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A Hydrozoan Interpretation of *Palaeoaplysina* (Enigmatic Organisms) Based on the Canal Arrangement and Structure

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Abstract—The study of the canal system of the enigmatic organism *Palaeoaplysina* Krotov, 1888 suggests a hydrozoan origin for these fossils. It is shown that the *Palaeoaplysina* canal system consists of three zones and can be interpreted as hydrorhizae that had their own function and morphology in each zone. In the basal part of the colony, the hydrorhizae consist of disconnected parallel stolons. It is possible that a soft body was attached to the substrate in the event of adverse environmental conditions to survive a diapause. In the central zone of the colony the hydrorhizae are strongly branched. That was the zone responsible for feeding. The terminal part of the colony has a characteristic reticulum of hydrorhizae and strongly branched dendritic shoots with hydrants. Hydrorhizae worked as a distributary system transporting nutrients between zooids.

Keywords: *Palaeoaplysina,* enigmatic organisms, hydrozoans, channel system, functional importance

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INTRODUCTION

Palaeoaplysina Krotov, 1888, a problematic fossil of uncertain systematic affiliation is found in the Upper Carboniferous–Lower Permian carbonates of the Northern Hemisphere (Chuvashov, 2009). These fossils are often interpreted as a component of Paleozoic reefs. Despite a wide stratigraphic range of *Palaeoaplysina* from the Moscovian (Vachard and Kabanov, 2007) to Artinskian (Chuvashov, 1973), all these organisms are identified as *Palaeoaplysina laminaeformis* Krotov, 1888. Chuvashov (1973) noted the low importance of *Palaeoaplysina* for stratigraphy, and considered that descriptions of new species cannot currently be substantiated because of the low variability of major skeletal elements of these organisms.

Palaeoaplysina fossils are composed of tabular plates (sometimes up to 1.0 m long), with a smooth basal and uneven upper surfaces, with a cellular structure and network of canals (Fig. 1a). Cellular tissue and canals are characters present in various organisms from various kingdoms (Flügel, 2004). Therefore there is not a single accepted view on the taxonomic affinity of *Palaeoaplysina*. At various times *Palaeoaplysina* has been attributed to hydroids (Ryabinin, 1955), sponges (Krotov, 1888; Flügel, 2004), stromatoporoids (Chuvashov, 1973), and compared to green codiacean algae similar to *Halimeda* (Davies and Nassichuk, 1973, etc.). The cellular tissue between the system of canals was interpreted as a thallus of red algae (Vachard and Kabanov, 2007; Andersson and Beauchamp, 2011).

Palaeoaplysina fossils are widespread in the Upper Carboniferous–Lower Permian carbonates of the western slope of the North Urals. Two paleoecotypes of *Palaeoaplysina*, differing in the thickness of plates and in the presence or absence of mamelons on the upper surface allowed the recognition of two paleoecotypes: thickly tabular paleoecotype characteristic of the Lower Permian skeletal mounds and thinly tabular paleoecotype usually found in association with micritic Upper Carboniferous carbonates (Ponomarenko, 2009).

The EPR (electron paramagnetic resonance) study of the *Palaeoaplysina* skeletons from the Lower Permian organic buildups of the South and North Urals showed the presence of radicals of organic matter of animal origin in the EPR spectra, which suggests that *Palaeoaplysina* belongs to Animals (Lyutoev et al., 2010; Antoshkin et al., 2010).

According to N.N. Marfenin (1993a, 1993b) the main character used for classifying hydroid colonies is the arrangement of the growth and budding zones. The functioning of these zones determines the morphology of the colony. The analysis of the skeletal structure identified the *Palaeoaplysina* morphotype as prostrate colonies, while the thickly tabular morphotype is referred to monopoidal colonies with terminal

