



General Palaeontology (Palaeoecology)

Lower Cambrian archaeocyathan bioconstructions

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Abstract

Archaeocyatha are now confidently considered as a Class within the phylum Porifera. Regulares and Irregulares are no longer a systematic division, but have only ecological significance. Topographic relief, biogenic framework and a wave-resistant capability are in favour of the reefal nature of archaeocyathan bioconstructions. Several types of boundstones are recognized, based on the relative proportion of the different framework builders. The same basic plan, characterized by component domains occupied by an association of lime mud, archaeocyaths calcimicrobes, growth cavities, shows little changes throughout the Early Cambrian. A four-stage ecological succession can be inferred, according to some documented cases of distinct biological zonation in archaeocyathan reefs. There is no consensus about the question of photosynthesis in those reefs. They follow the transgression of carbonate facies in sub-tropical areas during the Early Cambrian. **To cite this article:** F. Debrenne, C. R. Palevol 6 (2007).

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Résumé

Bioconstructions à archéocyathes (Cambrien inférieur). Les Archaeocyatha sont maintenant considérés unanimement comme une classe du phylum Porifera. Les anciennes distinctions entre Regulares et Irregulares n'ont qu'une valeur écologique et n'ont plus de valeur systématique. Le relief topographique, la charpente biogénique et une certaine capacité de résistance aux vagues font que les bioconstructions à archéocyathes sont de véritables récifs. La proportion relative des différents calcimicrobes et des archéocyathes dans le cœur du récif permet de distinguer plusieurs types de *boundstones*. Le même plan de base, caractérisé par un ensemble de domaines composés de l'association de boues calcaires, d'archéocyathes, de calcimicrobes, de cavités internes, persiste durant tout le Cambrien inférieur, sans modifications notables. Quatre stades de succession écologique, basés sur des zonations biologiques distinctes observées dans quelques cas, ont été établis. La présence de photosymbiontes est toujours controversée. Les récifs à archéocyathes suivent la progression des plates-formes carbonatées dans les zones intertropicales au Cambrien inférieur. **Pour citer cet article :** F. Debrenne, C. R. Palevol 6 (2007).

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Mots clés : Récifs Cambrien inférieur ; Consortium archéocyathes–calcimicrobes ; Données passées et actuelles

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Les premières bioconstructions à métazoaires contenaient un groupe d'affinités incertaines, les archéocyathes. Après les découvertes d'éponges

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corallines actuelles, les études comparatives ont montré que les Archaeocyatha formaient une seule classe dans le phylum Porifera [1,24]. La nature des bioconstructions a aussi été sujet à débat suivant les différentes conceptions du « récif » [5,23,49,56] : le mot « récif » [21] correspond à « une structure biogénique construite par l'activité d'organismes sessiles benthiques, formant un relief topographique et possédant une structure rigide », définition assez large pour inclure des bioconstructions variées. De nombreux auteurs ont étudié les formations à archéocyathes. En premier, des auteurs russes [61,63,64] ont établi différents types morphologiques de constructions et établi la liste des organismes les composant. Noël James [9,26,27] a fait connaître ces travaux en Occident et mis au point une méthode d'étude pour quantifier les caractéristiques lithologiques, biosédimentologiques, biologiques et environnementales des différentes constructions, et en faire la comparaison avec les récifs plus récents. Cette méthode est appliquée par la plupart des chercheurs depuis 1980.

Suivant les variations morphologiques des récifs, on distingue les kalyptrae (monticules) simples (Fig. 3–5) ou empilées (récif complexes) (Fig. 6–7) et des récifs massifs (Fig. 8) [63]. La méthode d'étude par cartographie de chaque kalyptre conduit à la distinction de régions (domaines) pour lesquelles on détermine les pourcentages des constituants biologiques et biosédimentologiques. Ces « domaines » sont définis par l'association de boues carbonatées, d'archéocyathes, de calcimicrobes et de ciment, avec possibilité de développer des cavités abritant des célobiontes. Les archéocyathes, suivant leur forme et les différences morphofonctionnelles dans la répartition du tissu vivant, ont un rôle différent dans la composition du récif. Les archéocyathes de type septal (ex-« réguliers », Fig. 1), chez lesquels les courants pénètrent la totalité du calice, prolifèrent sous forme de calices solitaires dans les substrats boueux, à la périphérie ou dans les cavités internes du récif. Les archéocyathes de type tænia (ex-« irréguliers », Fig. 2), dont le tissu vivant est limité à la partie supérieure du calice, développent des formes modulaires (pseudo-coloniales) et des expansions exothécales, et participent activement à la formation de la charpente du récif. Les récifs du Cambrien inférieur étaient construits par un consortium de calcimicrobes et d'archéocyathes suivant plusieurs types d'associations (Fig. 10). Leur position sur les plates-formes a été établie par James et Gravestock [28] (Fig. 11). Les récifs connus peuvent être rapportés à ce schéma. En fonction du constructeur dominant, on distingue les *boundstones* à calcimicrobes et rares archéocyathes [33],

à archéocyathes dominants [45] (Fig. 12), à *Renalcis* et archéocyathes [47], à *Epiphyton* dominants et archéocyathes [12,22,36], à *Girvanella–Epiphyton–Renalcis* construit par interaction complexe des constructeurs [14,34,40], les *boundstones* à archéocyathes et composants mineurs appartenant à des groupes énigmatiques (radiocyathes) ou à des formes morphologiquement proches ou rattachées plus précisément aux spongiaires et aux tabulés [13,35]. La surface supérieure peut être perforée ; une faune variée habitait à la périphérie du récif. Les récifs cambriens possèdent des traits communs avec les récifs post-paléozoïques (ciments synsédimentaires, cavités avec cryptobiontes). La présence de filtreurs passifs et de suspensivores qui nécessitent un milieu relativement riche en nutriments et le nombre limité d'espèces participant à la construction sont des conditions connues au Paléozoïque, mais qui contrastent avec celles de la plupart des récifs post-paléozoïques. Il n'y a pas actuellement de consensus sur l'éventuelle présence de symbiontes. La possibilité d'une zonation verticale a longtemps été niée ; elle a pu être établie dans quelques cas [45,47] (Fig. 19). Zhuravlev [59] reconstitue une succession écologique verticale théorique d'après les exemples connus, comportant les stades successifs : pionnier, de stabilisation, de diversification, de destruction, suivi ou non de la reprise de l'activité récifale (Fig. 18).

La répartition spatio-temporelle des récifs à archéocyathes (Fig. 4) correspond à l'extension des dépôts marins carbonatés et des habitats d'eaux peu profondes. De la Sibérie (Tommotien), ils gagnent l'Altai–Saïan, la Mongolie, l'Espagne, la France (Normandie), le Maroc (début de l'Atdabanien) ; à partir de nouveaux centres de dispersion (Europe méridionale et Maroc), ils colonisent la Chine du Sud, l'Australie et la cordillère Nord-Américaine (fin de l'Atdabanien–début du Botomien). À l'apogée de la transgression botomienne, ils migrent de l'Australie vers l'Antarctique, l'Extrême-Orient russe et la Laurentie. À la fin du Botomien et au Toyonien, deux épisodes régressifs et anoxiques éliminent progressivement les archéocyathes et les récifs par réduction des domaines d'eaux peu profondes [20,38,61].

