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The role of Archaeocyatha in Cambrian biostratigraphy and biogeography

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Abbreviated title: Archaeocyatha distributions in Cambrian

Abstract: The Archaeocyatha is group of Cambrian fossils successively considered as cnidarians or sponges or as an independent phylum convergent with many groups lacking clear affinities. Comparisons with Recent calcified sponges discovered in sub-marine caves have demonstrated that the sponge model is consistent with their structural organization. Thus their systematic position is now agreed as a class within the phylum Porifera, permitting now realistic investigations of their comparative physiology and life strategies. Archaeocyatha is an important part of research programmes on the Cambrian System, initiated by different commissions of the IUGS since 1970. Archaeocyathan biozones are available in some key regions. Faunal and palaeocommunities distribution, especially of the reefs they helped build in epeiric seas & migration pathways constrain Cambrian palaeogeographical reconstructions. A database, using recent compilations of the group, is now on line. This free access data source offers specialists a tool, easy to use not only as an identification key but also to establish faunal, geographical and stratigraphical distributions of archaeocyathan genera & a rapid first step towards Cambrian palaeogeographical reconstructions.

Keywords: Archaeocyatha, Porifera, Cambrian biozonations, palaeoecology, reefs, palaeogeography, migration pathways

Archaeocyatha represent the oldest calcified sponges and the first metazoans to build bioconstructions in association with calcimicrobes. They are a key group in biological and evolutionary studies, biostratigraphy, palaeoecology and the palaeogeography of the early Cambrian.

History of Systematic Studies

Archaeocyathans were first discovered in the middle of the 19th Century in the oldest fossiliferous rocks of Labrador (Canada); their geographical distribution is world-wide including Russia, Kazakhstan, Uzbekistan, Poland, Mongolia, China, Greenland, Canada, USA, Mexico, Argentina, France, Germany, Sardinia, Serbia, Spain, Morocco, South Africa, Antarctica & Australia. Following their discovery by Captain Bayfield, a hydrographer (Bayfield, 1845), sporadic new finds essentially formed the basis for discussions on the affinities of this enigmatic group. Only when large collections were made, authors had enough data to propose a coherent systematic approach: Bornemann (Sardinia) coined the name Archaeocyatha for a class within the Coelenterata (Bornemann, 1884) (Bornemann, 1886) “Über die Fortsetzung seiner Untersuchungen cambrischer Archaeocyathus-Formen und verwandter Organismen von der Insel Sardinien.,” 1884)

(Anon, 1884) and Taylor (1910), working on material from Australia, adopted the name and was the first to consider Archaeocyatha as an independent group intermediate between the Porifera and Coelenterata at the same taxonomic level (Taylor, 1910). The investigations world-wide really began in the 1930s with Vologdin and the Eastern school, Okulitch and the Bedfords and the Western school. Both groups based their classification on ontogenic stages but Okulitch's classification (Okulitch, 1943) was not accepted by other palaeontologists. A more logical pattern was established by Russian specialists based on abundant material with wide geographical and stratigraphical ranges. Vologdin (Vologdin, 1937) established two classes, whereas Vologdin & Zhuravleva (Vologdin and Zhuravleva, 1947) proposed a separate phylum for the Archaeocyatha. The modern systematic approach established by Zhuravleva (Zhuravleva, 1960) was based on the order of appearance and complexity of skeletal structures, determining key characters and consequently the hierarchy of systematics ranks, still in use today. Intensive studies have been carried out through international cooperation since 1970. At that time most of palaeontologists accepted the concept of an independent phylum and thereafter Archaeocyatha were seldom compared with Porifera except by some far-sighted zoologists. Technical progress in marine research by scuba-divers and the discovery of sponges capable of secreting massive calcareous skeletons with or without spicules, forced a reconsideration of the nature of a number of related fossils groups, e.g., stromatoporoids, chaetetids and archaeocyaths. There is now a consensus on the phylogenetic relationships of these enigmatic organisms: Archaeocyatha represent an extinct class of the phylum Porifera, close to the Demospongiae (Debrenne and Vacelet, 1984) (Debrenne and Zhuravlev, 1992).

