Theoretical Article

Innovation directions in paleoecology: evolutionary paleoecology

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Abstract

A new branch of paleoecology is defined here, evolutionary paleoecology, which covers the studies of the evolutions of the paleoecological habits of the taxa of all phyla in geological times. It is based on autecology and paleoautecology. The main methods in autecology are experiments and observations. More experimental studies are needed to determine what and how the environmental factors control the growth of taxa. The main paleoenvironmental factors for ancient taxa include the temperature, salinity, pH, DOT (dissolved oxygen content), and water-depth. The limitations of the methods to quantitatively determine the paleoenvironmental factors has hindered the development of paleoautecology. Many methods in the related disciplines, such as paleoatmospheric science, paleoceanography, paleogeography and sedimentology, can be used to quantitatively determine the paleoenvironmental factors. The urgent tasks in the future for paleoecologists are (1) to do more experimental researches in autecology, (2) to develop new methods for quantitatively determining paleoenvironmental factors, (3) to do researches on paleoautecology of taxa, (4) to do researches on evolutions of paleoautecological features of all taxa, and (5) to synthesize the results of the paleoautecological studies of all taxa, to develop evolutionary paleoecology.

Crinoids are an example of the taxa whose paleoecology has changed in geological times. In the Paleozoic Era crinoids were abundant in shallow water environments, but in present-day oceans crinoids are sparse and distributed at depth from 105 to 5000 m.

Our statistical research on the Late Ordovician calcified dasycladaleans in the Tarim Basin shows that all of them occurred in shallow water sedimentary facies, such as the platform margin

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reefs, platform margin banks, and open platforms, but not in the restricted platform facies such as lagoons. According to our analysis on the literature on the calcified dasycladaleans from the times after the Ordovician, we found that the paleoecology of the calcified dasycladaleans has never changed since their appearance in the Late Ordovician.

Key words: autecology, paleoautecology, experimental ecology, crinoids, dasycladaleans, paleoatomspheric science, paleoceanography.

1 Conceptions of ecology and paleoecology

Ecology is a discipline that studies the relationship between organisms and their environments, including in what environments they can live, their adaptions to the environments, their impacts on the environments, as well as the impacts of the environments on them. The main methods include experimental research, field observation, and model deduction.

The subdisciplines of ecology can be divided in many ways. Based on the research methods, it can be divided into: (1) **Experimental Ecology**. The impact of physical and chemical conditions on organisms can be determined by experiments, such as observing at what temperatures an organism dies, grows fast, and grows slow. Literature shows that experimental ecology is not treated as an independent subdiscipline in China. But a large amount of Chinese literature can be retrieved using "ecological experiments", indicating that there is a lot of researches in this field. There are many literatures, tutorials, collected works, and professional journals on experimental ecology abroad; (2) **Observational Ecology**. The controlling of physical and chemical parameters and their changes on organism can be determined through field observation and measurement. For example, the relationship between seawater temperature and the population composition of water-blooming cyanobacteria can be determined through observation and measurement; (3) **Mathematical Ecology**, in which various mathematical methods are used to analyze the relationship between the environments and organisms and that among populations.

Paleoecology studies the relationship between ancient organisms and their environments. Paleoecological research is not only based on the theories, methods, and results of modern ecology, but also on the unique theories and methods of paleoecology.

The sedimentary rocks contain a lot of information about the life and the environments in ancient times. Researchers decipher the information about ancient environment and organisms in the strata through paleoecological research.

Determining ancient environmental conditions is one of the core contents of paleoecological research. The environmental conditions for recent organisms include latitude, temperature, atmosphere, and rainfall for terrestrial organisms, and the latitude, water depth, temperature, salinity, dissolved oxygen content (DO), pH, and main nutrient contents for marine organisms. But, for ancient organisms, determining their environmental conditions is very difficult. Thus, the innovation in research method is very necessary.

