New Data on the General Organization of Conodonts: Euconodont Animals in Imprints from the Paleozoic of South Africa

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Abstract—The purpose of this work is to compare the morphology of two ecologically similar groups of marine animals. Conodonts comprise two types: protoconodonts (these are ancient imprints + extant chaetognaths) and the presumably extinct euconodonts. A new study of previously published photographs of imprints suggests that the general organization of two closely related phyla of conodonts and their possible survival in changing environments needs to be reassessed.

Keywords: soft tissues of a euconodont animal, morphological characters of proto- and euconodont animals, imprint, Upper Ordovician shales of South Africa

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INTRODUCTION

More than 150 years ago, in 1856, Christian Pander discovered microscopic tooth-like elements of an unknown animal in the Ordovician marine deposits of the Baltic Region, which he named conodonts. Bengtsson (1976) was the first to establish the differences of the internal structure and development modes of three morphological varieties of conodont dental elements and classified them into different histological types-protoconodonts, paraconodonts and euconodonts, differing in the mode of growth of the substance of the dental elements. The first soft tissue imprints of euconodonts [EU] suggested that these animals could belong to the Chaetognatha [CH] (Briggs et al., 1983). Soft tissue impressions of the "enigmatic animals" discovered by Walcott (1911) were, upon careful examination, recognized as protoconodonts and belonged to Chaetognatha [CH] (Szaniawski, 1982).

For a century, the study of conodonts has been accompanied by attempts to determine the systematic position of this "enigmatic group" in: they have been associated with animals of the most diverse types. The most fundamental work on the comparative characteristics of all animal groups is the monograph by O.M. Ivanova-Kazas, 1995.

Olga Mikhailovna supported the works of I.I. Schmalhausen (1940), who, working in the field of evolutionary morphology of animals, created the theory of growth, the theory of stabilizing selection and

the concept of the integrity of the organism in individual development. In the work of O.M. Ivanova-Kazas, 1995, it was shown that even at the egg stage the further position of the genitals in Chaetognaths was predetermined. Chapter two provides a detailed description of the embryonic development of Chaetognaths [CH] and provides evidence of the group's possible assignment to the deuterostomes based on some characters, while the general organization of CH is closer to protostomes (Ivanova-Kazas, 1995). According to the definition by Dogel (1981), Chaetognaths is a group independent of protostomes and deuterostomes, originating from unknown common ancestors, their early separation from the common stem of animals is certain. Ivanov (1976) recognized them in the superphylum Chaetognatha. The discussion of the possible closeness of EU to primitive chordate animals (Purnell at al., 2000) was ultimately shown to be untenable. Ultramicroscopic studies of EU, analysis of all internal structures showed the erroneous assumption that they have not only the rudiments of a notochord, but even internal nerve fibers, which refutes the possibility of considering EU as even a primitive chordate animal (Guravskaya and Kasatkina, 2023).

We conducted comparative morphological studies of the imprints of the world collection of euconodont animals (Guravskaya and Kasatkina, 2023). We also studied the entire collection of the Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow) of the earliest protoconodont imprints (Kasatkina et al., 1993). The earliest imprint of a primitive



Fig. 1. Imprint the EU spawning ground (photograph) after Gabbott et al., 1995. The spawning ground contains several EU imprints: a—an adult mature female during the breeding season (ovary o; tail section t); b—a young specimen, h—dental elements of a decomposed large specimen.

protoconodont was found in the Proterozoic beds (age—1 Ga): *Parmia anastassiae* Gnilovskaya, 1998, north-east of the Russian Platform (Fedonkin, 2003). Paleontologists associate the problems of animal survival with the environmental conditions (Fedonkin, 2003). However, new, more in-depth studies of the nature of organisms have revealed that various animals have different strategies of existence (Kasyanov, 2001), which can affect the survival of species.

The purpose of this work is to compare the morphological features of conodonts, two ecologically close groups of marine animals that live exclusively in the marine environment (Bengtson, 1976).