En conclusion, même si les récifs du Cambrien inférieur ont été surtout le fait de l'action constructrice des calcimicrobes, les archéocyathes ont participé à leur établissement comme support des calcimicrobes, comme toit des cavités internes et, plus rarement, comme constructeurs de la charpente principale. Dans les zones péri- et inter-biohermales, ils ont agi comme filtreurs et contribué au bon fonctionnement du biotope récifal au Cambrien inférieur.

Les exemples cités dans cet article ont été étudiés sur le terrain par Max et Françoise Debrenne.

1. Introduction

The earliest skeletal, metazoan-built reef ecosystem starts at the beginning of the second stage of the Early Cambrian, in Siberia. It spreads around the world and decreases at the end of the Early Cambrian, essentially corresponding to the temporal and spatial distribution of a pioneer group of sponges, the Archaeocyatha. This first episode of reef building by metazoans covers a time span equivalent to the Palaeocene, i.e. 11 Myr.

They were called by authors “archaeocyathan reefs”, but for a long time, the systematic position of archaeocyaths was controversial and, in the other hand, the definition of reefs differs according to biologists, geologists, palaeontologists or sedimentologists.

This paper is a review of literature and is mainly focused on the role of archaeocyatha in the establishment of Cambrian bioconstructions.

2. ‘Archaeocyathan reefs’, preliminary definitions

2.1. What are Archaeocyaths?

Archaeocyaths were marine sessile organisms, appearing in the Tommotian (521 Myr) and almost extinct in the Toyonian (510 Myr). Their biological affinities were much debated from their first find in Labrador in the mid-19th century to the discovery of living aspiculate sponges in the late 20th century [24]. From this point onwards, studies of comparative anatomy with calcified sponges, showing similarities in growth pattern, structure of the skeleton (primary and secondary), functional morphology and trends of evolution, conferred archaeocyaths a sponge grade of organisation [10]. It was established that all archaeocyaths went through the same stages of skeletal development and that the differences between ‘Regulares’ (septal type) (Fig. 1) and ‘Irregulares’ (taenial type) (Fig. 2) were linked to the position of living tissue in relation to the calcareous skeleton. Regulares and Irregulares belong to a single taxonomic unit, a Class within the phylum Porifera and have no systematic value [20].

2.2. What is a reef?

The use of the word *reef* differs from authors to authors: the literature is therefore plethoric [5]. The following definition by Flügel and Kiessling [21] according

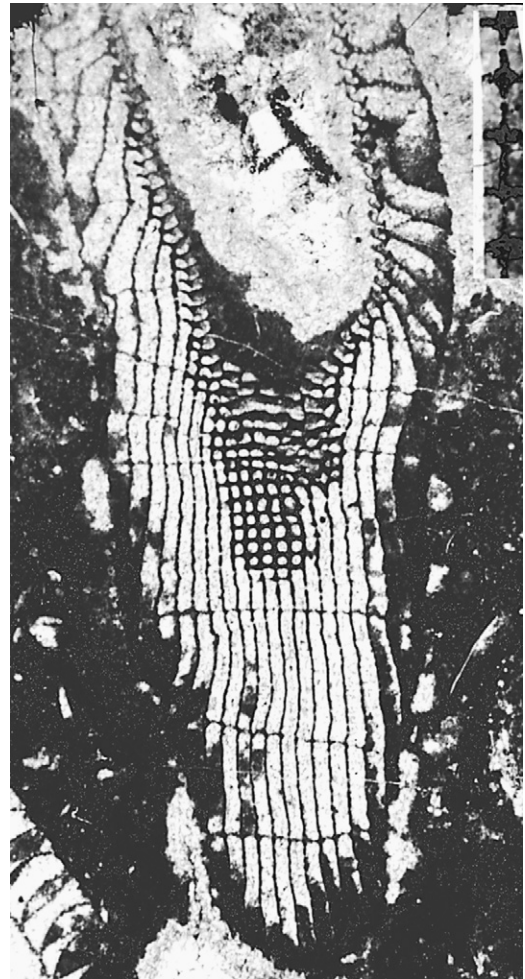


Fig. 1. Septal type: *Baikalocyathus rossicus* (Zhuravleva) Siberian Platform, Oy-Muran reef, Atdabanian. Longitudinal section: vertical porous septa, horizontal pectinate tabulae, inner wall with upward V-shaped canals. Coll. Rozanov (A315-130), M81084.

Fig. 1. Type septal : *Baikalocyathus rossicus* (Zhuravleva), plate-forme sibérienne, récif d'Oy-Muran, Atdabanien. Section longitudinale avec cloisons verticales poreuses, planchers pectinés horizontaux, muraille interne à canaux en V, ouverts vers le haut. Collection Rozanov (A315-130), M81084.

to which “reefs are laterally confined biogenic structures developed by the growth of activity of sessile benthic organisms and exhibiting topographic relief and inferred rigidity” is wide ranging enough to be generally accepted.

2.3. Are there Archaeocyathan reefs?

Archaeocyatha were interpreted, since the beginning, as being responsible for constructions comparable with the Great Barrier Reef [25]. But the observation of accumulations of archaeocyaths and ‘algae’ in muddy

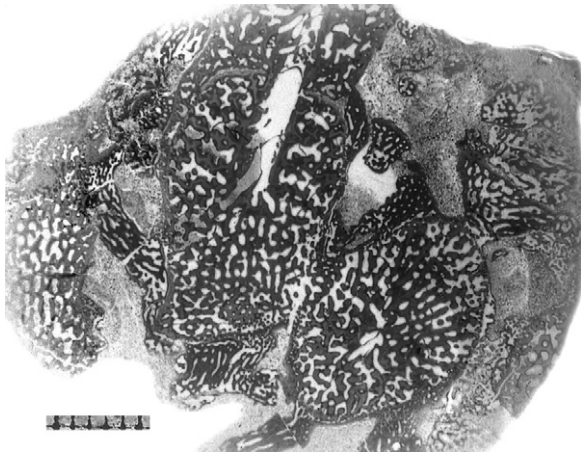


Fig. 2. Taenial type: *Archaeocyathus atlanticus* Billings, Fox Cove, Labrador, Upper Botoman–Toyonian. Framework consisting of modular cups, linked by exothecal outgrowths. Coll. F. & M. Debrenne, GSC62190.

