Rounded phosphatic structures (H elements) of euconodonts and their function (Euconodontophylea)

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Morphological analysis is done of the rounded structures in the head part of euconodont imprints from the Carboniferous deposits of Granton (Scotland), and the Ordovician Soom Shale (South Africa) and the rounded phosphatic structures present separately in the Upper Silurian and Upper Devonian deposits of Germany and Lower Triassic deposits of Primorsk Terr. (Russia). The identity of these structures in morphology and ontogenetic stages testifies that all of them belong to euconodonts. The rounded head structures of euconodonts, or H elements (Buryi & Kasatkina, 2001), appear to be analogous to the skeletal attaching plates of Chaetognatha. They were arranged in pairs in the anterior part of head in front of the tooth apparatus symmetrically to the sagittal axis of the euconodont and their surface was completely coated with a soft connective-muscular tissue like a cap. The H skeletal elements are rather a part of the mouth assemblage of euconodont animals along with the pharynx, P, M, and S elements of the tooth apparatus, and muscles (connective-muscular tissue). The presence of skeletal attaching plates (H elements) in euconodonts is responsible for the unique structure of the head part and of the whole animal (the euconodont mouth is arranged along the sagittal axis between the H elements). This supports recognition of these animals as a separate type, Euconodontophylea (Kasatkina & Buryi, 1999).

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Introduction

The rounded structures were first detected in the head part of euconodont imprints found in the Lower Carboniferous Granton Shrimp Bed of Edinburgh, Scotland (Briggs et al., 1983). A pair of such rounded structures, 1.4 mm long and separated by 0.5 mm space, is arranged symmetrically to the euconodont sagittal axis in front of the tooth apparatus of *Clydagnathus*. They look like “deep, inwardly hollow rings” (Aldridge et al., 1993). Very similar to these paired rounded structures, 2.1-3.1 mm long, were found in association with very large tooth elements of *Promissum* in the imprints of euconodont animals from the Upper Ordovician Soom Shale of South Africa (Aldridge & Theron, 1993). Aldridge et al. (1993) assigned the rounded structures to soft tissues (having called them “carbonized lobes”), probably because they discovered organic matter in these structures. They compared their findings with the fossilized agnaths, particularly with the Silurian anaspids *Jamoytius*, and suggested that these rounded structures were sclerotic cartilages, which surrounded the eyes. In the best preserved imprint of *Promissum pulchrum* from South Africa (GSSA C721), paired oval structures composed of white organic matter were found in its head part in the same position relative to the tooth apparatus as the “carbonized lobes” from Granton. This white tissue of a fibrous texture has been interpreted as an outer muscular system of the euconodont eyes (Gabbott et al., 1995).

Similar rounded phosphatic structures, 0.7 mm long, have been found in the Lower Triassic deposits from the south of Primorsk Terr., Russia (siltstone series of the Perevalny Creek, Kamenushka River basin, 50 m thick), assigned to the ammonite zone *Anasibirites nevolini*. They are of the same colour as the numerous associated euconodont elements (from light- to deep-brown) and have a similar texture of the surface. We proposed to consider these rounded structures to be the skeletal attaching plates of the euconodont mouth assemblage. They were designated as H

