

PATTERN OF EVOLUTION OF CAMBRIAN BENTHIC COMMUNITIES: ENVIRONMENTS OF CARBONATE SEDIMENTATION

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Riassunto. Vengono delineati alcuni aspetti delle comunità bentoniche del Cambriano, caratterizzate da sedimentazione carbonatica. La relativa ricchezza di queste comunità del Cambriano inferiore contrasta con le controparti impoverite tipiche del Cambriano Medio e dell'inizio del Cambriano Superiore. Tuttavia, si osserva uno stabile aumento della diversità nelle comunità durante il Cambriano. Viene dimostrato che lo spostamento delle comunità è un fenomeno comune e si ipotizza che intere comunità potrebbero migrare dalle loro aree di origine verso condizioni più favorevoli se la comunità precedente soffre di crisi.

Abstract. Features of Cambrian benthic communities that inhabited areas characterised by carbonate sedimentation are outlined. Relative richness of these Early Cambrian communities contrasts in comparison with their impoverished Middle and Early Late Cambrian counterparts. Nevertheless, a steady increase in the diversity of communities is observed during the Cambrian. It is shown that displacement of communities is a common phenomenon. It is suggested that entire communities might migrate from their area of origin into more favourable conditions if the former community suffered a crisis.

Introduction.

This paper deals with the diversity of Cambrian communities. Two principal settings, differentiated by the type of sedimentation, existed in the Cambrian: those where carbonate sedimentation dominated and those which were mainly characterized by siliciclastic deposition. The background controls of sedimentation were in general the climate and the size of area available for denudation. The Siberian Platform through the entire Cambrian, Laurentia since the middle Early Cambrian and Australia during the Early Cambrian exemplified carbonate-dominated habitats which are considered in the present paper.

The various communities are characterised seaward from the inner part of basin. The Siberian time scale is chosen for the Early to Middle Cambrian: Ne-

makyt-Daldinian (*in toto*, conformably to the decision accepted by the IGC of Kyoto in 1992, or only its upper part, according to most of the Russian authors, Tommotian, Atdabanian, Botoman, Toyonian, Amgan, Mayan), the Laurentian time scale for the Late Cambrian (Dresbachian, Franconian, Trempealeauan), because of their respective richness and well-studied paleontological remains.

Evaporite basins.

Evaporite basins, yielding carbonates and evaporites, were typified by low clastic input and high rate of evaporation. Their coastlines are characterised by chains of islands which shelter hypersaline lagoons with reduced tidal ranges where microbial mats are formed. They produced extensive stromatolites; good examples occur in the Toyonian Angara Formations of the Siberian Platform where stratiform and columnar stromatolites formed low but very wide buildups, up to several kilometres in length flanked by ooidal grainstones along their periphery (Korolyuk, 1968). This stromatolite community did not change appreciably during the Cambrian. However, various molluscs (rostriconchs and possible chiton-like grazers) occupied barrier complexes formed under generally higher salinities during the latest Late Cambrian in Australia (Druce et al., 1982).

Peritidal carbonate environments.

Peritidal carbonate environments include oolite shoals, carbonate sand shoals and beaches, and intertidal to subtidal flat settings. Since Atdabanian time *Ophiomorpha*-like trace producers as *Aulophycus* Fenton & Fenton, 1939, occupied mobile lime muds in shoal agitated back-reef conditions.

Ophiomorpha-type burrowings represent the innovative behaviour due to the ability to produce a pelleted

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burrow lining, which prevents burrow collapse in substrates of relatively low cohesive strength. The *Aulophycus*-community persisted through the entire Cambrian: Atdabanian Nokhoroy Unit, Botoman Kutorgina and Toyonian Keteme Formations of the Siberian Platform and Botoman Poleta Formation and Shady Dolomite of Laurentia (Balsam, 1974; Astashkin, 1985; Droser & Bottjer, 1988).

Shallow carbonate seas.

Shallow carbonate seas include several carbonate environments, all of which lie at or below fair-weather wave base. A high range of communities inhabits this zone, including reefal, level-bottom and hardground communities.