Fig. 2. Type taenial : *Archaeocyathus atlanticus* Billings, Fox Cove, Labrador, Botomien supérieur–Toyonien. Charpente constituée de calices modulaires liés par des excroissances exothécales. Coll. F. & M. Debrenne, GSC62190.

limestones higher than the enclosing beds led Zhuravleva and Zelenov [64] to consider them as bioherms (Fig. 3). They were the first to propose several types according to their biological components and stratigraphic position. James and Debrenne provided an English summary of reef studies published from 1966 to 1978, allowing specialists to have access to the Russian literature, otherwise not readily available [27]. Thus, westerner

scientists [2,3,9,16,17,22,28,33,36,46,47], prospecting the Cambrian reefs of the world, have documented the lithology and biosedimentology of reef-building communities, revealing features in common with recent reefs, as in situ organism–organism intergrowths, abundant marine cements, stromatactis structures, micro- and macroborings, and primary cavities containing diverse cryptobionts and photosymbionts trophic web, a presence which is however refuted by Wood [52,60]. Further systematic study of reef-dwelling species suggested that, ecologically, they were very different in terms of nutrient availability, energy flow, and trophic nucleus from the recent reefs, even setting in sedimentologically and climatically comparable environments [14–17,22,28,33,34,40,44,56]. Even if they are not similar to the Recent, there is currently no doubt as to the reefal nature of archaeocyathan bioconstructions.

3. Morphology and components of Lower Cambrian archaeocyathan reefs

3.1. Morphology

Between 1960 and 1966, Zhuravleva [62,63] initiated researches into characterisation of morphological variations in structure and composition of reefs. She distinguished two types. The ‘monolophoid’ reef is a plano-convex structure of 1.5 m in height to maximum 12 m in diameter, with a basal flat surface colonised by ‘algae’ (now named calcimicrobes, abbreviation for calcified microbial fossils [28]) and with a domed upper surface.



Fig. 3. Titiriktek stream, Lena River tributary, a single kalyptra reef.

Fig. 3. Rivière Titiriktek, affluent de la Lena, un récif formé d’une kalyptra isolée.

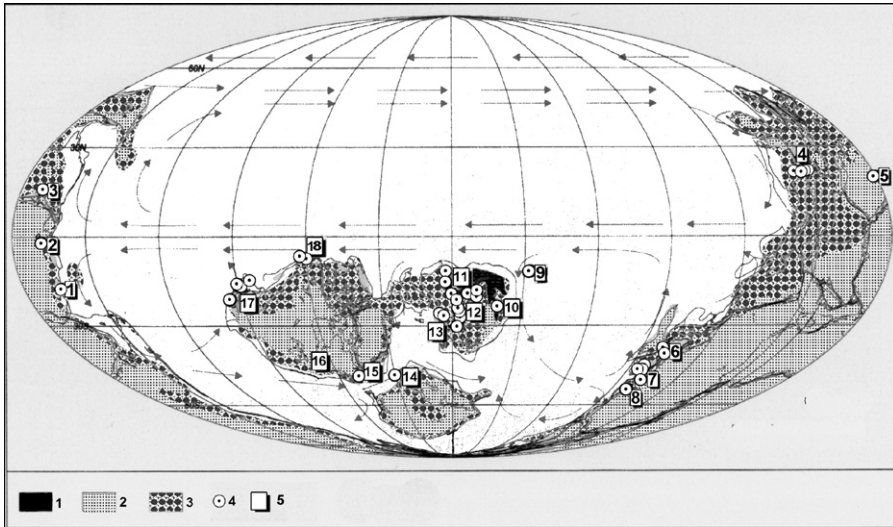


Fig. 4. Geographic distribution of Early Cambrian archaeocyathan reefs, bottom of map: (1) mountains; (2) land; (3) continental shelf; (4) reefs with archaeocyathans; (5) localities. Localities: 1–2, Antarctica; 3, Flinders Ranges (Australia); 4, South China; 5, Amadeus Basin (Australia); 6, Sardegna (Italy); 7, France & Spain; 8, Anti-Atlas (Morocco); 9, Mongolia; 10, Kija River (Kuznetsk Alatau); 11, Siberian platform (Yakutia); 12, Altai-Sayan; 13, Northern Siberia; 14, Germany; 15, Newfoundland & Labrador; 16, Virginia; 17, Cordillera Chain: Mexico, California, Nevada; 18, Rocky Mountains (Canada). From Rowland & Shapiro [48] (fig. 9, modified).

Fig. 4. Répartition géographique des récifs à archéocyathes du Cambrien inférieur, à la base de la carte : (1) montagnes ; (2) terre ; (3) plateau continental ; (4) récifs à archéocyathes ; (5) localités. Localités : 1–2, Antarctique ; 3, Flinders Ranges (Australie) ; 4, Chine méridionale ; 5, Amadeus Basin (Australie) ; 6, Sardaigne (Italie) ; 7, France & Espagne ; 8, Anti-Atlas (Maroc) ; 9, Mongolie ; 10, Kija River (Kuznetsk Alatau) ; 11, plateforme sibérienne (Yakutia) ; 12, Altai-Sayan ; 13, Sibérie septentrionale ; 14, Allemagne ; 15, Terre-Neuve & Labrador ; 16, Virginie ; 17, cordillère Nord-Américaine : Mexico, Californie, Nevada ; 18, Montagnes Rocheuses (Canada). D'après Rowland & Shapiro [48] (fig. 9, modifiée).

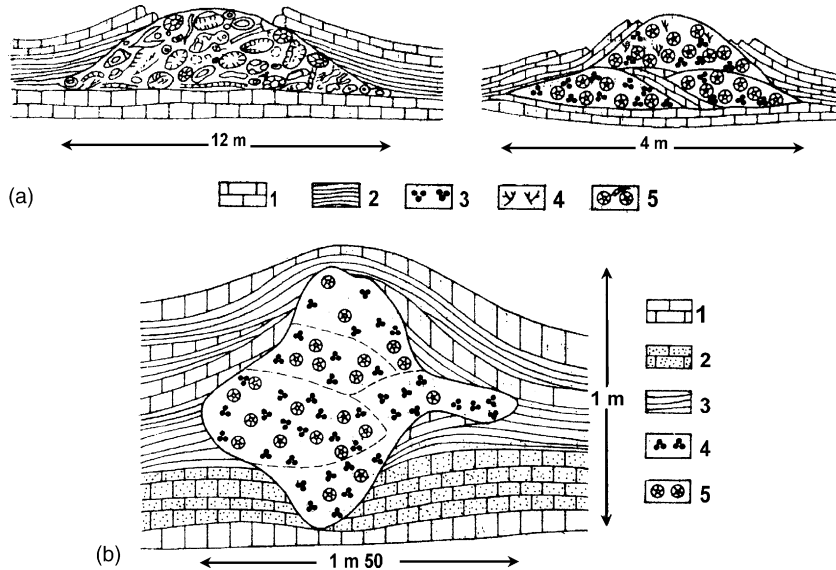


Fig. 5. (a) Monolophoid bioherm, single kalyptra (left); complex kalyptra reef (right). (b) A mound of dilophoid bioherms; from Zhuravleva [63] modified; (1) limestone; (2) sandy limestone; (3) argillaceous limestone, siltstone and shales; (4) calcimicrobes; (5) archaeocyathans.

Fig. 5. (a) Bioherme monolophoïde, kalyptra simple (à gauche); récif complexe à kalyptrae superposées (à droite). (b) Colline de biohermes dilophoïdes; d'après Zhuravleva [63] modifiée; (1) calcaire; (2) calcaire gréseux; (3) calcaire argileux, grès et schiste argileux; (4) calcimicrobes; (5) archéocyathes.



