

The Role of Arthropods in the Development of Continental Biota

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Abstract—Arthropods appeared in the Early Cambrian and by the end of this period had begun colonizing dry land and continental waters. Remains and supposed tracks of euthycarcinoids are already known by the end of the Cambrian. Ordovician deposits contain burrows of wormlike animals, which assimilated organic material from algal-bacterial mats and began creating hydromorphic proto soils by mixing this material with products of erosion. By the end of the Silurian, a coadapted complex of soil organisms, no less complex than the recent one, had already formed. Its principal components were arthropods. Then the algal-bacterial mats began being replaced by vascular plants. Slowly decaying lignin and cellulose significantly stabilized the soil ecosystems. The most important role in the formation of continental ecosystems was played by chelicerates and myriapod-like creatures, which were particularly characteristic of the Late Paleozoic. By the end of the Paleozoic, insects began to play an important role.

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INTRODUCTION

Arthropods have a special status in the Earth's biota. They are not only the most diverse group of animals, but also a crucial component of ecosystems, essentially being the builders of the Phanerozoic biosphere. If all the vertebrates, including humans, vanished from the Earth, it would only slightly affect the organization of the biosphere. But if arthropods vanished, the planet would most likely revert to the Cryptozoic state. Recently, the role of arthropods in the formation of the marine ecosystem received detailed, but still insufficient, attention. Below, I will attempt to demonstrate that arthropods played no lesser role in the formation of the continental part of the biosphere. Whatever genomic evidence, from the view point of a paleontologist, arthropods appeared in the Early Phanerozoic in the course of the Cambrian explosion, i.e., a fast, on the geological scale nearly instantaneous, appearance and spread of the major taxa of the organic world. Descriptions of Precambrian arthropods have universally turned out to be artifacts. Arthropods played a very important role in the Early Phanerozoic events; perhaps their ecological importance was even greater than that of the recent taxa. Yet, not only arthropods but also their hypothetical more primitive ancestors, Xenusia and Paleoscolecidae, enter the fossil record only in the Atdabanian, approximately 520 m.y. ago. It is important to keep in mind that isolated mineralized sclerites of Paleoscolecidae (*Hademopanella*) and Xenusia (*Microdictyon*) are broadly distributed in various facies together with other "small shell faunas," while the majority of ancient arthropods lacking a mineralized exoskeleton, are known only from localities of the Bur-

gess Shale type, which existed during limited periods of time, and do not document the entire life span of a group. Nevertheless, neither taxon has been found in the Tommotian.

It is prudent to consider here how justified was the re-setting of the lower boundary of the Cambrian to the time of the first appearance of *Treptichnus pedum* trace fossils. This decision ignores the fact that the lower boundary of the Cambrian marks the onset of the Phanerozoic, the eon of *visible* life, while the presence of trace fossils, combined with a nearly complete absence of remains of the actual organisms, seems more characteristic of cryptic life. That boundary marks no significant changes in ecosystems and, therefore, there are few reasons to accept it as a starting point of a new major stage in the evolution of the biosphere. The Tommotian is a different story. Here we obviously observe a radically new level of organization of biological systems. Earlier, stromatolites were built by complexes of organisms that interacted only through the environment, and the intensity of that interaction was low. In the Tommotian, archaeocyaths appeared and, even more importantly, became widely distributed. Their complex calcareous skeletons could not have been built without immediate cellular interactions with division of functions. Certainly, metazoans appeared much earlier, but their broad distribution in the Tommotian suggests a radical change in the organization and evolution of the biosphere during that period. Setting the lower boundary of the Phanerozoic below the Tommotian and the significant expansion of the "pre-trilobitic" Cambrian does not appear prudent. It is unfortunate that supporters of the new placement of the boundary see no other

rationale in attempts to keep its traditional position than “nationalistic clashes” (Budd, 2003, p. 160). Remains of mollusks and brachiopods also occur in the Tommotian, suggesting that the lineages of lophotrochozoans and ecdysozoans had already separated, but the latter still lacked mineralized sclerites. The biomineralization capability is not only less typical of ecdysozoans than of lophotrochozoans, but it also appears to have evolved in that lineage significantly later. With regard to biomineralization, these two groups are nearly the opposite of each other: a mineralized skeleton is almost a rule for lophotrochozoans and an exception among ecdysozoans.