Biostratigraphy

Subdivision of the Cambrian System was traditionally based on trilobite ranges. Zhuravleva (Zhuravleva, 1960) established the first stage subdivision based on Archaeocyatha on the Siberian Platform. Rozanov & Missarzhevskiy (Rozanov and Missarzhevskiy, 1966) discovered a rich archaeocyathan fauna on the Siberian Platform in some strata below the first appearance data (FAD) of trilobites & named a new stage, the Tommotian. Since then, archaeocyathans biozones have been used in key Cambrian areas such as Australia, Canada, Mongolia, Morocco, Siberia & Spain. The distribution of Archaeocyatha in time, mainly the early Cambrian with few relicts in the middle and late Cambrian, limits their use to stages 2 to 4 of the International Stratigraphic Chart. As the regional Siberian chronostratigraphical scale was the reference scheme for archaeocyathan

specialists to establish palaeobiostratigraphical correlations, this scale is used in this article: i.e. Fortunian, Tommotian, Atdabanian, Botomian and Toyonian.

When possible for many Cambrian localities where archaeocyathan and trilobites were well studied, two parallel scales, one based on trilobites the other on archaeocyathans are utilized. Under certain circumstances, archaeocyaths may actually provide finer biozones than do trilobites (Table 1).

Palaeoecology

Archaeocyathans were adapted to a narrow range of depths, salinity and temperature, but in association with calcimicrobes were the first widespread metazoan reef builders. Archaeocyaths were stenothermal organisms, corresponding to intertropical climatic conditions except to the South in South Morocco and South Europe occurrences & with some Chinese and possible Korean occurrences to the North (Debrenne and Courjault-Rade, 1994) (Fig. 1).

Archaeocyathans were stenohaline organisms. Increased salinity reduced the diversity of archaeocyathan communities; only forms, with simple walls and porous septa, tolerated higher salinities. During brief decreases in salinity, they were located in lime muds but not in evaporite environments (Debrenne & Zhuravlev 1996). Archaeocyaths were stenobathyal organisms, living anchored in soft substrates in intertidal to subtidal zones but probably not in the subphotic zone. They preferred shallow-water settings as supported by the following observations: 1, they mainly developed in carbonate-dominated lithofacies; 2, they are commonly associated with ooids and bioclastic limestones and with siltstones and quartz arenites indicating oscillating tidal-flat environments; 3, interbedded occurrences with a variety of hemispheroidal stromatolites and oncoids are observed and 4, they coexist with macroboring organisms in Labrador patch reefs (James & Kobluk 1978). In the deepest-water Tommotian bioherms of the Siberian Platform (Kruse et al., 1995), archaeocyathan communities are characterized by a significant development of secondary skeletal structures. On the other hand, episodic erosional events can be demonstrated only in Sardinia (Debrenne et al., 1989a) and Khara-Ulakh Mountains, where a distinctive archaeocyath life strategy consists of *Dictyocyathus* encrusting the biohermal surface (Debrenne & Zhuravlev 1996).

As passive filter feeders, archaeocyaths were better adapted to habitats with reduced turbulence and increased currents and nutrient supply, as are Recent calcified sponges. Certain morphological features are predominant within some archaeocyaths communities; it might be due to local environmental conditions such as turbulence, detrital input or volcanic ashfall (Zhuravlev 2001). They also were active bafflers at the periphery and on the top of reefs and constitute an abundant fauna in inter-reef environments.

Since their first occurrences, archaeocyathans were interpreted as being responsible for construction of the first metazoan reefs. The archaeocyathan-calcimicrobial bioconstructions have topographical relief, a biogenic framework & a certain capacity for wave resistance. They were seemingly initiated when mud input slowed down or ceased, thus allowing localized cementation or stabilization of seafloor mud. Archaeocyathans did not generally produce a real biological framework. Since the Tommotian, even when reefs were dominated by calcimicrobes, subordinate archaeocyathans have assisted reef building, supporting the builders and forming cavity roofs. Data on the analysis of biohermal communities and their architectures indicate that they reflect the relative development of the main reef-building components, dominant physical-chemical factors, mainly temperature and nutrient availability and the physiography of the depositional setting. The bioaccumulations show different reef building styles, 1, mud-supported simple to compound mounds locally with stromatolite-like cavities; 2, dendrolitic bioherms and crustose buildups with large shelter cavities and low synoptic relief; 3, cement supported skeletal reefs with wave resistant frameworks often associated with oolitic shoals & 4, bioclastic sands, developed at photic and

shallow sub-photoc depths on low-angle/low-energy ramps (1-2) or on high-energy conditions on platforms distally rimmed (3) or occasionally swept by storm currents (4) (Gandin & Debrenne 2010).