We examined the Euconodont collection of R. Aldridge in 2006 during a visit to the Natural History Museum, London, UK. A Uralian imprint of an euconodont animal was studied using a ZEISS EVO 50XVP scanning electron microscope without sputtering its surface in the secondary electron mode at an accelerating voltage of 20 kV. As a result, at magnifications from 120 to 10000 times, numerous structural details were observed, and a number of new morphological features of euconodonts were established, such as H-attachment elements, a food pouch, transverse muscle structures, and female reproductive organs of the EU were discovered. A study of a imprints from the Upper Ordovician Soom shale of South Africa led to the conclusion that the interpretation of the photograph by the authors (Gabbott et al., 1995), who considered a complex of animals of different individual ages as a single specimen, was erroneous. In fact, the photograph shows an imprint of the EU spawning ground with several specimens of EU animals. There are several imprints of EU individuals of different ages at the spawning ground: Fig. 1, a-an adult mature female during the breeding season (ovary-o; tail region—t); Fig. 1, b—a young specimen, Fig. 1, h tooth elements of a decomposed large specimen. The authors (Gabbott et al., 1995) examined some details (muscles) in detail, but did not consider the general organization of the animals, did not discuss the significance of the central organs. As a result of our study of

a well-preserved imprint (Fig. 1, a), paired ovaries were observed on the sides of the gut (Fig. 2, k), a breakthrough of the body wall with the laying of eggs outside the individual (Fig. 2, Ir, Irb). However, the tail region of this well-preserved specimen (Figs. 1; 2, t) is empty, it does not contain testes, the tail section contains only the intestine. Hence, we have discovered the imprint of a female euconodont animal. Unlike the hermaphrodite protoconodonts, individuals of which contain not only ovaries, but also testes, euconodont animals are not hermaphrodites (Figs. 1, a; 2). Studying the world collections of EU imprints, protoconodont imprints and a collection of their living representatives [CH], allows us to compare the morphology of protoconodonts (extant chaetognaths) with the presumably extinct Euconodonts.

COMMON CHARACTERS

Both types are characterized by the absence of not only individual organs, but even organ systems. There is no respiratory or excretory system, no oviducts or vas deferens. EU have no circulatory system, while CH have a primitive circulatory system (Malakhov and Berezinskaya, 2001). Both groups lack a trunk support system: there is not even a notochord. Some geologists mistook the intestinal tract of EU for a notochord, ignoring the fact that the notochord should be located dorsal to the intestine (Briggs et al, 1993). Both types have a support system only in the head in the form of skeletal plates to which powerful muscles of the alimentary apparatus are attached. Maturation of spermatozoa of both types occurs in the tail section. The eggs are located in the ovaries of both CH and EU: to the right and left of the gut tube(Figs. 1, o; 2, ov1, ov).

MORPHOLOGICAL DIFFERENCES

The most striking feature of the difference is the dental system. It is well known that the dental system of protoconodonts was formed as a result of the skeletonization of the surfaces of convex structures—tenta-



Fig. 2. Drawing of a mature specimen (female) of a euconodont animal. The eggs of a breeding female are laid out from two ovaries at once; a—ruptures in the body wall, release of eggs to the exterior; e—food sac with dental elements inside; Irb— eggs released outside from the left ovary; Ir—eggs, released from the right ovary; ka—anal opening; Ov1—left ovary.

cles (Bengtson, 1976). Unlike CH, the dental system of EU was formed inside the food sac (Fig. 2e) as secretions of muscle structure cells. Despite the similarities in nutrition—capture of surrounding animals and detritus, swallowing and pushing from the pharynx into the intestinal lumen are different. In CH, the food swallowed with water is pushed forward by the strong muscles of the back of the pharynx, and the water is expelled through the mouth. In EU, the food swallowed with water is compressed by the dental elements, and then pushed into the intestine, and the water is expelled through a special opening on the dor-