Many previous paleoecological researches focused on univariate analysis of the sedimentary environments, such as the hydrodynamic energy based on the texture of the sedimentary rocks (Flugel, 2010). Some scholars (Liu et al., 1997; Wang et al., 2012; Zhang et al., 2015) have studied the organism group adapting to different hydrodynamic energy, called them paleontological assemblages. Some researches assessed ancient water depths according to the uniformitarianism, for example, the fossil dasycladaleans are believed to live in shallow water by comparing them with modern dasycladaleans. Some researchers studied the sedimentary subfacies of the fossils using sedimentological methods. For example, Liu et al. (2017) had analyzed the relative abundance of the calcified cyanobacteria genera in different sedimentary subfacies in the Ordovician carbonate strata of the Tarim Basin, Xinjiang, China.

Division of marine environments The marine environments can be divided in different ways (Wilson, 1975; Tucker and Wright, 1990; Flugel, 2010), which caused confusion in the use of terminologies. In our opinion, the marine environments include coast, shallow sea or continental shelf, semi-deep sea or slope (continental slope), and deep sea. The coast can be divided into the backshore or supratidal zone, foreshore or intertidal zone, nearshore or subtidal zone (its lower limit is the fair-weather wave base). Carbonate platforms are divided into platform margins and platform interiors. The platform margins can be divided into platform margin reefs, platform margin bank, inter-reefs, or inter-bank. The platform interiors can be open or restricted. The restricted platform can be divided into lagoon, tidal flat, and island; and the open platform can be divided into open platform reef, open platform bank, inter reef, and inter-bank. Platforms may develop not only on the shelf, but also on the submarine volcanic cones at slopes and basins (Wang, 2001). There is an obvious shelf break between the continental shelf and the continental slope. If there is no slope break, it is called ramp. Ramp can be divided into inner ramp, mid ramp, and outer ramp.

2 The subdisciplines of paleoecology

The main subdisciplines of paleoecology are the follows:

(1) Paleoautecology Autecology studies the relationship between taxa and their environments. Paleoautecology studies the relationship between extinct taxa and their environments. The ecological habits of the different species in a phylum are generally different, and the ecological characteristics of the different populations of a species may also be different. For example, Tibet people are adapted to the low-oxygen environment in Tibet. However, the people who live on the plains are not adapted to the low-oxygen environment in Tibet, and when they travel in Tibet, they may have altitude sickness.

(2) Evolutionary paleoecology It is defined here to study the evolution of the ecological habits of taxa in geological times. Although the name of this discipline is similar to evolutionary ecology, a branch of ecology (Pianka, 1978; Cockburn, 1991), they are different. Evolutionary ecology focuses on the impact of the ecological characteristics of organisms on their evolution, such as the control of the long-term geographical barriers on the formation of new species. Abundant research results in evolutionary ecology have been published in the English journal "evolutionary ecology". It needs to be pointed out that although the term evolutionary paleoecology appears in many documents (e.g., Allmon, 1994; Allmon and Bottjer, 2001), its meaning is similar to evolutionary ecology but not the evolutionary paleoecology defined here, as evidenced by the statement "A traditional focus of evolutionary paleoecology has been the reconstruction of the selective forces that have affected evolving lineages through time". In order to avoid two meanings of the term, it is suggested here to limit the meaning of the term evolutionary paleoecology to that defined here.

Although evolutionary paleoecology is independent of evolutionary ecology, ecology, and evolutionary biology, it needs taxonomy and evolutionary biology as the basis. The prerequisite for the study of evolutionary paleoecology is the correct classification of fossils and living organisms. If several species are incorrectly assigned to one species, the chronostratigraphic range of the species will be artificially lengthened, causing incorrect interpretation of evolutionary paleoecology of the species. If one species is incorrectly split into several species, it will shorten the span of its ecological habits.

(3) Community paleoecology It studies the relationship among the species in a particular space and the relationship between the species and the environments. Its methods include qualitative analysis, quantitative analysis and establishment of quantitative models.

Organisms needs to use resources to survive. Generally, there are more than one species, more than one population, and more than one individual in a space. Therefore, in most cases, it is necessary to carry out community ecology research.