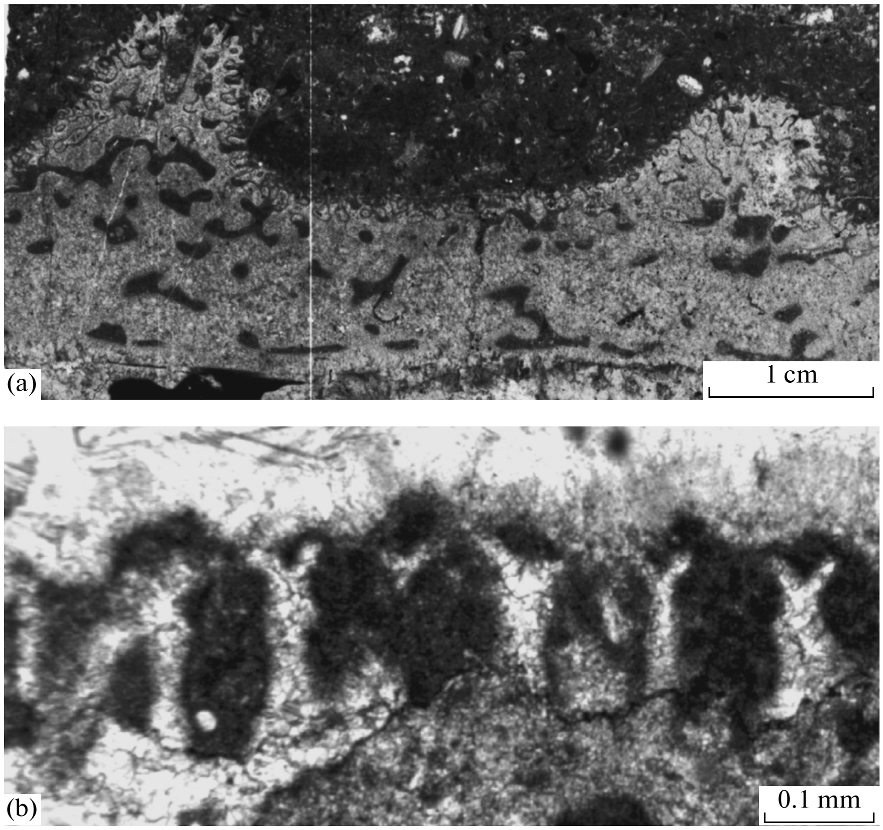

Fig. 1. Major elements of a *Palaeoaplysina* colony: (a) specimen GM A.A. Chernov, no. 327/3, skeletal morphology of *Palaeoaplysina* Krotov, 1888; Un'ya River, North Urals; Asselian, Kholodnyi Log Regional Stage; (b) specimen GM A.A. Chernov, no. 327/5, remains of hydrant on the surface of the skeleton preserved due to microbial encrustation (dark colored); Ilych River, North Urals; Asselian, Kholodnyi Log Regional Stage. Scale bar 0.1 mm.

growth zones (Ponomarenko, 2011). This allowed us to accept Ryabinin's (1955) hypothesis that *Palaeoaplysina* were hydroids similar to the modern *Hydractinia*.

However the relationship between the horizontal and vertical canals of thickly budded *Palaeoaplysina* remains unclear. This paper aims at revealing and describing major patterns of their arrangement in *Palaeoaplysina*.

MATERIAL AND METHODS

Material used as a basis for this paper was collected by one of the authors during the field examination of the Upper Carboniferous–Lower Permian carbonates in the North Urals in 2006–2009.

Microscopic examination showed that the hollow canals that remained after the death of the *Palaeoaplysina* colony and decay of their soft tissues were filled with mud only in the upper part of the plates. In the lower and middle parts, we observed crystalline sparite calcite in the canals, and the canals are poorly visible inside the recrystallized cellular tissue (Ponomarenko, 2009; Ponomarenko, 2011).

High-Resolution Computed Tomography (CT) was used to analyze the development of the canals, as a non-destructive method allowing the examination of the inner structure of an object based on measuring and computation of differences in of X-ray radiation of elements with different density. The study was conducted in the Kazan (Volga Region) Federal University using CT Phoenix V|tome|X S 240. A sample fixed on a support was placed in the CT chamber and was photographed in a nanofocused X-ray tube. The photography was performed at accelerating voltage 100kV and beam current 200mA. The resolution was 15 μm (size of 1 voxel). The photographs and video of 2D sections were made in PO VG Studio MAX 2.1. The 3D reconstructions were made using Avizo Fire 7.1.