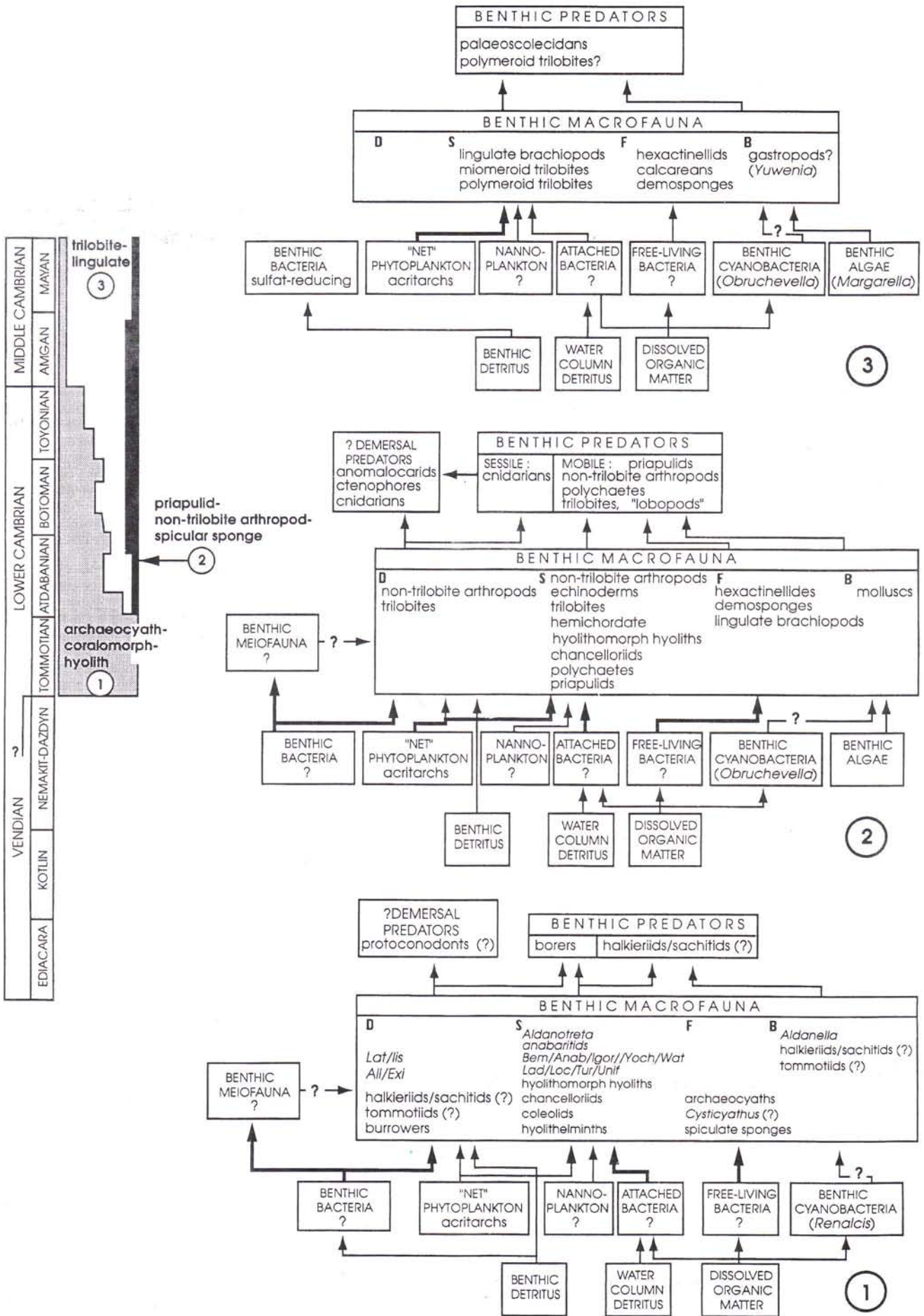
a) Reefal communities. The earliest Cambrian animal-autotroph reefs are calcified cyanobacterial bioherms in the early Nemakit-Daldynian on the Siberian Platform and Oman. They locally enclose *Anabarites* and *Cloudina* thickets (Luchinina, 1985; Mattes & Conway Morris, 1990). By the late Nemakit-Daldynian, bioherms of calcified cyanobacteria were widespread in the Siberian Platform, Altay-Sayan Foldbelt and Mongolia (Zadorozhnaya, 1974; Drozdova, 1980; Luchinina, 1985). The earliest Tommotian archaeocyath-*Renalcis* reef described from the Siberian Platform (Riding & Zhuravlev, 1995), however, was more complex as it contained the entire set of reef guilds: constructors (encrusting modular archaeocyathids), binders (monocyathids and *Renalcis*), bafflers (ajacicyathids, spicular sponges, and some orthothecimorph hyoliths), possible destroyers (borers), and diverse dwellers.

