Paratype, × 3, domed successive forms in growth position, Schooner Cove, Labrador.

PLATE 54



DEBRENNE and JAMES, *Retilamina*

(Pl. 55, fig. 1). The vesicles of the compact wall have varied forms: blisters, horns, and berry-like structures formed of tiny closed sacks. Besides these, some cylindrical chimneys opening upwards are also present. A tangential cut shows that they are fairly regularly distributed at the surface (Pl. 49, fig. 1). The stereoplasma is regularly developed and may encrust a complete individual, except near the openings and vesicles (Pl. 54, fig. 1).

Discussion. To our knowledge no similar form has been described from strata of Lower Cambrian age. At first glance these sheets and inverted bowls would seem to constitute a family of peculiar outgrowths similar to the exostructures habitually described in connection with archaeocyathans. In Labrador, however, it is clear that the skeleton is from an independent organism quite separate from the usual archaeocyathan cup and not an outgrowth of it. Detailed microscopic examination confirms that there is no continuity between an archaeocyathan skeleton and *Retilamina*. In contrast *Retilamina* commonly develops secondary thickening (a stereo-plasmic reaction) at the point of contact (Pl. 54, fig. 4). In addition, *Retilamina* are associated with cups that are upside down and so they could not have grown when the cup was upright and in growth position. Finally, domes formed by the stacking of several *Retilamina* skeletons are frequently encountered, quite independent of archaeocyathan cups. The development of stereoplasma in *Retilamina*, when in contact with other forms, is identical to the response of all archaeocyathans when two cups are in contact, suggesting that the two organisms may have phyletic relationships. The microstructure of the skeletal elements of *Retilamina* is different from typical archaeocyathan microstructure: here the crystallites are always smaller, more akin to the size of the crystallites in secondary thickenings on some archaeocyathans (e.g. *Archaeocyathus*).

Retilamina is remarkably similar to certain reef-associated stromatoporoids and calcareous algae that appear later in the Paleozoic. Devonian reef complexes in western Canada, for example, commonly contain 'encrusting' or sheet-like growth forms of the stromatoporoids *Hammatostroma*, *Stromatopora*, and *Synthetostroma* (Noble 1970) that resemble *Retilamina*. Although these forms commonly encrust skeletons such as tabulate corals and brachiopods they are equally as abundant growing directly on sediment in other facies. Calcareous algae such as *Archaeolithophyllum* that are the primary skeletal constituents of reef mounds in Pennsylvanian age carbonates (Johnson 1956; Wray 1964, 1977) are very similar to *Retilamina*. These ancestral corallines occur as solitary or multiple crusts or foliose arrays and often form the roofs of small cavities.

Retilamina, from its structure and the general organization of its skeletal meshwork, is closer to archaeocyathans than to any other known organism. Although a systematic position inside the phylum Archaeocyatha is most likely, the unusual organization of the 'wall', unlike that of any known archaeocyathan, prevents us from classifying it in any definite order. It may be an abberant Irregular adapted to a stabilization or encrusting habit in a biostromal and biohermal environment.