For example, there are four cases: (a) one sheep in a grassland of ten square meters, (b) ten sheep in the same grassland, (c) ten sheep and a wolf in the same grassland, and (d) ten sheep and ten wolves in the same grassland. In the first case, the sheep has enough grass to eat. In the second case, the grass cannot afford the ten sheep, and those eating slowly will starve to death. In the third case, the wolf will eat some sheep, and the left sheep can survive on the grass. In the fourth case, the ten wolves will eat all sheep, and will all starve to death, and the grass remains. Community ecology deals with the relationship between the sheep, wolf, and grass land.

Community paleoecology deals with the relationship between the organisms in a space and their relationship with their environments. The term community was used in different senses. According to the definition by Scott and West (1976), all the organisms in a space are a community. Generally, non-skeletal organisms cannot be preserved as fossils. Thus, incomplete preservation of the organisms in ancient communities is a common problem in the study of ancient communities. Only in the case of quick burial, the most species in an ancient community can be preserved, and a community paleoecology study can be performed in a decent sense. In most cases, however, the species in the ancient communities were incompletely preserved, and the community paleoecological studies were approximately performed.

Reefs are constructed by in situ skeletons of organisms. For ancient reefs, almost all skeletal organisms can be preserved as fossils. Thus, reefs are good materials for community paleoecological research. Up to the present, many community paleoecological studies have been done on the Paleozoic reefs in China (Wu 1991; Li and Gong, 1996; Yang et al. 2001; Guan et al. 2004; Gong et al. 2007; Cai et al. 2008; Li et al., 2011; Cai et al. 2014; Liu et al., 2014; Huang et al. 2017). Besides, many community paleoecological researches have been dong on non-reef shallow water benthic communities (Rong, 1986; Shen et al., 1994; Zhan and Rong, 1995; Liu et al., 1995; Zhan et al., 2002; Zhao et al., 2010).

3 The related disciplines of paleoecology

The development of paleoecology requires application of the knowledge and methods from other disciplines, such as paleoatmospheric science, paleoceanography, and paleogeography.

(1) Atmospheric science It studies the layered structure, chemical composition, and internal movements of modern atmosphere, and climate changes. It is necessary to study the composition and structure of the ancient atmospheres of different geological periods, and many studies in this field have been done. However, there is no formal disciplinary name for this field. Therefore, the name "**paleoatmospheric science**" is proposed here.

Paleoatmospheric science is a branch of earth science to study the composition and evolution of the ancient atmospheres in geological times. Some special methods of paleoatmospheric science can be used in paleoecological studies. One of the research hotspots of paleoatmospheric science is the evolution of the oxygen and carbon dioxide contents of the ancient atmospheres of geological periods (Lyons et al., 2014).

There are many methods and models for determining the oxygen contents of ancient atmospheres. A research frontier is how the atmosphere changed from its initial anaerobic status to its aerobic statue in the Great Oxidation Event. It is found that the oxygen content of the Mesoproterozoic atmosphere is 0.1% lower than that of modern atmosphere based on chromium isotopes (Planavsky et al., 2014). The carbon dioxide content of ancient Earth is also a hot topic.

The stomatal density of plant leaf fossils is an important method for assessing the carbon dioxide content of ancient atmospheres (McElwain and Chaloner, 1995; Sun et al., 2009; Wang et al., 2015).

Plants use the stomata on their leaves to breathe. The number of the stomata of per unit leaf area is different between different plants. For most present-day plants, there is a roughly inverse relationship between the number of the stomata of per leaf area and the carbon dioxide content of the atmosphere, and the relationship can be determined. For ancient plants, if they have close extant relatives, the stomatal density of their leaf fossils can be used for calculating the carbon dioxide content of the atmosphere of their time.

For example, *Ginkgo* appeared in the Jurassic Period, and still exists at present. The relationship between the stomatal density of modern *Ginkgo* leaves and the carbon dioxide content of modern atmosphere can be determined. Based on this relationship and the stomatal density of the Jurassic and Cretaceous *Ginkgo* leaf fossils, it was determined that the atmospheric CO2 content increased by about 700 ppm from the early Jurassic to the early Cretaceous (Sun et al., 2007, 2008; Li et al., 2019). Based on the stomata of the *Quercus* leaf fossils, the CO2 content of the Miocene atmosphere was 395 ppm (Jia et al., 2009).

