



Establishment of trophic structure in communities of the Late Precambrian and Early Paleozoic Epicontinental Seas

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The reconstruction of functioning of ancient ecosystems is based on many-sided comparisons with modern ecosystems, which allow the revelation of data on both feeding of particular organisms and the arrangement of the basic food chains. Similar morphology not always means identical physiological features of organisms, and the similarity in the taxonomic composition of communities not necessarily indicate similar food chains. This particularly concerns ancient ecosystems that appeared and developed in the Late Precambrian and Early Paleozoic. For example, cavitory digestion with enzymes is developed in extant echinoderms to the same extent as more primitive intracellular digestion based on phagocytosis. In addition, a significant role is played by feeding on dissolved organic matter and skin digestion is also recorded, i.e., enzymes excreted on the external surface of the body decompose organic matter outside the body cavity and, hence, provide its assimilation. A significant role in the preparation of food for assimilation is often played by bacteria. It is probable that at the beginning of the formation of the metazoan phyla and classes, the relationships of the basic modes of digestion mentioned above were different. In the Vendian, the skin digestion combined with intracellular digestion apparently prevailed in multicellular organisms. This assumption is supported by the recently discovered traces of discrete consumption of algal-bacterial mats by typical Vendian taxa, such as *Dickinsonia* and *Yorgia*. This is also corroborated by the absence of a mouth, anus, and food-gathering appendages needed for filtering food objects in the majority of Vendian metazoans. Certain taxa, such as *Parvacorina* and *Temnoxa*, were probably specialized for feeding

on organic matter decomposed by destructive bacteria. However, even in these taxa, skin digestion could have played the major role. In the Vendian, the primary food resource of benthos came from the photic layer only at the banks of cold-water seas, without thermoclines. In this area, algal-bacterial mats were widespread and provided food for many metazoans. In the Cambrian, the microbe loop of the photic layer was broken due to the appearance of pelagic filter-feeders. As a result, the wide area of the bottom of the epicontinental seas was filled with excessive food resources, which provided the Cambrian Evolutionary Explosion and distribution of various benthic taxa over this extensive area. The basic food resource for the majority of Cambrian benthic animals, including filter-feeders, detritophages, and scavenger, was the organic matter more or less decomposed by destructive bacteria and bacteria developing on this organic matter in a thin bottom water layer. Therefore, the Cambrian benthos was almost entirely confined to 10-cm thick bottom layer. Active predators specialized for preying on particular animals that could offer resistance played a minor role in both Vendian and Early Paleozoic communities. Therefore, Cambrian consumers made a minor contribution to the food chains, since most of them consumed organic matter decomposed by destructors and differed from each other mostly in the extent to which their food was decomposed and in the size of food objects rather than in the taxonomic position of prey. In the Ordovician, some pelmatozoan echinoderms, particularly crinoids, adapted to feeding on living plankton. It was provided not only by morphological novelties (an increase in the size of food-gathering grooves and elongation of the stalk) but also by the expansion of physiological potentiality resulting in digestion of more diverse food objects. The new food opportunities resulted in the appearance of a 1-m-thick stratification above the sea bottom and, eventually, provided the basis of the Ordovician evolutionary radiation. This study was supported by the Russian Foundation for Basic Research (projects 05-04-49244 and 06-05-64641); it also contributes to IGCP Project 503 and to Program 18 of the Russian Academy of Sciences "Origin and Evolution of the Biosphere."