Typical Early Cambrian reefs were reef mounds constructed by calcimicrobes and less by filter-feeding metazoans, i.e. archaeocyaths, radiocyaths, and coralomorphs, proliferating from the Tommotian to Toyonian within the palaeoequatorial belt on carbonate platforms, under normal salinity, in mesotrophic-eutrophic shallow waters conditions (Wood et al., 1993). These reefs being developed on soft mud-dominated substrates, largely, at or below fair-weather wave base act as a hard bottom substratum for relatively rare macroborers (*Trypanites*-type) and abundant cryptobionts (Kobluk et al., 1978; Kobluk & James, 1979; Zhuravlev & Wood, 1995). Metazoans preferred the soft-bottom reefal periphery or occupied reefal cavities. Early Cambrian reefs, although similar sedimentologically to those of the later Phanero-

zoic, differ greatly from them in ecological aspect (Wood et al., 1992, 1993). They were essentially microbially mediated mounds in a broad sense, full of lime mud and dominated by solitary or low modular soft-substrate dwellers. The analysis of trophic structure has shown an abundance of filter- and suspension-feeders and carnivores among the biota (Wood et al., 1993; Kruse et al., 1995) (Fig. 1.1). Deposit-feeders and grazers were relatively scarce. The food web was short and based mainly on bacteria rather than on algae. The low diversity of reefal communities (an average of 50-80 species per several dozens of km² of outcrops studied) (Wood et al., 1993; Kruse et al., 1995) reflects a low degree of niche splitting by the Cambrian reefal biota in comparison with Palaeozoic (60-400 species) and modern (over 1,200 species) reefal biotas occupying comparable space (Fagerstrom, 1987). Contrary to the commonly held view that the reef fall coincided with the quasi-extinction of archaeocyaths at the end of the Early Cambrian, Middle and early Late Cambrian buildups, although being purely calcimicrobial, were the largest framework reefs of the Cambrian (Astashkin et al., 1984). A few remaining archaeocyaths, coralomorphs, and problematic calcified sponges, as well as probable calcified algae, are found only in thrombolites. Trilobites were almost the only metazoan element of the Middle Cambrian reefs but both their diversity and abundance were low (Sukhov & Pegel', 1986). Pure calcimicrobial reefs (dendrolites) lack any metazoan or algal components. The earliest metazoan reefs to appear after the demise of archaeocyathan buildups are described from the upper Middle Cambrian of the Mila Formation, northern Iran (Hamdi et al., 1995). This reef was built by a branching demosponge together with minor probable bacterial sheaths.

A continuous decline of calcimicrobial diversity could have been a direct consequence of elimination of both potential tiny grazers and reef-building metazoans during the Early Cambrian extinction events (Zhuravlev, 1996). The Middle Cambrian dendrolites were replaced by thrombolites and stromatolites during the Late Cambrian (Aitken, 1967; Fedorov et al., 1986; Kennard & James, 1986). The availability of space was probably the only reason for a spread of stromatolites. Any attempt to explain stromatolite decline/proliferation by the development of favourable/unfavourable conditions for their grazers fails (Zhuravlev, 1996) because even the extreme conditions, such as restricted lagoons, sabkhas and thermal springs do not exclude grazer pressure; mo-

Fig. 1 - Trophic webs in principal Early Cambrian benthic communities: 1 - reefal archaeocyath-coralomorph-hyolith community (modified after Kruse et al., 1995); 2 - level-bottom open marine priapulid-non-trilobite arthropod-spicular sponge community (modified after Conway Morris, 1986); 3 - level-bottom dysaerobic trilobite-lingulate community.



reover this conditions eliminate the predators that consume grazers, then species adapted to such environment can dramatically inhibit the development of stromatolites. Under normal marine conditions, various ecophysiological adaptations, such as oxygen and H₂S coexistence in alternative laminae of oxygenic and anoxygenic photosynthetic cyanobacteria, production of extracellular slimes and nitrogen fixation are more significant to prevent grazing.

The first possible chitons appeared during the Late Cambrian (Trempealeuan) (Bergenhayn, 1960; Runnegar et al., 1979; Stinchcomb & Darrough, 1995). Stromatolite-thrombolite dominance persisted during the Early and early Middle Ordovician (Toomey, 1981; Pratt & James, 1989). A widespread intrusion of metazoans into the stromatolitic-thrombolitic consortium started to occur during the Middle Ordovician (but also in lower Early Ordovician) with the coral *Lichenaria* (Pratt & James, 1982, 1989). The success of new Ordovician metazoan reef-builders (tabulates, stromatoporoids, bryozoans) in the algal-cyanobacterial framework reefs lies in their modular and encrusting type of growth.

b) Level-bottom community. For taxonomic and trophic aspects, the Early and early-Middle Cambrian level-bottom communities resembled the coeval reefal associations but differed in the absence of heavily calcified organisms. In both cases, filter- and suspension-feeders dominate both in number and in diversity.