In addition to plant leaf fossils, calcified cyanobacteria fossils can be used to determine the atmospheric carbon dioxide content. According to the calcification event of the cyanobacteria in the Ordovician, Liu et al. (2020) determined that the atmospheric carbon dioxide content has declined to below 0.32% in the late Ordovician.

(2) Paleoceanography It studies the physical and chemical properties of oceans and their changes in geological times. The main research contents of paleoceanography include the temperature, salinity, oxygen content, pH value, nutrient content, water depth, stratification, isotopic compositions, and movement of currents of ancient oceans.

Paleotemperatures of ancient sea water One of the hotspots in paleoceanography is to calculate the quantitative temperatures of ancient seawaters according to the $\delta^{18}O$ of carbonate or phosphate minerals. The principle is that there is a quantitative relationship between the oxygen isotope composition (x) of the carbonate and phosphate minerals and the oxygen isotope composition (y) and temperature (t) of the seawater from which the minerals precipitated (Urey et al., 1951). Therefore, if any two variables of the three variables (x, y, and t) are known, the third can be calculated. The oxygen isotope composition of ancient carbonate or phosphate mineral can be tested. If the oxygen isotope composition of ancient sea water is known, the temperature of the ancient sea water can be calculated out.

This method has two difficulties. The first is the alteration of carbonate rocks by various diagenetic processes, which generally made their oxygen isotope composition become lighter than their original. The second is the lack of good way to determine the oxygen isotope composition of ancient seawater.

To overcome the first difficulty, the carbonate or phosphate mineral samples should be carefully selected, to avoid the parts that have been affected by diagenesis. Compared to carbonate rocks, brachiopod shells and conodonts are better, and micrites are better than other limestones, dolomicrites are better than other dolostones, because brachiopod shells and conodonts are more resistant to diagenesis (Joachimski and Buggisch, 2002; Joachimski et al., 2006; Bergmann et al., 2018; Hearing et al., 2018; Wotte et al., 2019).

To overcome the second difficulty, the oxygen isotope of ancient seawater was usually assumed to be a certain value depending on the total volume of the glaciers on continents. However, the oxygen isotope values of seawater kept changing during geological times, so, the assumed value does not represent the actual value. Consequently, the paleotemperature of ancient sea water determined in this way has only relative meaning, not absolute meaning, not being the actual temperatures. However, for a short geological time, in the case that the same assumed value for the oxygen isotope composition of the sea water is used, the paleotemperatures can be compared vertically, so as to see their change in a not long period. Studies have shown that important geological events are strongly related to the paleotemperature changes reflected by conodonts (Korte et al., 2005; Joachimski et al., 2009; Joachimski et al., 2012; Chen et al., 2013).

Redox state of ancient oceans The second hot spot in paleoceanography is the study of the redox state of ancient oceans, that is, whether the ocean was stratified or non-stratified, and hypoxic or aerobic. Many geochemical methods were used to assess the redox state of ancient oceans (Schaal et al., 2015). For example, whether the ancient ocean was anoxia can be determined by the anomalies of sulfur isotopes, the ratio of radioactive thorium to uranium, and the content of molybdenum. Some biomarker compounds can be used to indicate the degree of oxygen deficit in the ocean. The elevated level of biomarkers associated with green sulfur bacteria near the mass extinction horizon at the Permian-Triassic boundary of Meishan shows that anoxia occurs in the euphotic zone of the ocean (Grice et al., 2005). The anoxia of the shallow water of the Tethys after the end-Permian mass extinction was indicated by the strawberry-like pyrite (must be less than 5 μm in diameter) (Liao et al., 2010) and the uranium isotopes in the Zal profile in Iran (Zhang et al., 2018) and the Dawen profile in South China (Brennecka et al., 2011).

