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## Palaeoecology of the Early Cambrian Sinsk biota from the Siberian Platform

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### Abstract

The Sinsk biota (Early Cambrian, Botoman Stage, Siberian Platform) inhabited an open-marine basin within the photic zone, but in oxygen-depleted bottom waters. Its rapid burial in a fine-grained sediment under anoxic conditions led to the formation of one of the earliest Cambrian Lagerstätte. All the organisms of the biota were adapted to a life under dysaerobic conditions. It seems possible that the adaptations of many Cambrian organisms, which composed the trophic nucleus of the Sinsk Algal Lens palaeocommunity to low oxygen tensions allowed them to diversify in the earliest Palaeozoic, especially during the Cambrian. Nowadays these groups comprise only a negligible part of communities and usually survive in settings with low levels of competition. Nonetheless, the organization of the Algal Lens palaeocommunity was not simple, it consisted of diverse trophic guilds. The tiering among sessile filter-feeders was well developed with the upper tier at the 50 cm level. In terms of individuals, the community was dominated by sessile filter-feeders, vagrant detritophages, and diverse carnivores/scavengers. The same groups, but in slightly different order, comprised the bulk of the biovolume: vagrant epifaunal and nektobenthic carnivores/scavengers, sessile filter-feeders, and vagrant detritophages. The Algal Lens and Phyllopod Bed (Burgess Shale) Lagerstätten share a number of common features including a representativeness of certain groups, a relative percentage of fauna in terms of individuals and biovolumes, feeding habits, and substrate relationships.

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*Keywords:* Palaeoecology; Early Cambrian; Individual abundance; Biovolume; Trophic nucleus

### 1. Introduction

Siberian Platform sites containing organisms of exceptional preservation are confined to the outer shelf to slope-basin facies of the Yudoma-Olenek basin (Fig. 1). The basin faced the open ocean and to a

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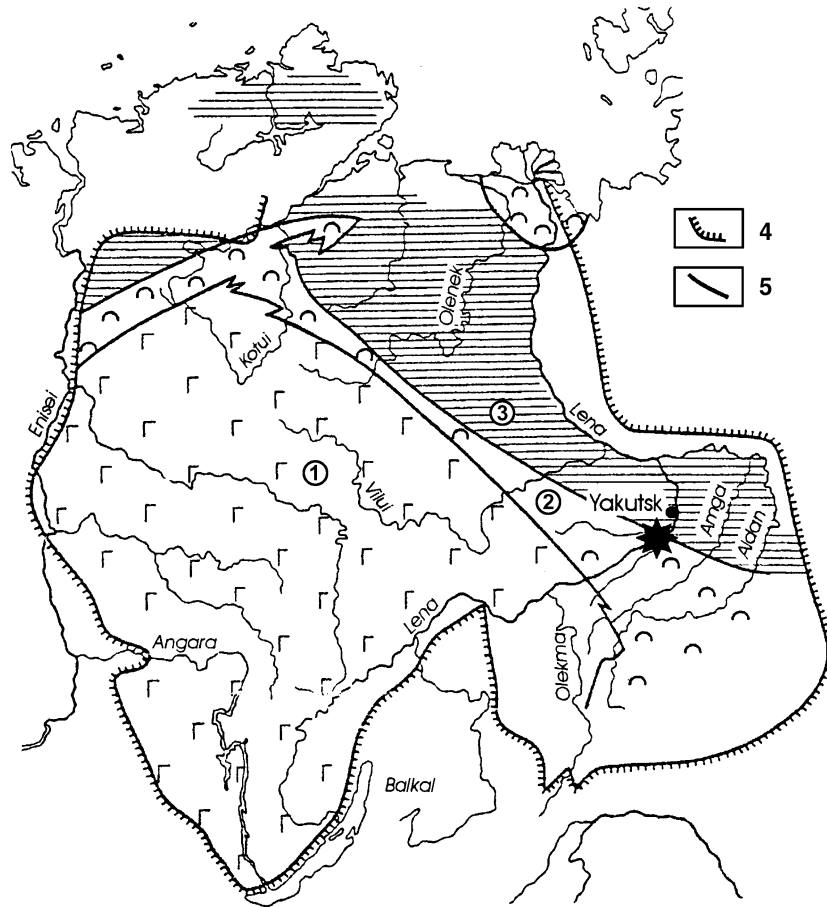


Fig. 1. Palaeogeographic map of the Siberian Platform in the Early Cambrian. Asterisk marks the Algal Lens Sinsk Lagerstätte. (1) Turukhans-Irkutsk-Olekma saliniferous basin (inner shelf); (2) Anabar-Sinsk reefal belt; (3) Yudoma-Olenek basin (outer shelf); (4) boundary of the Siberian Platform; (5) major facies boundaries (modified after Savitskiy and Astashkin, 1979).

certain extent was comparable to the outer detrital belt of Laurentia famous of its Burgess-Shale-type localities. Excavations of the Early Cambrian Sinsk Formation in the middle courses of the Lena River brought out a large number of relatively diverse and well-preserved fossils (Ivantsov et al., 1996; Ivantsov, 1998, 1999; Melnikova, 1998, 2000). The principal localities occur on the right bank of the Lena River in the vicinity of the mouths of the Achchagyy-Tuoydakh and Ulakhan-Tuoydakh rivers.

The main fossiliferous horizon is restricted to a calcareous shale bed at the lower Sinsk Formation of 0.5 m in thickness (Fig. 2). The shale is dark brown, thinly laminated with calcitic and clayey laminae. Only organisms with rigid enough covers (envelopes

and cuticles) such as seaweeds, palaeoscolecidans, some cnidarians, arthropods and spicular sponges are preserved. The Sinsk biota does not represent a typical Burgess-Shale-type preservation which often keeps tiny details of soft integuments. Nonetheless, the Sinsk localities should be attributed to Lagerstätten because they yield forms which are not usually fossilized and which contribute to a disproportionate amount and quality of palaeobiological information.

The age of the Sinsk biota is *Bergeroniellus gurarii* Zone of the Early Cambrian Botoman Stage (Astashkin et al., 1990). This biota is among the oldest soft-bodied Early Cambrian together with the late Atdabanian Sirius Passet fossils of Greenland and early Botoman Chengjiang fauna of China (Conway

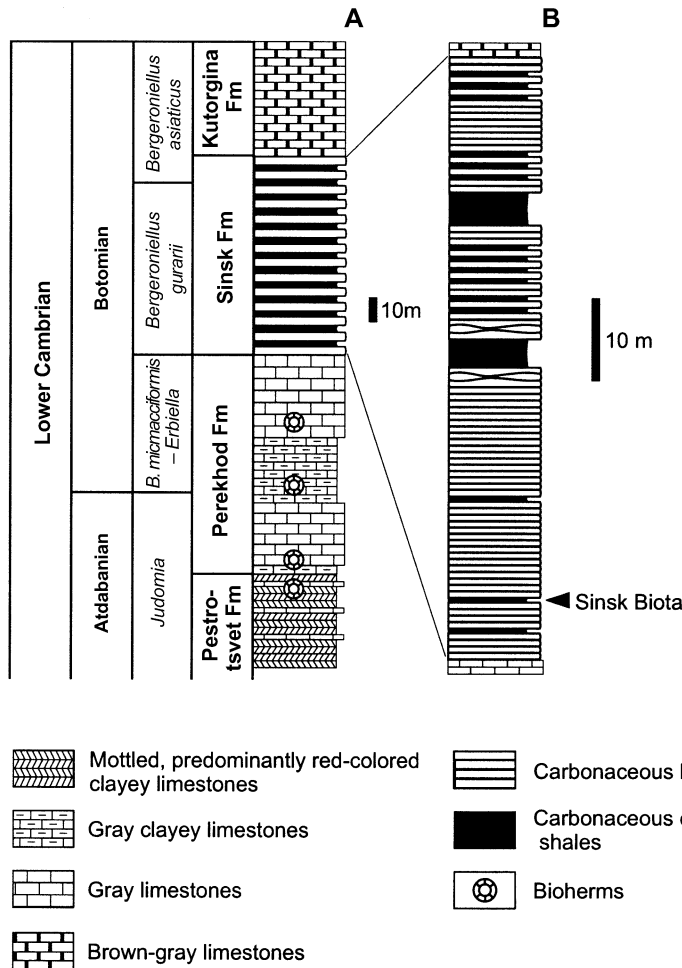


Fig. 2. Sections of the Sinsk Formation on the right bank of the Lena River middle courses. (A) Generalised section of the western Yudoma-Olenok basin; (B) section of the Sinsk Formation located 2.5 km downstream the Achchaggy-Tuoydakh River mouth, the level of the Sinsk Lagerstätten is indicated.