The difference in the composition of skeletons of *Palaeoaplysina* and cements is determined by the change in the abundance of MgO (Ponomarenko, 2012). These changes were insufficient to build a 3-D model using CT, but successive photographs of thin sections in various axes and a video made based on these photographs give a comprehensive interpretation of structure sufficient for analyzing of arrangement of the canal system in different zones of the change in the abundance of *Palaeoaplysina* plates.

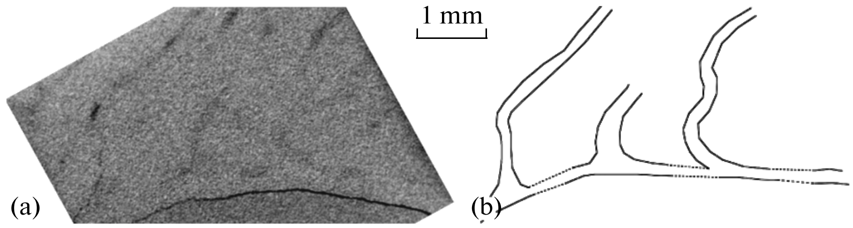

Fig. 2. Arrangement of stolons and shoots in zone A: (a) CT image of *Palaeoaplysina*, (b) a scheme of the canal system.

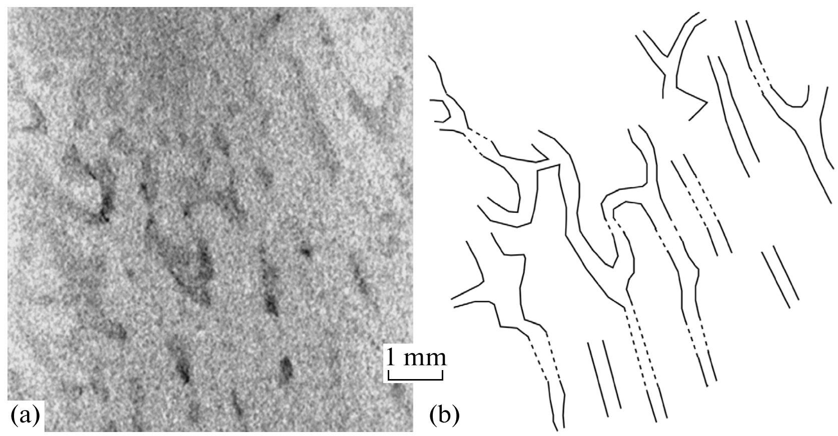

Fig. 3. Canal system of zone B: (a) CT image of *Palaeoaplysina*, (b) scheme of the canal system.

The *Palaeoaplysina* collection studied and samples of the host rocks are housed in the A.A. Chernov Museum at the Institute of Geology, Komi Scientific Center, Urals Branch, Russian Academy of Sciences (GM A.A. Chernov), no. 327.

RESULTS

Interior Structure of Palaeoaplysina Krotov, 1888

Our study revealed the zonal arrangement of the canal system in *Palaeoaplysina*. Patterns of canal branching support the assignment of *Palaeoaplysina* to hydroids. Using the terminology of colonial animals, canals can be interpreted as hollows left by a hydrorhiza (prostrate part of the colony), and hydrocauli (a shoot or erect parts of the hydrophyton).

Three zones can be recognized based on the character of their interaction.

Zone A. Basal zone of the plate has straight and rarely connecting stolons and shoots. The stolons (separate branches of the hydrorhiza) are arranged more or less in parallel, are straight and can extend along the entire length of the fragment of the plate (sometimes up to 10 cm). Sometimes they dichotomize. Hydrocauli from the hydrorhizae branch off every 1.0–1.5 mm at an angle up to 45° (Fig. 2), rarely at a right angle. Without coalescing they continue into the overlying zone B. Occasionally vertical shoots can coalesce with the overlying stolons. The overlying level of the hydrorhiza occurs above the basal but goes around shoots growing from the latter. The distance between the levels is usually 1.0–1.5 mm.

