Specific features of the head region in euconodont animals

Особенности строения головной части эуконодонтовых животных

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New data on morphology of the head region of euconodonts are discussed based on a study of its imprint from the Lower Carboniferous deposits of the Polar Urals (Russia); on its external ventral surface, the animal had an oval expansion of the head region, supposedly, a mouth food sac. A similar structure is also described in one of the imprints from Granton (Great Britain) exposed from internal surfaces. A hypothesis is put forward on the mechanism of functioning of the feeding apparatus in euconodonts which consists of hard S, M, and P tooth elements and *H* attaching skeletal elements as well as soft connective structures. The food sac probably served for filtering food particles from the water which was removed through special openings and for formation of the food bolus and transferring the latter into the alimentary canal (gut). These data gave to reasons for a new interpretation of feeding behaviour of euconodonts. It is suggested that the euconodont animals were filter feeders adapted to the near-bottom dwelling over substrates, where there was greatest concentration of small food items available for filtration.

Обсуждаются новые исследования морфологии головного отдела эуконодонтовых животных на материале отпечатка из нижнекарбоновых отложений Приполярного Урала (Россия), на внешней вентральной стороне которого наблюдается овальное расширение его головной части; сделано предположение, что это образование является пищевом мешком. Аналогичная структура также описана у одного из отпечатков из Грантона (Великобритания), обнаженного по внутренним плоскостям. Выдвинута гипотеза о механизме функционирования находящегося в пищевом мешке ротового аппарата эуконодонтовых животных, состоящего из твердых S, M, P зубных и H прикрепительных скелетных элементов, а также мягких соединительных образований. В нём, возможно, происходила фильтрация пищевых частиц от воды, которая удалялась через специальные отверстия, формирование пищевого комка и продвижение его в пищевой канал (кишку). Эти данные дают основание по-новому интерпретировать пищевое поведение эуконодонтов. Сделано предположение, что они являлись плавающими фильтраторами и были приспособлены к придонному обитанию, вблизи донного субстрата, где находилась наибольшая концентрация мелких пищевых объектов, доступных для фильтрации.

Key words: euconodonts, imprints, morphology, feeding, filtration, Euconodonta, Lower Carboniferous

Ключевые слова: эуконодонты, отпечатки, морфология, питание, фильтрация, Euconodonta, нижний карбон

INTRODUCTION

In the middle 1980s, in the Lower Carboniferous Shrimp bed of Granton (Great Britain), there were found several imprints of different states of preservation of the inner sections of a soft body of the unknown animals with an euconodont tooth apparatus in their head region (Briggs et al., 1983; Aldridge et al., 1986). Later (Buryi et al., 2010), a complete, uncovered on the outer side imprint of an euconodont from the Lower Carboniferous shales of the Polar Urals (Russia) were discovered. These findings served the basis for a detailed study of important morphological characters of euconodonts, first of all those connected with the head region, and the H skeletal attaching elements that earlier were considered to be the eye structures were described (Buryi & Kassatkina, 2003, 2004). Studies on other head structures of euconodonts continue. It is notable that when studying the euconodont imprints from Shrimp bed of Granton, Aldridge with co-authors (Aldridge et al., 1993, p. 410) first marked an obvious paradox in the arrangement of the tooth apparatus relative to other structures of the head: "Although the apparatus of specimen 1 is preserved in the standard lateral configuration, the symmetry of the eyes and other soft tissues in the head suggests the dorsoventral flattening". These researchers revealed also the fact that "in specimens 1 and 4 the feeding apparatus lies close to the line of the trunk axis, reflecting a dorsoventral orientation of the anterior of the animal. In the most specimens, however, the elements, although retaining their configuration within the feeding apparatus, are consistently offset to one side of the trunk axis and extend beyond the preserved traces of soft tissue (specimens 2, 5, 6, 8 and 10)" (Aldridge et al., 1993, p. 410).