Fig. 6. Oy-Muran complex stacked kalyptra reef; Lena River bank.

Fig. 6. Oy-Muran : récif complexe formé de kalyptres empilées ; berges de la Léna.

The second type, the ‘dilophoid’ reef, is a biconvex-shaped structure with a narrow base expanding to a maximum size and decreasing to a narrow apex, 1–2 m in height and 1.5–3 m in diameter (Fig. 5). The spatial arrangement of these mounds gives rise to a great variety of shapes. Later Zhuravleva and Miagkova [65] combined the different morphological types under one single name: calyptra from the geek *kaluptros* (a small cap), modified into kalyptra by Rowland & Gangloff [47], to

avoid confusion with ‘calyptra’, a botanical term, and defined as follows: “kalyptrae are loaf- or pillow-shaped mounds which are the primary component structure of a reef (0.5 m to 8.0 m in diameter; 1–2 m wide and rarely more than 1 m high). They occur singly or collectively, in some cases, stacked on top of one other, forming complexes up to 40 m high and up to 10 km wide, rarely more prominent than 1 m above the sea floor, as observed on Lena River bank (Oy-Muran, Siberia) (Fig. 6). This

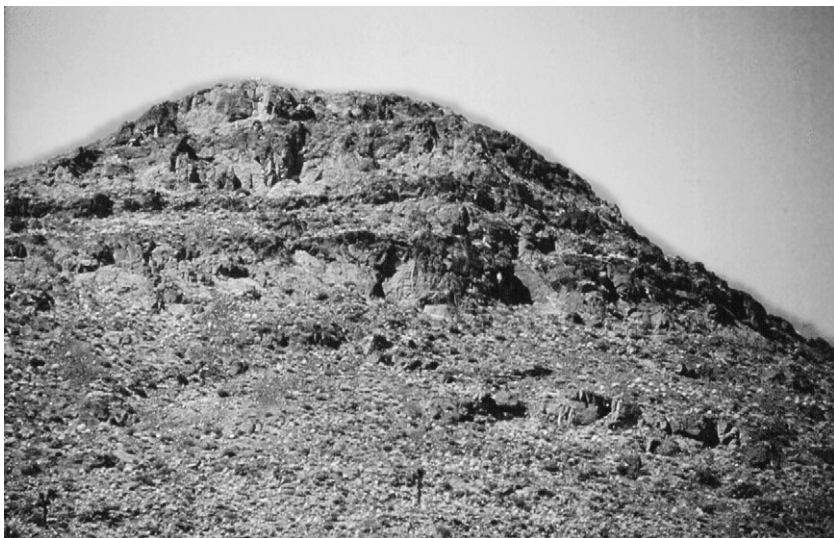


Fig. 7. Stewart’s Mill(Nevada): mudshales of Campito Formation overlaid by successive individual boundstones of specific composition, separated by mudshale facies (tidal channel) and capped by an oolite shoal [47 (p. 130)].

Fig. 7. Récif complexe de Stewart’s Mill (Nevada) : *mudshales* de la formation de Campito, surmontés par une succession de bioconstructions de composition spécifique, séparées par des faciès boueux (chenaux de marée) et coiffés d’une barrière oolitique [47 (p. 130)].



Fig. 8. Salaany Gol (Mongolia): massive non-kalyptra reef.

Fig. 8. Salaany Gol (Mongolia) : récif massif sans distinction de kalyptres.

biohermal complex of reefs is part of the Great Siberian Barrier Reef (200–300 km) stretching over northern Siberia from the Aldan to the Kotuiy Rivers [47,49].

Kalyptrate reefs are typical of Lower Cambrian reefs. Nevertheless, an archaeocyath–calcimicrobe consortium is able to construct massive, non-kalyptrate reefs as the 600-m-wide, 90-m-thick build-up of Schrimp Lake in Yukon Territories, northwestern Canada [41] interpreted as being formed in a quiet water setting or the archaeocyath calcimicrobial–reef/oolite shoal complex in the Poleta Formation (western Nevada), extending 200 km along the shelf margin of the northern margin of Laurentia [46,47] (Fig. 7).

Other exceptional individual bioherms are massive non-kalyptrate reefs (Fig. 8). Some are opened quarries of ‘marble’, used in architecture and decoration (Alconera, Spain; Funtana Calumba, Sardinia; Amagour, Morocco).

3.2. Reef structure

Specific investigations on structure and composition of Lower Cambrian reefs were not carried out until the late 1970s. The Russian authors [57,63] focussed their work on the morphological variation of reefs and on the systematic composition of building organisms during the Lower Cambrian. During the last 25 years, a number of detailed studies were undertaken worldwide to analyse the variations in structure and composition of Cambrian reefs and their evolution in time. Most importantly, Noël James developed a clear method of investigation, which he and his collaborators applied to reefs of Newfoundland (Kobluk and Debrenne), Australia (Gravestock), Siberia (Kruse and Zhuravlev). Most of the studies since 1980 have followed this method, which consists in dividing the studied mound into squares to which are mapped the percentage of biological components (main framework builders and subordinate organisms), and abiological estimate (matrix, cavities and cements), recorded and

quantified (Fig. 9). The role of the archaeocyathan shape inside and outside the build-up, the presence of cryptobionts dwellers and their interactions with calcimicrobes, are equally mapped for each kalyptra. Individual kalyptra can belong to one or two several domains (areal extent of a given lithology or environment), each recurring several times or creating a complex of different domains. Due to the variability in the shape of cups and the morphofunctional dissimilarity in the distribution of soft tissue, the role of archaeocyatha in a biohermal complex seems to have been quite different. The former distinction between ‘Regulares’ and ‘Irregulares’ reflects their ecological preferences: when the soft tissue fills the entire body (‘Regulares’), the water flows through all the aquifer system, while when the soft tissue is restricted, by the development of secondary skeleton, to the upper part only (‘Irregulares’), the water currents are more independent of the porosity. Solitary ‘Regulares’ (Ajacicyathida and Coscinocyathida) proliferated on mud substrata with a high rate of sedimentation, at the periphery or in cryptic niches within the bioconstructions; their high competi-



Fig. 9. Sampling method: square grid marked on the flank of a Serra Scoris bioherm, Sardinia.

Fig. 9. Méthode d'échantillonnage selon une grille tracée sur le flanc d'un bioherme à Serra Scoris, Sardaigne.

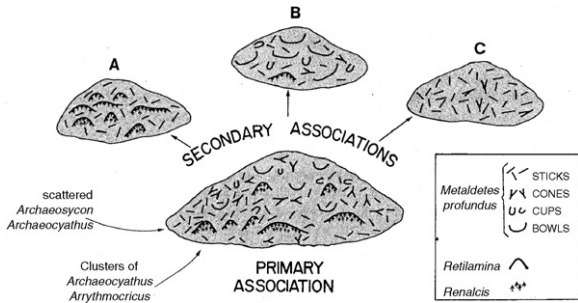


Fig. 10. Various spatial relationships between different archaeocyathans in kalyptrae, which make up the complex reefs of Labrador. The primary association is the most commonly observed with less common, but recurring, secondary associations (from [9], fig. 5).