Typically level-bottom communities were more diverse on the open shelves facing the ocean on siliciclastic rather than on carbonate platforms. The Middle Cambrian Phyllopod Bed and Wheeler Formation faunas (Laurentia), by the exceptional soft parts preservation, provide an unique insight into the structure of a bottom-level community (Conway-Morris, 1986; Robison, 1991) (Fig. 1.2). Because of the presence of soft-bodied animals, the characterization of Cambrian life of the Phyllopod Bed community does not correspond entirely with the classical one based on shelly components only. An unsuspected ecological complexity appears, with a finer niche partitioning: low levels were occupied mostly by brachiopods and rare edrioasteroids but sponges together with rarer pelmatozoan echinoderms, dominated at higher levels. More contrasting is the role of fleshy algae and cyanobacterians as primary producers and deposit feeding arthropods as consumers. Diverse predators are confirmed by the abundance of effectively soft-bodied carnivores, together with some carnivores with hard parts. Similar communities existed since the Early Botoman at least, for example the Chinese Chengjiang Biota (Chen et al., 1989).

The shallow level-bottom community underwent most significant changes during the Cambrian. After the

demise of the "Tommotian" Fauna by the end of the Early Cambrian, trilobites and lingulate brachiopods dominated until the Middle Ordovician, in Laurentia and on the Siberian Platform (Sepkoski & Sheehan, 1983; Sukhov & Pegel', 1986) (but also in Australia, China, Kazakhstan). Brachiopods and less commonly hyoliths, graptolites and pterobranchs occupied two suspension-feeding levels, while trilobites were deposit-feeders and possibly carnivores. During Middle Cambrian - Middle Ordovician, a reorganisation of communities proceeded by addition of new elements, especially gastropods, rostroconchs, cephalopods and articulate brachiopods, beginning in the Trempealeuan. In the Dresbachian-Franconian, trilobites account for two-thirds of the species present. By the Trempealeuan to Early Ordovician interval, palaeocommunity compositions are split more or less evenly between trilobites and molluscs (gastropods, cephalopods, and rostroconchs). In Northern China, the within-community diversity of molluscs exceeded that of trilobites (Chen & Teichert, 1983). Finally, during the Middle Ordovician interval, the number of trilobite species were maintained at the same level, while the number of other species increased to about one-third in their prior number of species. Thus, decline in the relative importance of trilobites in nearshore environments was a case of dilution, as species of new clades appeared, rather than an actual displacement (Westrop et al., 1995).

c) Hardground community. This community was a late innovation appearing only during the Late Cambrian and becoming widespread during the Ordovician. Although hardgrounds existed since Late Atdabanian at least (e.g., Sellick Hill Formation, South Australia) (Alexander & Gravestock, 1990), they were lacking a distinct fauna (A. Zhur. pers. observation). Only much later, the early Franconian - Trempealeuan Snowy Range flat pebble conglomerates of Laurentia exhibit evidence of early lithification. The resulting hardground was locally inhabited by solitary filter / suspension-feeding organisms, namely eocrinoids and other pelmatozoans, orthid brachiopods, and spicular demosponges (Brett et al., 1983). The Cambrian hardground community, not yet ecologically partitioned, was dominated by solitary forms (like the other Cambrian communities). The encrusting (especially bryozoan) and boring faunas on the upward-facing hardground surfaces, increased rapidly in diversity in Early and Middle Ordovician occupying the full range of levels above the substratum (Palmer, 1982). Open-framework burrow systems from the Late Cambrian Peerless Formation of Laurentia are attributed to *Thalassinoides*, which penetrated firm substrates and, thus, belonged to an intermediate firm substrate community (Myrow, 1995).

The rise of stalked echinoderms, starting in the Middle Cambrian, was one of the prerequisites for the development of hardground communities. The easy breakage of echinoderm skeletons into multiple fragments composing up to 30% of rock volume, increased the amount of calcareous detritus, rapidly lithified on the sea floor through the precipitation of cements (Wilson et al., 1992; Rozhnov, 1993). The echinoderms, thus, played an indirect taphonomic role in their own habitat, as their debris supported further attached echinoderms. Development of *Thalassinoides* burrows and hardgrounds during Late Cambrian to Ordovician and Middle to Late Cainozoic is notable, coinciding with calcitic-sea conditions. Then, the inorganic precipitation of carbonates - as mud, allochems, and cements - was exclusively calcite (Sandberg, 1983; Wilson et al., 1992). Thus, the switching from the Early Cambrian aragonitic-sea epoch to the Late Cambrian calcitic one may have somehow promoted the development of hardground communities.