Studies of the worldwide distribution of Cambrian reefs have described and illustrated the lithology and biosedimentology of reef-building communities (Debrenne 2007). Features in common with Recent reefs: in situ organism–organism intergrowths, abundant marine cements, stromatactis structures, micro- and macroborings, primary cavities containing diverse cryptobionts and photosymbionts trophic web have been observed. Even if they occur in sedimentologically and climatically comparable environments, some studies of reef-dwelling species suggested that, ecologically, they were very different from the Recent reefs, in terms of nutrient availability, energy flow and their trophic nucleus (Wood *et al.* 1992, Zhuravlev & Wood 1995).

Palaeogeography

Cambrian palaeogeographic reconstructions are notoriously difficult for the Precambrian-Cambrian intervals due to sparse reliable palaeomagnetic data and a lack of any usual climate indicators. Lands distributions are constrained by the distribution of reefs established in associated epeiric seas. Global palaeogeographical reconstructions are based herein on Jaccard's similarity coefficient which calculates a relationship between the numbers of distinct taxa present at two localities at the same time. The Jaccard's similarity coefficient values are calculated for both Archaeocyatha and the total faunas of Tommotian (528-521Ma), early Atdabanian (521-515Ma) and Botomian (515-510 Ma) age. The resulting pathways of archaeocyathan migration suggest the early Cambrian existence of East and West Gondwana, the rifting of Laurentia from the Australian-Antarctic margin & the drift of the Altay-Sayan and Mongolia suspect terranes towards Siberia (Fig. 2) (Debrenne *et al.* 1999). An exhaustive compendium of archaeocyath genera may provide material for the further definition of provinces and realms by cluster analysis (e.g. Kruse & Shi 2000). Five provinces are recognized after an initial phase of cluster analysis of generic distribution data: A, Siberia-Mongolia (including Siberian Platform-Kolyma, Altai Sayan, Tuva, Transbaikalia Mongolia Far-East-Higgan); B, Europe-Morocco; C, Central East Asia (including Kazakhstan-Tajikistan-Turkmenistan-Uzbekistan-Tarim-Kirgiztan,Urals, South China); D, North America – Koryakia; E, Australia-Antarctica (and possibly South America) (Fig. 3). Two realms are defined by the second phase cluster analysis: Eurasia (the first three provinces) and Laurastal (the last two provinces) (Fig. 4). In the early Tommotian the first appearance of archaeocyaths (FAD) occurred within the transitional Anabar-Sinsk tract of the Siberian Platform (Fig. 5a). They spread to the Altay-Sayan and Russian Far-East only in the late Tommotian. Other regions with phosphatic-rich sedimentation, extensive evaporite basins or fluvatile and deltaic siliciclastic sediments were not amenable to archaeocyath settlement. In the early Atdabanian the major marine transgression generated widespread carbonate sedimentation in Altay-Sayan, Russian Far-East and Mongolia with corresponding dispersion of archaeocyaths (Fig. 5a) & in the mid Atdabanian, archaeocyaths of Siberian affinities reached Western Europe and Morocco where a new center of diversification developed and endemic forms emerged (Fig. 5b). By the late Atdabanian, continuous transgression initiated carbonate accumulation and archaeocyath proliferation on Yantsi and Australia from Siberia and Morocco (Fig. 5c). The peak of the transgression was reached at the beginning of the Botomian, leading to the relative isolation of various regions and to a maximum diversity of mostly endemic faunas. At that time archaeocyaths of Siberian and Australian affinities reached the North America-Koryakia Province (Fig. 5d). In the mid Botomian, Australia became a new center of diversification spreading to Antarctica and possibly South America (Gonzalez *et al.* 2011) whereas West America archaeocyaths populated East America (Fig. 5e).The medial Botomian transgressive peak was marked by the extensive accumulation of black shales, thin bedded limestones in low latitudes and an anoxic/dysoxic event. Consequently the archaeocyaths survived only as low-diversity communities in localized refugia. The late Botomian-early Toyonian regression reduced

shallow marine platform areas and thereby removed the archaeocyaths which virtually disappeared at the beginning of middle Cambrian (Fig. 5f). The only archaeocyathan species of post-early Cambrian age are found in Antarctica which was the only one to remain in low latitudes due to the counter-clock rotation of Gondwana.