It appears that the very appearance of arthropods—coelomate animals with appendages consisting of articulated joints, brought into action by muscles attached to internal folds of the cuticle—was a crucial event in the evolution of the biosphere. Arthropods evolved in the course of arthropodization, i.e., parallel and on the geological scale almost simultaneous appearance of numerous forms with nearly arbitrary combinations of characters typical of various arthropod taxa among “pre-arthropods,” organisms with a metameric body plan without a well-defined head and with appendages driven by hydraulics. The resulting continuum of forms cannot be represented as a system of hierarchical taxa, and the cladistic concept of strictly dichotomous appearance of taxa cannot be applied to it (Whittington, 1979, Fryer, 1996, Ponomarenko, 2004). Despite their diversity, all the first arthropods differed from the majority of modern forms in displaying a low diversity of limb types within a body. There were only four idiosgments (segment types) bearing appendages: a segment with a pair of uniramous flagellate antennae, a segment with prehensile limbs, and numerous homonomous segments with walking limbs, either uniramous or biramous. The first two idiosgments could both be present in the same animal, or either type alone was present. Therefore, the prehensile limbs of almost identical structure could be non-homologous by their location. The dorsal integument could have been divided in a variety of ways. The number of segments varied from few to numerous. The cephalon and the pygidium were distinct. One- or two-part shells similar to shells of crustaceans have sometimes been developed. And yet, all the appendages, except for one or two anterior pairs, were identical. The head never bore masticatory mandibles or any other specialized appendages. This condition was retained by trilobites and pantopods, while in other arthropods the main evolutionary mode has been specialization of limbs. Trilobites existed during the entire Paleozoic but retained perfectly homonomous limbs along the entire body, having evolved no specialized appendages for gathering or chewing food. The majority of these forms rapidly became extinct. The character combinations of the surviving forms became robust syndromes of groups separated by distinct hiatuses. Parts of these groups also became extinct, further increasing hiatuses among the surviving groups. As a

result of divergence in new characters, the latter became the higher arthropod taxa with enormous diversity. Already as “pre-arthropods” these animals were capable of filtration and contributed significantly to the formation of marine ecosystems (Butterfield, 1997; Ponomarenko, 2004). Soon after their appearance, already in the Cambrian, arthropods began colonizing continental ecosystems, which they also transformed significantly. The present paper briefly describes this process.

In the evolution of continental ecosystems arthropods played no lesser part than in the seas. The most important here was participation of uniramians and terrestrial chelicerates in the evolution of pedogenesis. In this paper we consider the uniramian arthropods without Onychophora and Tardigrada, leaving in only euthycarcinoids, “myriapods,” and insects. The uniramous appendages of uniramians appear to be the original condition; thus we suggest their independent retention, rather than *de novo* appearance. In continental environments the uniramians (euthycarcinoids and “myriapods”) already appeared in the Cambrian. From the Lower Cambrian there are also known trackways ascribed to euthycarcinoids. In the Upper Cambrian marginal-marine continental eolian deposits appear trackways of some arthropods (MacNaughton et al., 2002). Most probably the first continental arthropods dwelled in the algal-bacterial mats since the Late Cambrian: euthycarcinoids mostly consumed the algae on the surface, while the myriapod-like kampecarids and “myriapods” together with oligochaetes were soil builders mixing the organic substance of the buried mats. For taphonomic reasons, this process is poorly known, but, judging from the early appearance of specialized chelicerate and chilopod predators, it progressed very quickly.

From school-days we know that the first vascular plants and vertebrates colonized the land in the late Silurian or the Devonian. Yet, the land and the continental waters had been colonized much earlier. Protocontinents had already appeared at the earliest stages of the evolution of the Earth’s surface; already in the Archean they comprised up to 10% of the area of the modern crust (Eriksson et al., 2004). Up on the cratons appeared sedimentary basins, such as the giant thousand kilometer Witwatersrand basin (3.3–2.7 b.y.) on the South African Kaapvaal craton, succeeded by the Ventersdorp basin (2.7–2.6 b.y.). Marine and lacustrine stromatolites are treated together (Sergeev et al., 2007); apparently, at that time the marine species, preserved in deposits of greenstone belts, did not differ significantly from the inhabitants of epicontinental basins. A recent review of the most ancient lakes (Park and Gierlowski-Kordesch, 2007) also does not mention any differences in the lacustrine biota of the Proterozoic and the Cambrian. Life on land had existed for as long as dry land itself existed, i.e., from the Paleoproterozoic. These were biofilms and algal-bacterial mats on flat surfaces regularly flooded with water. Eukaryotic algae and fungi

