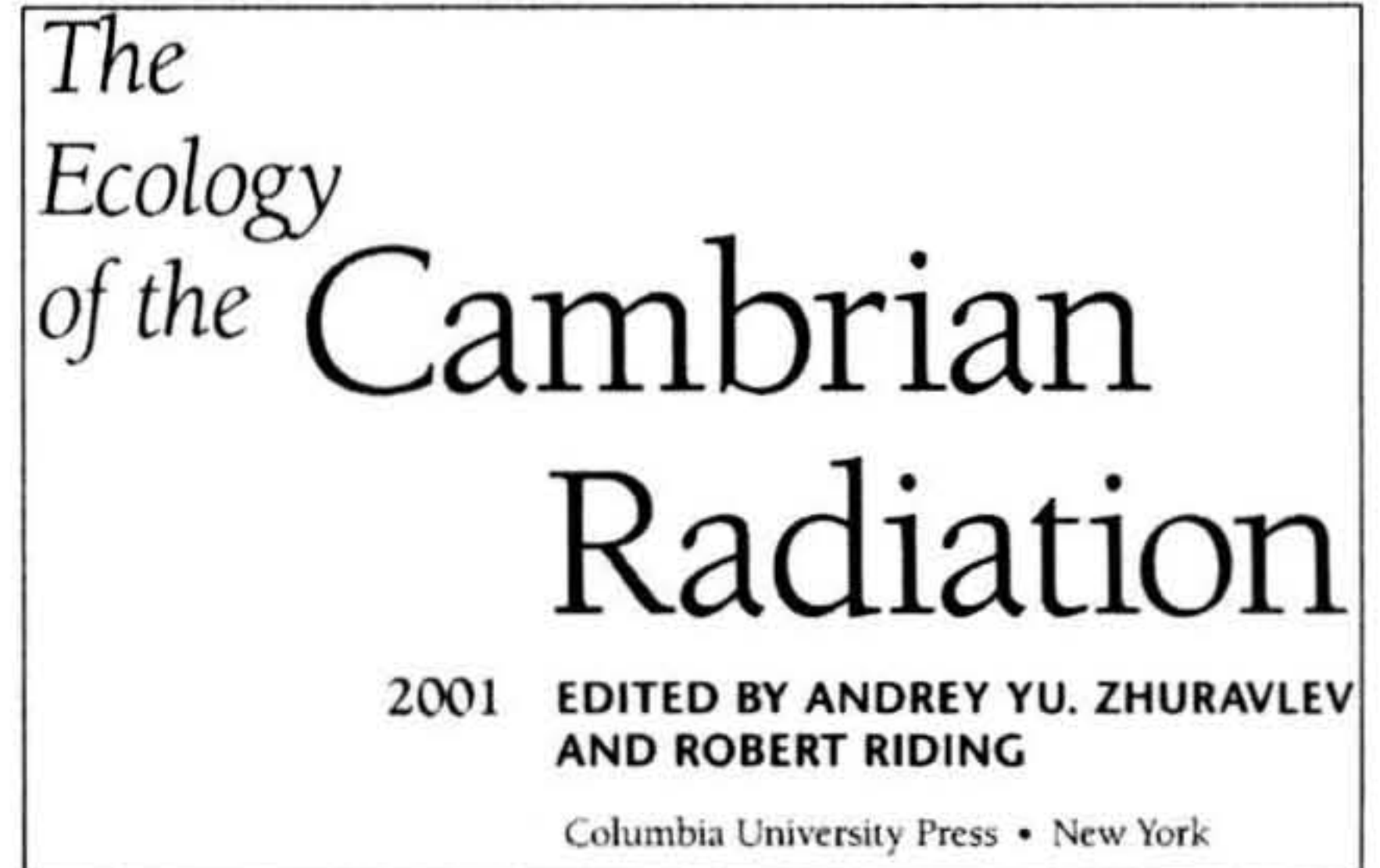


Sponges, Cnidarians, and Ctenophores



Sponges and coralomorphs were sessile epibenthic suspension feeders living in normal marine environments. Sponges with calcified skeletons, including archaeocyaths, mainly inhabited shallow to subtidal and intertidal domains, while other sponges occupied a variety of depths, including slopes. The high diversity of sponges in many Cambrian Lagerstätten suggests that complex tiering and niche partitioning were established early in the Cambrian. Hexactinellida were widespread in shallow-water conditions from the Tommotian; some of them may have been restricted to deep-water environments later in the Cambrian. Calcareans (pharetronids), together with solitary coralomorphs, thrived in reef environments, mostly in cryptic niches protected from very agitated waters. Rigid demosponges (anthaspidellids and possible axinellids) appeared by the end of the Early Cambrian and inhabited hardgrounds and reefs from the Middle Cambrian. The overall diversity of sponge and coralomorph types indicates that during the Cambrian these groups, like other metazoans, evolved a variety of architectural forms not observed in subsequent periods.

RAPID DIVERSIFICATION near the Proterozoic-Phanerozoic boundary implies the mutual interactions of ecosystems and biotas. One of the most striking features in the distribution of Early Paleozoic sessile benthos is the poor Middle–Late Cambrian record (Webby 1984).

The present contribution deals with the ecologic radiation of sponges and cnidarians.

SPONGES

Earliest Metazoans?

Sponges are a monophyletic metazoan group characterized by choanoflagellate cells (choanocytes). Based on studies made by Mehl and Reiswig (1991), Reitner (1992),

Müller et al. (1994), and Reitner and Mehl (1995), the first sponges originated in the Proterozoic from a choanoflagellate ancestor. The ancestral sponge was probably an aggregate of choanoflagellates, closely associated with various microbial communities. Important data are given by the analysis of metazoan β -galactose-binding lectins (S-type lectins) in sponges, hitherto analyzed only from vertebrates and one species of nematode (Müller et al. 1994). The development of this sponge lectin may have occurred before 800 Ma (Hirabayashi and Kasai 1993). Also remarkable are biomarker analyses made by McCaffrey et al. (1994), who detected C_{30} sterane, which is characteristic for demosponges, in 1.8-Ma-old black shales. This biochemical argument that sponges are Proterozoic metazoans is proven by new finds of undoubted sponge spicules and even entire phosphatized juvenile sponges with well-preserved sclerocytes (spicule-forming cells) from the late Sinian Doushantuo Formation of China (Ding et al. 1985; Li et al. 1998). Gehling and Rigby (1996) illustrate a nearly complete hexactinellid sponge from the Ediacarian Rawnsley Quartzite from South Australia. Additional specimens were described by them, but not all exhibit sponge affinities. The most convincing is *Paleophragmodictya*, which exhibits hexactinellid spicule patterns. Nevertheless, most previous records of Precambrian sponge spicules have proven upon examination either not to be sponges or not to be of Precambrian age (Rigby 1986a).

Sponges are represented in the fossil record as disarticulated spicules, soft-body casts, spicular networks, and spicular or calcareous skeletons. Since the review of Finks (1970), there has been a considerable number of new discoveries, but the ecologic history of sponges has yet to be revised.

Spicule Record

The oldest isolated spicules belong to the hexactinellids: stauractines, pentactines, and hexactines, in the Nemakit-Daldynian of Mongolia, Tommotian of Siberia, and Meishucunian of South China (Fedorov in Pel'man et al. 1990; Brasier et al. 1997). The Tindir Group (now dated by carbon isotopic correlation as Riphean—Kaufman et al. 1992) in Alaska contains possible hexactinellid spicules. Rare hexactine occurrences are found in pretrilobitic sequences, but hexactines become more numerous and widespread in the Atdabanian.

Genuine demosponge spicules are present in the upper quarter of the Atdabanian as tetractines with various additional elements that show much higher diversity than previously recognized (Bengtson et al. 1990).

By the Atdabanian, demosponges and hexactinellids seem to have become widespread in low-energy, offshore marine environments in Siberia and Australia (James and Gravestock 1990; Debrenne and Zhuravlev 1996), suggesting deeper-water occurrence.

In the Botoman, some microscleres are recognized, autapomorphic of the Tetracti-

nellida (Reitner and Mehl 1995). Spongoliths of pentactines and hexactines are known from the Sinsk and Kuonamka formations (Botoman of Siberia—Fedorov and Pereladov 1987; Rozanov and Zhuravlev 1992). In addition, these formations contain a large number of inflated pillowlike stauractines (e.g., *Cjulankella*), which may compose dermal armoring layers of hexactinellids (Rozanov and Zhuravlev 1992; Reitner and Mehl 1995). Armoring probably reflects development of protective structures against predators.

In the Ordian (late Early Cambrian) of the Georgina Basin, Australia, Kruse (in Kruse and West 1980) found sigmata microscleres, autapomorphic of the ceractinomorphic demosponges (Reitner and Mehl 1995).

Most tetractine spicules exhibiting diagenetic features have previously been recorded from Mesozoic siliceous sponges. In contrast, regular triaene spicules of the *Calcarea* are represented by a single crystal (Reitner and Mehl 1995). Among demosponges, the tetractines are restricted to the Tetractinellida. Additionally, typically modified dermal spicules (nail-type), monaxons (large tylostyles), and large aster microscleres (sterraster autapomorphic of the Geodiidae) have been found in the Early Cambrian, demonstrating the advanced state of tetractinellid evolution since that time. The rapid diversification of demosponges with clearly differentiated spicules occurred only in the Middle Cambrian.

The first calcarean spicules (Tommotian Pestrotsvet Formation, Siberian Platform—Kruse et al. 1995) have a triradiate symmetry. Their systematic position among the *Calcarea* is under discussion (Bengtson et al. 1990) (figures 14.1C,D). Previously known regular calcitic triaene spicules were Mesozoic. The Heteractinida, with multirayed spicules or characteristic octactines, are typical Paleozoic *Calcarea*. Regular triaene spicules of the Polyactinellida are common in early Paleozoic strata (Mostler 1985). The observed calcarean spicules have affinities with those of modern *Calcaronea*; spicules with calcinean affinities (regular triaenes) are rare in the Cambrian.

Sponge spicule assemblages are abundant in the Early Cambrian. In the lower Middle Cambrian of the Iberian Chains (Spain), spicules are so common with echinoderm ossicles that eocrinoid-sponge meadows are inferred for low-energy shallow subtidal environments (Alvaro and Vennin 1997). In general, spicule assemblages display high morphologic diversity, with many spicule types unknown in living sponges (Mostler 1985; Bengtson 1986; Fedorov and Pereladov 1987; Fedorov in Shabanov et al. 1987; Zhang and Pratt 1994; Dong and Knoll 1996; Mehl 1998). Their composition indicates the early appearance of hexactinellid, and possible calcarean, sponges in shallow-water archaeocyath-calcimicrobial mounds and the dominance of these sponges over archaeocyaths in deeper-water mounds. Relatively deep environments yield only demosponge and hexactinellid spicules, with the latter being prevalent (Fedorov and Pereladov 1987; James and Gravestock 1990; Zhang and Pratt 1994; Debrenne and Zhuravlev 1996; Dong and Knoll 1996).