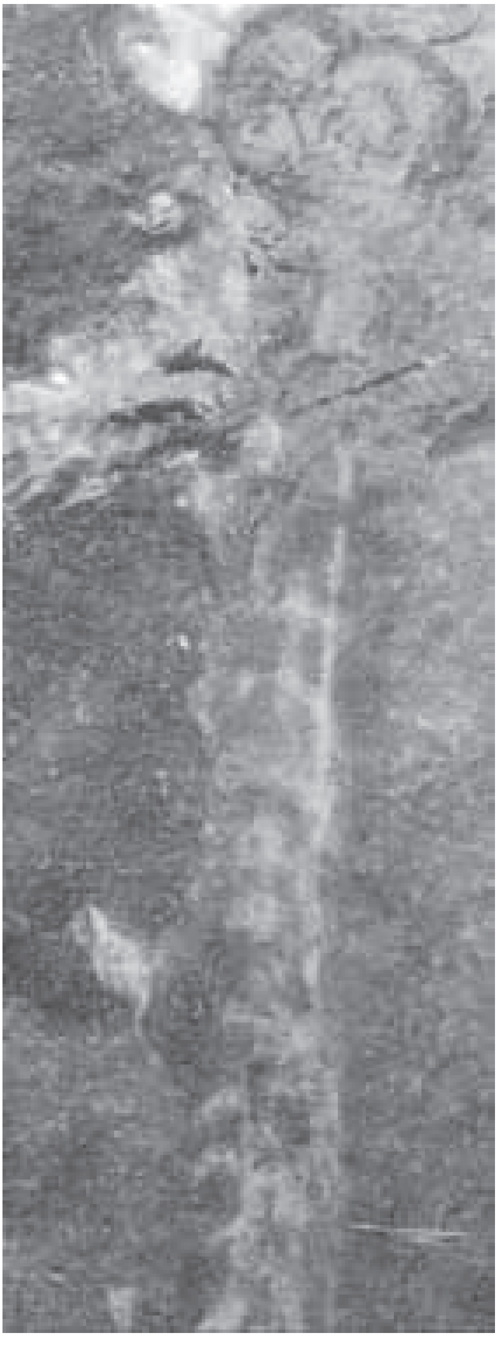

Fig. 1. Paired rounded structures in the head part of the euconodont animal from the Carboniferous deposits of Granton, Scotland, specimen no. 5 RMS GY 1992.41.1 (after Aldridge et al., 1993).

elements by analogy with the already known P, M, and S euconodont elements (Buryi & Kasatkina, 2001). Well before the findings mentioned above, phosphatic rounded structures, occasionally of somewhat lesser sizes (0.13-0.8 mm), were found in many regions of North America, Europe, and Asia, in the Cambrian to Devonian deposits, together with numerous euconodont elements and cephalopods. They were called "rings" and referred to unknown before representatives of colonial problematic Hyolithelminthes Fisher, 1962 (Müller et al., 1974). It is by far interesting to compare these at first glance dissimilar rounded structures.

Material for comparison

1. The paired rounded "carbonized" structures present in the head part of euconodont animals from the Carboniferous deposits of Granton, Scotland [specimen no. 5 RMS GY 1992.41.1 (Aldridge et al., 1993) (Fig. 1)] and the Ordovician Soom Shale of South Africa [specimens GSSA C351 and GSSA C721 (Aldridge & Theron, 1993) (Fig. 2)].
2. The rounded phosphatic structures present separately in the Upper Silurian deposits [specimen UB no. 532 (Taf. 18, fig. 1) (Figs 4a, 4b) and specimen UB no. 533 (Taf. 18, fig. 2)] and Upper Devonian deposits [specimen UB no. 561 (Taf. 20, fig. 5)] of Germany (Müller et al., 1974).
3. The rounded phosphatic structures (H skeletal elements) found separately in the Lower Triassic deposits in the south of Primorsk Territory (Russia): specimens DVGI 3B-1 (Fig. 3) and DVGI 3B-2. Together with them, numerous euconodont elements are present in sample no. 4035 (Buryi & Kasatkina, 2001): platform [*Neogondolella milleri* (Müller) – 22 specimens], segminate [*Neospathodus lanceolathus* Mosher – 1, *Smithodus discreta* (Müller) – 19, *S. cristagali* (Huckriede) – 1, *S. conservativa* (Müller) – 4], and ramiform [*Furnishius triserratus* Clark – 170, *Ellisonia triassica* Müller – 9, *E. meissneri* (Tatge) – 3, *E. magnidentata* (Tatge) – 4, *E. nevadensis* Müller – 3, *Hindeodella triassica* Müller – 36, *H. nevadensis* Müller –15, *H. raridenticulata* Müller – 15, *H. budurovi* Buryi – 7, *Parachirognathus symmetrica* (Staesche) – 4, *P. inclinata* Staesche –1, *Hadrodontina adunca* Staesche – 13, *H. subsymmetrica* (Müller) – 36, *H. symmetrica* (Staesche) – 30, *Xaniognathus curvatus* Sweet – 2].

Common morphological features

All three types of rounded structures have a similar irregular-circular ring-like shape.

Their outer diameters are as follows: 1.4 mm in the imprints from the Carboniferous deposits of the Granton area, 2.1-3.1 mm in the Ordovician imprints of South Africa, 0.72 mm in the H elements from the Lower Triassic deposits of Primorsk Terr., 0.13-0.8 mm in the rounded structures from the collection of Müller et al. (1974) (Cambrian-Devonian).

The thickness of the Lower Triassic H skeletal element, measured along its outer margin, is about 0.1 mm. In all rounded structures under comparison, the outer margin (*om*) (Fig. 3) is uneven, with numerous projections (*p*) and hollows. The upper surface is clearly subdivided in all structures into the outer and inner rings. The outer ring (*or*) is outlined from the outer margin towards the center as a rather wide band and represents a smooth, shining (as in euconodont elements) surface restricted on the inside by a circular ridge (*cr*) bearing faintly visible projections or papillae. From the circular ridge towards the center of the structure, the surface of the inner ring (*ir*) is composed of rough, sometimes concentrically arranged material, the thickness of which decreases gradually to the point of a hole (*h*) in the center.