Morris et al., 1987; Chen et al., 1989). The latter is approximately coeval with the Sinsk biota.

Despite of an apparent heterogeneity in fossil composition among different Sinsk sites (Algal Lens, Tuoydakh, and others) it is obvious that they represent oryctocenoses resulting from a catastrophic burial of organisms composing natural communities. Thus, Sinsk localities and especially the Algal Lens Lagerstätte provide a rare opportunity to reconstruct an ancient community in detail.

The Algal Lens oryctocoenosis itself supplies the principal data set of this study because it is the richest of the Sinsk Lagerstätten. It occurs on the right bank

of the Lena River, 300 m downstream the Ulakhan-Tuoydakh River mouth. The total excavated area encircles over 5 m<sup>2</sup>. The locality yields cyanobacteria, algae, sponges, cnidarians, brachiopods, arthropods, and other fossil groups.

Many typical Cambrian groups of animals preserved in the Algal Lens Lagerstätte became rare, including cephalorhynch worms, tardipolypodians, bradoriids, coeloscleritophorans, and eldonioideans. The cephalorhynchs comprise a phylum of primitive worms which include modern priapulids, loriciferans, kinorhynchs, and nematomorphs as well as a number of fossil groups of class rank, such as the Ancalo-

gonida and Louisellida (Malakhov and Adrianov, 1995). Of these, only lousellids (one species) are present in the Sinsk Lagerstätten. Palaeoscolecids also bear a number of characteristics typical of cephalorhynchids, including cuticular structure, features of the proboscis, alimentary tract, and caudal end (Conway Morris and Robison, 1986; Barskov and Zhuravlev, 1988; Märss, 1988; Müller and Hinz-Schallreuter, 1993; How and Bergström, 1995; Zhang and Pratt, 1996; Conway Morris, 1997). The entire set of features is consistent with features represented with the phylum Cephalorhyncha, to which palaeoscolecids are assigned as a class (Conway Morris and Robison, 1986). Palaeoscolecids are diverse in the Sinsk Lagerstätten, with five species from only the Algal Lens oryctocoenosis.

Tardipolypodians are ancient lobopodian animals often compared with onychophorans or tardigrades, but probably represent a separate extinct phylum (Chen and Zhou, 1997). Bradoriids, which were once considered to be ostracode-like crustaceans, are now classified as several independent groups of primitive bivalve arthropods due to structure of their appendages (Hou et al., 1996). Coeloscleritophorans are Cambrian in age, sclerite-bearing animals which can be a stem-group of brachiopods, mollusks, and annelids (Bengtson and Missarzhevsky, 1981; Conway Morris and Peel, 1995). The Sinsk Lagerstätten contains two different coeloscleritophorans: a sessile radially symmetrical calcareous spiny cancelloriid, and vagrant bilaterally symmetrical organic-sclerite wiwaxiid. Eldonioideans can represent either a stem-group of radial-symmetrical planktic deuterostomians or extremely deviated lophophorates (Conway Morris, 1993; Dzik et al., 1997; Friend et al., 2002).

The material under discussion is housed in the Palaeontological Institute of the Russian Academy of Sciences (Moscow), collection PIN 4349.

## 2. Environments

### 2.1. Burial facies

The combination of palaeomagnetic, sedimentological, and geochemical data revealed that the marine basin inhabited by Sinsk communities occurred at low latitudes and was characterized by

a humid warm climate (Savitskiy et al., 1972; Savitskiy and Astashkin, 1979; Nikolaeva, 1981; Smethurst et al., 1998).

The early-middle Botoman Sinsk Formation consists of mostly dark bituminous platy to flaggy, thinly laminated, variously argillaceous limestones. Both slump bedding and breccia are observed in places, as well as unidirectional current marks and aligned trilobite carapaces. Dark bituminous limestones are composed of clotted to finely peloidal varieties often altered to a neomorphic microcrystalline limestone. Gradational sorting of primary peloids and disseminated organic matter is well expressed. Microclotted limestone of the Algal Lens locality contains relatively less organic matter and argillaceous admixture than average Sinsk Formation rocks. The limestones are mostly calcisiltites and calcilutites consisting of redeposited aleuritic size peloids, the texture of which depends entirely on the degree of recrystallization and the amount of carbonaceous and argillaceous admixture.

The fine-grained sediment was likely accumulated under calm conditions below storm wave base. The complete absence of bioturbation as well as high organic and pyritic content further reveal dysaerobic conditions developed within the sediment and near-bottom water column (Byers, 1977; Coniglio and Dix, 1992; Anderson et al., 1994). The gradational structure reflects the deposition from suspension. Each layer accumulated rapidly during a single, short depositional event. The bedding structures, especially the bed foot texture indicate a deposition resulting from a loading of unidirectional fading flows. Judging by a low thicknesses and sharp erosional contacts at bed feet, with a gradational sorting and thin (aleuritic) composition of fabrics, low density suspension flows are inferred as the source of deposits (Eberli, 1991; Piper and Stow, 1991). The fine (submillimetric) horizontal lamination is also typical of such conditions.

X-ray fluorescence microscopy of Sinsk limestones has revealed an enrichment in minor and trace elements, which being corrected by elements to Al ( $10^4$ ) ratio, reach the following values: V=176, As=32, Cr=19, Cu=67, Ni=32. Such geochemical manifestations imply oxygen-depleted conditions during the accumulation of the Sinsk Formation and may be taken into account for the explanation of the

preservation of the Sinsk Lagerstätten (Zhuravlev and Wood, 1996). Anoxia might limit bioturbation and scavenger activity which resulted in the excellent preservation of rigid carcasses, but certainly was not a strong enough factor to prevent a rapid enzymatic degradation of organic structures (Allison, 1988; Butterfield, 1990). The preservation of microscopical details of cephalorhynch and tardipolypodian muscle fibres and of lingulate mantle cells in Sinsk phosphate replicas also infer tissue decay under oxygen-depleted conditions (Hof and Briggs, 1997).

Bearing in mind the distal position of the Sinsk Formation, the aforementioned strata are interpreted as microturbidites which were deposited from low density turbid flows generated by storms within relatively shallow water conditions, transported downslope, and accumulated below storm wave base under dysaerobic conditions. The peloids were probably the products of destruction of calcimicrobial reefs, and larger fragments of such reefs are common in the underlying Perekhod Formation representing more shallow water facies.

In summary, the Sinsk Lagerstätten are among the typical Lagerstätten, where the preservation of organic remains is due to the following factors: (1) the presence of tough, resistant cuticles, (2) a dysoxic milieu of accumulation, and (3) rapid burial in (4) a fine grained sediment (Fig. 3).

## 2.2. Pre-burial facies

Despite the dissimilar position of Cambrian low latitude Lagerstätten within basin in which they were formed (Siberian and Laurentian—at an open shelf, Chengjiang—at an open shelf influenced in places by estuarine or fluvial sources, Paseky—in a brackish lagoon, and Emu Bay—probably, within a closed basin), they preserved comparable biotas (Piper, 1972; Chlupáč, 1995; Lindström, 1995; Elrick and Hinnov, 1996; Nedin, 1997; Babcock and Zhang, 2001).