Zone B. This is a portion of the plate with strongly branching hydrorhizae and hydrocauli (Fig. 3). It is noteworthy that branching is more intense in the part with nodes, and begins somewhat lower than in the zones where there are no nodes. In this part of the skeleton, shoots from different zones of the hydrorhiza can coalesce. Nevertheless, the general direction of stolon growth can be traced.

Zone C. This is the terminal portion of the plate (about 0.1–0.2 mm) with intensely branching hydrocauli (Fig. 4). The hydrorhiza in this part of the skeleton looks like a network completely covering the plate, from which smaller and thinner shoots are growing.

DISCUSSION

Interpretation of Morphology

The zonal structure revealed in the canal arrangement within the plates of *Palaeoaplysina* needs to be functionally interpreted. To understand the meaning of the system of canals, it is necessary to interpret the functions of the entire biological organism.

Some researchers have previously attempted to explain the functionality of various elements of *Palaeoaplysina*. For instance, Krotov (1888) interpreted the small pores of the upper surface and the canals con-

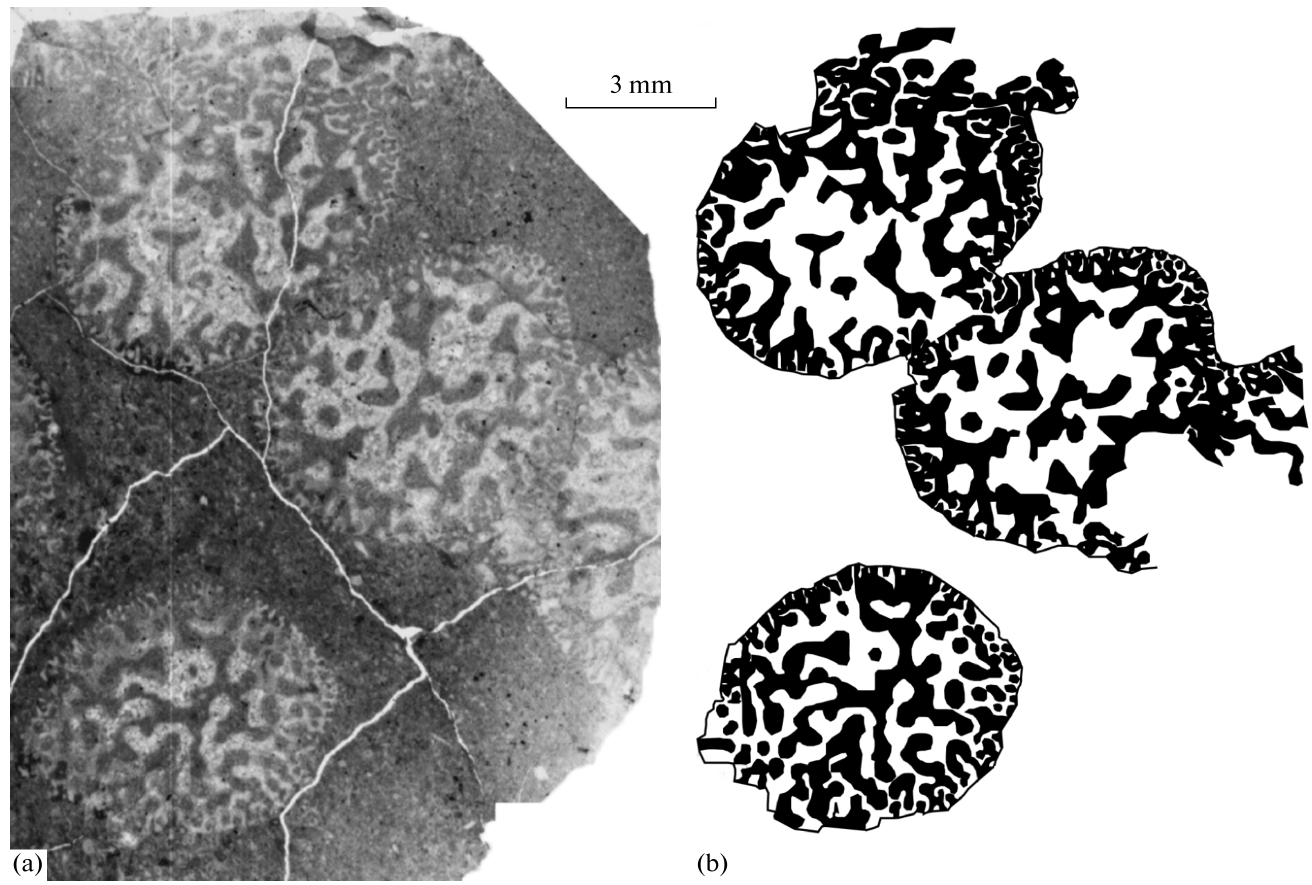

Fig. 4. Canal system of zone B: (a) specimen GM A.A. Chernov, no. 327/4, the section cuts through the mamelons. The terminal zone is on the periphery of the skeleton. The central part shows the canal system of zone B; Un'ya River, North Urals; Asselian, Shikhan Regional Stage; (b) a drawing over the image of the canal system.

necting them as irrigation system of a leuconoid sponge. Ryabinin (1955) suggested that through these pores feeding individuals and reproductive organs were connected to internal cavities. Chuvashov (1973) suggested that transverse septa in some vertical canals might indicate that canals could house hydrants.

