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LOWER CAMBRIAN BIOHERMS: PIONEER REEFS OF THE PHANEROZOIC

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Synthesis of information presently available on the makeup of Lower Cambrian bioherms indicates a gradual transition in their composition through time. The oldest bioherms (Lower Tommotian of the Siberian Platform) are mounds composed of lime mud and calcareous algae (*Epiphyton* and *Renalcis*) with archaeocyaths most common in the surrounding sediments. This trend continues throughout most of early Lower Cambrian time. In the middle part of the Lower Cambrian, archaeocyaths become an important part of the bioherm biota. By late Lower Cambrian time, as much as 50% of the limestone in bioherms is composed of archaeocyath skeletons and the structures illustrate the same sedimentological and ecological attributes as skeletal metazoan reefs later in the Phanerozoic.

Key words: Archaeocyatha, algae, bioherms, reefs, Lower Cambrian.

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INTRODUCTION

Bioherms in the stratigraphic record can generally be separated into one of two types: (1) algal mounds, composed of sediment-trapping and binding, or calcareous algae, which are most common in Precambrian and Lower Paleozoic time, and (2) reefs and reef mounds, structures composed primarily of skeletal metazoa and calcareous algae, which occur throughout the Phanerozoic. Until recently, reefs were generally assumed to have developed coincident with the appearance of large, skeletal metazoa such as corals, stromatoporoids and bryoza in Middle Ordovican (Wilson 1976). Detailed study of archaeocyath-rich bioherms of late Lower Cambrian age in Labrador, however, reveals that all of the sedimentologic and paleoecologic attributes we generally ascribe to reefs are present in these older structures. This suggests that the reef ecosystem, as we know it, developed somewhat earlier than generally assumed, in lower Cambrian time, possibly coincident with the appearance of archaeocyaths, one of the first skeletal metazoa. This assumption is, however, merely an assumption, because very few Lower Cambrian bioherms have been studied from the viewpoint of sedimentology and paleoecology.

This paper is a synthesis of all the information we known of concerning the major components of bioherms of Lower Cambrian age. The information presented is from literature and our own observations together with the yet unpublished information kindly given to us by B. Read (Calgary, Alberta) S. Rowland (Las Vegas, Nevada) and I. Zhuravleva (Novosibirsk, USSR). The purpose of the paper is to document when archaeocyaths became important contributors to bioherm development.

ARCHAEOCYATHS

Bioherms throughout the Phanerozoic are characterized by the inplace accumulation of numerous, relatively large, sessile skeletal metazoa, which exhibit a variety of growth forms. The only such metazoa present in Lower



Fig. 1. A plot of the number of archaeocyath genera with time for the Lower Cambrian: T Tommotian stage; A Atdabanian stage; L Lenian stage; E Elankian stage; unpublished diagram (Rozanov, A. Yu. and Debrenne, F.), by courtesy of A. Yu. Rozanov.

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Cambrian strata are archaeocyaths. These conical to bowl-shaped metazoa of uncertain affinity, many of which are superficially like sponges or rugose corals in shape, are amongst the earliest known skeletal body fossils but became extinct at the end of the Lower Cambrian time (Hill 1972).

The number of archaeocyath genera varied widely with time during the Lower Cambrian and is plotted in fig. 1. In the oldest strata, of the Tommotian stage, only a total of nine families are known, all from the Siberia. 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 dispersion, which was probably somewhere in the Altai-Sayan region of the eastern USSR. During the Lenian (Botomian of some authors) archaeocyaths illustrate their greatest geographic extent and widest diversity, coincident with the rapid expansion of trilobite genera (Rozanov and Debrenne 1974; Debrenne and James, in press). At this time differences in faunas between areas are strongly marked. There is a stock of world-wide faunas in addition to some well defined endemic forms. Towards the close of the succeeding Elankian Stage (Lenian of some authors) there is a dramatic decrease in the number of taxa as well as individual archaeocyaths. The remaining fauna evolved in place from the already diversified stock, probably in areas which were, at that time, completely separated and so provincialism is the rule.