The abundance and diversity of seaweeds and calcified cyanobacteria are indicative of the photic zone. Algae and cyanobacteria are particularly diverse in the Algal Lens and Chengjiang oryctocoenoses where they comprise over one-third of all fossils (Babcock and Zhang, 2001). These groups are numerous in the Phyllopod Bed of Burgess Shale as well (Conway Morris, 1986). In all three Lagerstätten, algae and cyanobacteria (mostly, *Marpolia*) are preserved as countless coverings. Only the Sirius Passet and Emu Bay sites completely lack algae. The Sirius Passet locality perhaps yields the deepest of similar biotas, because it does not express any features of transportation of its fossils (Vidal and Peel, 1993). On the contrary, the Emu Bay biota appeared to live under utterly unfavourable conditions of a shallow stagnant basin that resulted in its extremely low

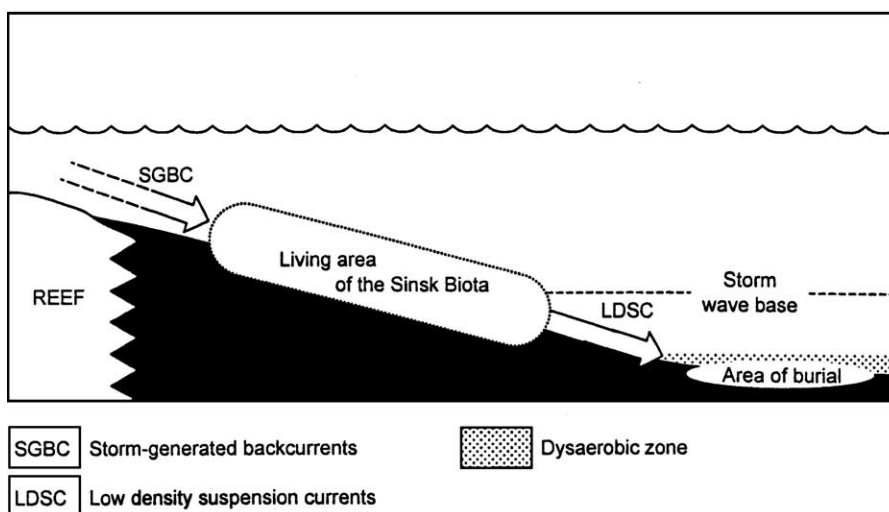


Fig. 3. Taphonomy of the Sinsk Lagerstätten. The benthic biota inhabiting photic zone were transported downslope into deeper dysaerobic environment.

diversity (11 species), and in a complete absence of Cambrian animals typical of normal marine conditions (sponges, brachiopods, mollusks, hyoliths, and echinoderms; Nedin, 1995). The composition of the brackish Paseky Shale biota is inferior, where 3 arthropod species are present, in addition to some acritarchs and filamentous cyanobacteria *Marpolia* (Chlupáč, 1995; Fatka and Konzalová, 1995; Steiner and Fatka, 1996).

The presence of hexactinellids, brachiopods including the rhynchonellate one, as well as mollusks and hyoliths in the Sinsk Lagerstätten shows, that the communities preserved as Algal Lens and Tuoydakh oryctocenoses inhabited a normal marine basin.

The modern seaweeds resembling the Sinsk algae are common under low intertidal to shallow subtidal conditions. They grow on rocky shores within bays free of severe storms. The restriction of the Sinsk living communities to the photic zone is followed from the presence of kunmingellids (bradoriids) with pronounced eyes (Shu et al., 1999). Additionally, all trilobites but miomeric *Delgadella*, as well as trilobitomorph *Phytophilaspis* possessed developed vision. The abundance of green algae allows us to suggest that the biota rarely lived below a hundred metres, but rather inhabited depths of 30–40 m of shallow subtidal zone.

In contrast to the Algal Lens palaeocommunity, the genuine biota of the Sinsk Formation, which comprises background oryctocenoses, probably was restricted to a deeper part of the basin, below the photic zone (Zhuravlev and Debrenne, 1996: Fig. 1.3). Seawards of the reefal Anabar-Sinsk belt (along the Yudoma and Maya rivers), fossil assemblages depauperate and, in the most remote localities, include miomeric trilobites and hexactinellid sponges, with only a few other fossils (Zhuravlev, Ivantsov, personal observations). Indeed, by comparison with demosponges, hexactinellids prefer deeper waters independently on a planktic food source (Krautter, 1997). A similar pattern of sponge distribution is observed in Sinsk localities: definite hexactinellids (*Lenica*) are restricted to Lagerstätten formed under deeper conditions while demosponges are typical of relatively shallow water ones.

A low number of mollusks, hyoliths, and rhynchonellate brachiopods possessing calcareous shells, as well as infaunal filter-feeders and detritophages

probably imply dysaerobic conditions (Byers, 1977; Morris, 1979; Savdra and Bottjer, 1986). Spicular sponges, which are able to survive anoxia, are very common. There is a high diversity and great abundance of cephalorhynch worms, including priapulids, and lingulate brachiopods are evident for low oxygen tensions because these animals rely upon hemerythrins for oxygen transportation (Runnegar and Curry, 1992). Brachiopods are very resistant to anoxic conditions and turbidity (Thayer, 1981; Tunnicliffe and Wilson, 1988; Ushatinskaya, 2001). Priapulids burrow in the mud even within anaerobic milieu (van der Land, 1970). Besides, wide pleurae of many Sinsk trilobites are the feature of well-developed gills, which are necessary in environments lacking enough oxygen (Fortey and Wilmot, 1991). Plentiful Sinsk bradoriids bore thin, densely porous carapaces pierced by a condensed net of branching vessels. They may have possessed paddle-like exopodites, which ventilated space under the carapace, especially in the vicinity of the main gas-exchange areas, crowded with vessels (Vannier et al., 1997; Shu et al., 1999). The entire set of bradoriid features indicates their adaptation to dysaerobic conditions. Indeed, in the Upper Cambrian of Scania (Sweden) bradoriids (*Cyclotron* sp.) are restricted exclusively to strata accumulated at low oxygen levels (Clarkson et al., 1998).

If the upper boundary of the oxygen minimum zone was high in Cambrian marine basins (Wright et al., 1987), it would not be surprising that dysaerobic biotas such as the Sinsk one occurred within the photic zone. These were biotops spreading out several dozens of meters below the belt where calcareous reefs proliferated. Both adjacent reefal and Sinsk biotas share common species of tardipolypodians, palaeoscolecidans, bivalved arthropods, cancelloriids, and pharetronid sponges (*Dodecaactinella*).

The Algal Lens community occupied a biotope abutting aerobic/dysaerobic interface. This was a space favourable to some groups of organisms which benefited by an enhanced nutrient recycling, especially phosphates, nitrates, and iron. The recycling has been stimulated by the absence of bioturbators, which are responsible for the burial of an excess organic matter under normal conditions, and by the presence of reducing conditions in the area of the biota burial



(see above). Over 50% of primary production in such a milieu is formed by a microbial regeneration of nutrients (Huntley et al., 1991). Increased nutrient regeneration and recycling could maintain the proliferation of abundant and often monotypic producers in Sinsk palaeocommunities.

The dominance of sessile filter-feeders (brachiopods, sponges, and cancelloriid *Archiasterella*) in the Algal Lens palaeocommunity (Table 1, Figs. 4, 5A and 6) infers permanent currents along Sinsk biotops, probably induced by storms and a slope gradient. These currents could scour sea bottom sediments in such a way that only animals adapted for deeper burrowing survived, specifically cephalorhynch. The presence of inverted proboscis indicates an ability to employ a hydrostatic system for locomotion and thus, for burrowing in advanced cephalorhynch worms. The same follows from an observation of developed

peripheral circular muscles of body-wall musculature, which are typical of burrowing worm-like invertebrates (Budd, 1998). The circular muscle fibers are organized in bundles of about 15–25  $\mu\text{m}$  across and well preserved in Sinsk cephalorhynch due to an early phosphatization. The sclerite cover pattern also reveals palaeoscolecidan burrowing abilities. One of species exhibits sclerites with hook-like nodes. Another palaeoscolecidan species bore sclerites oriented by their sharp edges across the trunk. In both cases, sclerites were well-shaped for an anchoring in the sediment.