Archaeocyaths on line

Archaeocyathan database and website

Establishing a database is nowadays is one of the powerful means to manage and analyze complex information. The archaeocyathan database has been produced initially to provide a flexible tool to identify archaeocyath genera (Kerner et al., 2011b). This has been developed with Xper², a free software to store, edit and manage descriptive data and to provide a free access key. (<http://www.infosyslab.fr/lis/?q=en/resources/software/xper2> (Ung et al., 2010). The database contains 307 valid genera, described with a set of standardized descriptive terms. Interactive identification requires the use of the same set of descriptors for each genus and an adapted terminology: terms are standardized and one term corresponds to a single morphological concept (Kerner *et al.* 2011a). An archaeocyathan description is composed of 85 morphological and ontogenetic characters. Specialists familiar with traditional terms can find a correspondence table between usual terminology and the computerized one. Each genus is illustrated by the type specimen of the type species; some additional specimens may be present. Each character and its states are associated with a definition and images. Additional data are present: Eight characters refer to stratigraphical and geographical information and 27 refer to traditional classification data. The database spans the entire Cambrian System and has world-wide coverage. As the regional Siberian stages were the traditional reference for archaeocyathan specialists before the establishment of the international stratigraphic chart, these stages are used in the database until correlations are refined.

The entire product is freely accessible on the internet within a website on Archaeocyatha: <http://www.infosyslab.fr/archaeocyatha>. This site is composed of three parts: 1, Archaeocyatha: introduction, role in Cambrian System, morphology and list of references; 2, knowledge base: introduction and some outputs like list of genera and their detailed sheets, list of characters, list of groups of characters and base properties; 3, interactive key: identification unit, user guide, matching terminologies and glossary.

Different tools available

Xper² offers a large range of tools to explore, analyze and interpreted the knowledge base with several approaches (Ung et al., 2010). The identification unit is a free access key. This kind of system is very flexible and is well adapted for palaeontological specimens that are often incomplete. At each step of the identification, the user can choose the adequate descriptor and one or several states. Doubt is possible and several tools are available. As the identification key is built from the database, it is not restricted to morphological information. The presence of stratigraphical and geographical data allows the rapid creation of some lists of genera for palaeobiogeographical or stratigraphical studies. For example, all genera from Canada present during the Botomian stage are found in few seconds contrary to traditional bibliographical studies. In the interactive key, two steps are sufficient: choosing the descriptor stratigraphical extension and the state Botomian and choosing geographical repartition and the state of Canada (Fig. 6a).

To obtain stratigraphical and geographical information for a particular genus it is possible to use another way. Each genus has a complete sheet with its descriptions, pictures and systematics information. Two ways allow access to the sheet. Firstly, the list of sheets is present on the page

named “genera: 307” of the website. There, it is enough to click on the name of the genus and go to “other information” part of the sheet. Secondly, in the interactive key, a double-click on the genus name, opens a new window with the same genus sheet as the website one. For example, *Archaeocyathus* stratigraphical extension is Botomian 2 to Toyonian 3 and possibly during Atdabanian 4; its geographical distribution is Antarctica, Australia, Canada, China (South China), Europe (Iberia, Sardinia), Mexico, Mongolia, Uzbekistan, Russia (Altay Sayan, Far East, Siberian Platform, Transbaikial, Tuva), USA (Fig. 6b).

Conclusion

The aim of this contribution is to present the current status concerning one of the most ancient fossil groups, the Archaeocyatha. Relevant studies have been published in various reviews ((Debrenne et al., 1990)(Debrenne and Zhuravlev, 1992), Debrenne *et al.* 2002, in press). A computer-aided identification tool for Archaeocyatha genera is now available online (<http://www.infosyslab.fr/archaeocyatha>). This database is firstly used as an identification key but can be also a driver for different areas of archaeocyathan research for instance, faunal geographical and stratigraphical distributions. The database will be an important tool for developing new palaeogeographical interpretations for the Cambrian Period.