GEOGRAPHICAL DISTRIBUTION AND CHRONOLOGY OF LOWER CAMBRIAN BIOHERMS

The most geographically widespread and most wide-ranging structures, in terms of geologic time, occur in the USSR. Along the northern margin of the Aldan Shield in Siberia bioherms are found throughout Lower Cambrian strata, but are most abundant in the lower half. In the Altai-Sayan-Tuva fold belt, on the other hand, bioherms are most common in younger strata, deposited in the upper half of Lower Cambrian time.

In the Mediterranean area, bioherms occur in Spain, Sardinia and Morocco. These structures occupy the middle part of Lower Cambrian.

In North America, bioherms are found both in the Appalachian and Cordillerian orogens. They occur in the latter half of the Lower Cambrian and are youngest in the Appalachian region.

In Australia, although many authors mention "barrier reefs", there are, to date, no records of true bioherms. Most of the archaeocyatha-bearing limestones are massive, 10—100 m thick biostromes or fine-grained carbonate units with scattered pockets of archaeocyaths. One of us (F.D.) has observed some mound-like bodies in the Ross River Formation, but these have not been studied.

STYLE OF LOWER CAMBRIAN REEF-LIKE STRUCTURES

In terms of geometry and internal structure Lower Cambrian reeflike structures can be classified either as bioherms or biostromes, similar to other structures later in geologic history (Debrenne 1959). The most important components in the reef rock or mound rock are archaeocyaths or the calcareous algae? *Renalcis* and/or *Epiphyton*, together with argillaceous lime mudstone to packstone and cement. The relative proportions of these components vary widely from mounds with predominantly archaeocyaths and little algae to mounds that are almost entirely algae and only rare archaeocyaths to mounds that are almost completely lime mudstone with only scattered archaeocyaths and no algae. Other common organisms associated with the bioherms are echinoderms, hyolithids, brachiopods, trilobites, sponges, and some *incertae sedis* organisms.

The biostromes are commonly nodular to massive limestones with the nodular strata often rich in archaeocyaths and algae while the massive beds are skeletal lime grainstones to packstones rich in archaeocyaths, echinoderm and brachiopod debris. Oolitic and oncolitic limestones are commonly associated with these biostromes. In many cases the archaeocyaths in these biostromes are upright and in place (Poleta Fm.: Gangloff 1976; Forteau Formation: Debrenne and James 1979) suggesting that they grew as archaeocyath thickets on the sea floor that were segmented into clusters by small submarine channels.

The bioherms are characteristically white to grey, massive and nodular limestone surrounded by bedded, often red to green-coloured siltstones, shales and carbonates. These bioherms have been most extensively documented in the USSR. The focus of work to date in the USSR has been in two directions: (1) on the morphology or external shape of the bioherms, and (2) on the taxonomy of the archaeocyaths. On the basis of the different morphologies, Yazmir (1960, 1961) and Zhuravleva (1966) have recognized two different styles which they have termed monolophoid (Zhuravleva) or biocupola (Yazmir) and dilophoid (Zhuravleva) or biolens (Yazmir).

Monolophoids. — These bioherms can best be described as plano-convex structures with a flat base and arched upper surface (fig. 2), generally small with heights of 1.5 and 3.0 m and may be up to 12 m in diameter. Numerous such bioherms occur in a single stratigraphic horizon, generally separated from one another by 3 to 5 m of inter-reef sediment. In any one sequence, individual bioherms may occur above one another in different succeeding stratigraphic horizons, once again separated by interreef sediment. In these monolophoids, the structure began as a community of algae and/or archaeocyaths covering a wide area of the sea floor. This accumulation of skeletal material formed the base upon which the subsequent communities thrived, building, with time, a reef-like structure.