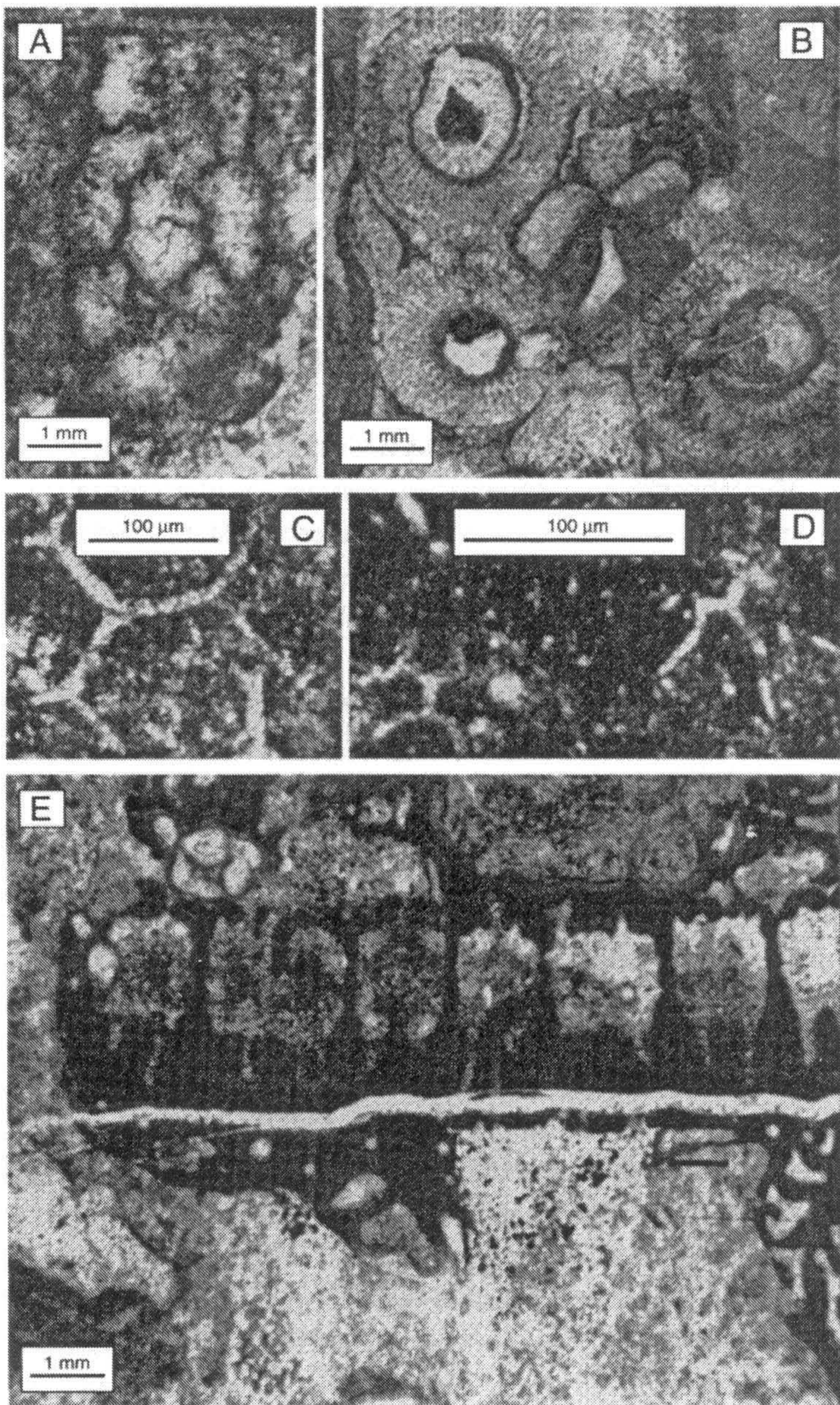


Figure 14.1 Thin sections. A, Cryptic thalamid sponge *Tanchocyathus amgaensis* (Vologdin 1963) PIN, Middle Cambrian, Mayan Tangha Formation (Amga River, Siberian Platform, Russia). B, Frame-building anthaspidellid demosponge *Rankenella* ex gr. *mors* (Gatehouse), IGS, Middle Cambrian, Kushanian Mila Formation (Elburz Mountains, Iran). C and D, Remains of modified tetractines (dodecaactinellids) described as *Calcarea*, Lower

Cambrian, Atdabanian Wilkawillina Limestone (Arrowie Basin, Australia). E, Cryptic pharetronid *Gravestockia pharetronensis* Reitner anchored on the inner wall of an archaeocyath cup and partially overgrown by its secondary skeleton, Lower Cambrian, Atdabanian Wilkawillina Limestone (Arrowie Basin, Australia). Source: Photographs A and B courtesy of Andrey Zhuravlev.

Soft-Bottom Communities of Sponges

Most sponges are soft-bodied animals, which means that their preservation potential is poor. Entirely preserved sponges are the exception. Sponges, such as coralline sponges, with a rigid skeleton do exist and include archaeocyaths and lithistid demosponges, which are characterized by a rigid framework of choanosomal spicules.

Preserved soft sponges are now recorded from the southern China Nunitang Formation at Sansha (Steiner et al. 1993), first attributed to Tommotian, since co-occurrence of the associated bivalved arthropod *Perspicularis* favors a younger age. A nearly complete hexactinellid spicule cluster of protospongid character has been found at the base of the formation (basal chert) (Steiner et al. 1993). The middle part of the formation bears a diverse fauna of complete specimens of hexactinellids, together with one doubtful demosponge taxon (*Saetaspongia*). The gray pelitic rocks, completely free of carbonate, probably correspond to a typical soft substrate under low-energy marine conditions; the sponges were morphofunctionally adapted to this environment. The hexactinellids demonstrate two main types of spicule architecture: rosselleid type (*Solactinella*) (figure 14.2B) and hyalonemid-like spicule root tufts (*Hyalosinica*) (figure 14.2A). Thin spicule mats have also been identified, on which grow numerous young hexactinellids, a strategy similar to the one observed on the top of the Recent Vesterisbanken Seamount in the Greenland Sea (Henrich et al. 1992).

Atdabanian rocks of northern Greenland (Sirius Passet) have yielded two genera of demosponges (Rigby 1986b) that are also known with a similar preservation in the younger Burgess Shale fauna. This soft-bodied fauna was deposited in deep-water shales on the margin of the outer detrital belt, on shelves facing the open ocean (Conway Morris et al. 1987; Conway Morris 1989). The forms noted as Paleozoic Dictyospongiidae are hexactinellids with bundles of long and large diactines (Mehl 1996).

After arthropods, Botoman sponges represent the most diverse metazoan group in the Chengjiang fauna, with at least 11 genera and 20 species (Chen et al. 1989, 1990; Chen and Erdtmann 1991; Rigby and Hou 1995). Those described by Chen et al. (1989, 1990) are hexactinellids and not demosponges. The spicule arrangement of the so-called leptomitid sponges has nothing in common with that of demosponges. The simple diactine spicules are very long (several mm to 1 cm), with a rectangular arrangement more characteristic of lyssacine hexactinellids. Some hexactinellids bear diactine spicules, which are actually reduced hexactines, with the typical hexactine cross in the center of the axial canal (Mehl 1992). For example, the modern Euplectellidae and most of lyssakiin hexactinellids exhibit this structure.

The Chengjiang sponges, embedded in mudstones of a low-energy environment, represent a sessile, suspension-feeding epifauna. Evidence of niche partitioning among them is visualized from their tiering complexity: choiids mostly occupying a lower-level epifaunal tier (<2 cm) or even being infaunal, and leptomitids feeding at the

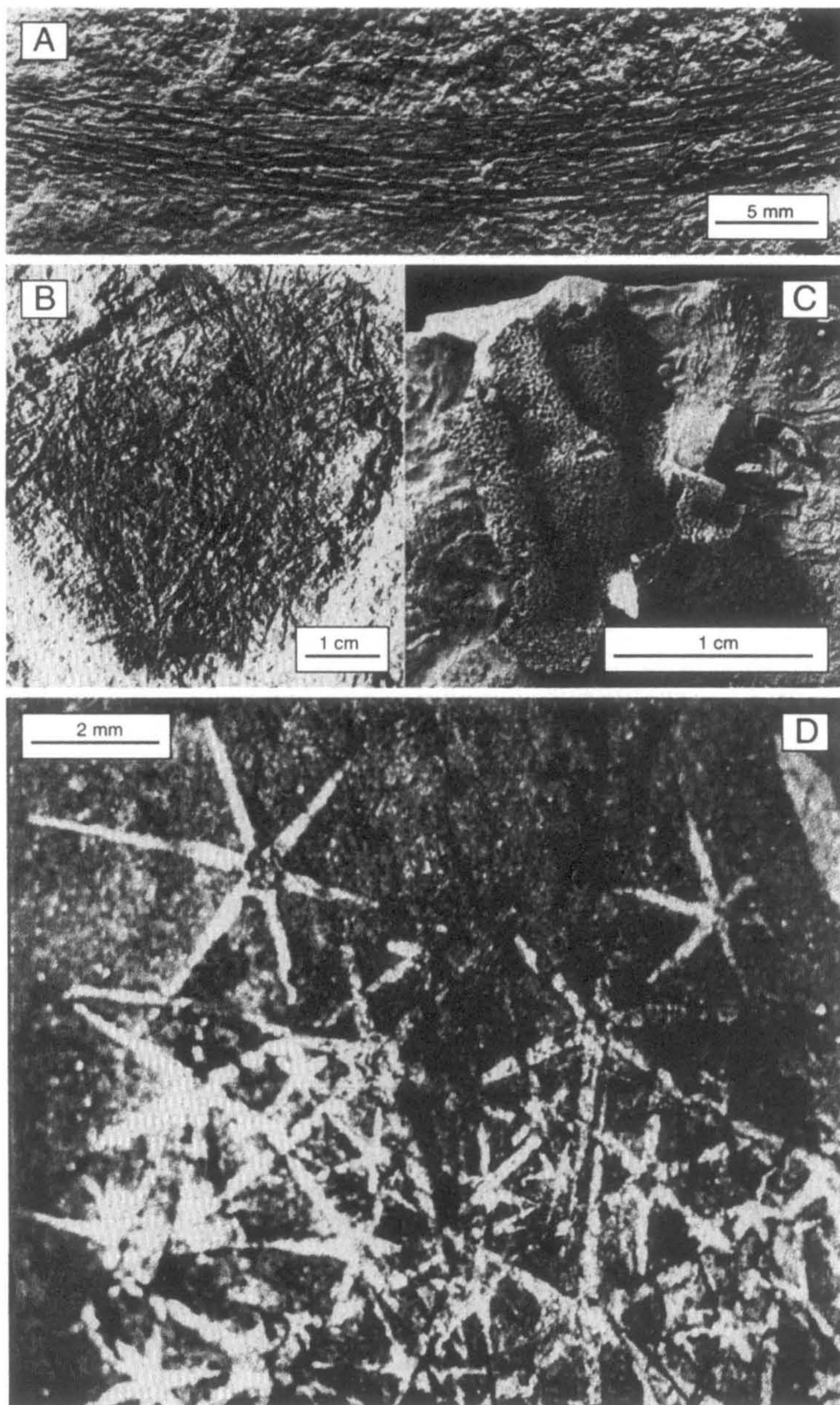


Figure 14.2 A, *Hyalosinica archaica* Mehl and Reitner with long spicule root tuft with small isolated hexactine on top, holotype SAN 109ab, Lower Cambrian, Qiongzhusian Niutitang Formation (Sansha, China). B, Hexactinellid sponge with strong lyssacyne character, *Solactinella plumata* Mehl and Reitner, holotype SAN 107ab, Lower Cambrian, Qiongzhusian

Niutitang Formation (Sansha, China). C, Encrusting anthaspidellid *Rankenella mors* (Gatehouse), weathered out and etched specimens, AGSO CPC 21244, Lower Cambrian, Ordian Arthur Creek Formation (Georgina Basin, Australia). D, Heteractinid *Eiffelia globosa* Walcott, USNM 66521, Middle Cambrian Burgess Shale (British Columbia, Canada).

intermediate level (5–15 cm), with a higher tier represented by a new globular sponge exhibiting a four-layered skeleton.

Early Cambrian articulated sponges have been recorded in Laurentia from Vermont (*Leptomitus*) and Pennsylvania (*Hazelia*), indicating that these two lineages had diverged by the end of the Early Cambrian (Rigby 1987).

Sponges constitute the most important Burgess Shale group in terms of number of specimens (Walcott 1920; Rigby 1986a; Ushatinskaya, this volume: figure 16.6), with at least 15 genera represented. The majority of these are hexactinellids resembling *Protospongia*: they consist of a single layer of parallel stauractines with rare pentactines, organized as a vasiform sheet. There are demosponges among them: *Choia*, *Hazelia*, and a probable keratose sponge, *Vauxia*. The calcareous heteractinid genus *Eiffelia* (figure 14.2D) has a thin-walled subspherical skeleton, with three ranks of oriented sexiradiate spicules. Most of these sponges are endemic, except for *Eiffelia* and *Choia*, the latter having also been reported from other localities of Laurentia, Europe, and possibly from South America and Australia (Rigby 1983).