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Figures captions

STAGES	SIBERIAN PLATFORM		ALTAI SAYAN		LAURENTIA	
	Archaeocyatha	Trilobita	Archaeocyatha	Trilobita	Archaeocyatha	Trilobita
Toyonian		<i>Anabaraspis splendens</i>	<i>Erbocyathus heterovallum</i>			<i>Nephrolenellus multinodus</i>
	<i>Irinaecyathus grandiperforatus</i>	<i>Lermontovia grandis</i>	<i>Irinaecyathus ratus</i>	<i>Kooteniella-Edelsteinaspis</i>	<i>Tegerocyathus greenlandensis/</i> <i>Pycnoidocyathus pearylandicus</i>	<i>Bolbolenellus euryparia</i>
		<i>Bergerionellus ketemensis</i>	<i>Claruscoscinus billingsi</i>	<i>Parapoliella-Oncocephalina</i>		A P
		<i>Bergerionaspis ornata</i>	<i>Syringocyathus aspectabilis</i>		<i>Archaeocyathus atlanticus</i> <i>Pycnoidocyathus serratus/Tabulaconus kordae</i> <i>Claruscoscinus fritzi/</i> <i>Metacyathellus caribouensis</i>	
Botoman		<i>Bergerionellus asiaticus</i> <i>Bergerionellus gurarii</i>	<i>Tercyathus altaicus</i>	<i>Poliellina-Laticephalus</i>		<i>Nevadella eucharis</i> <i>Nevadia addyensis</i>
	<i>Porocyathus squamosus/</i> <i>Botomacyathus zelenovi</i>	<i>Bergerionellus micmaciformis/</i> <i>Erbiella</i>	<i>Clathricoscinus</i>		<i>Ethmophyllum whitneyi/</i> <i>Sekwicyathus nahaniensis</i>	<i>Avefallotaspis maria</i>
Atdabanian	<i>Fansycyathus lermontovae</i>	<i>Judomia</i>	<i>Plicocyathus torosus</i>	<i>Sajanaspis-Kameshkoviella</i>		<i>Grandinaspis patulus</i>
	<i>Nochoroicyathus kokoulini</i>		<i>Nalivkinicyathus cyroflexus</i>			<i>Esmeraldina rowei</i>
	<i>Carinacyathus pinus</i>	<i>Delgadella anabara</i>	<i>Gordonicyathus howelli</i>	<i>Resimopsis</i>		<i>Fallotaspis</i>
	<i>Retecoscinus zegebarti</i>	<i>Repinaella</i> <i>Profallotaspis jakutensis</i>	<i>Nochoroicyathus marinskii</i>			<i>Fritzaspis</i>
Tommotian	<i>Dokidocyathus lenaicus/</i> <i>Tumuliolyntus primigenius</i>					
	<i>Dokidocyathus regularis</i>					
	<i>Nochoroicyathus sumnaginicus</i>					
Fortunian						

Table 1. Comparison of trilobites and archaeocyaths biozones (Kerner *et al.* 2011a, modified after Rozanov & Sokolov 1984, Mansy *et al.* 1993, Webster 2011, Hollingsworth 2011)

P => A: *Peachella iddingsi* then *Bristolia insolens* then *Bristolia mohaviensis* and *Arcuolenellus arcuatus*.