seem to have appeared rather early. The most ancient remains of eukaryotes were found in the 1.87-b.y.-old Negaunee Formation of the Menominee Group in the Lake Superior region (Han and Runnegar, 1992), but the biological markers of eukaryotes, steranes, are known from more ancient times, approximately 2.7 b.y. (Brocks et al., 1999). There exist numerous reports of still more ancient records, but currently most of those are considered erroneous (for a review, see Sergeev et al., 2007). Yet, in both the Archean and Proterozoic, the bulk of the biomass on land, as well as in the seas, was made up of prokaryotes. Prokaryotes had created a highly sophisticated system, where autotrophs and heterotrophs were virtually united symbiotically into a single superorganism. It was the excellent organization of this complex that allowed prokaryotes withstand the expansion of eukaryotes. For a long period of time eukaryotes existed as minor elements, while the biosphere remained mostly prokaryotic.

The landscape of the early land differed strongly from the modern one. It must have been significantly flatter due to strong erosion, which had not yet been controlled by vegetation. For the same reason, chemical weathering must have been weaker, and physical weathering stronger. Inclined loose substrates were absent, being quickly washed away by the overland runoff. Now strong erosion occurs only on plowed lands, while in natural areas it is controlled by vegetation. The most extreme examples of natural erosion can currently be seen in deserts, but even there the erosion is much weaker, since deserts develop due to shortage of precipitation. In general, under current conditions, the rate of erosion is inversely proportional to the amount of precipitation. Far back in the past, eroded landscapes had to develop in conditions with the maximum precipitation as well, so that the rate of erosion was directly proportional to the amount of precipitation. Also due to the absence of vegetation, there was no constant fluvial net, and the overland runoff was dominant. Rivers did not have regular beds, and most of them were meandering. A discharge of water, often in the form of mudflow, could happen in almost any place due to breaching of the lateral walls of the channel. Due to erosion of the inclined loose substrates the landscape was becoming troughlike, with wide flat valleys filled with “valley proluvium,” extending for tens and hundreds of kilometers between the sea and the mountains, and almost vertical outcrops of bare bedrock. Both water erosion and tidal waves washed through sediments and spread them uniformly over large areas, so that, despite weathering and erosion, the thickness of the sediments was small. Just that nearly horizontal surface was occupied by the algal-bacterial mat.

Algal-bacterial mats become easily buried under pelite material, which is unavoidable when the water is highly turbid as a result of strong erosion. The mat as a whole died but it could have been easily restored by self-assembly. Actively moving photosynthetic organisms of the *Microcoleus* came up to the surface, and

other components of the mat were also easily disseminating and rapidly reproducing. The buried organic matter was broken down by bacterial decomposers or became carbonized and preserved in the form of lignites. In both cases, the energy and biogenic compounds were lost from the ecosystem. Although such Archean formations have been described as “soil” (Watanabe et al., 2000, 2004), it is unlikely that they were true soil. Soil was not developing as a homogeneous, mostly inorganic system. The situation has changed with the appearance of oligochaetes and uniramian arthropods—euthycarcinoids, archidesmids, kampecarids, springtails, and mitelike chelicerates. There also existed unknown wormlike animals, similar to *Polyurida*, which has been described from the Carboniferous of Scotland (Almond, 1985) but remains unassigned to any group of animals. All these organisms began breaking up the organic matter of the mats, mixing it with products of weathering. This created the most ancient hydromorphic protosoils with tunnels, known from the Upper Ordovician (Retallack and Feakes, 1987). Myriapod-like forms are known from the Middle Silurian. Already by the Late Silurian a complex of coadapted soil organisms, similar to the recent one, had formed, which included not only phytodetritophages, but also some highly specialized predators (Jeram et al., 1990). A significant increase in the abundance and diversity of detritophages, particularly springtails and mites, is characteristic of the Lower Devonian localities. Apparently it was associated with the appearance of abundant, slowly decaying debris of the first vascular plants. The literature about early stages of plant life on land is much more extensive than that on the life of early land animals.