More-complex complete bodies of spicular sponges have been found only in Laurentia: *Hintzespongia*, occurring in slightly younger rocks than the Burgess Shale, and thin-walled *Ratcliffespongia*. These sponges have, beneath an outer (dermal) layer of stauract spicules, an inner (endosomal) layer of stauractines and hexactines in a non-parallel arrangement, surrounding numerous circular aporhyses, covered externally by the outer layer (Finks 1983). Sponges of these lineages appear to have had their origin in the moderate deep shelf, in relatively constant temperatures and similar-chemistry waters of the shelf and outer margin of the continents (Rigby 1986a). The early hexactinellid sponges seem to have lived in warm shallow-water and high-energy environments and in rather deep and quiet water, on muddy sea floors, and colonizing sandy limestone substrates by the end of the Cambrian.

These sponges were sessile epibenthic suspension feeders on picoplankton and/or dissolved organic matter. Detailed investigations of the Chengjiang and Burgess faunas suggest that various niches existed: nutrients differing in type and size were ingested by different species at different heights (tiering), showing that the fundamental trophic structure of marine metazoan life was established very early in metazoan evolution (Conway Morris 1986) and that the maximum height of the community above the sediment-water interface was greater than suggested in the tiering model of Ausich and Bottjer (1982).

Reefal and Hardground Sponges

In addition to the secretion of siliceous and calcareous spicules, nonspicular calcareous skeletons have been independently acquired at different times, both in Demospongia and Calcarea.

Archaeocyaths

Functional and constructional analyses of archaeocyaths support a poriferan affinity for the group (Debrenne and Vacelet 1984; Kruse 1990; Zhuravlev 1990; Debrenne and Zhuravlev 1992), possibly with demosponges (Debrenne and Zhuravlev 1994). As sessile benthic filter-feeding organisms, archaeocyaths appeared in the Tommotian, progressively colonizing Atdabanian carbonate platforms, reaching their acme of development in the Botoman, and then declining in the Toyonian. Only a few forms persisted into the Middle and Late Cambrian.

Archaeocyaths are divided into two groups, according to the reconstructed position of their soft tissues: the Ajacicyathida (Regulares) and the Archaeocyathida (Irregulares). In the Regulares (Debrenne et al. 1990b), soft tissue filled the entire body and nutrient flows circulated through a complex aquiferous system corresponding to the different types of skeletal porosity. In the Irregulares (Debrenne and Zhuravlev 1992), the living tissue was restricted to the upper part of the cup, and a secondary skeleton developed that separated dead from living parts; thus nutrient flows in the Irregulares were less dependent on skeletal porosity, which is not as diverse as it is in the Regulares. The respective position of the living tissue in both groups also influenced their ecologic responses (figure 14.3A).

Archaeocyaths are associated with calcimicrobes but commonly play a subordinate role in reef building (Wood et al. 1992; Kruse et al. 1995; Pratt et al., this volume). Regulares were mainly solitary, with a high degree of individualization and thus with limited possibilities of being efficient frame builders. They tended to settle on soft bottoms in environments with low energy and low sedimentation rate, commonly at reef peripheries. Irregulares had a higher degree of integration that was propitious for modularization and for tolerance of associations with other species; they produced abundant secondary skeletal links between adjacent cups (figure 14.4A). All these features enhanced frame-building ability. They settled on stable substrates, after stabilization of the soft bottom, and were supported by cement and calcimicrobes—the principal reef builders (Pratt et al., this volume: figures 12.1A and 12.2A). Archaeocyaths differentiated from the late Tommotian into distinct open-surface and crypt dwellers (Zhuravlev and Wood 1995). Solitary ajacicyathids and modular branching archaeocyathids dominated open-surface assemblages, while solitary archaeocyathids and solitary chambered forms (capsulocyathids and kazachstanicyathids) were preferentially housed in crypts. Some species of *Dictyofavus*, *Altaicyathus*, and *Polythalamia* were obligate cryptobionts (figure 14.4B; Pratt et al., this volume: figure 12.1B).

Overall, archaeocyaths were adapted to restricted conditions of temperature, salinity, and depth. They were limited to tropical seas, as confirmed by paleomagnetic continental reconstructions (McKerrow et al. 1992; Debrenne and Courjault-Radé 1994). Under conditions of increased salinity, archaeocyath assemblages became depleted, and they were represented by the simplest forms (Debrenne and Zhuravlev 1996).

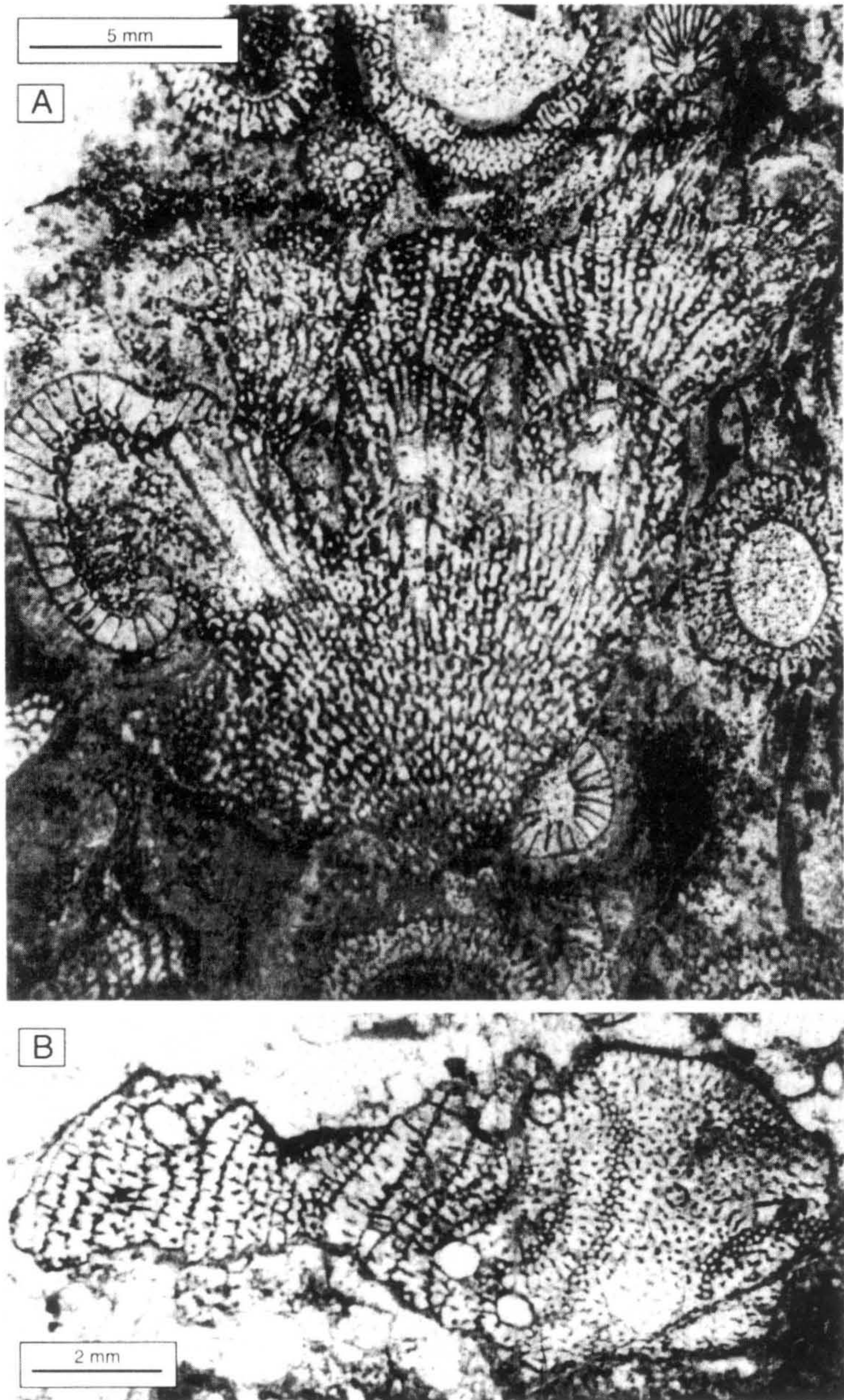


Figure 14.3 Archaeocyaths in thin section. A, Modular Archaeocyathida (*Archaeocyathus arborensis* Okulitch and *Arrhythmocricus macdamsensis* [Handfield]) and solitary Ajacicyathida (*Robustocyathellus pusillus* [Debrenne] and *Palmericyathus americanus* [Okulitch]), MNHN

M83075, Lower Cambrian, Botoman Puerto Blanco Formation (Cerro Rajón, Mexico). B, Stromatoporoid *Korovinella sajanica* (Yaworsky), MNHN M81017, Lower Cambrian, Botoman Verkhneomonok Formation (Karakol River, Western Sayan, Russia).

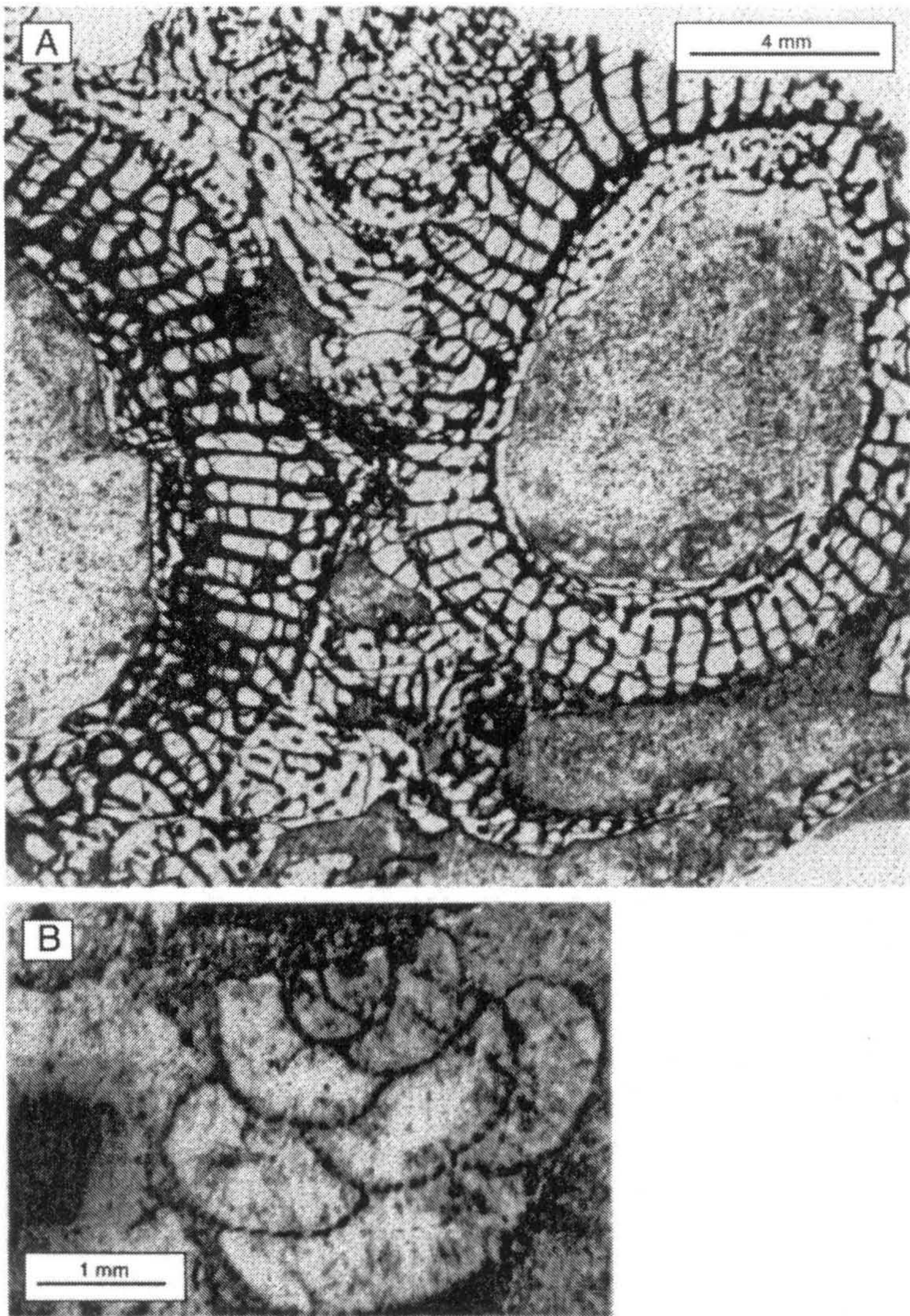


Figure 14.4 Archaeocyaths in thin section. A, Modular *Metaldetes profundus* (Billings), GSC 62113, Lower Cambrian, Botoman Forteau Formation (Labrador, Canada). B, Cryptic thalamid *Polythalamia americana* Debrenne and

Wood, anchored to cyanobacterial crust-forming crypt, USNM 443584, Lower Cambrian, Botoman Scott Canyon Formation (Battle Mountain, Nevada, USA).