Paleo-water-depth It is one of the most important environmental factors in paleoecology. Many indicators can be used to determine the paleo-water-depth, such as the size, sorting, and roundness of sedimentary particles. However, there is no good way to quantitatively calculate paleo-water-depth, although a lot of researches on paleo-water-depth have been done. For examples, some researchers used brachiopod assemblages to indicate the paleo-water-depth of Paleozoic ocean, and at least six brachiopod assemblages were defined for different paleo-water-depths (Ziegler, 1965; Zhan et al., 2002; Rong et al., 2018). Foraminiferal fossils were to determine the paleo-water-depths of the Cenozoic seas. And the facies of reefs were used to determine the paleo-water-depths of Permian seas (Wu and Fan, 2001; Wu and Fan, 2003).

Salinity It is also an important environmental factor in paleoecology. At present, there is no effective method to quantitatively calculate the salinity of ancient seawaters. Fluid inclusions of minerals seem to be a potential method. Based on the fluid inclusions of Archean quartz, it was determined that the seawater at that time had low salinity, and the potassium content was 40% lower than modern ocean (Marty et al., 2018). But the fluid inclusions are not easy to obtain and their origins are not monogenic.

pH of ancient sea water It is one of the important parameters of ancient marine environments. Few researches have been done for quantitatively determining the pH of ancient seawater. One promising approach is the boron isotope of carbonate minerals, whose value was thought to be related to the pH of seawater (Honisch, 2007). A research indicates that the boron isotopic composition of modern coral skeletons in the South China Sea is related to seawater pH (Liu et al., 1999). An empirical formula for calculating the pH of ancient seawater using the boron isotopes of foraminifera shells since 20 Ma has been established (Sanyal et al., 1995, 2001), but there is no report that boron isotope can be used to determine the pH of pre-Cenozoic seawater.

(3) Paleogeography It aims to decipher ancient geographic environments according to the features of sedimentary rocks, the paleoecology of fossils, and geochemical indicators (Feng, 2009).

Geographic environments include land and ocean. Land includes desert, glaciers, rivers, lakes, and alluvial fans. Marine environments include coasts, deltas, lagoons, reefs, shallow seas, continental shelves, continental slopes, and sea basins. Different environments have different sediments, sedimentary structures, biological compositions, and geochemical compositions. For example, glacial sediments lack sorting, and coastal tidal flats are featured by desiccation fissures, gypsum, and tidal bedding. There are many methods to assess paleogeographic environments (Feng, 2004; Shao et al., 2019), and these methods can be used in the paleoecology.

The main branches of paleogeography are **biopaleogeography** and **lithofacies paleogeography**. Biopaleogeography restores paleogeographic environments mainly based on fossils (Feng, 2009). Lithofacies paleogeography assesses paleogeographic environments on the basis of the petrological and sedimentological characteristics of sedimentary rocks. Since biopaleogeographic research needs the knowledge of paleoecology, biopaleogeography can be regarded as an applied science of paleoecology. The application of the method of paleogeography in paleoecology means the use of the knowledge and methods of lithofacies paleography rather than of biopaleogeography. Otherwise, it becomes a circulation. For example, based on the two premises that dasycladalean fossils occur in a Middle Permian stratum and that modern dasycladaleans live in shallow water, it is inferred that the Middle Permian stratum was formed in shallow water environment. This is a biopaleogeographic research. But it is a scientific question whether the habits of the Middle Permian dasycladaleans resembles present-day dasycladaleans. This question needs to be determined through some specific researches. The above inference lacks a reliable basis before this scientific question be solved.

Paleobiogeography and biopaleogeography are similar in names, but have different contents. The former studies geographical distribution of paleontological taxa and their changes in geological time. A lot of biopaleogeographic studies have been done in China (Yin, 1988; Wang, 1989; Chen, 1993; Wang et al., 2003, 2013; Xie et al., 2007; Wang et al., 2013), but there are few studies in paleobiogeography (Liu, 1955).

4 Two basic principles in paleoecology

(1) Sample size determines the research results

The quality of the research results of observational ecology is related to the number of observation points. Chlorophyta is considered to be the ancestor of all green plants. Dasycladaleans, an Order of Chlorophyta, has important significance for understanding the origin and evolution of green algae. There are few experimental ecological studies on dasycladaleans. And the understanding of the ecology of dasycladaleans is still incomplete.