Dilophoids. — These bioherms have a lens-like or biconvex shape with a narrow basis expanding to a maximum size and decreasing to a narrow apex (figs 3, 4). Each bioherm is, in turn, composed of numerous small mounds or lenses. The spatial arrangement of these mounds can give rise to a great variety of shapes. Individual mounds range in size 1 to 2 m in height and 2 to 3 m in diameter. In contrast to the planoconvex monolophoids, these structures begin with one or two colonies of algae and/or archaeocyaths and with time expand both upward and outward. Once the maximum size has been reached the structure decreases.

These different bioherm morphologies have recently been combined under a new term calyptra (Gr. kaluptra = veil, $kalupt\bar{o} = to cover$) (Zhuravleva and Miagkova 1975). This term is used for the primary component structure (0.5 to 8.0 m in diameter and rarely higher than 1 m) that may occur alone or as a component of larger biostromes or bioherms, or bioherm complexes. This appears to be synonymous with the term "mound" as used in western literature. Various different types of calyptra or mounds are recognized but the forms which are of interest here are: (1) bun-shaped calyptra — corresponding to the plano-convex bioherms or monolophoids, and (2) spherical calyptra — corresponding to the biconvex bioherms or dilophoids.

The sedimentology and structure of very few of these bioherms has been studied in detail. Recent examination of the superbly exposed bioherms in the Forteau Formation at the northern end of the Appalachians, however, indicates that these bioherms at least have most of the sedimentologic/biologic attributes that characterize reefs throughout the geologic record (James and Kobluk 1978). The reefs are typically biconvex bioherms (dilophoids) averaging 10 m in diameter and 6 m high and sometimes forming reef complexes up to 200 m across. Each bioherm is composed of many small loaf-shaped mounds (spherical caluptra) stacked on top of one another and are best classified as "stratigraphic reefs" (Dunham 1970). The limestone of each mound comprises archaeocyaths (30 to $50^{\circ}/_{\circ}$), renalcids (20 to 30%) in a matrix of lime mudstone rich in sponge spicules, trilobite carapaces, hyolithid and brachiopod skeletons. The interior of the reef contains numerous growth cavities, roofed by pendant renalcids floored by geopetal sediment and containing a variety of cavity-dwelling invertebrates (Kobluk and James 1979). The surfaces of many mounds are bored, penetrated by the ichnogenus Trypanites sp. Sediments and skeletons of the reefs were cemented on the sea floor by finely crystalline to fibrous calcite and cement comprises 10 to 30% of the bioherms.



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VARIATION IN BIOHERM STRUCTURE AND COMPOSITION IN LOWER CAMBRIAN TIME

Bioherms can be expected to show wide variation in structure and composition depending upon varying environmental parameters such as water depth, climate, tectonism, sediment influx and other physiochemical constraints. With this in mind, we have summarized in fig. 5 and table 1 most of the information presently available and discuss the variation with age below.

The percentage of components in most cases is an estimate, gleaned either from the literature, personal communication or personal observation and is intended as a generalization rather than a fixed number. In our experience the precipitated calcite cement in these structures is often ignored. Examination of thin sections and outcrops indicates that cement between calcareous algae often comprises $50^{\circ}/_{\circ}$ of the elements called "algae" and likewise cement in voids and cavities may make up as much as $30^{\circ}/_{\circ}$ of the rock volume in some cases. Because cement is rarely reported, we have restricted our tabulation to the obvious sedimentary/biotic components, archaeocyaths, calcareous algae ? and matrix.

Tommotian. — The oldest bioherms occur in the Lower Tommotian' (Sunnagine) on the Aldan and Succharicha Rivers of the Siberian Platform. These small bioherms (dilophoids) rarely exceed 2 m in total height and based on reef-interreef relationships were less than 20 cm above the sea floor. The core of the bioherm is algae, dominated by *Renalcis* (fig. 3). Archaeocyaths are rare and represented predominantly by the large discshaped Okulitchicyathus together with Archaeolynthus and Aldanocyathus localized around the periphery. These algal bioherms are preceded by small stromatolites and numerous oncolites. They are located adjacent to a paleoshoreline and are associated with abundant terrigenous sediment (Zhuravleva 1966). In the Upper Tommotian (Keniada), bioherms are wide-

Fig. 4. A small mound that makes up part of a dilophoid bioherm, from Zhuravleva 1966: fig. 10B. 1 Limestone; 2 Sandy limestone; 3 Argillaceous limestone; 4 Renalcis; 5 Archaeocyatha.