Archaeocyaths occupied the intertidal to subtidal zones. Basinward, the communities became impoverished and commonly were associated with hexactinellid sponge spicules, suggesting that with increasing depth, spicular sponges came to dominate sponges with a calcified skeleton (e.g., the Atdabanian of the Lena River—Debrenne and Zhuravlev 1996; Pratt et al., this volume: figure 12.2). Deeper-water bioherms (e.g., Sellick Hill Formation, Australia) contain oligotypic assemblages of archaeo-

cyaths developing exocyathoid buttresses, interpreted as a response to higher water pressure (Debrenne and Zhuravlev 1996). Erosional features may also be observed in some places (e.g., Khara Ulakh, Siberian Platform, and Sardinia) that are indicative of peritidal conditions in which some archaeocyaths existed.

As filter feeders, archaeocyaths were better adapted to environments with sufficient current activity to transport nutrients. Complex outer walls promoted inhalant-exhalant flow through the cup, while annular inner walls accelerated the initial speed of the exhalant current (Debrenne and Zhuravlev 1996). Metallic models in fume tanks have shown that porous septa are better adapted to low-energy currents and aporous septa to high-energy environments (Savarese 1992); these conclusions are in accordance with the observations of Zhuravlev (1986) of an archaeocyath reef facies assemblage where genera have mostly aporose septa, whereas in back-reef facies their analogs have porous septa.

In conclusion, archaeocyaths were stenothermal, stenohaline, stenobathic marine sessile filter-feeding organisms, employing both active and passive current flow to move water through their systems. The nature of their food remains uncertain (Signor and Vermeij 1994); like their modern poriferan relatives, they probably fed primarily on bacteria and similarly sized particles. Whether some archaeocyaths possessed photosymbionts remains controversial (Camoin et al. 1989; Wood et al. 1992; Surge et al. 1997; Riding and Andrews 1998), but if photosymbionts were associated with archaeocyaths, they were rare, as in Recent marine sponges.

Thalamid Coralline Sponges ("Sphinctozoans")

A thalamid grade of organization is recognized in various classes of calcified sponge (Archaeocyatha [Capsulocyathida], Demospongea, and Calcarea) and in one species of Hexactinellida that lacks a calcareous skeleton. This type of skeleton is thus polyphyletic (Vacelet 1985; Reitner 1990), and the term *sphinctozoan* is only morphologic and without systematic significance.

Apart from archaeocyaths (see above), sphinctozoans of Early Cambrian age described from Australia either are not sponges or lack a sphinctozoan grade of organization. Simple sebergasiids have been found in marginal shelf deposits of New South Wales (Pickett and Jell 1983). Some of these are of doubtful affinity: single-chambered *Blastulospongia*, considered as a possible ancestor for the whole group, has been reinterpreted as a radiolarian (Bengtson 1986). Nonetheless, its large size and apparent attachment to the substrate do not fit closely to the radiolarian model of the type *Blastulospongia* species. As for the multichambered and cateniform *Nucha* and *Amblysiophonella?*, reexamination of the holotypes (Reitner and Pickett, unpubl. data) suggests that they might not be sponges.

Coeval "sphinctozoans" *Jawonya* and *Wagima* (Kruse 1987) have been found in platform deposits (Tindall Limestone) of northern Australia. Upon reexamination, Wood

(in Kruse 1990; Rigby 1991) noted the presence in these of spicules. They are modified octactines, confirming *Jawonya* as a heteractinid sponge (Wewokellidae). Kruse (1996) has recently demonstrated that *Jawonya* is in fact two-walled, with a complicated exopore architecture. The related genus *Wagima* is also considered to be two-walled. They lived in a low-energy, open-shelf environment on the muddy substrate, stabilized by calcimicrobes (Kruse 1996).

Questionable *Jawonya*, from older Atdabanian strata of South Australia (Kruse 1987), is a rimmed single-chambered form (not with "sphinctozoan" grade of organization). It differs from contemporaneous one-walled archaeocyaths in its size and inferred microstructure; its affinity remains uncertain. This form is intimately associated with reefal facies (in this case, calcimicrobial-archaeocyath mounds).

Tanchocyathus amgaensis (Vologdin 1963), from the Middle Cambrian of Siberia, is probably a thalamid, nonarchaeocyathan sponge that lived in cryptic communities (Zhuravlev 1996) (see figure 14.1A).

Stromatoporoid Coralline Sponges

Forms exhibiting a stromatoporoid grade of organization have been noted from the Botoman. The archaeocyath order Kazachstanicyathida (Debrenne and Zhuravlev 1992) has the thalamid type of cup development and a stromatoporoid growth pattern, even with astrorhizae (figure 14.3B). They are associated with calcimicrobial-archaeocyathan reefs.

Calcarea with a Rigid Skeleton ("Pharetronida")

Apart from isolated regular calcitic spicules, one articulated taxon is known from the Flinders Ranges, South Australia, in beds of Atdabanian equivalent age: *Gravestockia pharetronensis* Reitner (Reitner 1992). This is a pharetronid sponge with a rigid skeleton of cemented choanosomal simple tetractine calcareous spicules and diactine free dermal spicules. It is anchored on an archaeocyath inner wall in a cryptic niche (figure 14.1E) and may in turn have been locally overgrown by the archaeocyath's secondary skeleton. *Gravestockia* is associated with calcimicrobial-archaeocyath bioconstructions.

Bottonaocyathus, from the Botoman of the Altay Sayan Foldbelt, Tuva, Morocco, and Mongolia, was originally described as an archaeocyath. It is now considered a probable sponge with a calcified skeleton. It lived together with archaeocyaths in reefal environments (Kruse et al. 1996).

Demosponges with Desma-Type Spicules ("Lithistida")

The "Lithistida" are a highly polyphyletic group of demosponges, including taxa of both Tetractinellida and Ceractinomorpha (Reiner 1992). The oldest known (Ordian

to early Templetonian) desma-bearing sponge, the anthaspidellid *Rankenella*, inhabited a low-energy, shallow subtidal marine environment, with abundant mud and high productivity (Ranken Limestone) (see figure 14.2C), and also even anaerobic low-energy shelf areas of limited circulation (Arthur Creek Formation) (Kruse 1996). A similar sponge has been identified from the late Early Cambrian to early Middle Cambrian Dedebulak Formation of Kyrgyzstan (Teslenko et al. 1983). Such sponges are restricted to a stable soft bottom and are presumed to be encrusting forms. From the late Middle Cambrian, anthaspidellid and axinellid demosponges became ubiquitous elements of fossil assemblages in Laurentia, Altay Sayan, and Iran (Wilson 1950; Okulitch and Bell 1955; Zhuravleva 1960). They encrusted hardgrounds (Brett et al. 1983; Zhuravlev et al. 1996) and even built their own reefs—Mila Formation, Iran (Hamdi et al. 1995; see also figure 14.1B) and Wilberns Formation, USA (Wood 1999; Pratt et al., this volume: figure 12.2C).

COELENTERATA

Soft-Bodied Cnidaria and Ctenophores

In contrast with the Precambrian Ediacara fauna, which is dominated by medusoids, representatives of the soft-bodied cnidaria and ctenophores are relatively poorly represented in the Cambrian. A great number of Cambrian forms have been assigned to Cnidaria with varying degrees of uncertainty. Impressions of putative jellyfish have been reported in Cambrian rocks since Walcott (1911), but most of them have been reinterpreted as trace fossils, sponges, echinoderms, arthropod appendages, or worms; others have been designated as *incertae sedis* or are unrecognizable forms (Harrington and Moore 1956; Conway Morris 1993a). The discovery of annulated disks alone is insufficient to place them in the chondrophores. The Tommotian records are still doubtful. Associated with *Lapworthella*, 50 m above the Cadomian peneplain, forms provisionally attributed to scyphozoans have been recorded (Doré 1985) (figure 14.5B).

Other discoidal fossils have been described in Europe but have not recently been reinvestigated, so their possible attribution to cnidarians remains uncertain. *Ichnusina cocozzai* (nom. correct. herein) (figure 14.5A)—from Sardinia, Italy, at the base of the “Arenarie di San Vito” (Middle-Upper Cambrian)—is one of these. It consists of a hemispheric body with undifferentiated center, dichotomized radial lobes and peripheral tentacles. If considered as a possible cnidarian, then this organism would have had a swimming or floating lifestyle.

Within the Middle Cambrian Burgess Shale-type fauna, some specimens resembling elements of the Ediacara fauna have a cnidarian affinity (Conway Morris 1993b). *Thaumaptilon* is a bilaterally symmetrical foliate animal with a holdfast and is related to pennatulaceans. It was benthic, and its mode of feeding rather conjectural, probably trapping the food particles by means of small tentacles of putative zooids. *Ge-*

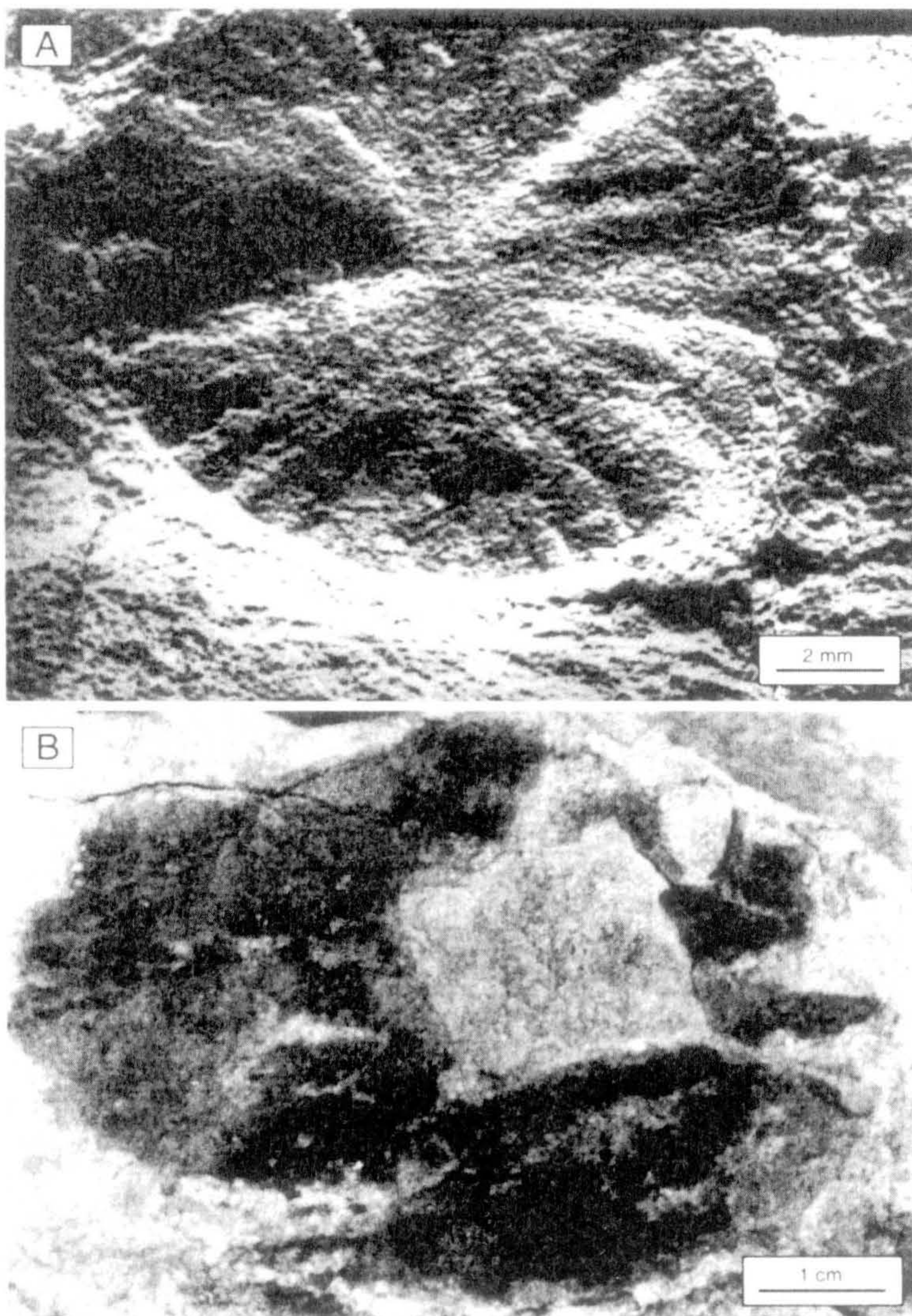


Figure 14.5 A, Disk of a possible chondrophore cast of *Ichnusina cocozzai* (Debrenne), MNHN M84160, Middle-Upper Cambrian (Sardinia, Italy). B, Cubic medusoid with square central part (gastrogenital cavity?), with a tentacle springing from the lower right angle

of the manubrium (?), surrounded by a dark organic circle (umbrella?), N 1368A Caen University, Lower Cambrian "Schistes et calcaires" Formation (Normandy, Val de May, Normandy, France). Source: Photograph courtesy of Francis Doré.