Fig. 10. Les différentes relations spatiales dans la répartition des archéocyathes dans les kalyptres qui composent les récifs complexes du Labrador. L'association primaire est la plus fréquente ; les associations secondaires sont moins fréquentes, mais récurrentes (d'après [9], fig. 5).

tivity and incompatibility to other organisms prevented them from being good binders. The development of secondary skeleton allowed 'Irregulares' (Kazachstanicyathida and Archaeocyathida) to be better builders; their higher integration and tolerance to other organisms favoured the process of modularity and strengthened their reef-building capability as binders and bafflers [13,55].

The studies of reefs from different localities and age show that they have the same basic plan and can be categorised into component domains occupied by associations of lime mud, archaeocyathans, calcimicrobes

and/or cement, with opportunities for cavity development. Domains reflect microenvironmental variations (Fig. 10).

3.3. Reef components

Most of the Lower Cambrian reefs were built by a consortium of calcimicrobes and archaeocyaths. Archaeocyaths themselves did not generally produce a real framework, but were an obligate substrate for dominant calcimicrobes, for cement, and provided additional opportunities for cavity development. Archaeocyaths were relatively abundant in bioherms built by calcimicrobes of the *Renalcis*-group, but rarer in those built by the *Epiphyton* group. The *Renalcis* group was probably less influenced by high sedimentation rate than *Epiphyton* and relatives, which had a more important growth rate than archaeocyaths in the absence of sedimentation rate stress [52].

The carbonate platform of South Australia was intensively examined to investigate as many different palaeoenvironments as possible with their influence on archaeocyathan reef development [28]. Their results have a global value and the Lower Cambrian reefs can be ascribed to the types based on their main components and their corresponding palaeoenvironmental distribution (Fig. 11).

Characteristics of archaeocyathan reefs are based on core components. Then, the archaeocyath-calcimicrobial reefs can be classified according to

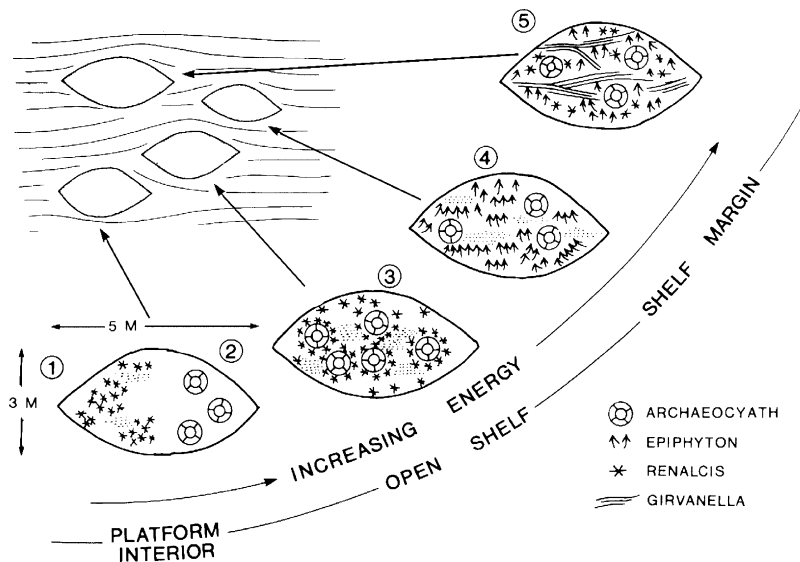


Fig. 11. The different types of calcimicrobes–archaeocyath reefs and their distribution according to the energy spectrum; from [28] (fig. 11, modified).
 Fig. 11. Les différents types de récifs à calcimicrobes et archéocyathes et leur répartition en fonction de leur position et de l'énergie, d'après [28] (fig. 11, modifiée).

the type of dominant builder. Among the archaeocyathan reefs now listed among the Cambrian rocks of the world, the following examples given below are those that my husband Max and I had the opportunity to visit or from which I have received material for study.

3.3.1. *Calcimicrobe boundstone*

It is a complex intergrowth of different calcimicrobes. Few or no archaeocyaths are found in their core. They occur in inner shelf locations under low-energy environments. *Renalcis* is dominant in Siberian Platform bioherms through the Tommotian [33], in some Atdabanian–Botoman reefs of southern Australia, [28] and in some Toyonian reefs of Antarctica [45].

3.3.2. *Archaeocyath boundstone*

In some rare cases archaeocyaths may be the dominant reef framework. Their bioconstructions are generally limited to some individual bioherms.

Riding and Zhuravlev [45] found, at Ulakhan-Sulugur, just above the base of the Tommotian stage, the oldest known reef on the Siberian Platform in which individual cups of *Cambrocyathellus tschuranicus*, a bowl-shaped archaeocyath, are intergrowing with other cups to form a rigid cavernous framework (Fig. 12). Cavities are colonised by cryptobionts: renalcids and some

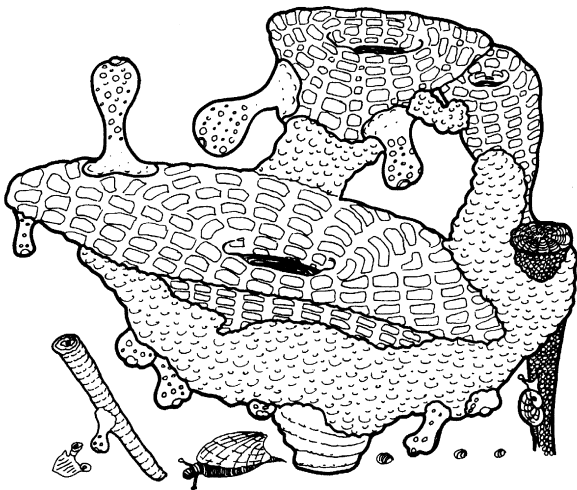


Fig. 12. Humoristic sketch of a Tommotian Ulakhan-Sulugur reefal community with large cups of frame building archaeocyaths, delimiting cavities with cryptic small monocyathid cups and renalcids; presence of in-situ bafflers (hyoliths, left) and reef dwellers molluscs; from [45] (fig. 4).

Fig. 12. Schéma humoristique d’une communauté récifale d’Ulakhan-Sulugur (Tommotien), charpente formée d’archéocyathes évasés délimitant des cavités habitées par des monocyathides cryptiques et des renalcides; présence de bafflers en place (hyolithes à gauche) et de mollusques [45] (fig. 4).

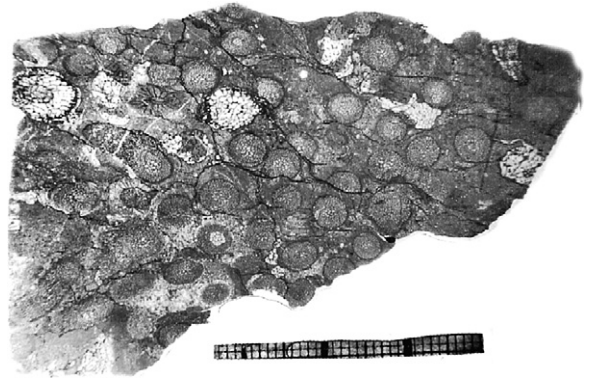


Fig. 13. Archaeocyath boundstone in Matoppa reef (Sardinia), coll. F. & M. Debrenne. MNHN MT6.