The sea floor probably consisted of a mixture of calcareous sand and mud, loose enough for burrowers but lithified rapidly to provide a firm ground for seaweeds, pharetronid sponges, and large brachiopods. Storm-generated currents provided food and some oxygen for Sinsk animals, while processes at the

Table 1  
The composition of the Algal Lens oryctocoenosis

Name	Affinity	<i>N</i> (specimens)	Biovolume	Feeding habit	Life habit
<i>Diagoniella</i>	sponge	1	15.5 cm <sup>2</sup>	filter-feeder	sessile epibenthos
<i>Lenica</i>	sponge	2?	84.0 cm <sup>2</sup>	filter-feeder	sessile epibenthos
<i>Wapkia</i>	sponge	4	10.0 cm <sup>2</sup>	filter-feeder	sessile epibenthos
Demosponge n.gen.	sponge	3?	18.0 cm <sup>2</sup>	filter-feeder	sessile epibenthos
<i>Cambrorhytium</i>	cnidarian	4?	0.3 cm <sup>2</sup>	filter-feeder?	sessile epibenthos
<i>Corallioscolex</i>	cephalorhynch	2	1.8 cm <sup>2</sup>	carnivore/scavenger	burrowing infauna
Palaeoscolecid n.gen.1	cephalorhynch	1	2.0 cm <sup>2</sup>	carnivore/scavenger	burrowing infauna
Louseillid n.gen.	cephalorhynch	1	0.9 cm <sup>2</sup>	carnivore/scavenger	burrowing infauna
Palaeoscolecid n.gen.2	cephalorhynch	3	2.2 cm <sup>2</sup>	carnivore/scavenger	burrowing infauna
Palaeoscolecid n.gen.3	cephalorhynch	2	3.6 cm <sup>2</sup>	carnivore/scavenger	burrowing infauna
Palaeoscolecida	cephalorhynch	1	4.2 cm <sup>2</sup>	carnivore/scavenger	burrowing infauna
<i>Microdictyon</i>	tardypolipodia	1	sclerite	carnivore/scavenger	vagrant epibenthos
<i>Xenusia</i> indet.	tardypolipodian	1	1.8 cm <sup>2</sup>	carnivore/scavenger	vagrant epibenthos
Tardipolypoda	tardypolipodian	1	1.8 cm <sup>2</sup>	carnivore/scavenger	vagrant epibenthos
<i>Delgadella</i>	trilobite	~10	1.3 cm <sup>2</sup>	filter-feeder?	vagrant epibenthos?
<i>Jakutus</i>	trilobite	6	648 cm <sup>2</sup>	carnivore/scavenger?	vagrant epibenthos
<i>Edelsteinaspis</i>	trilobite	5	26.9 cm <sup>2</sup>	?	vagrant epibenthos
<i>Bergeroniaspis</i>	trilobite	3	5.3 cm <sup>2</sup>	carnivore/scavenger?	vagrant epibenthos
<i>Bergeroniellus</i>	trilobite	~10	28.6 cm <sup>2</sup>	carnivore/scavenger?	vagrant epibenthos
<i>Binodaspis</i>	trilobite	1	0.3 cm <sup>2</sup>	?	vagrant epibenthos
<i>Sinskolutella</i>	bradoriid	64	26.1 cm <sup>2</sup>	detritophag?	vagrant epibenthos
<i>Yakutingella</i>	bradoriid	3	1.1 cm <sup>2</sup>	detritophag?	vagrant epibenthos
<i>Phytophilaspis</i>	arthropod	11	863.5 cm <sup>2</sup>	carnivore/scavenger?	vagrant epibenthos
<i>Eoobolus</i>	lingulate	12	0.9 cm <sup>2</sup>	suspension-feeder	sessile epibenthos
<i>Linnarssonina</i>	lingulate	120	1.8 cm <sup>2</sup>	suspension-feeder	sessile epibenthos
<i>Botsfordia</i>	lingulate	37	1.4 cm <sup>2</sup>	suspension-feeder	sessile epibenthos
<i>Nisusia?</i>	rhynchonellate	1	2.9 cm <sup>2</sup>	suspension-feeder	sessile epibenthos
<i>Wiwaxia</i>	wiwaxiid	1	3.4 cm <sup>2</sup>	grazer?	vagrant epibenthos
<i>Archiasterella</i>	cancelloriid	3?	36 cm <sup>2</sup>	suspension-feeder?	sessile epibenthos
<i>Eldonia</i>	eldonioidean	39	477.8 cm <sup>2</sup>	carnivore?	nektobenthos?

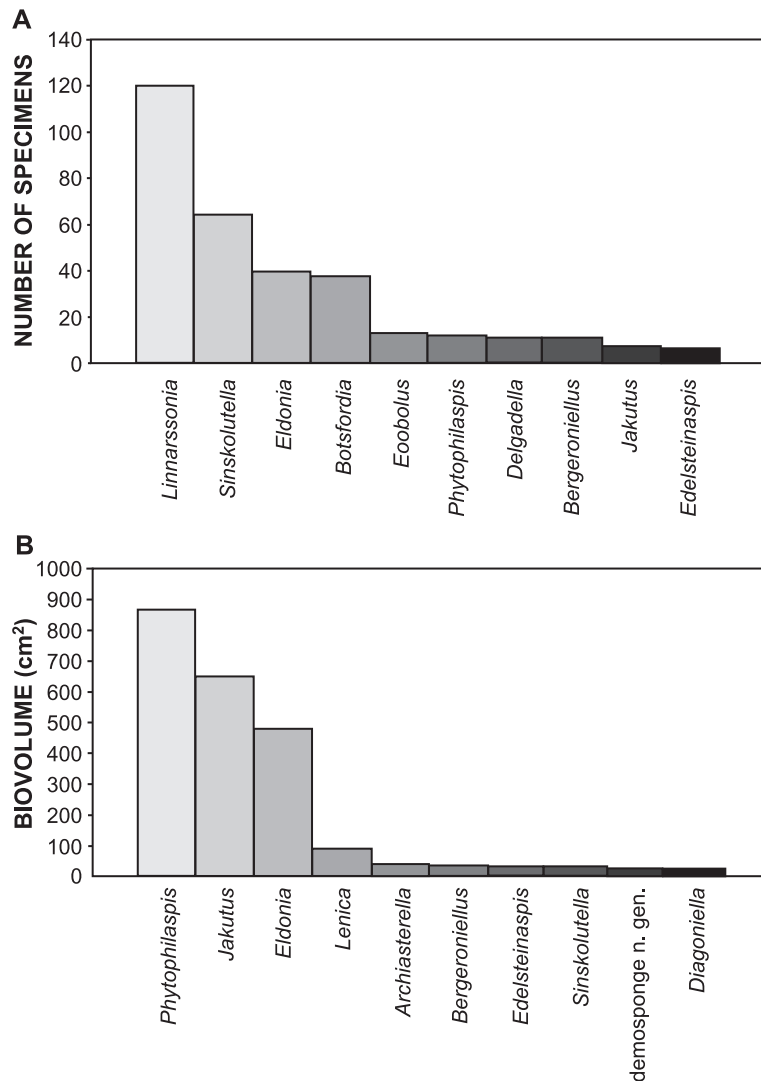


Fig. 4. Relative percentages of different species in the Algal Lens oryctocoenosis. (A) Number of individuals, (B) biovolume.

aerobic/dysaerobic interface supplied nutrients for abundant planktic and benthic producers (Fig. 3).

### 3. Composition of the Algal Lens oryctocoenosis

The Sinsk Lagerstätten contain remains of all principal groups of organisms typical of Cambrian Lagerstätten which are seaweeds, spicular hexactinellids and demosponges, cnidarians, cephalorhynch worms, tardipolypodians, trilobites, bradoriids, other arthropods, coeloscleritophorans, and eldonioideans.

The localities lack anomalocaridids, annelids, and echinoderms. Likewise, anomalocaridids rarely occur in the early Middle Cambrian Kaili Formation (South China), and echinoderms are absent from Sirius Passet, Chengjiang, and Emu Bay of South Australia which are the oldest Cambrian Lagerstätten. The absence of echinoderms can be related to their low diversification by that time. As to annelids, their relatively thin cuticle does not preserve in extremely suitable conditions only (Briggs and Kear, 1993), which are not typical of the Sinsk Lagerstätten as well as of Sirius Passet, Kaili, and Emu Bay ones. Similar