The excellent collection of such structures presented in the work by Müller et al. (1974) gives an important additional material for understanding their morphology and function. All of them are similar and represent different variations of the same rounded structures depending on their age and preservation. The young structures are thinner and hollow inside and have only the outer ring (see Taf. 20, Fig. 5 in Müller et al., 1974; Fig. 3 in Buryi & Kasatkina, 2001; and specimen GSSA C351 from South Africa, Aldridge & Theron, 1993). The investigations by Müller et al. (1974) showed that the outer ring has a lamellar texture similar to that of the euconodont elements. As an organism became adult, the space between the outer ring and the center decreased and was filled with structureless, often concentrically arranged material. The thickness of this inner ring gradually decreases towards the center.

The rounded structures from the collection of Müller et al. (1974) are covered with remains of a soft, probably connective tissue, which was called the outer skin. Many observations by Müller et al. (1974) showed that "the outer skin is folded around the adhering surface and is discontinuous on the upper margin". Their text-table 3b (our Fig. 4b) demonstrates "the specimen of the outer skin, from which the ring is detached. The position of its upper margin is, however, recognizable on the outer skin at a distinct interval. The outer skin is folded inwards on the lower margin".

It is obvious that the rounded structures under discussion are in lifetime coated from above with a soft connective tissue (the outer skin) like a cap; the diameter of such a cap is close to the outer diameter of the rounded structure. Being

Fig. 2. Paired rounded structures in the head part of the euconodont animal from the Ordovician Soom Shale of South Africa, specimen GSSA C 351 (after Aldridge & Theron, 1993).

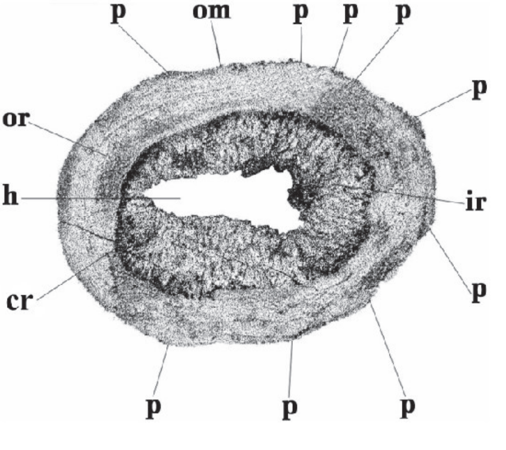

Fig. 3. Rounded phosphatic structure (H skeletal element) from the Lower Triassic deposits of Primorsk Terr., specimen DVGI 3B-1 (*om*, outer margin; *p*, projection; *cr*, circular ridge; *or*, outer ring; *ir*, inner ring; *h*, hole);

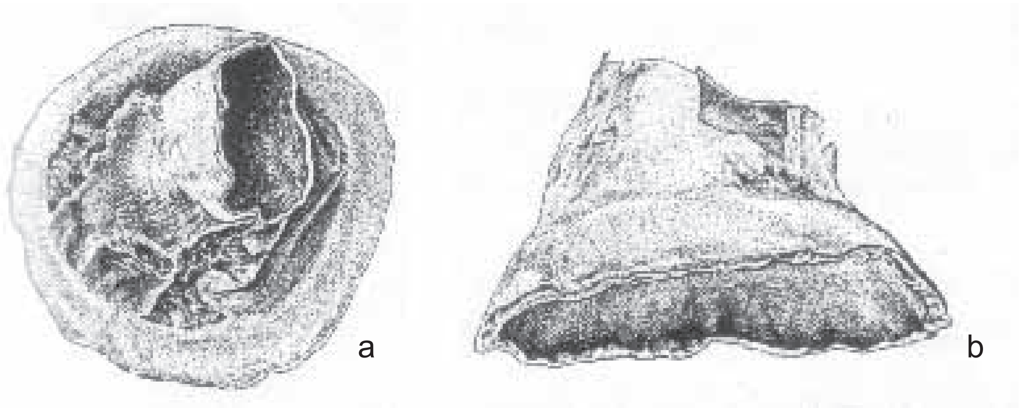

Fig. 4. Rounded phosphatic structure from the Upper Silurian deposits of Germany, specimen UB no. 532 (after Müller et al., 1974) (a, rounded structure coated with a soft connective tissue; b, cap of the soft connective tissue).

combined with this structure and attached on the circular ridge with the help of its projections, the connective tissue widened and coated the structure surface beginning from the circular ridge towards the outer margin of the ring, then it was bent downward from the outer margin to its lower surface, and then bent again and extended on the lower surface over a small distance towards the center (see Taf. 18, Figs 1a, 1b, and 1c in Müller et al., 1974).

Probably, the remains of this connective tissue are present in the Granton animal imprint as a dark band on the outer ring and in part on the inner ring in the center of this structure (the remains of the tube). Apparently, such a connective tissue coats the rounded structure in specimen GSSA C721 from South Africa.