lenoptron is tentatively assigned to chondrophorines (Conway Morris 1993b), together with some undetermined disks with spaced annulations and tentacles. *Emmonsaspis* from the Early Cambrian Parker Slate of the Appalachians is tentatively interpreted as a benthic suspension feeder or microcarnivore (Conway Morris 1993b).

The trace fossil *Dolopichnus* is interpreted as a possible cnidarian burrow (Alpert and Moore 1975; Birkenmajer 1977). It contains trilobite debris, indicating a carniv-

orous diet. Such trace fossils might be produced by animals similar to the Early Cambrian *Xianguangia* or Middle Cambrian *Mackenzia*. *Xianguangia* from Chengjiang is interpreted as an anthozoan-like cnidarian on account of a basal disk, a polyp-like body with possible septal impressions, and a distal crown of tentacles bearing closely spaced pinnules (Chen and Erdtmann 1991). *Mackenzia costalis* Walcott, having a baglike body with possible internal partitions, is compared with some putative actinians (Conway Morris 1993b).

Ctenophores, representatives of another branch of the coelenteratan grade, were active swimmers that combed the pelagic realm in search of tiny metazoans and larvae (Conway Morris and Collins 1996; Chen and Zhou 1997).

Coralomorphs

The mass radiation of Metazoans included mineralized skeletons of solitary calcium carbonate cups and, later, slender irregular cerioid polygonal tubes, near the beginning of the Cambrian. These were originally grouped as coralomorphs because of their probable cnidarian affinities (Jell 1984). New descriptions of Early Cambrian coralomorphs, including studies of the biocrystals characteristic of their microstructure, their systematic position, and their stratigraphic distribution, have recently been made (Zhuravlev et al. 1993; Sorauf and Savarese 1995).

The oldest coralomorph, *Cysticyathus* (figure 14.6B), occurs in middle Tommotian calcimicrobial-archaeocyath bioherms of Siberia. It was previously included in archaeocyaths, despite its aporous skeleton. Tannuolaiids (=khasaktiids) (figure 14.6A) appeared in the Atdabanian of Siberia, diversifying as they migrated throughout the Ural-Mongolian Belt, and are always associated with reefs.

Hydroconozoa began with the Atdabanian but are not known later than the Botoman, when modular ramose forms developed. The skeletal microstructure of *Hydroconus* is most likely similar to that of genuine corals (Lafuste et al. 1990).

The Botoman was the acme for all Cambrian coralomorphs. In addition to tannuolaiids and hydroconozoans, which are characteristic of Siberia, one of the most convincing cnidarians, *Tabulaconus* (low modular) (Debrenne et al. 1987) (figure 14.6C), also appeared in Laurentia, along with the solitary *Aploconus* (Debrenne et al. 1990a) and the high modular *Rosellatana* (Kobluk 1984). In Australia, *Flindersipora* occurs. It was thought to comprise the oldest tabulate corals (Lafuste et al. 1991) (figure 14.6D) but is considered by Scrutton (1992) to be an unassigned early skeletonized anthozoan lacking linear descent to any major coral group. The newly discovered *Moorowipora* and *Arrowipora*, with their cerioid coral forms and typical coralline wall structure, short septal spines, and tabulae, suggest an assignment with Tabulata (Fuller and Jenkins 1994, 1995; Sorauf and Savarese 1995). The latter authors also propose inclusion of *Tabulaconus* in the Tabulata, thereby greatly extending the stratigraphic range of the group. Scrutton (1997), however, prefers to classify Cambrian

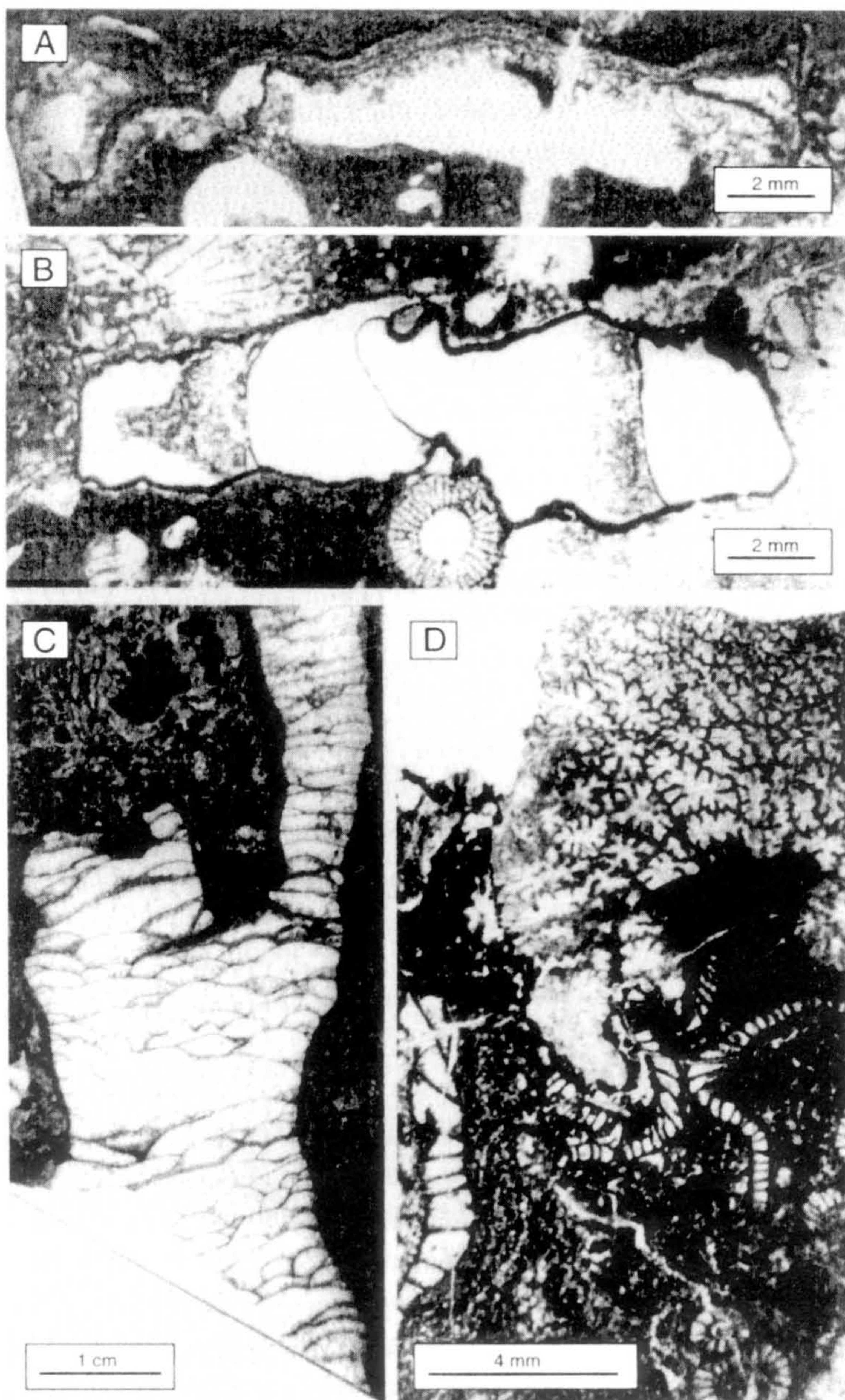


Figure 14.6 Coralomorphs in thin section. **A**, Encrusting *Khasaktia vesicularis* Sayutina, PIN, Lower Cambrian, Atdabanian Pestrotsvet Formation (middle Lena River, Siberian Platform, Russia). **B**, Branching *Cysticyathus tunicatus* Zhuravleva, MNHN M81016, Lower Cambrian, Tommotian Pestrotsvet Formation (middle Lena River, Siberian Platform, Russia).

C, Branching *Tabulaconus kordae* Handfield, UA 2526, Lower Cambrian, Botoman Adams Argillite (Tatonduk area, Alaska, USA). **D**, Association of archaeocyaths (*Ajacicyathus aequitriens* [Bedford and Bedford]) and tabulate *Flandersipora bowmanni* Lafuste, MNHN M42048, Lower Cambrian, Botoman Moorowie Limestone (Arrowie Basin, Australia).

zoantharian corals as a separate order Tabulaconida without an assignment to other Paleozoic coral clades.

All Atdabanian and Botoman coralomorphs are associated with calcimicrobial-archaeocyath reef environments, with *Flindersipora* and *Yaworipora* even participating in bioconstruction (Zhuravlev 1999). *Khasaktia* and *Rosellatana* can be cryptobionts in calcimicrobial-archaeocyathan reef cavities.

The modular Laurentian *Labyrinthus* is known from the late Botoman Forteau Formation of Labrador. Colonies are often attached to archaeocyath skeletons, indicating a preference for hard substrates. They are found in the "upper biostrome complex," which underlies and interfingers with ooid beds containing oncoids and diverse skeletal fragments. This implies shallow, agitated water conditions in the vicinity of a bioconstruction (Kobluk 1979).

Lipopora and *Cothonion*, from New South Wales, Australia, are the latest Early Cambrian (Ordian) coralomorphs (Jell and Jell 1976). Solitary or modular, they occur in carbonate beds, associated with *Girvanella* oncoids and a rich fauna of trilobites, brachiopods, mollusks, and sponges. The high faunal diversity, the predominance of cyanobacteria, and the carbonate petrology suggest a warm shallow-water carbonate bank environment.

Other proposed Early Cambrian cnidarians have doubtful records (inorganic concretions, algae, bryozoans, or synonyms of already described tannuolaiids or hydroconochozoans) and consequently are not considered here.

A Middle Cambrian (Floran-Undillan) coralomorph *Tretocylichne* is found in reworked clasts within inner submarine fan deposits of northeastern New South Wales (Engelbretsen 1993). The single example of a possible Late Cambrian coral is found in Montana (Fritz and Howell 1955).