Fig. 3. Drawing of the tail section of the male sixth euconodont imprint from the Lower Carboniferous Granton deposits after Aldridge et al., 1993 (d—pellets; k—gut; m muscles; s—spermatophores; t—tail section),

sal side of the head, and not through the mouth. In CH, food is pushed through without compression, entirely, since the midgut has expansions (e.g., in P. samamithion Schram, 1973: Paleozoic, Carboniferous, Pennsylvanian, <300 mL). The main difference between these two types: EU and CH, may be in the organization of the reproductive system. In EU, spermatophores leave the caudal region, where sperm maturation occurs, through ruptures in the integument and settle on long, straight hairs around the caudal region (Fig. 3, s). Spermatophores in CH break through the integument in the tail region and enter the bulge of the body—the seminal vesicle (Fig. 4, s). Unlike EU, CH individuals do not release a spermatophore into space (Fig. 4, sm) but transfer it to their mating partner by attaching it to the mouth of the seminal receptacle, into which (Fig. 5, sc) the sperm flows. Fertilization of CH is internal. Fertilized eggs enter the marsupial sac through a rupture in the body wall (Fig. 6, bo), and then get into the exterior. In both types, eggs leave the body cavity through a rupture in the body wall due to the absence of oviducts. The spawning of eggs by a breeding female EU occurs from both ovaries at once (Figs. 50; 6, Ir). The EU's spawning strategy is the same as that of the CH. CH eggs break through the body wall and emerge, remaining in a common membrane with other eggs (in the marsupial sac). EU eggs rupture the body wall on their own and emerge without a marsupial sac. The EU female has laid almost half of her ovarian resources, although the left ovary is emptier than the right. Apparently, the fertilization of EU eggs occurs not internally, but



Fig. 4. Section of the caudal region with spermatophore and mature seminal vesicle (f^1 -lateral fin; f^2 -caudal fin; *s*-spermatophore in the seminal vesicle).

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Fig. 5. The ovary section with the seminal receptacle (ov— mature egg in the ovary; sc—cavity of the seminal receptacle; sm— mouth of the seminal receptacle).

externally. This act makes EUs fundamentally different from CHs. Unlike EU, CH has a seminal receptacle organ, which opens with its opening onto the surface of the fin (Kasatkina and Stolyarova, 2010). Thanks to this organ, the fertilization strategy of CH is more perfect. At the time of reproduction, CH species gather in flocks and sexually mature individuals transfer (throw) their spermatophore from the tail end to other partners. The eggs of the EU female come out in a packet, after breaking through the covers. In CH, the spermatophores are deposited, during the process of convergence of individuals, on the fin of the partner, next to the opening leading to the seminal receptacle (Kasatkina and Stolyarova, 2010). Fertilization occurs internally: each egg cell makes its way to the seminal



Fig. 6. Area of the body with a ruptured marsupial sac (*bo*): eggs released.

receptacle with amoeboid movements and after fertilization makes its way again to the body wall, breaks through it, coming out on the fin, where it is retained, and together with other developing eggs enters a special marsupial sac (Fig. 6, bo).

Fertilization occurs internally: each egg cell makes its way to the spermatheca with amoeboid movements and after fertilization makes its way again to the body wall, breaks through it, exits onto the fin, where it lingers, and together with other developing eggs enters a special marsupial sac (Fig. 6, *bo*).

ECOLOGY

In the Paleozoic, conodonts were abundant (several thousand per cm3 in some deposits). This was a successful group until the end of the Triassic, when they disappeared from the paleontological record. Protoconodonts [CH] reappear in modern oceans, which is confirmed by the facts of their record [CH]. However, euconodont animals, unlike CH, cannot be observed in large numbers in the modern ocean. There is only one suspected modern specimen of EU, from the bottom layer of the Laptev Sea; it requires histological examination to identification.

CONCLUSIONS

In addition to external environmental factors, the survival of organisms is undoubtedly influenced by features of their external structure and reproductive strategy, as was previpously demonstrated for other large animal groups (Kasyanov, 2001). Studies of the general organization of conodont animals can confirm earlier discoveries (Kasyanov, 2001). Perhaps the main reason for the disappearance of the once numerous EU group, in contrast to the numerous surviving living protoconodont animals [CH], probably lies in the structure of the reproductive system and in the reproductive strategy, i.e. with different methods of spawning and fertilization of individuals.

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This work does not contain any studies involving human and animal subjects.

CONFLICT OF INTEREST

The authors of this work declare that they have no conflict of interest.

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