Fig. 2. Monolophoid bioherms, from Zhuravleva 1966: fig. 3 and 4. 1 Limestones; 2 Argillaceous limestone, silstone, shale; 3 Renalcis; 4 Epiphyton; 5 Archaeocyatha.

Fig. 3. A series of dilophoid bioherms in a nearshore environment; Early Tommotian, Aldan River; from Zhuravleva (1966: fig. 6). 1 Accumulation of biofragments; 2 Argillaceous limestone; 3 Renalcis; 4 Archaeocyatha.

Fig. 5. A diagram illustrating the different types of Lower Cambrian bioherms and their temporal as well as geographic distribution; numbers refer to areas listed in table 1. 1 Limestone; 2 Argillaceous limestone, silstone, shale; 3 Bioherms in which algae predominate, but archaeocyaths are present; 4 Bioherms in which archaeocyaths are predominant; 5 Nodules rich in archaeocyaths; 6 Bioherms in which algae, Epiphyton+Renalcis predominate, rare archaeocyaths; 7 Stromatolites; 8 Bioherm composed of mudstone with rare archaeocyaths and algae; 9 Sandy limestone; 10 Accumulation of fragmental archeocyaths (taphoherms).



Fig. 6. A sketch illustrating a typical Lower Cambrian bioherm and the composition of the individual mounds (calyptra) that make up the bioherm in Early and Middle versus Middle and Late Lower Cambrian time.

spread in the Aldan and Lena River Basins of the Siberian Platform. Titiriktek is one well studied example of these structures. Once again the bioherms are predominantly renalcids and lesser *Epiphyton*, with archaeocyaths restricted mainly to the periphery of the bioherms and interreef sediments. The individual mounds are characteristically isolated structures but occasionally occur as bioherms or bioherm complexes (Zhuravleva 1966).

Table 1

An estimate of the abundance of major constituents of Lower Cambrian bioherms

AGE		LOCALITY	CONSTITUENTS - 2		- 7	REFERENCE
			ARCHAEO	ALCAE	MATRIX	
1. Low	er Tommotian	USSR-Dvorsty, Aldan-Jura	5	35	60	Zhuravleva, 1966
2. Mid	-Upper Tommotian	USSR-Aldan, Lena	5	35	60	Zhuravleva, 1972
3. Atd	abanian	SPAIN-Las Ermitas	1-2	80	20	Zamarreño-Debrenne, 1977
4. Atd	abanian	MOROCCO-Jbel Taissa	1-20	30-80	50	Personal observation
5. Mid	-Upper Atdaba- nian	USSR-Kokoulin, Oi-Muran, Lena	0-20	30	50	Zhuravleva, 1966, 1972, pers. comm.
6. Upp	er Atdabanian	USSR-Bazaikh River (Altai-Sayan-Tuva)	0-5	60	30	Zadorozhnaya, 1974
7. Len	ian	USSR-Sanachtygkol	0-5	60	40	Zhuravleva, pers. comm.
8. Len	ian	SARDINIA	20	30	50	Personal observation
9, Len	ian	MOROCCO-Issafenien	20-30	20-70	50	Zersonal observation
10. Len	ian	USA-Nevada and Califor- nis	20-30	0-40	50-70	Gangloff, 1976; Morgan, 1976; Rowland, pers. comm.
11. Len	ian	CANADA - Yukon	30	30	40	Read, pers. comm.
12. Ela:	nkian (Obruchev)	USSR-Altai-Sayan	5-10	30-40	40	Zhuravleva, pers. comma.
13. Ela	nkian (Obruchev)	CANADA-Labrador	30-50	20-40	40	James and Kobluk, 1978; Debrenne and James, in press