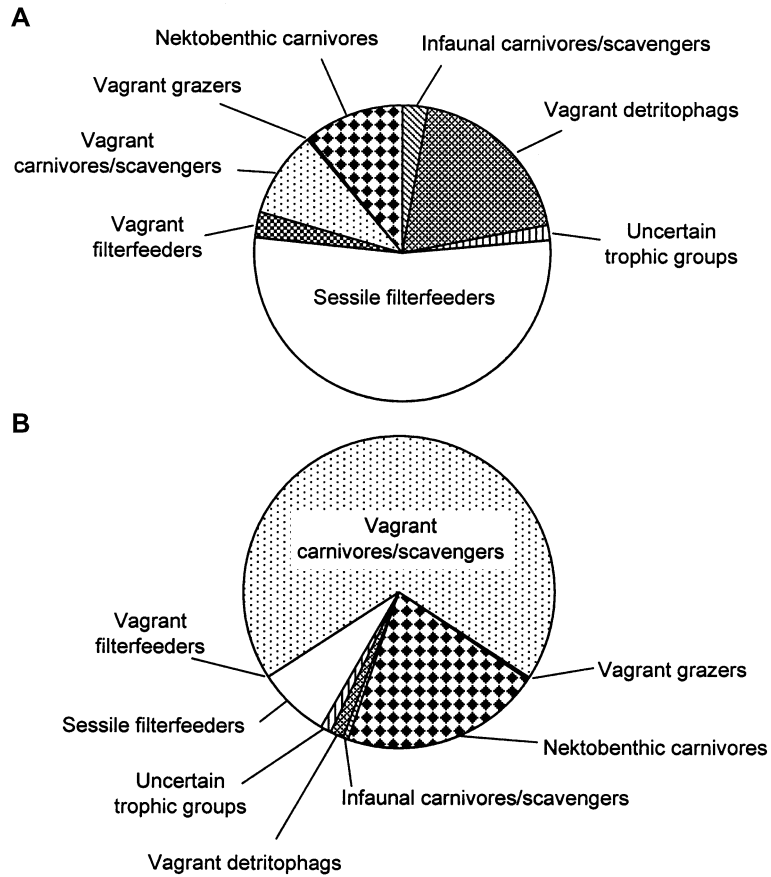


Fig. 5. Trophic nucleus of the Algal Lens palaeocommunity. (A) Individuals, (B) biovolume (in cm<sup>2</sup>).

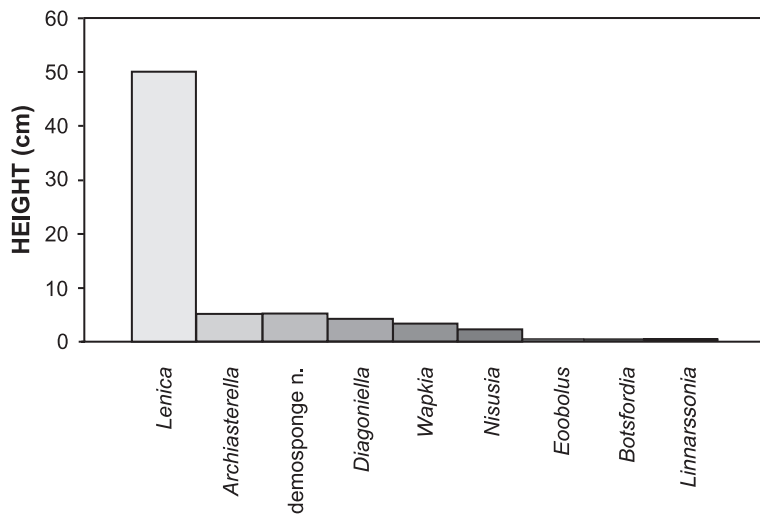


Fig. 6. Tiering among epifaunal sessile filter-feeders of the Algal Lens palaeocommunity.

to many Lagerstätten of this age, mollusks, hyoliths, and rhynchonellate brachiopods are represented by one–two species in Sinsk localities, although they are common in coeval strata formed under shallow water well-oxygenated conditions within the neighbouring Anabar-Sinsk belt.

By comparison with other Lagerstätten, a noticeable feature of Sinsk localities is a lack of non-trilobite arthropods, and a proliferation of bradoriids. There are only 4 such fossils there: concilitergan trilobitomorph *Phytophilaspis*, large bivalved *Tuzoia*, and fragments of two other probably different arthropods. A similar number of non-trilobite arthropods occur in Emu Bay (4), Niutitang Formation of South China (4), and inadequately studied Kinzers Formation of the Appalachians (5) (see Glaessner, 1979; Nedin, 1995; Briggs and Nedin, 1997 for Emu Bay; Zhao et al., 1999a for the Niutitang Formation; Resser and Howell, 1938; Sprinkle, 1973; Briggs, 1978; Rigby, 1987; Garcia-Bellido Capdevila and Conway Morris, 1999 for the Kinzers Formation). However, all aforementioned localities contain a relatively poor fauna in general and therefore, the proportion of non-trilobite arthropods is still high (40%—Emu Bay, 18%—Niutitang Formation, and 23%—Kinzers Formation), whereas they comprise only 11% in the Sinsk Lagerstätten. There are 17% of such arthropods in the Kaili Formation, but they are not of good preservation. Noteworthy, that both the Sinsk and Kaili Lagerstätten occur within dominantly carbonate facies while other Cambrian Lagerstätten are restricted to siliciclastics. The argillaceous Paseky Shale (Czech Republic) formed under brackish conditions, and does not contain any trilobites at all (Chlupáč, 1995).

The total number of fossil animals in the Algal Lens oryctocoenosis is 353 counting out isolated spicules and sclerites (Table 1). Algae, cyanobacteria, and acritarchs are so plentiful that their remains are beyond the computation. In places, algae completely cover an area over several square metres. Intact skeletons of sponges, coeloscleritophorans, some trilobites, and *Phytophilaspis*, coiled cephalorhynch bodies, articulated brachiopod shells and bradoriid carapaces led us to suggest that these organisms were buried alive. For instance, of 120 individuals of brachiopod *Linnarssonina rowelli*, 104 individuals (86.7%) represent complete shells with intact valves,

and only 16 of them are detached valves. In ordinary localities of the same age, intact shells of the same species comprise less than 1.5% in a sampling unit (Pelman, 1977; Ushatinskaya, personal observations). Many specimens preserve imprints of the mantle and other fine features of the soft body structure. These peculiarities also reveal that the brachiopods were buried alive. Merely a few brachiopods and bradoriids were preserved as disarticulated shells and carapaces, which belonged to animals that either died before transportation to the place of their burial, or had been squashed during digestion by carnivores/scavengers. In situ trilobite exuviae are common in the Sinsk Formation and their number in oryctocoenoses is significant. However, the Algal Lens Lagerstätte lacks exuviae. Thus, the proportion of trilobite remains in the fossil assemblage can, with a good degree of accuracy, reflect the representation of this group as a living community.

#### 4. The analysis of fauna

##### 4.1. Species diversity and composition

The Algal Lens oryctocoenosis consists of 30 species. Arthropods represent the most diverse group (9 species or 30%). Following arthropods are the Cephalorhynch worms (6 species or 20%), sponges, and brachiopods (4 species or 13.3% each). It should be noted that in the Algal Lens oryctocoenosis, as well as in other Cambrian Lagerstätten, genera are almost exclusively monospecific (Table 1, Fig. 4).

By the species composition, the Algal Lens oryctocoenosis resembles the famous early Middle Cambrian Phyllopod Bed from the Burgess Shale (British Columbia) where arthropods (38%), sponges (16%), and cephalorynchs (6%) prevail similarly. [Here and hereafter the Phyllopod Bed data are mostly from Conway Morris (1986).] Problematic animals are also significant in the Phyllopod Bed (21%). In this paper, the ‘problematic’ label is assigned to tardipolypodians, coeloscleritophorans, cnidarians, and eldonioideans. Altogether they comprise a comparable figure of 23.3%. Taking into consideration the diversity of spicules which represent at least 7 more species of sponges, the structure of both oryctocoenoses appears to be systematically comparable.

A similar share of the principal systematic groups is typical of other Early Cambrian Lagerstätten, though their sampling units seem to represent more time-averaged data on several different communities. In Chenjiang (Haikou, Ercaicun locality, Yu'an-shan Formation), arthropods constitute 43.5%, sponges—14.5%, and cephalorhynchs—10%. Tardipolypodians—8.7%, chordates—4.3%, and brachiopods—4.3%, are also important [calculation of Wang et al.'s (2001) data]. According to a recent computation by Babcock and Zhang (2001), arthropods account for more than three-quarter of 140 species and two-thirds of all specimens in the Chengjiang biota. In the Kinzers Formation, the same three main groups give the number of 46.4% (arthropods), 3.6% (sponges), and 7.1% (cephalorhynchs), respectively (another 7.1% are of echinoderms). In Emu Bay, arthropods comprise 54.5%, anomalocaridids—27.3%, cephalorhynchs—18.9% but the sampling unit itself is too small to provide a statistically significant figure. The Middle Cambrian Kaili, Wheeler, and Marjum formations as well as the Spence Shale (the last three are in Utah), arthropods share from 42% to 57%, sponges—from 5% to 26%, and cephalorhynchs—from 2% to 6% (see Mao et al., 1992; Huang et al., 1994; Zhao et al., 1996, 1999b for the Kaili Formation; Robison, 1990, 1991; Robison and Wiley, 1995; Rigby et al., 1997; Sumrall and Sprinkle, 1999 for the Wheeler and Marjum formations and Spence Shale). The species composition of brachiopods (10–12%) and echinoderms (6–8%) becomes also weighty in the Middle Cambrian Lagerstätten.