If dasycladaleans are present at water depth from 50 to 90 m, and no observations or sampling are performed at this depth range, the presence of dasycladaleans at this depth range cannot be found. If no dasycladalean is present at this depth range, the research result based on one sample from this depth range is the same as that based on many samples. If few dasycladaleans are present at this depth range, and few samples are collected from this depth range, the dasycladaleans are hard to be collected. If there are abundant dasycladaleans at this depth range, and numerous samples are collected from this depth range, the presence of the dasycladaleans at tis depth range will surely be found.

The quality of the results of paleoecological researches is also highly dependent on the number of samples. The discovery of the ancient organisms in any environments in geological time depends on the number of samples. For example, dasycladaleans were distributed in the low-latitude shallow seas in the Late Ordovician time, but their distribution was patchy rather than continuous. If the outcrops of the Late Ordovician limestone are very sparsely sampled, the dasycladaleans may not be sampled. If the outcrops are densely sampled, and the distribution of the samples is uniform, the dasycladaleans can be sampled.

(2) Backward reasoning doesn't work

The occurrence of an organism in a place indicates that all main environmental factors of the place meet the requirements of the organism. Conversely, if a particular organism does not appear in a place, it does not mean that all main environmental factors do not meet the requirements of the organism but that one or some environmental factors of the place do not meet the requirements of the organism. For example, the environmental requirements of dasycladaleans include normal salinity, >17°C, low water turbulence, pH >7, and relatively clear water. If some dasycladaleans appears in a place, it means that all the environmental factors meet the requirements of the dasycladaleans. On the other hand, if no dasycladaleans occurred in a place, it means one or some factors were beyond the tolerance range of all dasycladaleans. For example, if the temperature is <17°C, no dasycladaleans can survive.

5 Examples of evolutionary paleoecological research

Here are three examples of how to do evolutionary paleoecological research:

(1) Has *Lingula* changed?

An example of the evolutionary paleoecological study is *Lingula*, a genus of Lingulidae of Phylum Brachiopoda (Emig, 2003; Rong et al., 2017). This genus is generally believed to have existed since 550 Ma ago and always occurred in the intertidal zone, and can be regarded as a representative of that kind whose ecological habits have never changed. However, some researchers suspect it is a living fossil (Emig, 2003), and this is an issue depending on the standards of the classification. If one believes that the 550-million-year-old fossils are the same as the extant *Lingula*, he will reach the conclusion that the ecological habits of *Lingula* have not changed since its appearance. Otherwise, he will reach a different interpretation. In our opinion, the photos of the Ordovician (Fig. 1) and modern (Fig. 6) *Lin-*

gula specimens in the plates of Emig (2003) are very similar, and the ecological habits of *Lingula* may not have changed.

(2) Have Paleozoic crinoids changed?

Crinoids are a group of animals of the Phylum Echinodermata, and are generally thought to have changed in their ecological habits from the shallow water in the Paleozoic to the deep sea of present day (Flugel, 2010). Crinoids were very common in Paleozoic shallow water limestones. For example, crinoids are widely distributed in the shallow subtidal environments of the platform margin bank and open platform bank facies in the Tazhong area of the Tarim Basin, Xinjiang, China, and in the shallow water limestones of the Upper Ordovician Beiguoshan Formation of Shijiezigou, Ningxia, China (Zheng et al., 2018). Crinoid stem fossils are common in the Middle and Upper Permian calcisponge reefs in south China. These cases and a lot of other observations as well as literature indicate that, Paleozoic crinoids mainly appeared in shallow waters, usually within euphotic zone, less than 80 m.

The crinoids in deeper water environments are small and sparse. For example, scattered small crinoids occur in the dark-colored thin bedded argillaceous limestone of the Late Ordovician Taoqupo Formation at Taoqupo reservoir, Yaoxian, Shaanxi province, China.