If a hydrant (feeding zooid) is treated functionally as the anterior portion of the digestive system with all necessary organs of sensation, grasping, swallowing, and partial digestion of food, a coelenterate colony in that sense is a "multi-mouth organism" (Marfenin, 1993a, p. 34). Therefore, the connection of hydrants to the entire body of the colony could occur through pores of the upper surface. However, no direct evidence has so far been found for the existence of hydrants in *Palaeoaplysina* because the soft body is not preserved in the fossils. Preservation of zooids could only happen if they were encrusted by other organisms. A good example of that comes from Paleozoic hydroid organism *Fistulella*, in which the soft body of the head zones was preserved due to encrustation by the cyanobacteria *Ikella*, which allowed recognition of small feeding polypid (hydrants) and blastostyles with gonophores in these organisms (Shuiskii,1973).

The encrustation of *Palaeoaplysina* by cyanobacteria or problematic organisms *Tubiphytes* is uncommon, hence the authors conducted special investigation to search for the remains of hydrants in microbial communities encrusting plates of *Palaeoaplysina*. Unique data were obtained from material of the Asselian buildups on the Ilych River and Tyagla Creek (drainage divide area between the Pechora and Un'ya rivers). In these samples, the fields of dark-colored microbial accumulations contained structures observed in thin sections as hollows filled by sparite (Fig. 1b). They vary in shape and size. The largest reach 0.5 mm with a width of about 0.1 mm, whereas the small ones are 0.1 mm wide and 0.01–0.05 thick. The width at the base of these hollows corresponds to the width of small pores in zone B of the skeleton of *Palaeoaplysina*, with which they are often interconnected. The above facts allowed these structures to be interpreted as remains of *Palaeoaplysina* hydrants.

The environment for sessile organisms is always anisotropic, so the influence of favorable factors, such