Deeper carbonate seas.

Two principal deeper water communities, aerobic and dysaerobic, occupied well and/or poorly oxygenated sites. They did not change significantly during the Ordovician preserving relicts of the Cambrian Fauna (Cook & Taylor, 1977).

a) **Aerobic community.** Several fossil assemblages are recognised in the late Middle Cambrian (Mayan Stage) of the Siberian Platform. Pterobranchs, eocrinoids (?), graptolites, *Brooksella*?, hyoliths, abundant trilobites and brachiopods (mainly lingulates) are described from outer slope, open-sea facies which occurred distally on the Siberian Platform, Olenek Province, from the Zele-notsvet, Dzhakhtar and Siligir Formations (Fedorov et al., 1986; Durman & Sennikov, 1993). The Late Cambrian Hales Limestones of Laurentia and the Chopko Formation of the Siberian Platform contained faunas living probably below 350 m, below the thermocline (Cook & Taylor, 1977; Barskov & Zhuravlev, 1988; Varlamov & Pak, 1993). The trilobite fauna is not diverse, the burrows and the infauna sparse, but the presence of palaeoscolecidans, benthic bradoriids, conodonts, and abundant sponge spicules suggests the presence of filter and suspension-feeders and carnivores.

b) **Dysaerobic community.** A typical Early Cambrian example is studied by Zhuravlev and Wood (1995) from the Botoman Sinsk Formation of the Siberian Platform (Fig. 1.3). The Sinsk biota was represented by the calcified bacterium *Obruchevella* and abundant green

fleshy algae *Margaretia* as primary producers, spicular sponges as filter-feeders, hyoliths, lingulate brachiopods and eodiscids trilobites as suspension-feeders, rare parastropods as grazers, palaeoscolecidans and protolenid trilobites as carnivores. Polymeroids with wide thin exoskeleton, multiple thoracic segments and enlarged pleurae, were nekto-benthic trilobites adapted to low oxygen tension (Repina & Zharkova, 1974; Fortey & Wilmot, 1991). Volumetrically, trilobites and lingulates dominated. The latter might have fed on an abundant but monotypic acritarch flora. A similar community occurred on the Siberian Platform over the late Early - early Middle Cambrian (Pel'man, 1982). Later, agnostoids and olenids, replaced eodiscids and protolenids respectively.

Conclusions.

The Ediacaran benthic fauna was chiefly composed of passive filter or/and suspension feeders and of a few deposit feeders (Lipps et al., 1992), independently of the systematic interpretation of its members. Although this biota is known from shallow-water onshore and offshore sandstones, deep-water turbidites and shallow-water carbonates, it may be attributed to a single community. A large diversity of communities was deployed during the Early Cambrian; some others were added by the Late Cambrian. Relatively diverse Early Cambrian benthos represented by the Tommotian Fauna was replaced during the Middle Cambrian by a simpler, trilobite-dominated Cambrian Fauna s.s. which, in turn, was replaced by the Palaeozoic Fauna during the Late Cambrian. This process is obvious in the reefal and level-bottom communities. The proximal communities were the most conservative; the distal, deep water communities grew permanently by adding of new elements, and the intermediate shallow shelf subtidal communities were the most changeable in taxonomic composition. The displacement of communities was a common phenomenon: the earliest deep water communities were derived from former shallow water elements; a trilobite-lingulate community, which occupied normal marine conditions during the Middle Cambrian, at first appeared in dysaerobic Early Cambrian basins.

A typical Cambrian food chain, acritarch / bacterioplankton - hyolith / lingulate? / arthropod - priapulid / "lobopodian" - anomalocarid is short and simple, in spite of the presence of second order consumers, and is comparable with diatom - anchovies / krill - tuna / sea bird - marine mammals' web of Recent eutrophic areas. Trace fossil data of Crimes (1992) indicate that the Cambrian biota consisted of 60% of deposit-feeders, 15% of filter- and suspension-feeders and 30% of probable car-

nivores and scavengers. Volumetric analysis of single communities, however, indicates bacterial primary producers, filterers, suspension-feeders and carnivores. Deposit-feeders and grazers were less common. Such a ratio of guilds is typical of communities which have thrived in eutrophic conditions (Jean & Thouzeau, 1995). This fact does not imply that each Cambrian community proliferated in such conditions but it reveals that Cambrian communities were potentially adapted to them. In the absence of terrestrial vegetation, and at the begin-

ning of the filter - /suspension-feeding niche, the early Phanerozoic shallow epicontinental waters, indeed, might have been turbid and nutrient-rich.

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