Fig. 13. Boundstone à archéocyathes du récif de Matoppa (Sardaigne), coll. F. & M. Debrenne. MNHN MT6.

one-walled archaeocyaths. In the Matoppa Formation (Botoman equivalent) of Sardinia [22], Gandin and Debrenne described a reef framework consisting of dominant modular *Dictyocyathus tenerrimus* and branching *Archaeopharetra ertashkaense* with encrusting *Renalcis* (Fig. 13). In the Moorowie Formation (Upper Botoman equivalent, Flinders Ranges, South Australia), atypical reefs displayed a solid framework, essentially composed of the first known tabulate coral *Flindersipora bowmanni*, the modular intergrowing *Ajacicyathus aequitriens* linked by stereoplasma and exothecal tissue anchoring the archaeocyathan cups to the top of the *Flindersipora* colonies (Fig. 14) [35]. A second tabulate genus was found later in the same reef complex [50], setting in an arid sea marginal fan under high-energy environment. At Cerro Rajon (Sonora NW Mexico), in

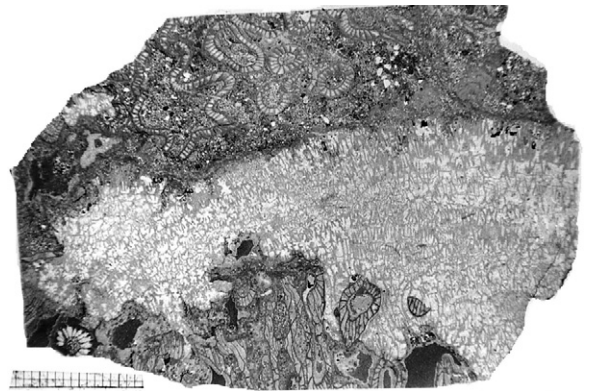


Fig. 14. The tabulate coral *Flindersipora*, with attached archaeocyath *Ajacicyathus*, Moorowie Mine, Botoman, Australia, Coll. B. Bowman, MNHN M42048.

Fig. 14. *Flindersipora* (tabulé), support de l’archéocyathe modulaire *Ajacicyathus*, Moorowie Mine, Botomien, Australie, Coll. B. Bowman, MNHN M42048.

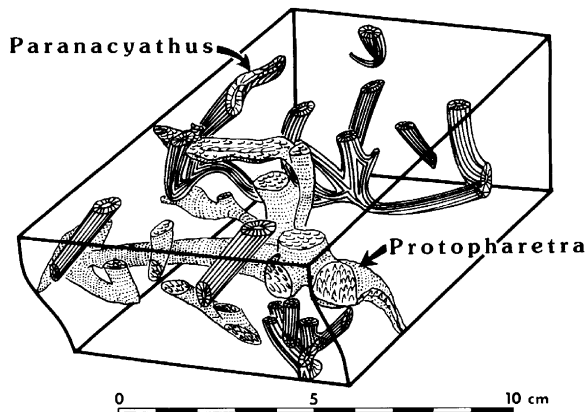


Fig. 15. Archaeocyath boundstone from Sonora (Mexico); reconstruction of the *Paranacyathus*–*Protopharetra* intergrowing community; from [47] (fig. 14).

Fig. 15. Boundstone à archéocyathes de Sonora (Mexico); reconstitution de la croissance simultanée de la communauté à *Paranacyathus*–*Protopharetra*; d'après [47] (fig. 14).

type-1 reefs [14], branching archaeocyaths and exothecal outgrowths formed a dense, rigid framework, waved resistant, shelf-margin setting, in which *Renalcis* were subordinate (Fig. 15). By the late Early Cambrian, in Labrador [9], rigid individual constructions are formed by exothecally bound archaeocyaths and by complete fusion of several branching units of modular forms to produce a genuine framework (Fig. 16). In other kalyptrae of the same area, sheets and arched domes of *Retil-*

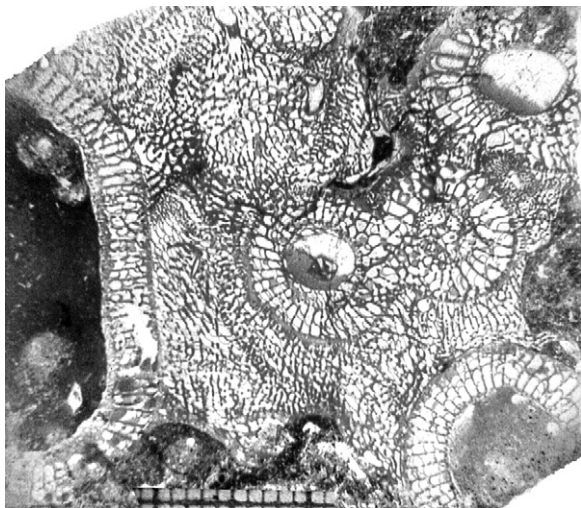


Fig. 16. Archaeocyath boundstone from Labrador; *Metaldetes* modular cups linked by exothecal outgrowths to form a solid reefal framework. Coll. F. & M. Debrenne, GSC 6211.

Fig. 16. Boundstone à archéocyathes du Labrador; calices modulaires de *Metaldetes* reliés par des structures exothécales formant une charpente récifale solide. Coll. F. & M. Debrenne, GSC 6211.

amina amourensis, piled up on the top of one another, sheltered a cavity-dwelling fauna of calcimicrobes and microfauna (Fig. 17)

3.3.3. *Renalcis*–archaeocyath boundstone

The most frequent framework builder of Cambrian reef is *Renalcis*, generally encrusting archaeocyath cups, accompanied by other calcimicrobes not volumetrically significant. They occupied the inner shelf, in a low-energy environment. Examples: lower Petrotsvetsk Formation, Siberia [63], Campito and Poleta Formations (western USA) [47], Sekwi Formation [43] and Forteau Formation (Canada) [9,26], Lower Wilkawillina (Australia) Shackleton limestone (Antarctica) [44].

In rarer cases, archaeocyaths are dominant or equally associated with a consortium of calcimicrobes often being cryptobionts. They have an open shelf, middle- to high-energy environment setting and are often associated with *Renalcis*-dominant mounds in composite kalyptrate reefs of the areas quoted above.

3.3.4. *Epiphyton*–archaeocyath boundstone

Epiphyton often developed spectacular bushes growing on archaeocyath cups or surrounding them. This type of reef is mainly settled on a shelf margin, in a high-energy environment. Examples are frequent in Morocco [12,17], Normandy [7], Spain [36,37,39,58], Sardinia [18,22], of Atdabanian to Lower Botoman in age. In Antarctica [45], Toyonian mounds with *Epiphyton* dominant are the most frequent, settled on platform margin in low-energy facies. In Yangtze (Huangling section) [16–23], *Epiphyton*, associated with *Renalcis*, *Girvanella* and taenial archaeocyaths forms small constructions on a muddy continental platform in low-energy conditions.