EXPLANATION OF PLATE 55

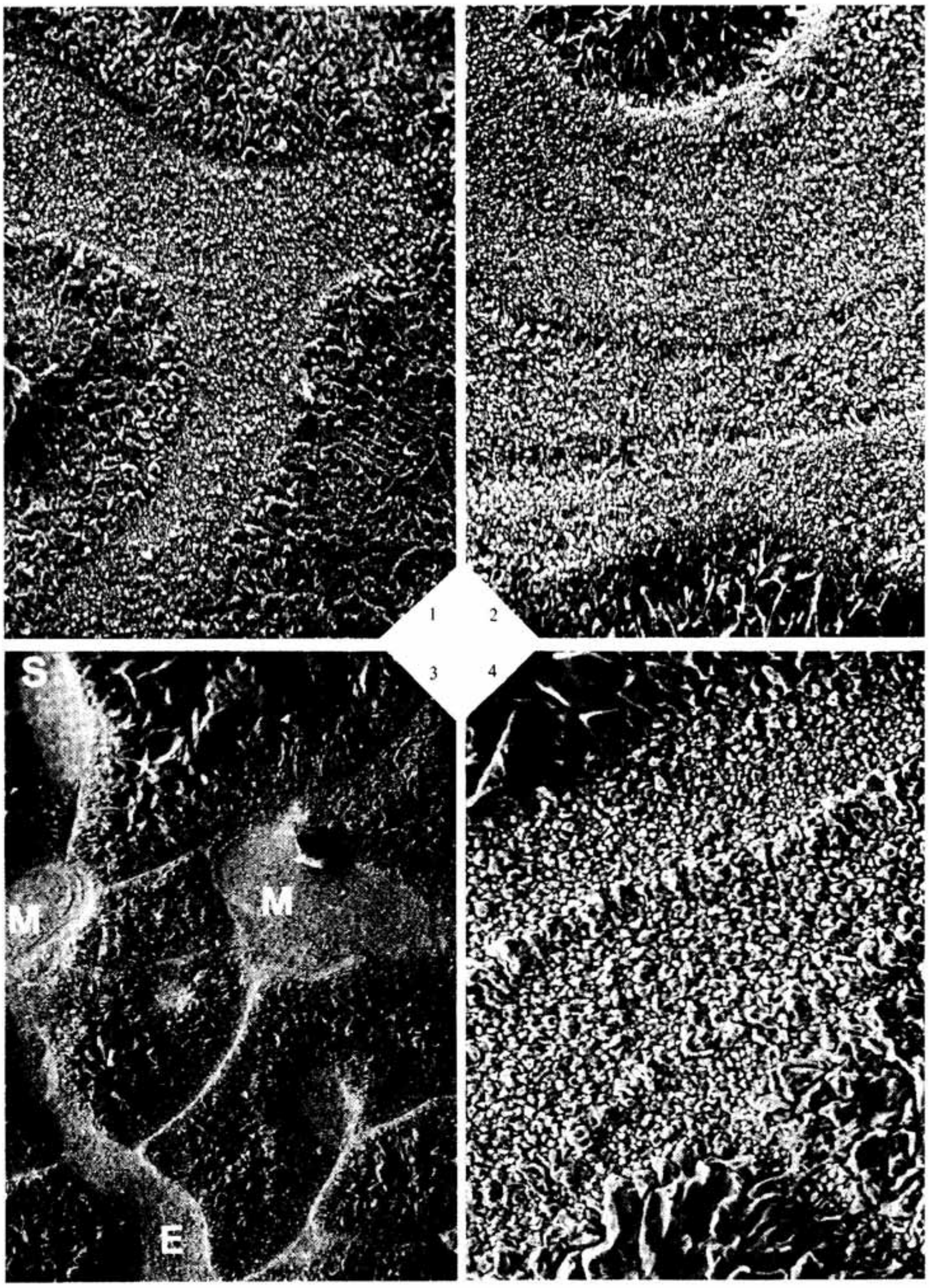
Fig. 1. *Retilamina amourensis* Debrenne and James, × 200, element of the dictyonemal mesh with fine-grained external limit. GSC 62127.

Fig. 2. *Archaeocyathus atlanticus* Billings, × 200, primary skeletal element of a taenia limited by palissading tissue and coated by layers of secondary thickening (stereoplasma) with fine-grained external limit. GSC 62107.

Fig. 3. *Metaldetes profundus* Billings and 'Exocyathus', × 70, the skeletal microstructures are identical; indicating the impossibility of finding a limit of the secretion of skeleton between both structures. GSC 62113. S = septa, M = wall, E = exostructure.

Fig. 4. *Archaeosycon billingsi* Walcott, × 400, same structure as in *Archaeocyathus*, primary skeleton-palissading tissue and layers of stereoplasma. GSC 62117. Photographs by Camebas-Institut de Paléontologie Paris—Technician: S. Laroche.