In Fig. 1b on Table 18 in the paper by Müller et al. (1974), one can see such a connective tissue as being mounted on the rounded phosphatic structure. On the wrecking of this tissue, isolated bunches of darker colour are clearly seen. They are suggested to be muscular tissue impregnated into a thick tube of the connective tissue, which narrows upwards from the rounded structure.

About the function of the rounded phosphatic structures (H elements) and their soft tissues in euconodont animals

Our analysis has revealed a great similarity of the rounded structures discussed above. One can observe identity of all details of their morphology and ontogenetic stages. Only the sizes of these structures are somewhat different. They vary from 0.13 mm in the finest “rings” from the collection of Müller et al. (1974) to 3.1 mm in the imprints from Soom Shale of South Africa. These variations are not beyond the scope of individual variability.

A serious barrier to the unification of these rounded structures is the fact that they are considered soft tissues composed of a white organic material with fibrous texture in the imprints of euconodont animals from Granton and Soom Shale (Donoghue et al., 2000), whereas the rounded structures from Primorsk Terr. and from the collection of Müller et al. (1974) are composed of solid calcium phosphate and have a lamellar texture. However, the material from the collection of Müller et al. (1974) demonstrates that these rounded structures were coated in their lifetime with a soft connective tissue like a cap, and it is natural that the connective tissue has been preserved in the imprints of the euconodont animal in its lifetime state. This is especially well seen in specimen GSSA C 721 from South Africa, in which the connective-muscular tissue completely coats the solid structures, and in part it is observed in specimen 5 from Granton. So, when discussing the rounded structures existing on the imprints, it is important to take into account the fact that in lifetime state these solid phosphatic structures were completely coated with a soft connective-muscular tissue.

As the paper by Müller et al. (1974) was published before the important findings of the euconodont animal imprints, those workers could not compare their “rings” with the rounded structures present in imprints from Granton and Soom Shale. Müller et al. (1974) were restricted in their suggestions, and this explains why they assigned the “rings” to the colonial Hyolithelminthes Fisher, 1962. The rounded structures from the Lower Triassic of Primorsk Terr. were found in 1974 and have been placed under problematic in our collection. Only after publications on the unique imprints from Granton and Soom Shale it became clear that the rounded structures from Primorsk Terr. belong to euconodont animals.

The complete similarity of all solid rounded structures testifies that they belong to euconodonts, as the imprints from Granton and Soom Shale, and suggests the commonness of their origin and function. As the rounded structures are composed of such a solid material as calcium phosphate, there is no need to suggest further that they were scleritic cartilages surrounding the eyes of euconodont animals. Moreover, the association of the rounded structures with traces of the connective-muscular tissue may indicate just the function of this tissue is to connect the euconodont elements and to govern them in work.

Probably, it would be more correct to compare the rounded structures of euconodonts with the attaching skeletal plates of modern chaetognaths. In chaetognaths, the chitinous hooks and the prehensile apparatus teeth are governed just by the attached to them two prolate semi-transparent plates arranged on the ventral and dorsoventral sides of the head. Besides, these skeletal plates served the support, to which all muscular tissues of the animal were attached (Kasatkina, 1982, p. 16, Fig. 6b).

Eventually, we are inclined to believe that the rounded head structures of euconodonts (H elements) are analogous to the skeletal attaching plates of chaetognaths. The Granton animal imprints demonstrate that they were arranged in pairs in the anterior part of the head in front of the tooth apparatus symmetrically to the euconodont sagittal axis. The H skeletal elements appear to be a part of the mouth assemblage of the euconodont animal. Other elements of the mouth assemblage are the pharynx, P, M, and S elements of the tooth apparatus, and muscles (connective-muscular tissue). The connective muscles, the remains of which have been preserved on the "rings" from the collection of Müller et al. (1974), were most likely attached to the projections of the outer margin and circular ridge of the H elements.

Conclusion

The presence of the skeletal attaching plates (H elements) in euconodonts makes unique the structure of their head and of the whole animal. The euconodont mouth is arranged along the sagittal axis between the H elements. Immediately behind the H elements there are S elements. They are connected to and governed by the attaching connective-muscular tissue (fibres) that starts from the H elements coating them. Here also the pharynx starts extending further backwards, and, where it widens, two pairs of P elements are arranged above and below. M elements are probably arranged not far from S elements or in front of the mouth entry. Sagittal arrangement of the H skeletal elements makes the euconodont animal quite different from fish and all of chordates.

Thus, the presence of the rounded structures (H elements) in the head part of euconodonts gives further support to recognize them as a separate type, Euconodontophylea (Kasatkina & Buryi, 1999).

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