3.3.5. *Girvanella*–*Epiphyton*–*Renalcis* boundstone

This reefal type consisted of complex intergrowths of calcimicrobes dominant and archaeocyaths, in which *Girvanella* crusts were the most abundant; the proportion of other components was variable. They developed on shelf margin, in high-energy conditions. They were studied in Mongolia, Zavkhan Basin [34,51], Mexico (Sonora type 2 build-ups) [14], Battle Mountains (Iron Canyon) [15], Sardinia (rio Cannas) [22], Spain (Cantabrian Chain) [1,8,40].

3.3.6. Reef minor components

They are associated with the main builders, but volumetrically not significant, such as the calcarean sponges *Gravestockia* (Australia) [13]), enigmatic radiocyaths,

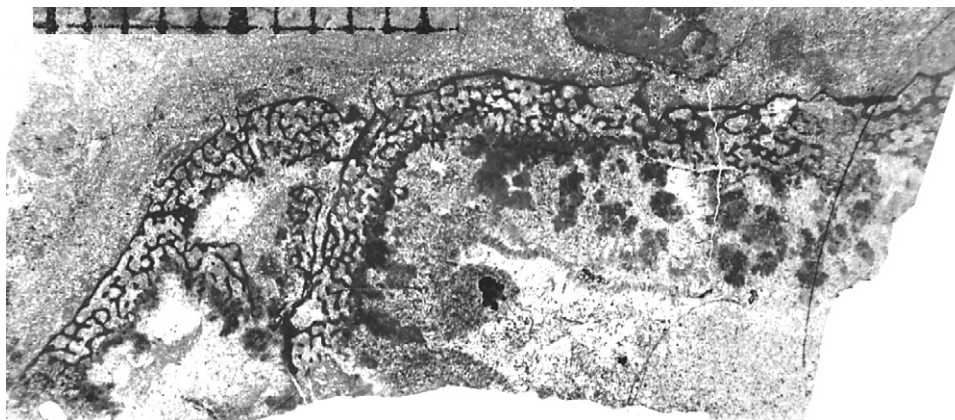


Fig. 17. *Retilamina* roofing a inner cavity with pendant *Renalcis*, Coll. F.& M. Debrenne. GSC 62127.
 Fig. 17. *Retilamina* au toit d'une cavité interne avec des *Renalcis* pendants, Coll. F. & M. Debrenne. GSC 62127.

subordinate to archaeocyath or forming their own thickets (Australia) [30,32], Mongolia [34,51,56], Morocco [12], Siberia [42], some putative tabulate corals *Flindersipora*, *Moorowipora* (Australia [35,50]).

4. Ecology of Lower Cambrian reefs

Archaeocyathan-calcimicrobial bioconstructions have topographic relief, a biogenic framework, and a certain capacity for wave resistance. Reefs were presumably initiated during episodes when the mud input slowed down or ceased, thus allowing localised cementation or stabilisation of seafloor mud [33,45,48]. Archaeocyathan reefs possess syndepositional cements and growth-framework cavities housing cryptobionts [29,33,61] like in later Phanerozoic reefs. There is not yet a consensus on the question of photosymbiosis among archaeocyath specialists. The observation of putative bacteria within the skeletal elements of archaeocyaths might suggest a symbiotic relationship similar to that practised by many Recent sponges. In Early Cambrian reefs, evidence for the presence of photosymbionts is necessarily indirect, as indicated by the possible reconstruction of the trophic structure [47,48,53–55]. Many archaeocyaths do possess a large skeletal surface area mantled by a thin veneer of soft matter amenable to photosymbionts. However, such forms tended to be mud dwellers favouring turbid waters presumably inimical to photosymbionts [33,59].

In matrix or in peri-reefal beds of some Lower Cambrian reefs are locally found trilobites; disarticulated valves of ostracodes, valves of inarticulate brachiopods, hyoliths, salterellids, helcionelloids, echinoderm ossicles, chancelloriids, sponge spicules [42], attesting the presence of various reef dwellers. Macroborings are

rarely present; *Trypanites*, occurs on the upper surface of Lower Cambrian reefs of Labrador [31].

The Early Cambrian reef ecosystem was largely composed of generalists and opportunistic passive filter- and active suspension-feeders, which were dependent upon a relatively high supply of nutrients. Many reefs were

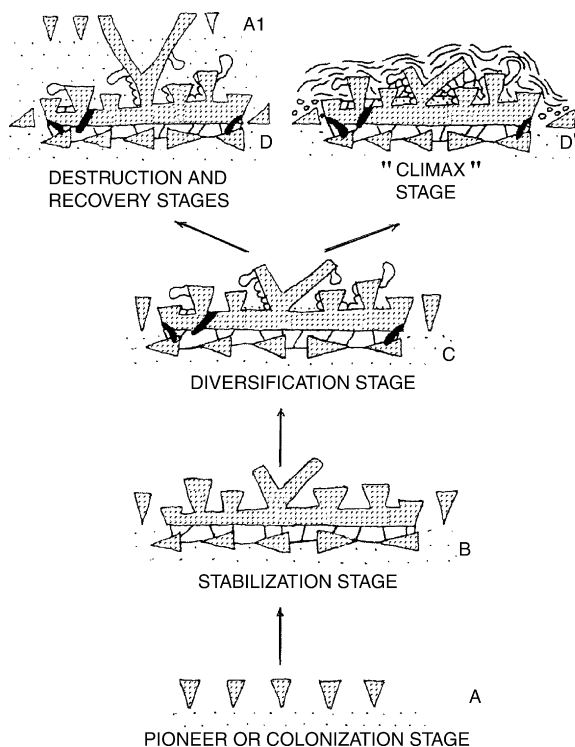


Fig. 18. Ecological succession on an Early Cambrian reef, reconstitution from [59] (fig. 10, modified).
 Fig. 18. Reconstitution de la succession écologique dans la construction d'un récif du Cambrien inférieur d'après [59] (fig. 10, modifiée).

dominated by just one or two archaeocyathan species, implying that these communities were the result of rapid colonisation and subsequent growth from one or a few larval spat falls [56]. Such a trophic organisation is similar to some other Palaeozoic reefs, but contrasts fundamentally with some Mesozoic and most of the Cainozoic and Recent reefs, which are dominated by mixo- and phototrophs adapted to low-nutrient conditions [52–54].

Lower Cambrian reefs were long time thought not to display vertical zonation [42]. Ecological succession in Cambrian reef ecosystem was discussed by Copper [4] and an obvious zonation was proposed at the same time

by the detailed study of Stewart Mill Reef, Poleta Formation, Nevada [47] (Fig. 19). This serves as a proof to argue that Cambrian reefs have ecological succession like younger metazoan reefs (Fig. 18). Nonetheless, it is not a character frequently observed in other archaeocyathan reefs.