PLATE 55



DEBRENNE and JAMES, Archaeocyathan structure

SUMMARY AND CONCLUSIONS

All of the reef-associated archaeocyathans in Labrador and Newfoundland belong to the class Irregulares. The fauna is composed of five genera and six species: *Archaeocyathus atlanticus* Billings, 1861; *Metaldetes profundus* (Billings 1865); *?Metaldetes simpliporous* sp. nov.; *Archaeosycon billingsi* (Walcott 1886); *Arrythmocricus kobluki* gen. et sp. nov.; *Retilamina amourensis* gen. et sp. nov. The population is dominated by *M. profundus*, which exhibits extreme polymorphism. *Retilamina* has many of the characteristics of archaeocyathans, but it has such a bizzare growth form that we have, for the time being, described it as of uncertain order.

Despite the low diversity, the fauna is one of extremely high density. This combination of low diversity and high abundance likely reflects time and environment. These archaeocyathans lived at a time well past the acme of archaeocyathan evolution, just prior to extinction of the phylum when there are a few recorded genera, in a shallow, nearshore environment that was favourable for the growth of macroinvertebrates, as demonstrated by the associated fauna.

Detailed taxonomic study has resulted in a more precise definition of several important genera. The relationship between *Archaeocyathus* Billings, 1861 and the forms *Protopharetra* Bornemann, 1887, *Retecyathus* Simon, 1939, *Pycnoidocyathus* Taylor, 1910 and *Flindersicyathus* Bedford, 1937 has been resolved. The genus *Archaeosycon* Taylor, 1910 has been compared to *Claruscyathus* Vologdin, 1932, *Clarucoscinus* Handfield, 1971, *Metacoscinus* and *Paracoscinus* Bedford, 1936 as well as *Tabulacyathidae* Missarzhevskiy, 1964. *Cambrocyathus* Okulitch, 1937 is now a junior synonym of *Metaldetes* Taylor, 1910 while *Metethmophyllum* Okulitch also falls into synonymy with *Metaldetes*. *Arrythmocricus*, a new genus of the class Irregulares characterized by an annular inner wall, is established.

One of the most puzzling problems for many years has been the origin and significance of the exostructures associated with archaeocyathan cups. As a result of this study it is now clear that the dissepimental tissue previously described as *Exocyathus canadensis* by Okulitch (1943) is part of the genus *Metaldetes*. Acting as coenchyme it gives the cups a massive habit resembling that of corals. From this tissue stolons and large ribbons surround other cups, dead or alive, of the same or different genus to form a massive structure. Buds of very simple structure swarm from these exostructures and most commonly occur in the cavities sheltered by *Retilamina*, in central cavities of other archaeocyathids or free and developing larger *Protopharetra*-like structures with central cavities. Buds with coarser structure are attached to *Archaeocyathus* and *Archaeosycon* but are not found elsewhere and are of limited development.

The new, enigmatic, sheet-like form *Retilamina* is not known from any other strata of Lower Cambrian age. The growth form is remarkably like many other encrusting skeletal organisms, notably the ancestral coralline alga *Archaeolithophyllum*, bryozoa, stromatoporoids, and corals that play a vital role in reefs at a later stage in geologic history. The prone to arched growth form of *Retilamina* resulted in cavities within the growing reef. Although shelter voids may have occurred in older reefs by the fortuitous accumulation of archaeocyathan skeletons, these are the earliest recorded examples of growth cavities produced directly by the growth habit of the major skeletal component of the reefs. These cavities provided a new and predictably recurring habitat within which a separate fauna and flora began to evolve (Kobluk and James 1979).

There is no clear-cut succession of archaeocyathans in the patch reefs, although there is a trend for *Retilamina* to be commonest at the base of the mounds and ?*M. simpliporous* to be commonest at the tops of the mounds. In the biostrome this trend is clearly established, with *Retilamina* and *Archaeocyathus* abundant at the base of any one subunit and *M. profundus* forming an almost monospecific assemblage in the middle and upper parts of the subunit.

Although the archaeocyathan fauna is entirely Irregulares, which have a long geologic time range, the composition of the fauna is clearly similar to that found in the Obruchev horizon of the Elankian Stage on the Siberian Platform. On the basis of trilobites the strata are equivalent to the middle part of the *Bonnia-Olenellus* Zone in age.

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