Abundant complete crinoid fossils have been found in the Late Triassic Carnian dark-colored fine-grained layered mudstone in Guanling, Guizhou province, China, which was regarded to represent anoxic sea (Wang et al., 2006; Wang, 2006). However, some researchers believed that the sedimentary facies of the mudstone was a tidal flat (Zeng, 2010). Based on the delicately preserved fern leaf fossils (Meng et al., 2002), we believe that the crinoids and fern fossils were buried by the quick deposition of the fine sediments of some debris flows, and the living environment of the crinoids was not anoxic. Based on the lithology, the sedimentary environment of the mudstone may be the outer shelf. Present-day stalked crinoids include 75 to 80 species, all living in oceans (Clark, 1957; Hess et al., 1999), most at the depth of 200 to 5000 m, and a few in the outer shelf. The stalked crinoids from the western Pacific at the depth of 100 m, and those from the western Atlantic at the depth of 170 m (Hess et al., 1999). The Paleozoic crinoid fossils were abundant at the depth from shallow subtidal zone to inner shelf, but no crinoids were found from modern subtidal zone and inner shelf. Therefore, it is reasonable to refer that the paleoecological habits of the crinoids have changed. However, there three possibilities: (1) The current shallow sea environments are different from those of the Paleozoic Era, that is, the Paleozoic shallow seas were suitable for crinoids, but, present-day's shallow seas are not; (2) The Paleozoic crinoids have become extinct, and they have not left any descendants in present-day seas; (3) The researchers failed to sample the crinoids in present-day shallow seas. Therefore, more research is needed.

(3) Evolutionary paleoecology of dasycladaleans

Quantitative statistical analysis of the dasycladaleans from the Late Ordovician limestone in the Tarim Basin shows that they are mainly in the open platform and platform margin facies, not in the lagoon and tidal flat facies. Previous studies revealed that dasycladaleans occurred in the strata from Silurian to Holocene, occurring in the reef, bank, open platform and tidal flat facies (Abate et al., 1977; Barattolo and Bigozzi, 1996; Ruffer and Zamparelli, 1997; Jamaican et al., 2011; Bucur and Sasaran, 2012; Mircescu et al., 2014; Bao et al., 2016; Ohba et al., 2017). Based on the sedimentological and paleontological information we read from the literature, we determined that the lagoon facies in the literature were not the lagoons in geological sense, but the lagoons in geographic sense. The lagoons in geological sense are water bodies with very low species diversity due to abnormal factors such as very high or very low salinity causing by geographic barriers. The geographical lagoons refer to the water bodies surrounded by reefs or behind reefs, regardless of the salinity and biological diversity. For example, in the book "Coral Reef Sedimentology in the South China Sea" (Wang, 2001), the water bodies inside the atolls in the South China Sea are all called lagoons. Most of these water bodies have living corals, which indicates that the salinity of water bodies is normal. These water bodies have almost normal seawater exchange with the open sea, but weaker wind and waves. Such water bodies should be called open platform in geological sense, not lagoons. A typical example of geological lagoon occurred in the strata of the fourth to second member of the Upper Ordovician Lianglitag Formation of the Tazhong platform, Tarim Basin, Xinjiang, China. The lagoon facies limestones are mainly dark-colored micrites, representing low-energy environments. The biotas are very monotonous, containing only cyanobacteria and ostracods. During the same period, various organisms, including coral, stromatoporoids, bryozoans, brachiopods, and echinoderms occurred in the platform margin facies, but were absent from the interior of the platform, which shows that the interior of the platform was limited, and some environmental factors were abnormal. The characteristics of the rocks and paleocommunities were those of restricted water bodies. Previous researchers proposed that the interior of the platform was open platform facies (Chen et al., 1999; Gu et al., 2005; Qu et al., 2014). Our study does not support their viewpoints (Liu et al., 2017).

Based on the literature and our research, dasycladaleans did not appear in any geological lagoons. And modern dasycladaleans do not occur in the lagoons in geological sense (Berger and Kaever, 1992).

Our research on the evolutionary paleoecology of dasycladaleans concluded that the paleoecological habits of dasycladaleans have not changed since their appearance in the Late Ordovician time. The dasycladaleans in geological times and today live in the shallow, warm water in low-latitude seas with normal salinity.

6 The innovative directions of paleoecology

Based on our research and the literature, we propose the following four main research directions of paleoecology in the future.