The principal difference of the Algal Lens and Phyllopod Bed oryctocoenoses lies in the species diversity of trilobites. They are divers in the Algal Lens Lagerstätte but not variable in the Phyllopod Bed, neither in Sirius Passet, Chenjiang, nor in Emu Bay assemblages.

#### 4.2. Individual abundance

Lingulate brachiopods are the most abundant group within the Algal Lens oryctocoenosis (169 specimens or 47.9%). Subsequent groups are arthropods (113 specimens or 32%) [namely, bradoriids (67 specimens or 19%), trilobites (35 specimens or 9.9%), and *Phytophilaspis* (11 specimens or 3.1%)], eldonioideans (39 specimens 11%), cephalorhynchs, and

sponges (10 specimens or 2.8% each). Bearing in mind the proportion of alive and dead by the time of burial individuals, one can draw even a larger brachiopod share in the natural community (Table 1, Figs. 4B, 5A and 6).

In the Phyllopod Bed oryctocoenosis, arthropods lead in the number of individuals (58%). They are followed by hemichordates (17%), mollusks including hyoliths (12%), and cephalorhynchs (5%) (Briggs and Whittington, 1985; Conway Morris, 1986). Brachiopods comprise 3% only of individuals, and eldonioideans counting together with echinoderms—about 2%. In Chengjiang (Haikou and Anning sites of 186 and 319 individuals in total, respectively), again arthropods form the majority of individuals (48–50%): bradoriids (27–23%), trilobites (2–21%), and others (19–7%). Other significant groups are cephalorhynchs (22–2%), brachiopods (4–24%), anomalocaridids and eldonioideans (about 1% each) (Zhang et al., 2001). Some similarity of the Algal Lens, Phyllopod Bed, and Chengjiang oryctocoenoses in the species abundance is observed in the significance of arthropods, but neither bradoriids, nor trilobites comprise a high share of the Phyllopod Bed arthropods. In terms of arthropod species abundance, some Chengjiang oryctocoenoses are much closer to that of almost coeval Algal Lens: bradoriids encompass over 70% of individuals representing 7.4% only in the generic diversity (How and Bergström, 1991; Babcock and Zhang, 2001). In Algal Lens, these tiny bivalve arthropods encompass almost 20% of individuals in total while providing 6.7% only of the generic diversity (2 species of 2 genera) (Figs. 4A,B and 6). However, trilobites are scarce in Chengjiang—1.5% of preserved arthropods only (Babcock and Zhang, 2001).

#### 4.3. Biovolume

When a Recent community is analyzed, a relative biomass of each group is examined in order to measure energy flows along a trophic web. It is difficult to estimate a biomass of long vanished bodies in a palaeocommunity, but some approximation is possible with use of data on biovolume (e.g., Conway Morris, 1986). Conway Morris computed a biovolume of each genus as the average length of an individual multiplied by the number of individual specimens

with use of formulae for standard shapes. Here, the biovolume is calculated for each species. Two measurements have been used for every individual: the diameter and height—for sessile forms, or the width and length—for vagrant ones. The sum of these figures is expressed in square centimetres (Table 1 and Figs. 4B, 5B and 6). The number of mature and juvenile individuals is counted separately because they differ significantly in size.

Arthropods dominate by biovolume in the Algal Lens oryctocoenosis—70.5%. Other voluminous groups are eldonioideans (21%), sponges (5.6%), coeloscleritophorans (1.7%), and cephalorhynch (0.6%).

The Phyllopod Bed fossils make up a comparable pattern: 49% of arthropods, 17% of sponges, about 15% of eldonioideans, and 10% of cephalorhynch. In both Phyllopod Bed and Algal Lens arthropod biovolumes, trilobites comprise a minor part.

## 5. Palaeoecological characteristics of the Algal Lens community

### 5.1. Ethological-trophic groups

Several producent groups are widespread in the Algal Lens oryctocoenosis. Among acritarchs, two monotypic assemblages are recognized. These assemblages consist of either diminutive (less than 20 µm in diameter) spiny forms resembling *Micrhystridium* (Zhuravlev and Wood, 1996) or relatively large (from 50 to 300 µm in diameter) spherical smooth envelopes of *Leiosphaeridia*-group acritarchs. The same two major groups of phytoplankters (small acanthomorphs and large sphaeromorphs) are recognized in the Phyllopod Bed and Kaili Formation oryctocoenoses (Conway Morris, 1986; Yin and Yang, 1999) (Table 1, Fig. 5A,B).

Benthic producentes include abundant seaweeds (4 genera and 4 species) and filamentous cyanobacteria (*Marpolia*). Relatively large fronds of green siphonous algae and their rhizoids dominate in number. Another representative of the same group possesses a smaller bushy thallus with slender, dichotomous-fastigated branches and filiform terminal branches. Only a relatively rare species which has an articulate frond is conditionally affiliated to red algae. Addi-

tionally, calcified cyanobacteria (*Obruchevella*) are common.

Several trophic levels can be distinguished among consumers. The first level or primary consumers are represented by filter-feeders, detritophages, and possible grazers and browsers. Secondary and even higher level consumers (carnivores/scavengers) can be inferred.

Miscellaneous guilds of filter-feeders are represented by fine filter-feeders or filter-feeders sensu stricto, namely abundant hexactinellids, demosponges, and pharetronids, as well as by coarse filter-feeders or suspension-feeders, which are lingu- late brachiopods and possibly cancelloriids. However, the latter lacks the distinct features of filter-feeders (Bengtson and Hou, 2001). The examples of cancelloriid scleritomes with a bent basal part indicate that these animals have been anchored in a soft mud (Mehl, 1996). Immobile cancelloriid life style is confirmed also by an in situ immuration of their scleritomes with early marine cements (Zhuravlev, 2001).

Miniature lingu- late brachiopods were attached to algal thalli as an attempt to gain levels of stronger water currents and to escape mud clogging. Such settlements (*Eoobolus* brachiopod on *Margaretia* green siphonous algae) are recognized in other Sink Lagerstätten, but are absent from the Algal Lens.

Cnidarians (*Cambrorhytium*) could be either tiny predators or filter-feeders like modern corals of a similar size (Sorokin, 1990). *Cambrorhytium* commonly occurs in dense settlements along ribbon-like structures possibly of algal origin. The epiphytism on seaweeds is indeed common among modern small cnidarians, mostly hydrozoans, with a short life span which escaped hostile soft mobile substrata (Morri et al., 1991).

The zooplankton, which was the food source for some filter-feeders, consisted of abundant trilobite and lingu- late brachiopod larvae at least as well as problematic embryos.

The presence of several filter-feeding guilds was expressed in distinct tiers, where the uppermost tier (above 25 cm) was occupied by hexactinellid *Lenica*, intermediate tiers (from 3 to 5 cm) were deployed by two demosponge species (*Wapkia* and new one), by hexactinellid *Diagoniella*, and by cancelloriid *Archiasterella*, while the lowermost tier (below 1

cm) was lined up by lingulate brachiopods and by *Cambrorhythium* (Fig. 6). The latter two groups were able to move to an upper tier by attaching themselves to algal thalli. The majority of Sinsk brachiopods were epifaunal anchored forms by their life habits (Ushatinskaya, 2001).

Unquestionable browsers and grazers are very rare in Cambrian strata. Mobile epifaunal coeloscleritophoran *Wiwaxia* possessing a radula probably grazed bacterial scum on algal thalli (Conway Morris, 1985). The few gastropods (*Nomgoliella?* sp.) were browsers (Kruse et al., 1995). Their remains are not distinguished in Algal Lens itself, but such shells are very fragile and are etched from the Sinsk Formation with difficulty.