Atdabanian. — Bioherms of this age are found both in the USSR and in the Eurafrica region. On the Siberian Platform, the main reefal structures in lower strata are biostromes, composed of over $80^{0}/_{0}$ algae with less than $1^{0}/_{0}$ archaeocyaths. These are succeeded by plano-convex bioherms (monolophoids) which in turn grade up into biconvex bioherms (dilophoids) forming large reef complexes or massifs that are well studied through the Lena River basin (e.g. Kokoulin, Oi Muran) and in Altai-Sayan mountains. These bioherms comprise $30^{0}/_{0}$ algae, $20^{0}/_{0}$ archaeocyaths and $50^{0}/_{0}$ lime mudstone (Zhuravleva 1969, 1972; Zadorozhnaya 1974).

In Spain, the bioherms are up to 20 m in diameter and 10 m high and comprise $80^{0}/_{0}$ algae, 1 to $2^{0}/_{0}$ archaeocyaths and $20^{0}/_{0}$ lime mudstone. These algal bioherms are surrounded and underlain by nodular limestones with common archaeocyaths (Debrenne and Zamarreño 1977).

The bioherm complex of the Jbel Taissa (Morocco) is composed of similar alga-rich mounds (2 m \times 1 m) which together form a large com-

plex which is, in places, 100 m thick. The mounds vary greatly in composition from $80^{0}/_{0}$ algae and $1-2^{0}/_{0}$ archaeocyaths to $30^{0}/_{0}$ algae and $20^{0}/_{0}$ archaeocyaths. The nodules surrounding the complex are rich in archaeocyaths.

Lenian. — On the margins of the Siberian Platform, bioherms are small and consist primarily of algae but are surrounded by extensive beds of skeletal debris. In the Sanachtygkol region of the Altai-Sayan fold belt, however, bioherm complexes and massifs are common. There are, however, once again primarily algal with only $0.5 - 5^{0/0}$ archaeocyaths (Zhuravleva, pers. comm.; Zadorozhnaya 1974).

In Sardinia, most of the limestone units within the "Arenarie" are long lenses composed either of oolitic lime sands and fragments of archaeocyath or lenticular biostromes whose main constituents are renalcids and minor *Epiphyton* with scattered archaeocyaths. In the bedded limestones surrounding this facies, archaeocyaths are abundant, as individuals in the sediment or in nodules (Funtana Calomba, Sant Angelo: Debrenne, Gandin and Simone in press). True bioherms are not yet recorded; the successive mounds observed at Gonnesa appear to be of a similar type as the lenticular biostromes. These limestones contain about $30^{0}/_{0}$ algae, $20^{0}/_{0}$ archaeocyaths, particularly saucer-shaped forms belonging to either *Coscinocyathus* or *Anthomorpha* and some *Exocyathus*-like forms.

In Morocco, bioherms extend in a trend from Dra to Jbel Irhoud and are particularly well developed at Issafenian. These bioherms are complex associations of mounds that may be as much as 50 m high. The mounds are composed of 20 to $30^{\circ}/_{\circ}$ archaeocyaths, mainly the budding form *Agastrocyathus* and colonial form *Halysicyathus*. and of 20 to $70^{\circ}/_{\circ}$ algae. Some bioherms are without algae.

Bioherms in the Cordillera of North America are mostly of this age and occur primarily in western Nevada and Eastern California in the USA and in British Columbia, the Yukon and the Northwest Territories of Canada. In the USA, these bioherms are small, with the largest 9 m high and 60 m long and are encased in shale, siltstone and argillite. The most common shape corresponds to the monolophoid. In the Montenegro Formation and Harkless Formation, the bioherms are essentially mounds of lime mudstone with $20 - 30^{0}/_{0}$ archaeocyaths and no algae. In the Poleta Formation, between the other two formations, the bioherms contain abundant *Epiphyton* and *Renalcis* which form clumps around the archaeocyaths. No bioherms with only algae, have been found to date (Gangloff 1976; Morgan 1976; Rowland, pers. comm.).