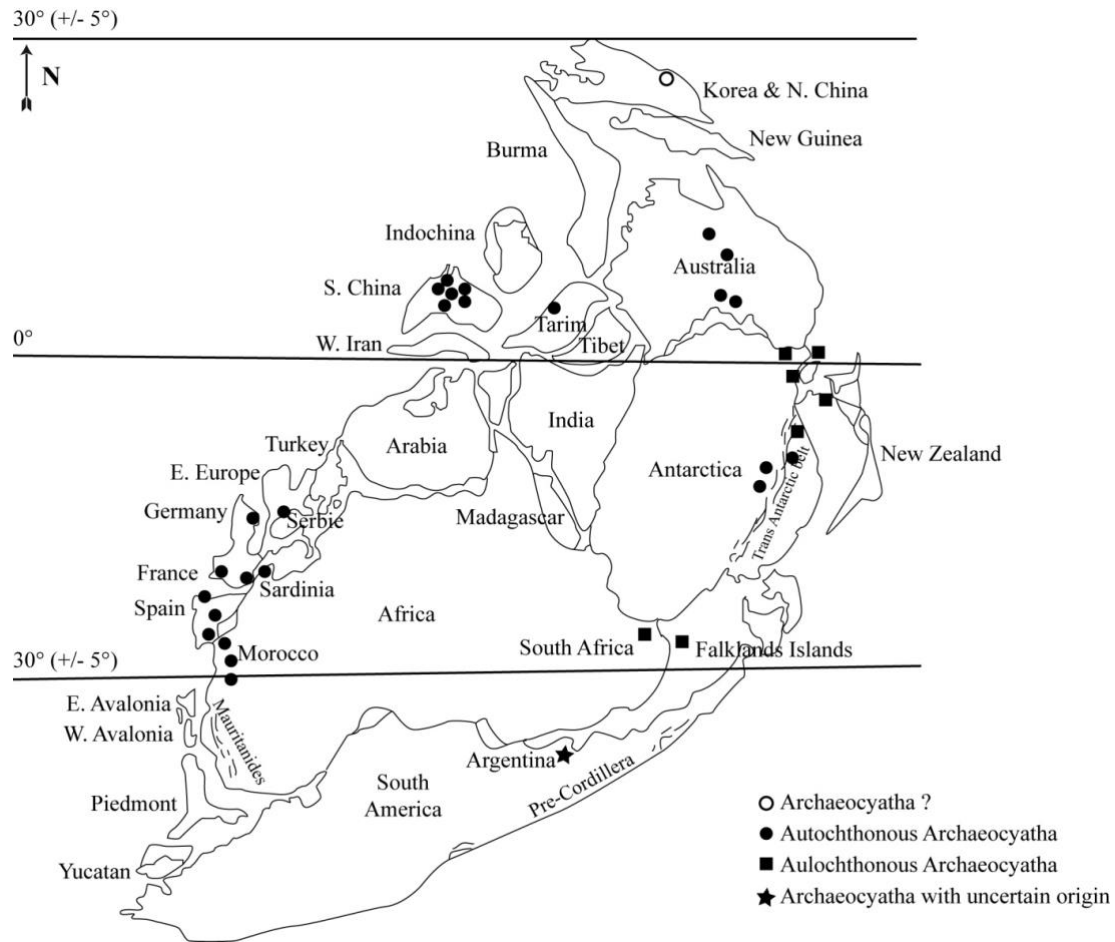


Figure 1: Distribution of archaeocyathan bioconstructions on the Gondwana margins (Atdabanian-Botomian stages) (Debrenne and Courjault-Rade, 1994).

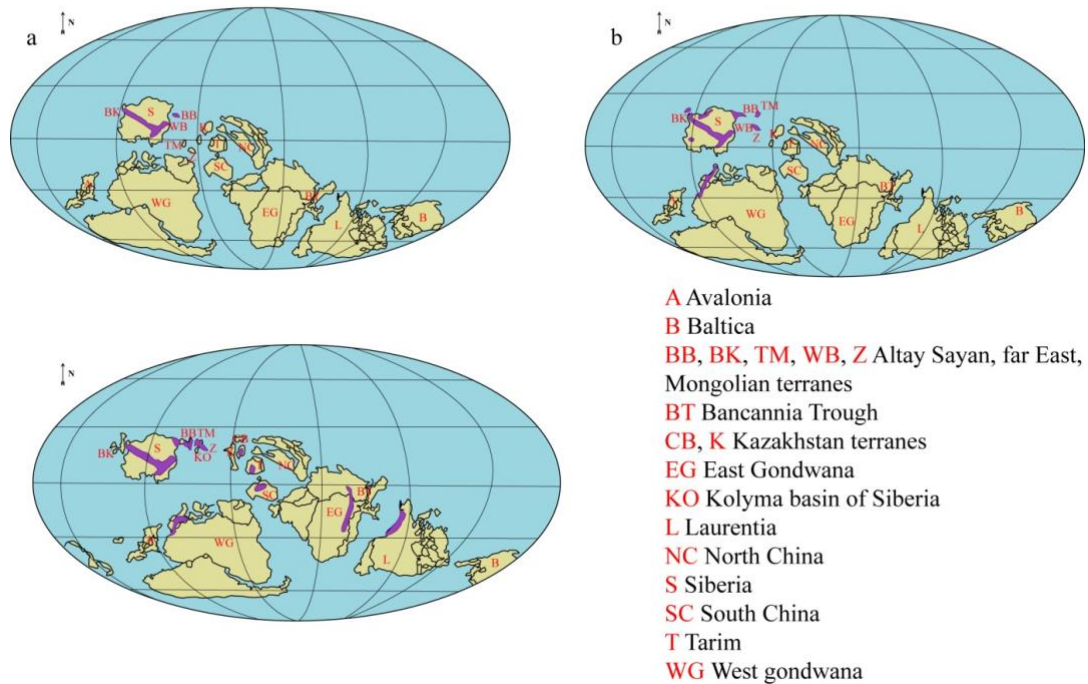


Figure 2: Global paleogeographical distribution for the early Cambrian and archaeocyathan distribution (violet). a, Tommotian Stage; b, Atdabanian Stage; c, Botomian Stage (Debrenne et al., 1999).