Bradoriids (at least kunmingellids) and miomeric and some polymeric trilobites are assigned here to detritophages. Dumpy bradoriids moved on postantennular appendages and stirred up the sediment surface in order to capture edible particles by the frontal postantennular spiny appendages (Hou et al., 1996; Shu et al., 1999). The natant hypostome of miomeric eodiscid trilobites implies a somewhat benthic life style and feeding on detritus including algal debris (Fortey and Owens, 1999).

Palaeoscolecidans and lousellid were probably predators like modern large cephalorhynchids and Cambrian ones furnishing with an armed spiny proboscis (Conway Morris, 1977b, 1986; Malakhov and Adrianov, 1995).

Tardipolypodians could be either microphagous predators or scavengers because they lacked any jaws or teeth, but the majority of them were discovered in usual accumulations with other animals, such as sponges, worms, and eldonioideans (Conway Morris, 1977a; Whittington, 1978). *Microdictyon* was confined strictly to *Eldonia* (Chen et al., 1995a,b). None of 70 individuals of this tardipolypodian show an alimentary tract filled with mud, as is typical of detritivorous animals (Chen et al., 1995b).

After etching with a weak acetic acid, sponge spicules and particulated brachiopod shells have been distinguished in the middle part of the gut of a single trilobite individual ascribed to *Bergeroniellus spinosus*. There is some regularity in the arrangement of the scraps: broken spicules alternate with brachiopod shells along the gut. One can suggest that the trilobite was able to select the food and macerate solid

particles. Polymeric trilobites and *Phytophilaspis* from Algal Lens commonly preserve a narrow stripe following the rachis. Its width is usually comprised of one fifth of the rachis width, but varies along the rachis bulging transversely up its entire width. In some individuals, the stripe can be traced along the entire thorax to the pygidium. The axial position, linearity, almost constant width, and sharp boundaries of this structure are typical of an arthropod alimentary tract.

The hypostome and bases of anterior limbs in *Phytophilaspis* are anomalous in size (Ivantsov, 1999: Figs. 3 and 4B). The presence of hypostome suggests an orientation of the mouth rearwards. The transportation of the food to the mouth was maintained by a metachronic rhythm of appendages. The data on other Cambrian arthropods with well-developed appendages and hypostome are evident for a predator propensity of *Phytophilaspis* (cf. Briggs and Whittington, 1985; Fortey and Owens, 1999). Trilobite *Bergeroniaspis lenaica* preserves undissolved isometric phosphatic structures under the glabella, some of which can be the stomach content. Usually a straight gut and an absence of mud infill in it are typical of arthropods preferring fleshy food (Chatterton et al., 1994; How and Bergström, 1997). In such a case, the phosphatic nodules could originate from highly chemically reactive organic matter rich in phosphate (Briggs and Whittington, 1985; Butterfield, 2002).

Altogether, these features allow us to consider *Bergeroniellus*, *Phytophilaspis*, and to a certain extent *Bergeroniaspis* as possible predators and/or scavengers, although in the absence of appendages, it is difficult to find out their exact trophic orientation.

Many have suggested a planktic life style for eldonioideans and closely related paropsonemids (Clarke, 1900; Durham, 1974; Stanley, 1986), and Conway Morris (1986) emphasized the significance of *Eldonia* among nektobenthos of the Phyllopod Bed community. Recently Dzik (1991) and Dzik et al. (1997) judged that, by their anatomy (inflexible aboral cover, absence of any organs suitable for floating) and by the restriction of epibiont settlements to the oral surface margin of *Rotadiscus* from the Kaili Formation, implied a passive position of this animal on organic-rich mud. However, this interpretation does not match well to cosmopolitan distribution of eldonioideans without any restriction to certain facies.



They are equally widespread as in relatively deep-water siltstones and mudstones as in coarse-grained shallow-water sandstones (van der Meer Mohr and Okulitch, 1967; Masiak and Żylińska, 1994; Dzik et al., 1997). Besides, they are concurrent only with other representatives of pelagic fauna (Conway Morris, 1979; Friend et al., 2002), while a distinct asymmetry of the catching organ does not fit well with the anatomy of a sedentary, radially symmetrical animal. Nektobenthic life style is preferable for eldonioideans. They could live in the water column at the density interface where food was plentiful. Under such conditions, epibionts would still fix upon margins of floating disc facing the upper water layer rich in oxygen whereas the rigid lower part maintained the animal buoyant. Miomeric trilobites would be a suitable food for *Eldonia* then.

In summary, sedentary filter-feeders (53% of individuals), mobile epibenthic detritophages (19%), as well as nektobenthic eldonioideans (11%), vagrant epibenthic (9.4%) and infaunal (2.8%) predators/scavengers, and mobile filter-feeders (2.8%) formed the Algal Lens community in terms of individuals (Fig. 5A). The same guilds comprised also the bulk of biovolume, though in a slightly different order (Fig. 5B): vagrant epibenthic (68.2% of biovolume) and nektobenthic predators/scavengers (21%), sessile filter-feeders (7.5%), and mobile epibenthic detritophages (1.2%). The data on the Phyllopod Bed palaeocommunity gives a similar figure (Conway Morris, 1986). Among individuals, vagrant (64%) and sessile epibenthos (30%, *Cambrorhytium* was incorrectly assigned to attached infauna) as well as mobile infauna (6%) dominated. By biovolume, vagrant (51%) and sessile (22%) epibenthos, nektobenthos (18%, eldonioideans only), and mobile infauna (10%) prevailed.

### 5.2. Trophic nucleus

The trophic nucleus concept was developed by Neyman (1967) and successfully applied to the analysis of the Phyllopod Bed oryctocoenosis by Conway Morris (1986). According to this concept, the trophic nucleus consists of species comprising over 80% of the community biomass. In terms of biovolume of the Algal Lens oryctocoenosis, these species are *Phytophilaspis* (vagrant epibenthic pre-

dator/scavenger—38%), trilobite *Jakutus* (vagrant epibenthic predator/scavenger—28.5%), *Eldonia* (nektobenthic predator—21%), hexactinellid sponge *Lenica unica* (sessile epibenthic filter-feeder—3.7%), cancelloriid *Archiasterella* (sessile epibenthic filter-feeder—1.6%), and trilobite *Bergeroniellus* (vagrant epibenthic predator/scavenger—1.3%). In terms of individuals, the bulk of the oryctocoenosis consists of lingulate brachiopods *Linnarssonina* (34%), *Botsfordia* (10.5%), and *Eoobolus* (3.4%) (sessile epibenthic filter-feeders), bradoriids *Sinskolutella* (vagrant epibenthic detritophag—18.1%), *Eldonia* (11%), and *Phytophilaspis* (3.1%). In both accounts, 6 species only, although different, represent the trophic nucleus of the palaeocommunity. Individually the trophic nucleus consists of epibenthic filter-feeders while volumetrically it is formed by predators, mostly because of the inclusion of the largest fossils (*Phytophilaspis* and *Jakutus* up to 50 cm and 15 cm in length, respectively). However, the number of predators can be overestimated due to the presence of exuviae among fossils. Independently of this fact, the trophic nucleus was homogenous (filter-feeders and predators) and, therefore, the community was low structuralized and highly dominant (Fig. 5A,B).

### 5.3. Trophic web

Two producent groups built the base of the trophic web of the Algal Lens community. Among planktic producents, these were “net” phytoplankton (acritarchs) and, probably, bacterioplankton (free-living and attached bacteria). The sponge proliferation depends on the bacterioplankton abundance (Reiswig, 1971; Wilkinson et al., 1984). Abundant, although low diverse lingulate brachiopods and their planktic larvae, on the contrary seemingly preferred acritarchs representing large “net” phytoplankton, which is the main phosphate source for their shell growth (Chuang, 1959; Pan and Watabe, 1988). Other filter-feeders (cancelloriids and miomeric trilobites) could like a catholic diet (Fig. 7).