(1) To do more experimental ecological research

Compared to Earth's history, today is just a moment. This moment is very valuable for paleoecologists, because most ancient taxa had living representatives or relatives, and the environmental factors of the representatives or relatives can be directly observed and measured, or be determined through cultivating experiments.

In the past, many observations and measurements of ecological features of the living organisms have been done, but the experiments on the environmental factors of the living were sparse. So, the general environmental requirements of most organisms are known, but the threshold values of the limiting factors of most living organisms have not been determined.

It is necessary to know the ecological characteristics of modern organisms for the evolutionary paleoecologists. Contemporary ecologists are mainly concerned with the high-grade issues such as the community structure, energy flow, and quantitative models, but few are concerning individual ecology. We believe that the study of autecology is still important. For example, although we already know the general ecological characteristics of Cyanophyta, the ecological habits of each genera still need to be studied. Some cyanobacteria can live in the hot springs with the temperature >70°C (Deng and Xu, 1997), but it is unclear what cyanobacteria can survive in high temperature, low oxygen, and acidic environments. For a particular species, it is not known how its shape, size, and physiological characteristics will change when the environmental factors change. This is a problem that needs to be solved through experimental ecological studies. After sufficient amount of such experimental studies are performed, it is necessary to summarize and integrate the results into a systematic knowledge system.

(2) To do more paleoautecological studies

There were numerous organisms in the Phanerozoic Eon, such as foraminifers, radiolarians, chitin, calcareous sponges, siliceous sponges, hexactinellid sponges, tabulata corals, rugose corals, stromatoporoids, bryozoans, echinoderms, trilobites, ostracods, gastropods, bivalves, graptolites, conodonts, cyanobacteria, dasycladaleans, Codiaceae, *Solenopora*, coral algae, ferns, gymnosperms, angiosperms, and so on. The paleoecological habits of these organisms can be constrained by the methods of sedimentology, geochemistry, and paleoecology. This kind of research has been carried out in some taxa before, such as brachiopods, trilobites. But there are no similar studies in other taxa. These studies should be done in the future, and the results be added to the textbooks of paleontology. In the future, the studies in paleoecology should not always focus on some single factor such as paleo-water-depth or hydrodynamic energy. Researches on more environmental factors are needed. It is necessary to do a more comprehensive analysis on the main environmental parameters of ancient organisms, such as the temperature, salinity, pH, seawater oxygen content, and nutrient content. We should first learn the paleoecological habits of each genera, and then of the family, order, class, and phylum, and finally do a summary.

(3) To do more research on the evolutionary ecology

Based on the studies of the paleoecological habits of the paleontological taxa in the geological times, the research on the evolution of the paleoecological habits of the taxa should be conducted, and then make the summary of each phylum.

(4) To do more studies for new technologies and methods

It is essential to explore the new technologies and methods for paleoenvironmental research, and strive to establish the methods to quantitatively determine the paleoenvironmental parameters of ancient organisms, such as the method to determine the oxygen isotope composition of ancient seawater, to quantitatively determine the ancient water depth, and to quantitatively calculate the salinity and pH of ancient sea waters, so as to realize the transformation from qualitative research to quantitative research. There are already some researches of this kind, and more are needed. Such kind of researches are a challenge to earth science, but they will be solved eventually with the relentless efforts of all paleontologists.

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Comments by Bogusław Kołodziej :

In my opinion it is not possible to write: "A new branch of paleoecology is defined here, evolutionary paleoecology". The title of the paper can be "A new approach to evolutionary paleoecology ".

Reply by Hongxia Jiang:

Thank you for your comments. Research on evolution of ecological habits of taxa is a new research direction. In order to promote the research in this direction, I prefer to regard it a new direction, instead of approach.

Note by the chief-editor:

Disagreement are common among researchers. Biopetrology does not reject different opinions.

Innovation scored by: Fritz Neuweiler, Santanu Banerjee, Hua-Xiao Yan, Giorgio Bianciardi.
Innovation score (0-5): (1.5+3+5+5)/4=3.6
Comments by: Bogusław Kołodziej.
Detailed reviewed by: Hua-Xiao Yan, Santanu Banerjee.

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