An informative review on the early land plants (480–360 Ma) has been published by Kenrick and Crane (1997). The oldest remains of vascular plants are tetrads of spores, apparently belonging to liverworts. Spores of bryophytes are known beginning from the Middle Ordovician. It can be assumed that plants already began colonization of the inclined loose substrates and gradual replacement of mats on the horizontal, periodically flooded surfaces. Liverworts, attached to the substrate with numerous rhizoids situated along the entire thallus, can resist erosion rather efficiently. The first records of Zygomycetes, possibly already being mycorrhizal fungi, came from the same time (Redecker et al., 2000). Later, the diversity and abundance of the tetrads decreased, giving way to individual spores of Anthocerotae and other mosses, and the first vascular plants (“Protracheophyta,” ancestral Lycopodiophyta). Algal-bacterial mats are being actively pushed out of their original habitats into suboptimal ones. By that time the soil fauna, including bacteria, protozoans (testate amoebas), fungi, and invertebrates (oligochaetes, euthycarcinoids, “myriapods,” including oligomeric ones, and mites and other arachnids), has already been almost formed. With the appearance of vascular plants pedogenesis accelerated significantly.

Stems of tracheophytes, rich in slowly decaying cellulose and lignin, provided a poorly nutritious yet abundant food for the soil fauna. Over time, vascular plants (Rhyniopsida and Lycopodiophyta) had occupied nearly all the habitats originally taken by the algal-bacterial mats. The turnover of matter and energy with the detritivore pathway strongly dominating over the herbivore pathway, so typical of terrestrial ecosystems (Shurin et al., 2005), began evolving already in the Early Paleozoic.

It is essential to give but a brief account of the evolution of euthycarcinoids, which were important as one of the first freshwater and terrestrial herbivores. For a long time euthycarcinoids remained unclassified within arthropods. They turned out to be a unique uniramian lineage, which appeared already in the Later Cambrian (Vaccari et al., 2004). Starobogatov (1988) reviewed the classification of euthycarcinoids and suggested treating them as a class of "Trilobitomorpha." However, the presence of two pairs of uniramous or one pair of biramous "antennae" and of mandibles contradicts that placement. The structures described as mandibles were very large sclerites lacking any appendages and occupying nearly the entire segment. The inclusion of Aglaspidae into Euthycarcinoidea seems precarious; more likely it was a "trilobitomorphan" group. It seems more appropriate to consider Euthycarcinoidea as belonging to Uniramia. Their body consisted of a two-segmented head and a trunk including two tagmata. The anterior, wider tagma bore two or three pairs of appendages under each tergite. Euthycarcinoids are unknown from the Ordovician but have been found in the Silurian (McNamara and Trewin, 1993). They were particularly abundant in the Devonian; their remains have been described from the Windyfield volcanogenic cherts near Rhynie in Scotland (Anderson and Trewin, 2003). Some known deposits are literally stuffed with isolated segments that have been described as the *Maldybulakia* myriapods (Tesakov and Alekseev, 1992; Edgecombe, 1998) but most probably belonged to cast-off exuvia of immature euthycarcinoids. While in myriapods all the body segments are of the same width, in *Maldybulakia* they are approximately of the same length but their width varies more than 1.5-fold. This is characteristic of euthycarcinoids, which had a wide and a narrow body regions. It has been suggested that the narrow segments represent the collar, but in that case they would be ten times less common than the wide segments, while in reality both types are approximately equally frequent. In diplopods, the anterior tergite of each pair overlaps the posterior one, and their structure is completely different. On the isolated segments of *Maldybulakia* such a difference must be easily discernible, yet all the segments in the available collections, which include hundreds of specimens, show identical structure. Finally, the collection of Borissiak Paleontological Institute includes a specimen from the type locality that comprises four connected segments. The tergites in that specimen do not overlap, and the last segment is

only 0.67 times as wide as the preceding ones, indicating that the body was divided into a wide and a narrow tagmata, which is characteristic of euthycarcinoids but not diplopods. In the Carboniferous there existed narrower myriapod-like forms with a larger number of segments (*Sottyxerxes*), but there also occurred some wider, flatter ones (*Smithixerxes*, *Kottyxerxes*) (Schram, 1971; Shram and Rolfe, 1982; Wilson and Almond, 2001). They still occurred in the Permian (Schneider, 1983) and the Triassic (Gall and Grauvogel, 1964; Schram, 1971), but from the younger deposits their remains are unknown.