A reconstruction of trophic chain beginning from benthic producents is more difficult. Single *Wiwaxia* and molluscs only are interpreted as grazers and browsers. Possibly, the bulk of dead phytoplankton and phytobenthos was directed strictly to detritus because large accumulations of acritarchs and algae



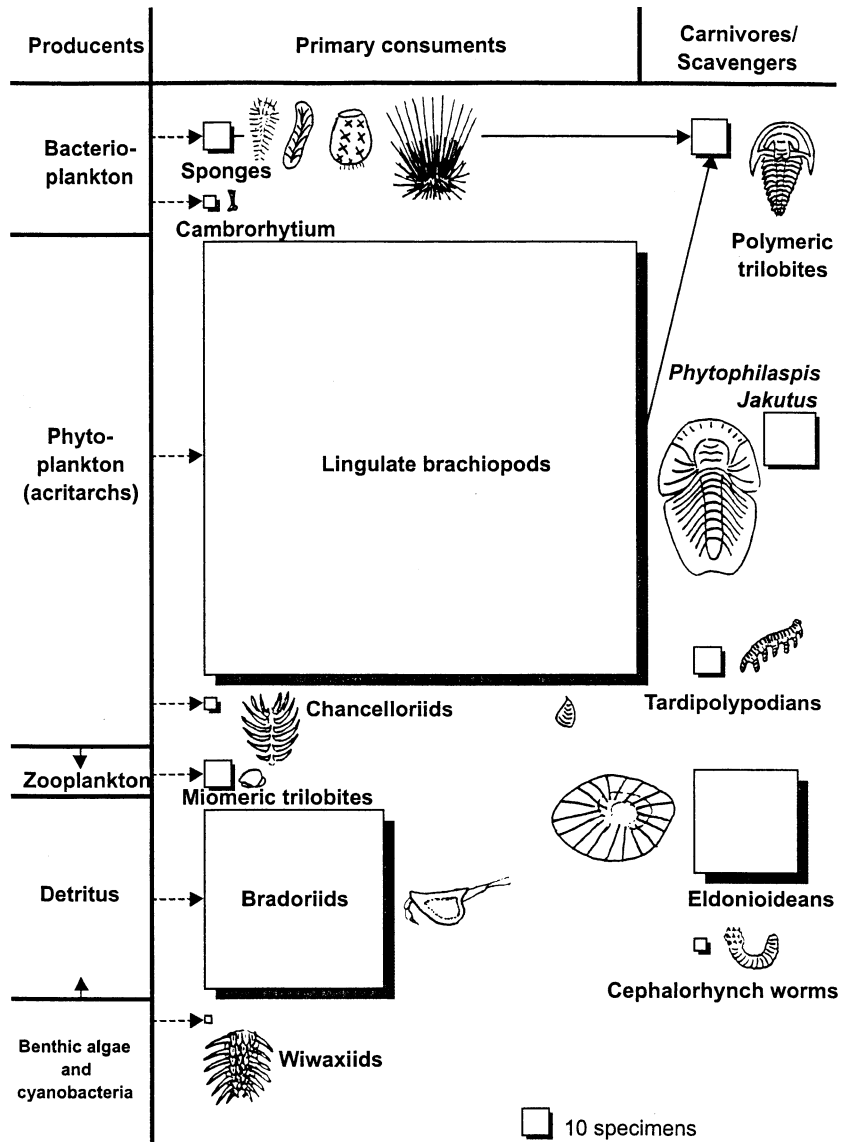


Fig. 7. Tentative reconstruction of the trophic web in the Algal Lens (Sinsk Formation) palaeocommunity in terms of number of individuals alive at the time of burial. Confirmed energy flows are shown by continuous arrows, inferred ones are indicated by dashed arrows. Square area indicates the number of individuals in each group of animals.

definitely was not required by any animals and preserved intact until nowadays. Some bradoriids, miomeric and polymeric trilobites perhaps fed on the detritus. In modern seas under oxygen shortage, the number of infaunal detritophages decreases and unutilised organic matter is accumulated (Kuznetsov, 1980). The abundance of anchoring in soft mud

epibenthic filter-feeders (sponges and juvenile brachiopods) proves indirectly the insignificance of detritophages in Sinsk communities. Under favourable conditions, detritophages overcompete sedentary filter-feeders due to amensalism (Thayer, 1983).

Cephalorhynch, tardipolypodians, possibly eldonioideans, and some polymeric trilobites were second-

dary consumers. Large sizes of *Phytophilaspis* and trilobite *Jakutus* (14–15 cm in length) perfectly allowed them to be consumers of the third level and preyed on other predators, for instance cephalorhynch worms. Trace fossils of trilobitomorph hunting on infaunal worms are described in many Cambrian localities (Jensen, 1990). Moreover, carapace segments of the largest trilobite *Jakutus* are ornamented by long axial spines that probably are evident for a predator pressure even on such sizeable animals.

The study of lingulate brachiopod shells revealed three different groups of destructors at least in the Algal Lens palaeocommunity. These were bacteria which, probably, destroying the organic matter incorporated within shell laminae, possible actinomycetes, and boring algae or cyanobacteria. The borers were parasites of living animals which repaired injuries in the surface shell layer and rehabilitated its healthy development.

## 6. Conclusions

A comparison of the number of primary (filter-feeders, detritophages, grazers, and browsers) and secondary consumers (counting out possible consumers of the third level) allow us to imply a relative amount of energetic transfer between these two levels. It comprises 25% at the individual level (Fig. 7). In modern communities the amount of energetic transfer approaches 10–12%. This fact merely means that we have lost about a half of primary information rather than energetic transfer was approximately as twice as higher in the Cambrian. This is not too much for an analysis of fossil communities.

In summary we would like to emphasise the following features of the Algal Lens palaeocommunity.

1. All organisms once upon a time comprising the community were adapted to a life under dysaerobic conditions.
2. The trophic web was firmly based on phytoplankton and bacterioplankton. Possibly, a dynamic upwelling bringing onto the Siberian Platform by early Botoman transgression together with increased rates of nutrient cycling occurring within the water column at the aerobic/dysaerobic interface created conditions which were favourable for the phytoplankton and bacterioplankton blooms (Zhuravlev and Wood, 1996). These blooms extracted significant oxygen volumes utilised on the oxygenation of organic necromass and, thus, maintained a wide dysaerobic zone.
3. These conditions led to the development of low structuralized and highly dominate community.
4. Nonetheless, the organisation of the Algal Lens palaeocommunity was not simple. It comprises diverse feeding habits and various substrate relationships and the tiering among sessile suspension-feeders was well developed with the upper tier at the 50 cm level.
5. A number of similar features of the Algal Lens and Phyllopod Bed (Burgess Shale) palaeocommunities studied by Conway Morris (1986), such as a significance of different groups of organisms in species composition, a relative percentage of fauna in terms of number of individuals and biovolumes of major groups, feeding habits, and substrate relationships, suggest a relative stability (during ca. 25 my) of Cambrian communities occupying similar subtidal settings. This stability is expressed also in the presence of the same genera and possibly even species (*Cambrorhytium*, *Wiwaxia*, *Eldonia*, many sponges and algae).
6. Cephalorhynchs, tardipolypodians, sponges, eldonioideans, and non-trilobite arthropods played a significant role in the organisation of the Algal Lens palaeocommunity, as well as in many other Cambrian marine communities. This is well expressed in a relative percentages of these groups in species composition as well as in individual abundance and biovolumes. In modern marine communities these animals either completely absent (tardipolypodians, eldonioideans, bradoriids) or their role is negligible (cephalorhynchs). Usually, they survive as meiobenthos, cryptobionts, or dysaerobic mud inhabitants. The communities, where diverse trilobites and lingulate brachiopods predominated and which are commonly taken for the typical Cambrian communities, appeared during the late Middle Cambrian only.
7. Despite of an apparent difference in composition between inhabitants of shallow water well-oxygenated environments and those of dysaerobic zone, the basic features of the Early Cambrian

communities on the Siberian Platform were alike (Burzin et al., 2001). Both were dominated in terms of individuals and biovolume by filter-feeders: spicular sponges, tiny cnidarians, and lingulate brachiopods under dysaerobic conditions; calcified sponges (archaeocyaths and pharetronids), calcareous minute cnidarians, and different brachiopods as well as hyolithomorph hyoliths and stenothecoids within well-oxygenated bottom waters. They were followed by detritophages: bradoriids and miomeric trilobites and orthothecimorph hyoliths, respectively. Finally, the same carnivores/scavengers represented by cephalorhynchids, tardipolydians, and large polymeric trilobites were significant in both environments, although their sclerites and fragments only are preserved in limestones formed in well-agitated milieu.

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