Our investigations of imprints of euconodont animals from Granton (type collection kept in the Museum of Natural History in London) confirm the fact that these tooth apparatuses truly display an unusual arrangement relative to other head structures. In specimen 1 (described by Briggs et al., 1983), two rhomb-like lobes belonging to the H skeletal attaching plates (Buryi & Kassatkina, 2004) and an opening between them leading to the mouth occur in the frontal projection symmetrically to the trunk axis, while the tooth apparatus, in the lateral projection. This apparent discordance in the position of different parts of the anterior of the animal was initially explained by possible consequences of the degradation of tissues supporting the mouth tooth apparatus that could result in its offset relative to other structures of the head (Morris, 1989; Aldridge et al., 1993). Interesting is also the fact that the tooth elements on the imprints are arranged rather regularly in separate groups. Immediately behind the H-skeletal elements, there are Sc, Sb, and M ramiform elements oriented obliquely to the animal axis. Farther backward, single ozarkoginoform Pb elements are placed, and, a little posterior, scaphate platform Pa elements lie with their axes perpendicular to the animal axis. The tooth apparatus of specimen 2 from Granton is composed also of ramiform (S and M) and pectiniform (P) elements, which lie, in contrast to specimen 1, at a distance of 1.5 mm beyond the animal body. The tooth apparatuses in imprints 4 and 5 are arranged in a similar way (Aldridge et al., 1986). However, at present, there is no explanation to the fact that the tooth apparatuses are, in most cases, oriented in the projection different from that of other head structures and lie as if beyond the trunk of euconodont animals.

The purpose of this article is to discuss some new data on the structure of the head region of euconodonts in order to explain the existing contradictions. New insights into functional roles of ramiform, pectiniform, and H connective elements and soft connective structures will allow to hypothesise on functioning of the feeding system in the whole group of euconodonts.

MATERIAL AND METHODS

Material examined. An imprint of an euconodont animal from the Lower Carboniferous of Polar Urals, **Russia**: specimen DVGI 2007 Tz-59-1/95 (Buryi et al., 2010). Eight imprints of euconodont animals from the Lower Carboniferous, Granton shrimp bed of Edinburgh, Scotland, **UK**: specimen 1, IGSE 13821 (part) and 13822 (counterpart) (Briggs et al., 1983); specimen 2, RSM GY 1986.17.1, part and counterpart (Aldridge et al., 1986); specimen 3, HU Y221, part and counterpart (Aldridge et al., 1986); specimen 4, BM X1065, counterpart (Aldridge et al., 1986); specimen 5, RMS GY 1992.41.1, part and counterpart (Aldridge et al., 1993); specimen 6, RMS GY 1992.41.2, part and counterpart (Aldridge et al., 1993); specimen 8, RMS GY 1992. 41.4, part (Aldridge et al., 1993); specimen 10, HU Y35a,b, part and counterpart (Aldridge et al., 1993).

The imprint of the euconodont animal found on the territory of Russia was studied using a MBC-10 microscope. It was established that it is a long (about 4.8 mm), narrow (0.3–0.4 mm), worm-like body with the exposed outer side, slightly curved in horizontal and vertical planes (see Buryi et al., 2010, p. 150). This imprint of the euconodont animal was also studied using a scanning electron microscope ZEISS EVO 50XVP without spraying of its surface. Observations were carried out in the regime of the secondary electrons at accelerating voltage of 20 kV. With small magnifications (×50), a total image of the euconodont animal body was obtained. With magnifications of 120 to 10000 times, numerous details of its structure are visible. Most interesting are the fibrous structures, first found on the surface of the euconodont animal. They are isolated fiber-like formations about 0.3×10^{-5} m thick and 1×10^{-5} m to 0.7×10^{-4} m long arranged as a rule by diagonal or across the euconodont body (Buryi et al., 2010, p.151).

DESCRIPTION OF MOUTH FOOD SAC OF EUCONODONT ANIMALS

While studying the morphology of the head region of the imprint from the Lower Carboniferous deposits of the Polar Urals (Buryi et al., 2011), we found an oval mouth broadening on the ventral side of the animal. As the Ural specimen is uncovered on the outer side, the tooth apparatus, situated, in our ideas, inside this broadening, is not visible. In the connection with this feature of our specimen we referred to the imprints of the earlier discovered euconodont animals from the Lower Carboniferous deposits of Granton (Aldridge et al., 1993). It was established that the head region of specimen 5 from Granton on the ventral inner side has also a significant broadening of the animal trunk, which, maybe, was an accumulating sac too (Fig. 1). Inside this food sac, there is a soft lobe with a branched system of muscular fibers with the ramiform and pectiniform tooth elements attached to them. We think that these tooth elements with the help of the soft lobe were connected with each other and with the paired skeletal H elements (Fig. 2). Most likely, the same muscular fibers governed the position and sizes of the mouth food sac. The soft food sac appears to be able to broaden and take big volumes of food. When the accumulating sac was filled with water and food particles it stretched and became broadened (as it often observed in nature in many animals of different groups). When muscles contracted, the sac was pulled up to the head and shrunk. Such state is observed in specimen 1 from Granton, where, in our opinion, the food sac is compressed and pushed to its apical part. The food sac of the Ural specimen appears also to be empty or not straightened. The external morphology of the head region of euconodont animals suggests that initially food together with water was supplied to the mouth cavity through the slit-like mouth situated between the H attaching elements (Fig. 3). Fine food, composed, most likely, of detritus, bacteria, and unicellular algae (Aldridge & Purnell, 1996), was together with water pulled into the sac-like constituent (accumulating sac). Then it arrived onto the “sieve” of S elements, which performed intricate movements in the accumulating sac. With their help the fine food