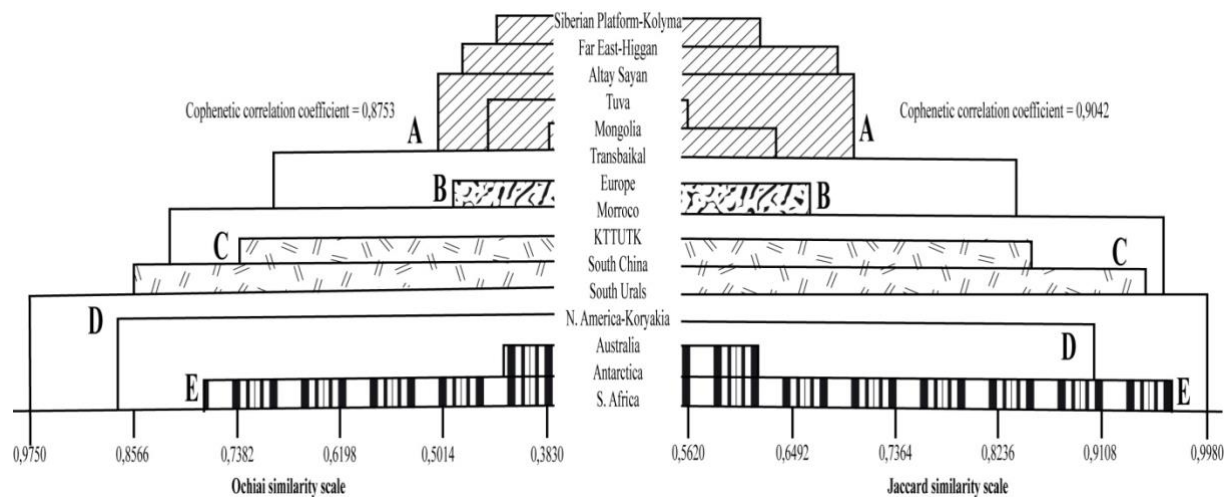


Figure 3: First-phase cluster analysis of binary data matrix of presence/absence of 310 archaeocyathan and radiocyathan genera from 15 regions of the world. (Kruse and Shi, 2000).

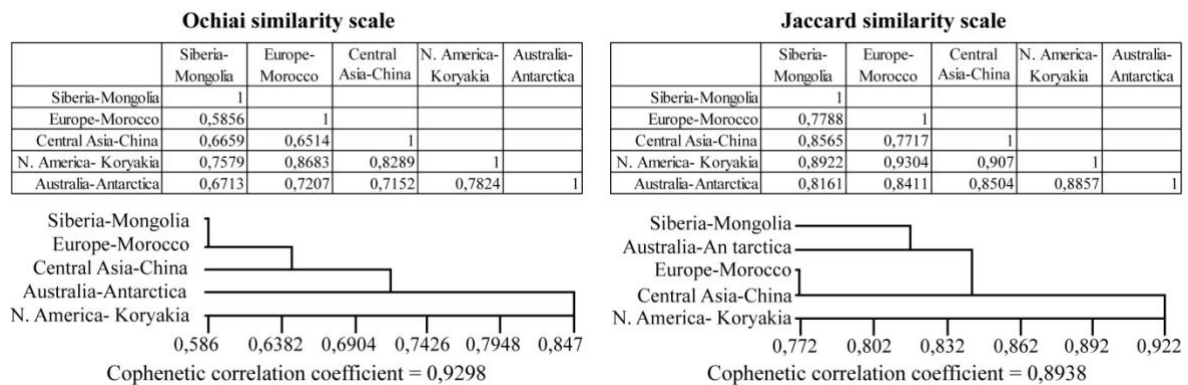


Figure 4: Second-phase cluster analysis of binary data matrix of presence/absence of 310 archaeocyathan and radiocyathan genera allocated to the five provinces deduced from the first-phase analysis. (Kruse and Shi, 2000).