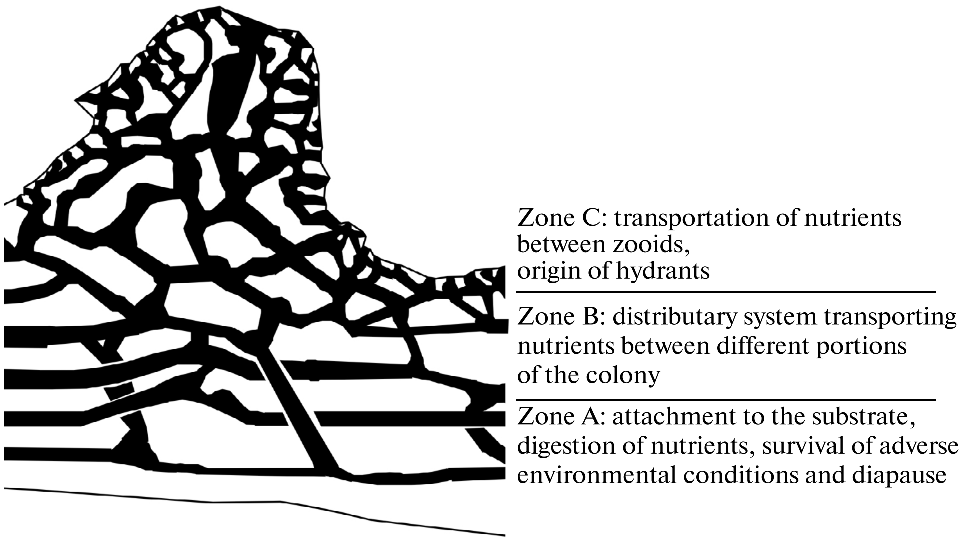

Fig. 5. Functional interpretation of zones in Palaeoaplysina.

as light, oxygen, influx of nutrients, etc. cannot be the same for the entire colony. A developed distributary system is necessary for supplying different parts of the colony with food (Marfenin, 1993a), a system which can transport nutrients from one zooid to another and to distant parts of the colony also needing nutrients. In *Palaeoaplysina* this function was performed by zones B and C (Fig. 5).

Zone B was apparently responsible for transportation of nutrients between the zooids. This is indicated by the presence of a developed network of the upper hydrorhiza with extending shoots. The strongly branching zone B served to transfer nutrients between the more distant zones of the colony, around the zooids, and also to transport nutrients to basal zone A.

Zone A is the basal portion of the *Palaeoaplysina* colony. However, its organization was not complicated, and it has only a few morphological characters, in fact, as in the extant hydroids, it was equally significant and functionally important part of the organism (Marfenin, 1993a). Apart from the attachment to the substrate and digestion of nutrients, stolons play an important role in surviving adverse conditions and seasonal diapause. Many extant hydroids have a diapause in winter (in summer in some taxa), when the colonies exist in an inactive form with no hydrants (Marfenin, 1993a). Polteva et al. (1987) showed that at that time, the coenosarc persists, while in the stolons the hypertrophic gastrodermis (lining of the gastral cavity) acts as a depot of nutrients and stem cells, from which after the end of the diapause (when the metabolism slows down) the colony revives.

CONCLUSIONS

New data on the morphology of the canal system of *Palaeoaplysina* Krotov, 1888 were obtained using X-ray computer tomography. The increased complexity of the canal system was observed upward in the plate. Consequently three zones were recognized in the colony: (A) lower half of the plate with straight and rarely connected hydrorhizae and hydrocauli; (B) upper part of the plate with mamelons and strongly branching and curved hydrorhizae and hydrocauli; (C) the uppermost portion of the plate (about 0.1–0.2 mm) with actively branching hydrocauli. Based on the published material and the data obtained using the method of electron paramagnetic resonance (EPR) (Lyutoev et al., 2010), we agree with Ryabinin's interpretation that *Palaeoaplysina* are representatives of the class Hydrozoa. Additional study revealed the presence of a hydrant extending directly from the skeletons of these hydroids. Preservation of the soft body parts was possible due to lifetime microbial encrustation. Comparison with the extant hydroid colonies allowed evaluation of the role of hydrorhizae and hydrocauli in different parts of the colony. Stolons and shoots in zone A were responsible for attachment to the substrate, digestion and worked as a distributary system transferring nutrients between portions of the colony. In zone B, the hydrorhizae form a network covering the entire skeleton of *Palaeoaplysina*, from which hydrants were growing. This acted as a distributary system transporting nutrients between zooids.

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