A. Zhuravlev [59] synthesised the result of previous studies and proposed a model represented here (Fig. 18): (A) a pioneer stage obtained by settlement on muddy substrate of solitary ajacyathides tolerant of turbid conditions; (B) a stabilization stage, where modular archaeocyaths encrusted the resulting grainstone–packstone to

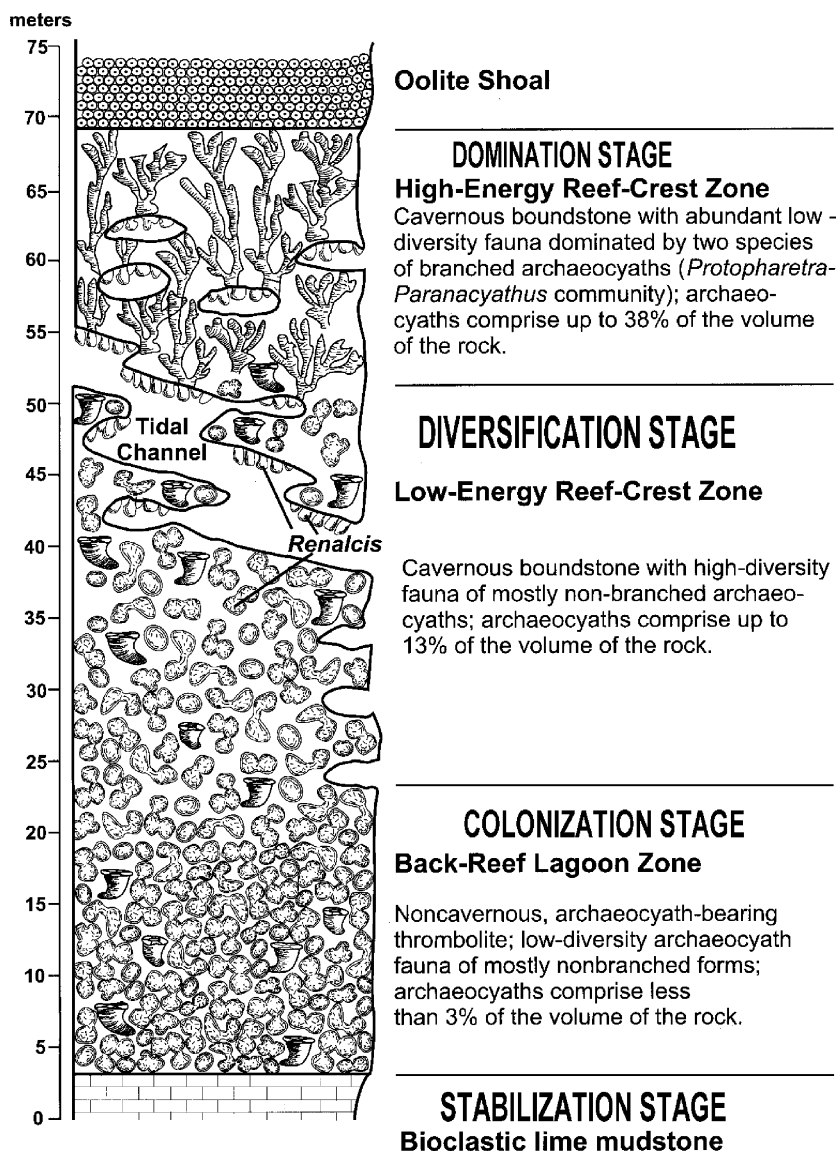


Fig. 19. Facies zonation and interpreted depositional environments in the massive reef complex of Stewart's Mill (Nevada); from [48] (fig. 5, modified).

Fig. 19. Zonation et interprétation des environnements des faciès dans le récif massif de Stewart's Mill (Nevada); d'après [48] (fig. 5, modifiée).

produce framework; (C) a diversification stage that strengthened the framework by binding *Renalcis* and occupied reef cavities by an assemblage of cryptobionts such as archaeocyaths (monocyathides, capsulocyathides), *incertae sedis* organisms (cribricyaths), hydroconozoans and borers; (D₁) a destruction stage, corresponding to the drop in the sea level or to a storm action that buried the framework in loose sediments, followed by either (A₁) a recovery stage, provided by surviving modular archaeocyathids or (D₂) a climax stage, by growth into the marginal peritidal or surf zone (shallow and agitated environment), with development of crusts (*Razumovskia* or *Retilamina*); in both cases, the new association was species-impooverished, with commonly a monospecific archaeocyathan community.

Despite their small size, a number of Early Cambrian reefs represent complete ecological successions. Others were initiated and dominated by calcimicrobes, with archaeocyaths as subordinate dwellers, contributing only modestly to reef construction.

5. Space and time distribution of archaeocyathan–calcimicrobial Lower Cambrian reefs

If not all archaeocyaths occur in limestones, as a few examples are found in siliciclastic facies, the vast majority live in carbonate-dominated environment facies and their palaeogeographic distribution coincides with the extension of marine carbonate deposits and of shallow marine habitats. Their association with calcimicrobial/stromatolitic reefs and oolite shoals and the proximity of evaporitic basins are in favour of an adaptation to warm waters, limited to intertropical areas [11]. Then, conditions are optimal for archaeocyaths to be involved in reef construction. Not all archaeocyaths are reef builders, but most of them lived within, or associated with reefs.

Palaeogeographic reconstructions indicate that the regions farthest from the palaeoequator were Morocco and southern Europe to the south, possibly the Yangtze (South China) and an enigmatic (though non-confirmed) locality in Korea to the north [6] (Fig. 4).

The archaeocyathan proliferation followed the continued transgression initiating the carbonate accumulation [19] from Siberia (Tommotian) to Sayan-Altay, Mongolia, Spain, France (Normandy), Morocco (Early Atdabanian), then from European an Moroccan new centres of dispersion, following the northern margin of Gondwana, to South China, Australia and the North American Cordillera (Late Atdabanian–Early Botoman). When the Lower Cambrian transgression reaches its

maximum (Botoman), from Australia to Antarctica, Russian Far East and Laurentia, the Late Botoman and Toyonian were characterised by two major regressions and anoxic episodes, progressively eliminating the archaeocyaths and the reefs through the reduction of shallow waters domains [20,38,61].

6. Conclusions

Even when reefs are dominated by calcimicrobes, subordinate archaeocyaths contribute as dwellers to the reef construction since the Tommotian, as support for the builders and as cavity roofs. They were active bafflers at the periphery and the top of reefs and constitute an abundant fauna in the inter-reef domains. The basic metazoan-calcimicrobial construction did not change significantly through the Early Cambrian, even if archaeocyaths became more modular, so more significantly reef builders. It may be that the archaeocyathan-calcimicrobial competitive interactions, in which dendritic renalcids were dominant, contributed to the eventual near-total elimination of archaeocyaths from the Cambrian reef biota in the Toyonian stage. Recent researches have corrected some common ideas. For example, the Lower Cambrian reefs were not all small kalyptrae individual or compound. Calcimicrobe and archaeocyath bioconstructions may be massive, ecologically zoned, associated with oolite shoal. A consensus has not yet been found concerning photosynthesis: if absent in the Cambrian, then the archaeocyath reefs would be different from Mesozoic and Cainozoic reef communities. It is the next challenge for archaeocyathan reefs to become integrated in the model of the Recent.

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¹ Photos in Figs. 1–3, 6–9, 13, 16, and 17 are by Max Debrenne.

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