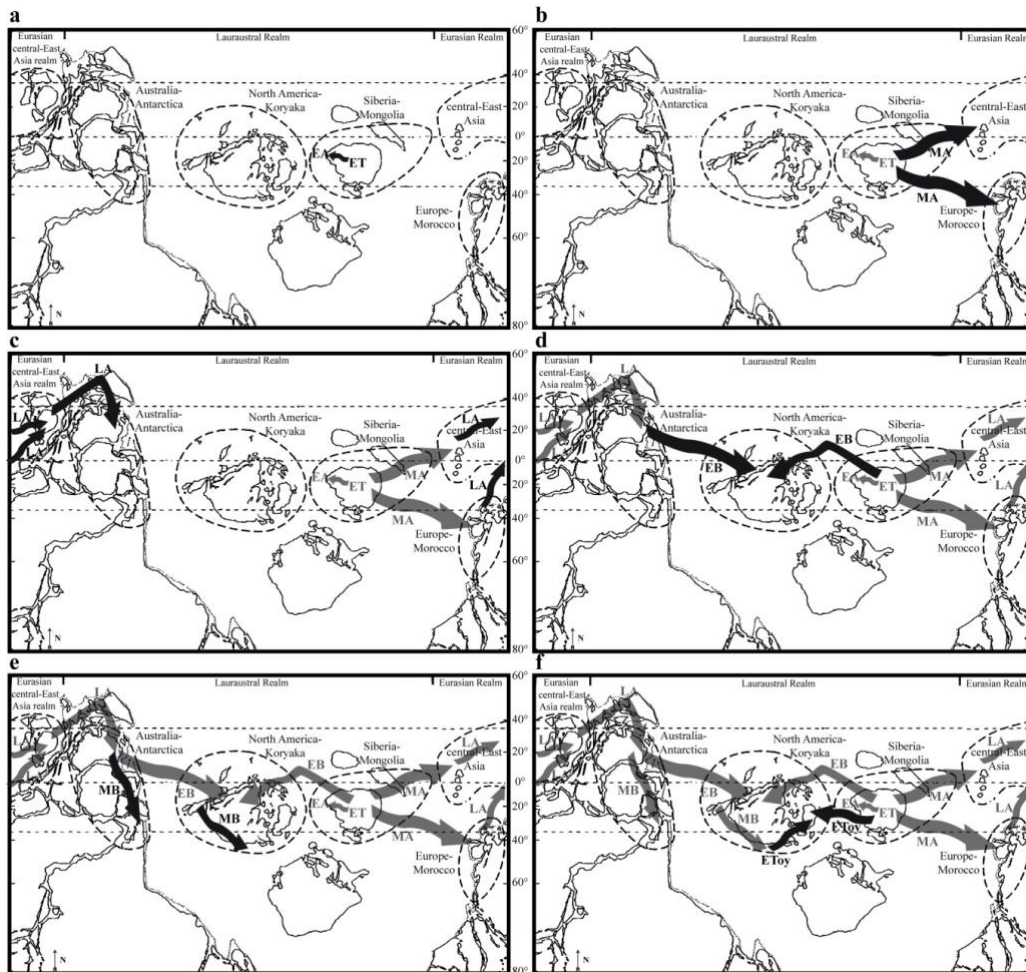


Figure 5: Early Cambrian global palaeogeographical reconstruction and archaeocyathan migration paths. a, early Tommotian (ET) to early Atdabanian (EA) map; b, middle Atdabanian (MA) map; c, late Atdabanian (LA) map; d, early Botomian (EB) map; e, middle Botomian (MB) map; f, early Toyonian (EToy) map (Kruse and Shi, 2000).

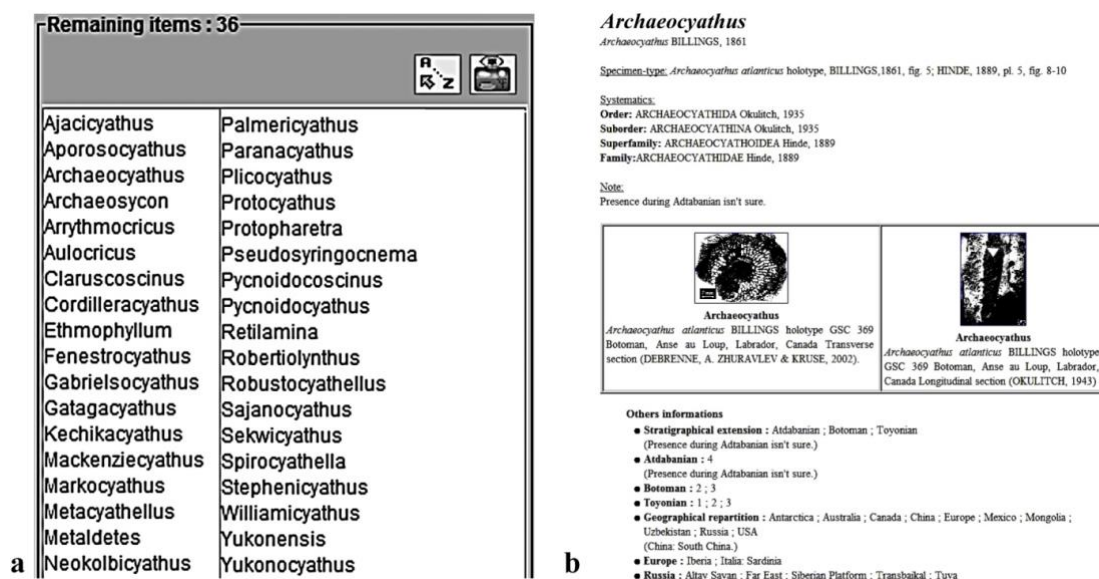


Figure 6: a, list of Canadian genera during the Botoman. B, *Archaeocythus* detailed sheet with geographical and stratigraphical ranges.