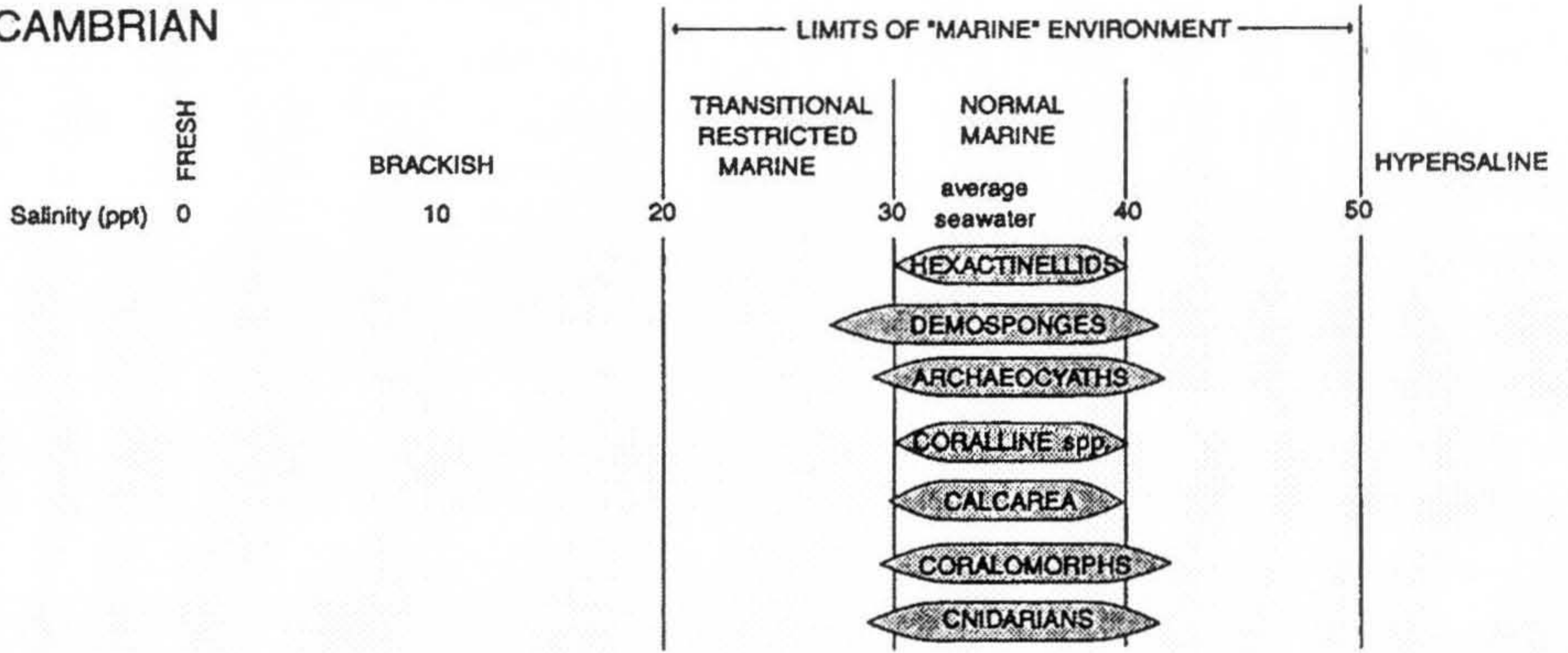
Coralomorphs were suspension feeders living in warm waters and generally associated with calcimicrobial-archaeocyath bioherms as coconstructors or cryptobionts. Some lived in agitated waters near biostromes or carbonate banks.

Other Possible Skeletal Cnidarians

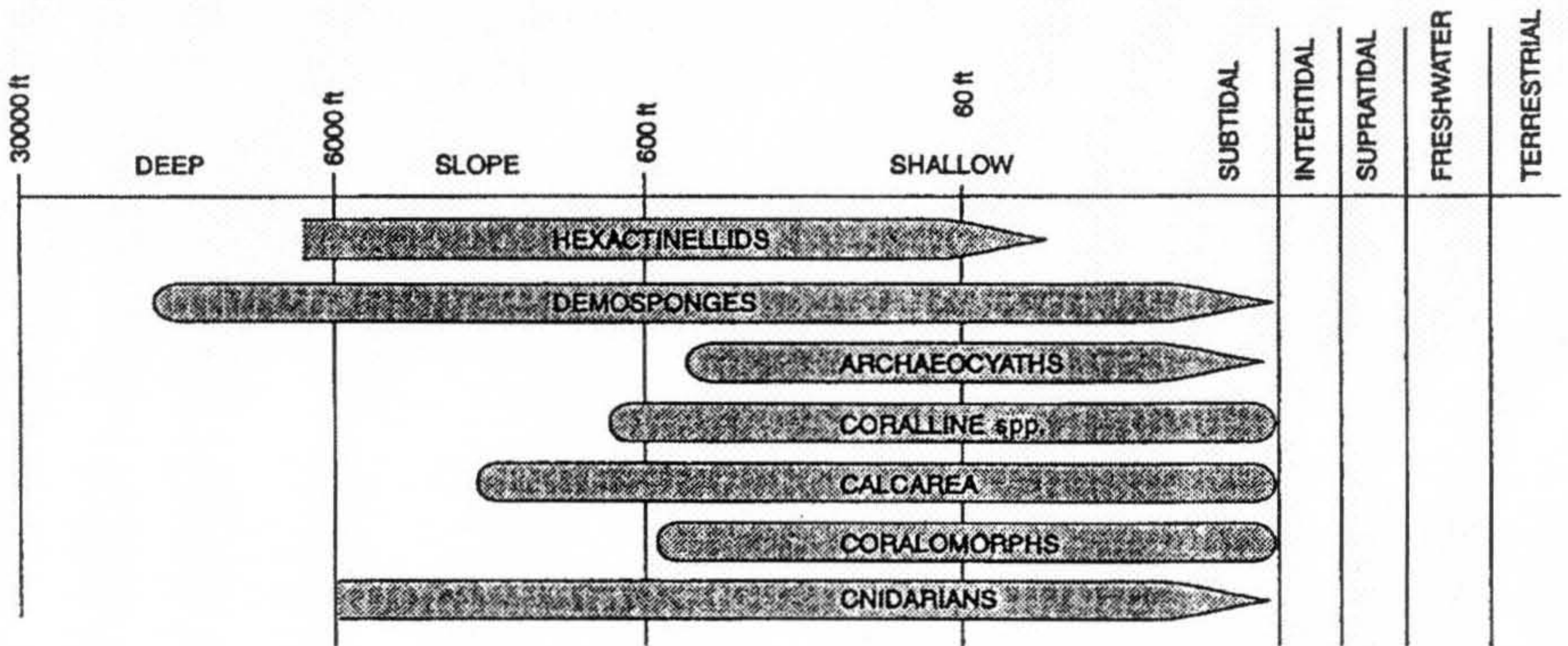
Among Cambrian small shelly fossils, a number of tiny, often septate, conoidal tubes have been suggested to be of cnidarian affinity, namely, paiutiids, quadriradial carinacnitiids and hexangulaconulariids, triradial anabaritids, and byroniids (for reviews, see Conway Morris and Chen 1989, 1992; Bengtson et al. 1990; Rozanov and Zhuravlev 1992). Except for byroniids, these animals are restricted to the Early Cambrian. Most of them are suggested to be sessile forms. Tentacle-bearing *Cambrorhytium* might be a cnidarian possessing an organic-walled tube (Conway Morris and Robison 1988). It is worth noting that phosphatized spheroids, in Nemakit-Daldynian strata containing anabaritids, resemble nonplanktotrophic cnidarian actinula larvae (Kouchinsky et al. 1999).

A

CAMBRIAN



B



C

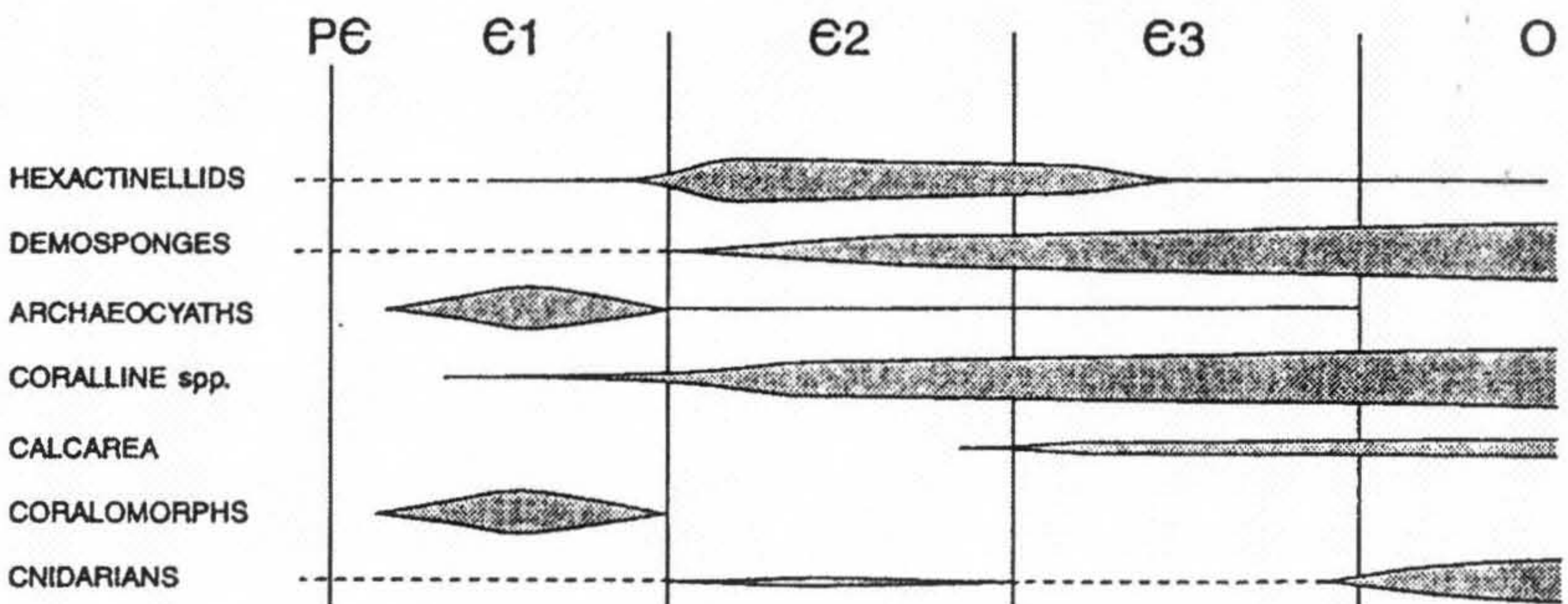


Figure 14.7 Distribution of sponges and cnidarians in relation to salinity (A), in relation to depth (B), and in relation to time (C).

CONCLUSIONS

Siliceous sponges, either as spicules or complete bodies, are known since the Ediacarian. From the Atdabanian and later, they were widespread in low-energy offshore marine environments (figure 14.7), suggesting a deep-water origin on open ocean-facing shelves. Ceractinomorphs are found only from the Middle Cambrian; they appear to have occupied shallow waters.

Calcified skeletons occur in different groups: archaeocyaths, pharetronids, and wewokellids. Archaeocyaths (first appearance in the Tommotian) occupied intertropical, intertidal to subtidal environments of low to normal salinity (figure 14.7), in well-agitated waters associated with reefs. Archaeocyaths with a stromatoporoid grade of organization were present in reefs, whereas the chambered forms ("sphinctozoans") were crypt dwellers.

Calcareous spicules are rare in the Early Cambrian. The known pharetronids grew on Atdabanian archaeocyath-calcimicrobe reefs, whereas late Early Cambrian heteractinids (Wewokellidae) were level-bottom dwellers.

The Middle Cambrian Burgess Shale fauna contains possible chondrophores and pennatulaceans. If the interpretation of forms unrecognizable and/or difficult to interpret as chondrophores is correct, they would have had a pelagic mode of life, because frondlike organisms were sessile organisms. In general, fossils of free-swimming cnidarians are rare in the Cambrian.

All Atdabanian and Botoman coralomorphs (Siberia, Australia, Laurentia) were associated with calcimicrobial-archaeocyath Tommotian to Botoman reefs, as open-surface and crypt dwellers. Late Early Cambrian coralomorphs from Australia were probably dwellers of warm agitated water with carbonate banks.