The taxonomic position of the majority of Paleozoic animals referred to as myriapods is unknown. The most ancient remains, nearly identical to the Carboniferous "myriapods," have been described from the Upper Cambrian of Siberia (Budd et al., 2001). They, indeed, had a long multisegmented body, mostly with two pairs of legs on each segment. These animals are considered diplopods, although in only a few of them the characteristic overlapping of tergites has been found. In most of these forms, including the giant *Arthropleura*, there were two pairs of legs under one segment, as in euthycarcinoids. The structures of palaeosomatids, interpreted as pro- and metazonites (Hannibal and Krzemiński, 2005), do not resemble the pro- and metazonites of diplopods, looking instead like a single sclerite. The structure and segmental composition of the head are unknown for the majority of forms. On the contrary, for kampecarids, which do not belong to Diplopoda, the overlap between tergites has been demonstrated, as illustrated on the widely circulating yet still unpublished reconstruction by John Almond. It appears that the Paleozoic "myriapods" included animals of profoundly different structure and, perhaps, of different origin.

The early stages of the evolution of the terrestrial biota were characterized by a remarkable abundance of chelicerates, which had appeared in habitats transitional between the sea and the land by the Cambrian. By the end of the Paleozoic, xiphosurans, which were much smaller than they currently are, became predominantly freshwater animals and could also partly live on land. Some of the fossil xiphosurans have been found "camouflaged" by fallen leaves of lepidophytes. Similarly, eurypterids were moving from seas into fresh waters, and in the Late Carboniferous and the Permian also onto the land, as indicated by their very long posterior legs. Marine scorpions also transformed first into freshwater, and then into terrestrial animals; from the Carboniferous onwards we encounter exclusively land scorpions with characteristic paired claws. In all these groups we can observe the same gradual transition to living in fresh waters and on land. The history of arachnids was different. Already in the Late Silurian we encounter completely formed trigonotarbid, and in the Early Devonian spiders and modern-looking mites. By that time arachnids had already completed a long period of time when they were living in soil and had

become true terrestrial animals. In both the Devonian and Carboniferous, trigonotarbids were the most abundant arachnids. They lacked such specialized traits as spinnerets or venomous chelicerae and were apparently omnivorous.

The Carboniferous and Lower Permian localities often contain remains of arachnids, diplopods, and the apterygote insects, monurans. These groups occurred in the Upper Permian as well, but then almost disappeared from the record, although their actual diversity and abundance most probably remained unchanged. One has to suggest that, in the Paleozoic, these animals had a different life style, which increased the probability of their fossilization. Hoffman (1969) believed that the Paleozoic myriapods were either aquatic or semi-aquatic. The burial of insects in water usually takes place far from the shore. Because it is unlikely that surface currents could transport rapidly drowning apterygote insects and even less so large and heavy myriapods, there must have existed large swimming objects to carry out that transport.

Arthropodization started as a single process for both sea and land because it was originally almost certainly associated with the large transitional zone in between the two, which existed in the Precambrian and was gradually shrinking during the Paleozoic. Later, however, the processes on sea and on land diverged. The task of transforming the marine landscape was easier as it did not require any substantial geomorphological changes and could be solved from the photic zone above as well as from below, by evolution of sestonophages (originally vagile and better adapted to unstable conditions, while the sessile sestonophages dominated in the next, Paleozoic fauna, which came into existence in the Ordovician). The process of transforming the land was more difficult and took longer. Neither the algal-bacterial mats by themselves, nor the wormlike animals that became engaged in processing organic matter were capable of influencing the most dangerous factor for that ecosystem—the high turbidity of the overland runoff resulting from the uncontrolled erosion. Algae and lichens living on hard substrates only increased that turbidity by contributing to chemical weathering. The situation has changed only with the appearance of soil and the spread of vascular plants. This circumstance delayed the arthropodization of land animals by at least two geological periods (i.e., by approximately a hundred million years), compared to the arthropodization of marine animals.

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