Bioherms occur scattered throughout strata of Lower Cambrian age in the Yukon and N.W.T. of Canada (Fritz 1976, 1978) and range in age from Lenian to Elankian, but few have been studied. In the Pelly Mountains, Yukon, one complex contains numerous bioherms, the largest of which is 500 m across and 80 m in height and biconvex in shape. In these structures, archaeocyaths comprise $30^{\circ}/_{\circ}$ of the rock, algae $30^{\circ}/_{\circ}$ and argillaceous lime mudstone the remaining $40^{\circ}/_{\circ}$ (Read, 1980).

Elankian. — During the final stages of the Lower Cambrian the number of archaeocyath taxa decreased in number dramatically and became isolated into provinces. In the USSR, bioherms of this age are known from the Siberian Platform (uppermost Elankian) where they are very small and composed of small regular archaeocyaths and from the Altai-Sayan-Tuva region where they form extensive bioherm complexes or massifs. These bioherm complexes are composed of 5 to $10^{0}/_{0}$ archaeocyaths (mainly large irregular forms), 30 to $40^{0}/_{0}$ algae and argillaceous lime mudstone (Zhuravleva, pers. comm.).

In the northern part of the Appalachians in North America (Labrador and Newfoundland), the bioherms are extensive and composed of 30 to $50^{\circ}/_{\circ}$ archaeocyaths (mainly large irregular forms), 20 to $30^{\circ}/_{\circ}$ algae and the remainder lime mud (Kobluk and James 1979; Debrenne and James, in press).

DISCUSSION

Bioherms in the Lower Paleozoic, specifically in the Cambrian and Lower Ordovician (Sauk Sequence: Sloss 1963), prior to the worldwide regression in the basal Middle Ordovician and subsequent appearance of numerous large, sessile, skeletal metazoa, are characteristically algal. Structures composed of Renalcis and/or Epiphyton, along with other calcareous algae are known from the Middle and Upper Cambrian (Ahr 1971; Lohmann 1976) and Lower Ordovician (Toomey 1970; Riding and Toomey 1972). Viewed in this context, the bioherms of the Lower Cambrian are part of this overall style of structure, composed primarily of algae but with archaeocyathids as a common accessory skeletal component. Only in the middle and late Lower Cambrian time when archaeocyathids became larger, possibly semi-colonial and developed polymorphism did the skeletal reef community develop. This could only occur because of the combination of prolific skeletal production and the great variety of new ecologic niches which could be inhabited by a variety of skeletal-sediment producing taxa.

SUMMARY

When viewed in total, several trends emerge from the foregoing synthesis:

 Lower Cambrian bioherms are composed of a series of small mounds (calyptra of Soviet authors), with each mound less than 2 m in diameter and 0.2 to 2 m in height;

- 2. the earliest bioherms, in the Tommotian Stage, are small and less than 2 m in size but by the middle part of the Atdabanian Stage individual bioherms are large and coalesce to form extensive bioherm complexes or massifs;
- 3. in the lower and middle parts of the Lower Cambrian (Tommotian and Atdabanian) bioherms are composed primarily of the calcareous algae *Renalcis* and *Epiphyton* with archaeocyath skeletons scattered irregularly throughout the structure or, more commonly around the periphery of the bioherm in nodular peri-reefal sediments; the relative proportion of archaeocyaths within the bioherms becomes significant (over $20^{0}/_{0}$) in parts of the Atdabanian, Lenian and especially in the Elankian; in this last stage of the Lower Cambrian, just prior to the extinction of archaeocyaths, bioherms contain up to $50^{0}/_{0}$ archaeocyath skeletons, similar to skeletal reefs later in the Phanerozoic;
- 4. when archaeocyaths occur in the reefs, they always exhibit budding and exothecal development;
- 5. in late Lower Cambrian time the archaeocyath-rich bioherms contain archaeocyaths that are exceptionally large, are sometimes bound together by coenosteum-like exostructures and exhibit a wide range in polymorphism.

The trends outlined above appear valid at the time of writing, but can still only be seen "through a glass darkly" and much more detailed documentation of these "pioneer" reefs is needed before a truely clear picture emerges.

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