REFERENCES

- Alpert, S. P. and J. N. Moore. 1975. Lower Cambrian trace fossil evidence for predation on trilobites. *Lethaia* 8:223–230.
- Alvaro, J. J. and E. Vennin. 1997. Episodic development of Cambrian eocrinoid-sponge meadows in the Iberian Chains (NE Spain). *Facies* 37:49–64.
- Ausich, W. I. and D. J. Bottjer. 1982. Tiering in suspension-feeding communities on soft substrata throughout the Phanerozoic. *Science* 216:173–174.
- Bengtson, S. 1986. Siliceous microfossils from the Upper Cambrian of Queensland. *Alcheringa* 10:195–216.
- Bengtson, S., S. Conway Morris, B. J. Cooper, P. A. Jell, and B. N. Runnegar. 1990. Early Cambrian fossils from South Australia. *Association of Australasian Palaeontologists, Memoir* 9:1–364.
- Birkenmajer, K. 1977. Trace fossil evidence for predation on trilobites from Lower Cambrian of South Spitsbergen. *Norsk Polarinstitut Årsbok* 1976:187–195.
- Brasier, M. D., O. Green, and G. Shields. 1997. Ediacarian sponge spicule clusters from southwestern Mongolia and the origins of the Cambrian fauna. *Geology* 25:303–306.
- Brett, C. E., W. D. Liddell, and K. L. Derstler.

1983. Late Cambrian hard substrate communities from Montana/Wyoming: The oldest known hardground encrusters. *Lethaia* 16:281–289.
- Camoin, G., F. Debrenne, and A. Gandin. 1989. Premières images des communautés microbiennes dans les écosystèmes cambriens. *Comptes rendus sommaires de l'Académie des Sciences, Paris*, 2d ser., 308: 1451–1458.
- Chen, J. and G. Zhou. 1997. Biology of Chengjiang fauna. *Bulletin of the National Museum of Natural Science, Taichung, Taiwan* 10:11–105.
- Chen, J.-Y. and B. D. Erdtmann. 1991. Lower Cambrian fossil Lagerstätte from Yunnan, China: Insights for reconstructing early metazoan life. In A. M. Simonetta and S. Conway Morris, eds., *The Early Evolution of Metazoa and the Significance of Problematic Taxa*, pp. 57–76. Cambridge: Cambridge University Press.
- Chen, J.-Y., X.-G. Hou, and H.-Z. Lu. 1989. Lower Cambrian leptomitids (Demospongia), Chengjiang, Yunnan. *Acta Palaeontologica Sinica* 28:17–30.
- Chen, J.-Y., X.-G. Hou, and G.-X. Li. 1990. New Lower Cambrian demosponges—*Quadrolaminella* gen. nov. from Chengjiang, Yunnan. *Acta Palaeontologica Sinica* 29:402–413.
- Conway Morris, S. 1986. The community structure of the Middle Cambrian Phyllopod Bed (Burgess Shale). *Palaeontology* 29: 423–467.
- Conway Morris, S. 1989. The persistence of Burgess Shale-type faunas: Implications for the evolution of deeper-water faunas. *Transactions of the Royal Society of Edinburgh (Earth Sciences)* 80:271–283.
- Conway Morris, S. 1993a. The fossil record and the evolution of the Metazoa. *Nature* 361:219–225.
- Conway Morris, S. 1993b. Ediacaran-like fossils in Cambrian Burgess Shale type—fauna of North America. *Palaeontology* 36:593–635.
- Conway Morris, S. and M. Chen. 1989. Lower Cambrian anabaritids from South China. *Geological Magazine* 126:615–632.
- Conway Morris, S. and M. Chen. 1992. Carinachitiids, hexangulaconulariids, and *Punctatus*: Problematic metazoans from the Early Cambrian of South China. *Journal of Paleontology* 66:384–406.
- Conway Morris, S. and D. H. Collins. 1996. Middle Cambrian ctenophores from the Stephen Formation, British Columbia, Canada. *Philosophical Transactions of the Royal Society of London B* 351:279–308.
- Conway Morris, S. and R. A. Robison. 1988. More soft-bodied animals and algae from the Middle Cambrian of Utah and British Columbia. *University of Kansas Paleontological Contributions* 122:1–48.
- Conway Morris, S., J. S. Peel, A. K. Higgins, N. J. J. Soper, and N. C. Davis. 1987. A Burgess Shale-like fauna from the Lower Cambrian of North Greenland. *Nature* 326:181–183.
- Debrenne, F. and P. Courjault-Radé. 1994. Répartition paléogéographique des archéocyathes et délimitation des zones intertropicales au cambrien inférieur. *Bulletin de la Société géologique de France* 165:459–467.
- Debrenne, F. and J. Vacelet. 1984. Archaeocyatha: Is the sponge model consistent with their structural organization? *Palaeontographica Americana* 54:358–369.
- Debrenne, F. and A. Yu. Zhuravlev. 1992. *Irregular Archaeocyaths*. Paris: Cahiers de Paléontologie, Éditions du Centre National de la Recherche Scientifique.
- Debrenne, F. and A. Yu. Zhuravlev. 1994. Archaeocyathan affinities: How deep can we go into the systematic affiliation of an extinct group? In R. W. M. Van Soest, T. M. G.

- Van Kempen, and J. C. Braekman, eds., *Sponges in Time and Space*, pp. 3–12. Rotterdam: Balkema.
- Debrenne, F. and A. Yu. Zhuravlev. 1996. Archaeocyatha, palaeoecology: A Cambrian sessile fauna. In A. Cherchi, ed., *Autoecology of Selected Fossil Organisms: Achievement and Problems. Bollettino della Società Paleontologica Italiana, Special Volume 3*: 77–85.
- Debrenne, F., M. Debrenne, R. A. Gangloff, and J. G. Lafuste. 1987. *Tabulaconus* Handfield: Microstructure and its implication in the taxonomy of primitive corals. *Journal of Paleontology* 61:1–9.
- Debrenne F., A. Gandin, and R. A. Gangloff. 1990a. Analyse sédimentologique et paléontologique de calcaires organogènes du Cambrien inférieur de Battle Mountain (Nevada, USA). *Annales de Paléontologie* 76:73–119.
- Debrenne, F., A. Yu. Rozanov, and A. Yu. Zhuravlev. 1990b. *Regular Archaeocyaths*. Paris: Cahiers de Paléontologie, Éditions du Centre National de la Recherche Scientifique.
- Ding, Q.-X., Y.-S. Xing, and Y.-Y. Chen. 1985. Metazoa and trace fossils. In *Biostratigraphy of the Yangtze Gorge Area. 1: Sinian*, pp. 115–119. Beijing: Geological Publishing House.
- Dong, X.-P. and A. H. Knoll. 1996. Middle and Late Cambrian sponge spicules from Hunnan, China. *Journal of Paleontology* 70: 173–184.
- Doré, F. 1985. Premières méduses et premières faunes à squelette dans le Massif Armoricaïn: Problème de la limite Précambrien-Cambrien. *Terra Cognita* 5:2–3, 235.
- Engelbretsen, M. J. 1993. A Middle Cambrian possible cnidarian from the Murrawong Creek Formation, NE New South Wales. *Association of Australasian Palaeontologists, Memoir* 15:51–56.
- Fedorov, A. B. and V. S. Pereladov. 1987. Kremnevye spikuly gubok iz Kuonamskoy svity severo-zapada Sibirskoy platformy [Siliceous sponge spicules from the Kuonamka Formation of the northeastern Siberian Platform]. In S. P. Bulynnikova and I. G. Klimova, eds., *Novye vidy drevneishikh bespozvonochnykh i rasteniy iz fanerozoia Sibiri* [New species of ancient invertebrates and plants of the Phanerozoic of Siberia], pp. 36–46. Novosibirsk: Siberian Scientific-Research Institute of Geology, Geophysics, and Mineral Resources.
- Finks, R. M. 1970. The evolution and ecologic history of sponges during Palaeozoic times. In W. G. Frey, ed., *The Biology of the Porifera*, pp. 3–22. New York: Academic Press.
- Finks, R. M. 1983. Fossil Hexactinellida. In T. W. Broadhead, ed., *Sponges and Spongiforms: Notes for a Short Course*, pp. 101–115. University of Tennessee, Department of Geological Sciences, Studies in Geology 7.
- Fritz, M. A. and B. F. Howell. 1955. An Upper Cambrian coral from Montana. *Journal of Paleontology* 29:181–183.
- Fuller, M. K. and R. J. F. Jenkins. 1994. *Moorowipora chamberensis*, a coral from the Early Cambrian Moorowie Formation, Flinders Ranges, South Australia. *Royal Society of South Australia, Transactions* 118: 227–235.
- Fuller, M. K. and R. J. F. Jenkins. 1995. *Arrowipora fromensis*, a new genus and species of tabulate-like coral from the Early Cambrian Moorowie Formation, Flinders Ranges, South Australia. *Royal Society of South Australia, Transactions* 119:75–82.
- Gehling J. G. and J. K. Rigby. 1996. Long expected sponge from the Neoproterozoic Ediacara Fauna of South Australia. *Journal of Paleontology* 70:185–195.
- Hamdi, B., A. Yu. Rozanov, and A. Yu. Zhuravlev. 1995. Latest Middle Cambrian meta-

- zoan reef from northern Iran. *Geological Magazine* 132:367–373.
- Harrington, H. J. and R. C. Moore. 1956. Medusae incertae sedis and unrecognizable forms. In R. C. Moore, ed., *Treatise on Invertebrate Paleontology, Part F: Coelenterata*, pp. F153–F161. Boulder, Colo.: Geological Society of America.
- Henrich, R., M. Hartmann, J. Reitner, P. Schäfer, A. Freiwald, P. Dietrich, and J. Thiede. 1992. Facies belts and communities of the Arctic Vesterisbanken Seamount (central Greenland Sea). *Facies* 27:1–352.
- Hirabayashi, J. and K. Kasai. 1993. The family of metazoan metal-independent β -galactose-binding lectins: Structure, function, and molecular evolution. *Glycobiology* 3:297–304.
- James, N. P. and D. I. Gravestock. 1990. Lower Cambrian shelf and shelf-margin build-ups, Flinders Ranges, South Australia. *Sedimentology* 37:455–480.
- Jell, J. S. 1984. Cambrian cnidarians with mineralized skeletons. *Palaeontographica Americana* 54:105–109.
- Jell, P. A. and J. S. Jell. 1976. Early Middle Cambrian corals from western New South Wales. *Alcheringa* 1:181–195.
- Kaufman, A. J., A. H. Knoll, and S. M. Awramik. 1992. Biostratigraphic and chemostratigraphic correlation of Neoproterozoic sedimentary successions: Upper Tindir Group, northwestern Canada, as a test case. *Geology* 20:181–185.
- Kobluk, D. R. 1979. A new and unusual skeletal organism from the Lower Cambrian of Labrador. *Canadian Journal of Earth Sciences* 16:2040–2045.
- Kobluk, D. R. 1984. A new compound skeletal organism from the Rosella Formation (Lower Cambrian), Atan Group, Cassiar Mountains, British Columbia. *Journal of Paleontology* 58:703–708.
- Kouchinsky, A., S. Bengtson, and L.-A. Gershin. 1999. Cnidarian-like embryos associated with the first shelly fossils in Siberia. *Geology* 27:609–612.
- Kruse, P. D. 1987. Further Australian Cambrian sphinctozoans. *Geological Magazine* 124:543–553.
- Kruse, P. D. 1990. Are archaeocyaths sponges, or are sponges archaeocyaths? *Geological Society of Australia, Special Publication* 16:310–323.
- Kruse, P. D. 1996. Update on the northern Australian Cambrian sponges *Rankenella*, *Jawonya*, and *Wagima*. *Alcheringa* 20:161–178.
- Kruse, P. D. and P. W. West. 1980. Archaeocyatha of the Amadeus and Georgina basins. *BMR Journal of Australian Geology and Geophysics* 5:165–181.
- Kruse, P. D., A. Yu. Zhuravlev, and J. P. James. 1995. Primordial metazoan-calcimicrobial reefs: Tommotian (Early Cambrian) of the Siberian Platform. *Palaios* 10:291–321.
- Kruse, P. D., A. Gandin, F. Debrenne, and R. Wood. 1996. Early Cambrian bioconstructions in the Zavkhan Basin of western Mongolia. *Geological Magazine* 133:429–444.
- Lafuste, J., F. Debrenne, and A. Yu. Zhuravlev. 1990. Les fuscicules, type nouveau de biocristaux dans le squelette d'*Hydroconus* Korde 1963, coralomorphe du Cambrien inférieur. *Comptes rendus sommaires de l'Académie des Sciences, Paris, 2d ser.*, 310:1553–1559.
- Lafuste, J., F. Debrenne, A. Gandin, and D. Gravestock. 1991. The oldest tabulate coral and the associated Archaeocyatha, Lower Cambrian, Flinders Ranges, South Australia. *Géobios* 24:697–718.
- Li, C.-W., J.-Y. Chen, and T.-E. Hua. 1998. Precambrian sponges with cellular structures. *Science* 279:879–882.
- McCaffrey, M. A., J. M. Moldowan, P. A. Lip-

- ton, R. E. Summons, K. E. Peters, A. Jenkinson, and D. S. Watt. 1994. Paleoenvironmental implications of novel C₃₀ steranes in Precambrian to Cenozoic age petroleum and bitumen. *Geochimica et Cosmochimica Acta* 58:529–532.
- McKerrow, W. S., C. R. Scotese, and M. D. Brasier. 1992. Early Cambrian continental reconstructions. *Journal of the Geological Society, London* 149:599–606.
- Mehl, D. 1992. Die Entwicklung der Hexactinellidae seit dem Mesozoikum: Paläobiologie, Phylogenie, und Evolutionsökologie. *Berliner geowissenschaftliche Abhandlungen, Reihe E* 2:1–164.
- Mehl, D. 1996. Phylogenie und Evolution-ökologie der Hexactinellida (Porifera) im Paläozoikum. *Geologische Paläontologische Mitteilungen der Universität Innsbruck, Sonderband* 4:1–55.
- Mehl, D. 1998. Porifera and Chancelloriidae from the Middle Cambrian of the Georgina Basin, Australia. *Palaeontology* 41:1153–1182.
- Mehl, D. and H. L. Reiswig. 1991. The presence of flagellar vanes in choanomeres of Porifera and their possible phylogenetic implications. *Zeitschrift für Zoologische Systematik und Evolutionsforschung* 28:312–319.
- Mostler, H. 1985. Neue heteractinide Spongien (Calcispongea) aus dem Unter- und Mittelcambrium Sudwestsardiniens. *Berichte des Naturwissenschaftlich-medizinischen Vereins Innsbruck* 72:7–32.
- Müller, W. E. G., H. C. Schröder, and V. Garmulin. 1994. Phylogenetic relationship of ubiquitin repeats in the polyubiquitin gene from the marine sponge *Geodia cyonium*. *Journal of Molecular Evolution* 39:369–377.
- Okulitch, V. J. and W. G. Bell. 1955. *Gallatinospongia*, a new siliceous sponge from the Upper Cambrian of Wyoming. *Journal of Paleontology* 29:460–461.
- Pel'man, Yu. L., V. V. Ermak, A. B. Fedorov, V. A. Luchinina, I. T. Zhuravleva, L. N. Repina, V. I. Bondarev, and Z. V. Borodaevskaya. 1990. Novye dannye po stratigrafii i paleontologii nizhnego kembriya r. Dzhandy (pravyy pritok r. Aldan) [New data on the Lower Cambrian stratigraphy and paleontology on the Dzhandanda River (Aldan River right tributary)]. *Trudy, Institut geologii i geofiziki, Sibirskoe otdelenie, Akademiya nauk SSSR* 765:3–32.
- Pickett, J. and P. A. Jell. 1983. Middle Cambrian Sphinctozoa (Porifera) from New South Wales. *Association of Australasian Palaeontologists, Memoir* 1:85–92.
- Reitner, J. 1990. Polyphyletic origin of the sphinctozoans. In K. Rützler, ed., *New Perspective in Sponge Biology: Third International Sponge Conference 1985*, pp. 33–42. Washington, D.C.: Smithsonian Institution Press.
- Reitner, J. 1992. "Coralline Spongien" der Versuch einer phylogenetisch-taxonomischen Analyse. *Berliner geowissenschaftliche Abhandlungen, Reihe E* 1:1–352.
- Reitner, J. and D. Mehl. 1995. Early Paleozoic diversification of sponges: New data and evidences. *Geologische Paläontologische Mitteilungen der Universität Innsbruck, Sonderband* 20:335–347.
- Riding, R. and J. E. Andrews. 1998. Carbon isotopic evidence for photosynthesis in Early Cambrian oceans: Comment. *Geology* 26:191.
- Rigby, J. K. 1983. Fossil Demospongia. In T. W. Broadhead, ed., *Sponges and Spongiforms: Notes for a Short Course*, pp. 12–39. University of Tennessee, Department of Geological Sciences, Studies in Geology 7.
- Rigby, J. K. 1986a. Sponges of the Burgess Shale (Middle Cambrian), British Columbia. *Palaeontographica Canadiana* 2:1–105.
- Rigby, J. K. 1986b. Cambrian and Silurian sponges from North Greenland. *Rapport*

- Grønlands Geologiske Undersøgelse* 132:51–63.
- Rigby, J. K. 1987. Early Cambrian sponges from Vermont and Pennsylvania, the only ones described from North America. *Journal of Paleontology* 61:451–461.
- Rigby, J. K. 1991. Evolution of Paleozoic heteractinid calcareous sponges and demosponges—Patterns and records. In J. Reitner and H. Keupp, eds., *Fossil and Recent Sponges*, pp. 83–101. Berlin: Springer Verlag.
- Rigby, J. K. and X.-G. Hou. 1995. Lower Cambrian demosponges and hexactinellid sponges from Yunnan, China. *Journal of Paleontology* 69:1009–1019.
- Rozanov, A. Yu. and A. Yu. Zhuravlev. 1992. The Lower Cambrian fossil record of the Soviet Union. In J. H. Lipps and P. W. Signor, eds., *Origin and Early Evolution of the Metazoa*, pp. 205–282. New York: Plenum Press.
- Savarese, M. 1992. Functional analysis of archaeocyathan skeletal morphology and its paleobiological implications. *Paleobiology* 18:464–480.
- Scrutton, C. T. 1992. *Flindersipora bowmani* Lafuste and the early evolution of tabulate corals. *Fossil Cnidaria and Porifera Newsletter* 21:29–33.
- Scrutton, C. T. 1997. The Palaeozoic corals. 1: Origins and relationships. *Proceedings of the Yorkshire Geological Society* 51:177–208.
- Shabanov, Yu. Ya., V. A. Astashkin, T. V. Peggel', L. I. Egorova, I. T. Zhuravleva, Yu. L. Pel'man, V. M. Sundukov, M. V. Stepanova, S. S. Sukhov, A. B. Fedorov, B. B. Shishkin, N. V. Vaganova, V. I. Ermak, K. V. Ryabukha, A. G. Yadrenkina, G. P. Abaimova, T. V. Lopushinskaya, O. V. Sychev, and T. A. Moskalenko. 1987. *Nizhniy paleozoy yugo-zapadnogo sklona Anabarskoy anteklizy (po dannym bureniya)* [Lower Paleozoic of the southwestern slope of the Anabar Anticline (according to boring data)]. Novosibirsk: Nauka.
- Signor, P. W. and G. J. Vermeij. 1994. The plankton and the benthos: Origins and early history of an evolving relationship. *Paleobiology* 20:297–319.
- Sorauf, J. E. and M. Savarese. 1995. A Lower Cambrian coral from South Australia. *Palaentology* 38:757–770.
- Steiner, M., D. Mehl, J. Reitner, and B. D. Erdtmann. 1993. Oldest entirely preserved sponges and other fossils from the lowermost Cambrian and a new facies reconstruction of the Yangtse Platform (China). *Berliner geowissenschaftliche Abhandlungen, Reihe E* 9:293–329.
- Surge, D. M., M. Savarese, J. R. Dodd, and K. C. Lohmann. 1997. Carbon isotopic evidence for photosynthesis in Early Cambrian oceans. *Geology* 25:503–506.
- Teslenko, I. L., A. M. Mambetov, I. T. Zhuravleva, E. I. Myagkova, and N. P. Meshkova. 1983. *Dedebulakskaya biogermnaya gryada i istoriya ee razvitiya* [The Dedebulak Bioherm Belt and the history of its development]. *Trudy, Institut geologii i geofiziki, Sibirskoe otделение, Akademiya nauk SSSR* 569:124–138.
- Vacelet, J. 1985. Coralline sponges and the evolution of Porifera. In S. Conway Morris, J. D. George, R. Gibson, and H. M. Platt, eds., *The Origins and Relationships of Lower Invertebrates*, pp. 1–13. Systematics Association Special Publication 28. Oxford: Clarendon Press.
- Vologdin A. G. 1963. *Pozdne-srednekembriyskie arkheotsiaty basseyna reki Amgi (Sibirskaya platforma)* [Late Middle Cambrian archaeocyaths from the Amga River basin (Siberian Platform)]. *Doklady Akademii nauk SSSR* 151:946–949.

- Walcott, C. D. 1911. Cambrian geology and paleontology 2: Middle Cambrian holothurians and medusae. *Smithsonian Miscellaneous Collections* 57:145–228.
- Walcott, C. D. 1920. Cambrian geology and paleontology 4: Middle Cambrian Spongiae. *Smithsonian Miscellaneous Collections* 85:1–46.
- Webby, B. D. 1984. Early Phanerozoic distribution pattern of some major groups of sessile organisms. In *Palaeontology*, vol. 2 of *Proceedings of the 27th International Geological Congress, Moscow, 1984*, pp. 193–208. Utrecht: VNU Science Press.
- Wilson, J. A. 1950. Upper Cambrian pleospongiid (?). *Journal of Paleontology* 24:460–461.
- Wood, R. 1999. *Reef Evolution*. Oxford: Oxford University Press.
- Wood, R., A. Yu. Zhuravlev, and F. Debrenne. 1992. Functional biology and ecology of Archaeocyatha. *Palaios* 7:131–156.
- Zhang, X. G. and B. R. Pratt. 1994. New and extraordinary Early Cambrian sponge spicule assemblage from China. *Geology* 22:43–46.
- Zhuravlev, A. Yu. 1986. Evolution of archaeocyaths and palaeobiogeography of the Early Cambrian. *Geological Magazine* 123:377–385.
- Zhuravlev, A. Yu. 1990. Sistema arkheotsiat [Systematics of archaeocyaths]. In V. V. Menner, ed., *Sistematika i filogeniya bespozvonochnykh: Kriterii vydeleniya vysshikh taksonov* [Systematics and phylogeny of invertebrates: Criteria of high taxa establishing], pp. 28–54. Moscow: Nauka.
- Zhuravlev, A. Yu. 1996. Reef ecosystem recovery after the Early Cambrian extinction. In M. B. Hart, ed., *Biotic Recovery from Mass Extinction Events*, pp. 79–96. Geological Society Special Publication 102.
- Zhuravlev, A. Yu. 1999. A new coral from the Lower Cambrian of Siberia. *Paleontologicheskii zhurnal* 1999 (5):27–33.
- Zhuravlev, A. Yu. and R. Wood. 1995. Lower Cambrian reefal cryptic communities. *Palaeontology* 18:443–470.
- Zhuravlev, A. Yu., F. Debrenne, and J. Lafuste. 1993. Early Cambrian microstructural diversification of Cnidaria. *Courier Forschungsinstitut Senckenberg* 164:365–372.
- Zhuravlev, A. Yu., B. Hamdi, and P. D. Kruse. 1996. IGCP 366: Ecological aspects of the Cambrian radiation—field meeting. *Episodes* 19:136–137.
- Zhuravleva, I. T. 1960. Tip Porifera: Gubki [Phylum Porifera: Sponges]. In L. L. Khalfin, ed., *Biostratigrafiya paleozoya Sayano-Altayskoy gornoy oblasti. Tom 1, Nizhniy paleozoy* [Paleozoic biostratigraphy of the Sayan Altay Mountain region. Vol. 1, Lower Paleozoic], pp. 140–141. Novosibirsk: Siberian Scientific-Research Institute of Geology, Geophysics, and Mineral Resources.