Fig. 1. Head region of specimen 5, RMS GY 1992.41.1., Granton, Scotland; from Aldridge et al. (1993).

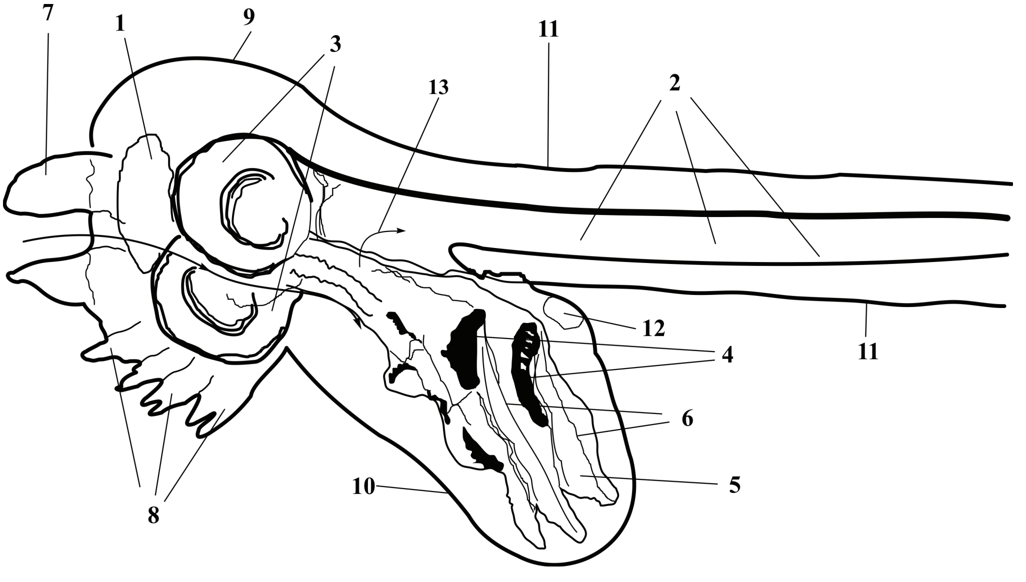

Fig. 2. Interpretative scheme of head region of specimen 5, RMS GY 1992.41.1., Granton, Scotland (anterior to left): 1, mouth; 2, putative food canal (gut); 3, H skeletal elements; 4, tooth elements; 5, soft muscular lobe; 6, muscular fibers; 7, tentacles (tactile, sensitive, and for driving food items); 8, head lobes; 9, head boundary; 10, boundary of food sac; 11, wall of body; 12, putative water outflow opening; 13, gut entry opening.

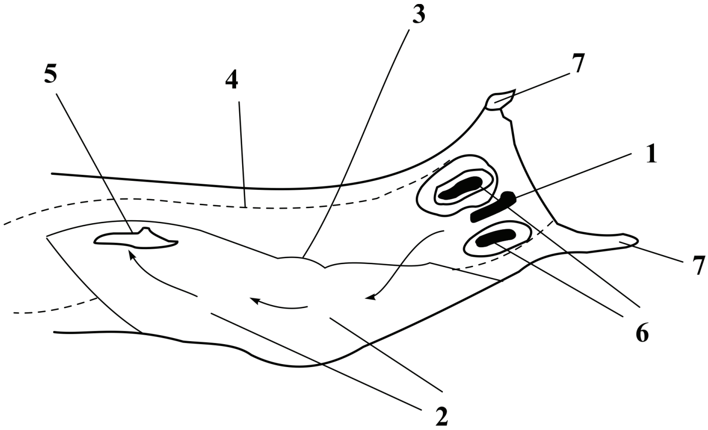

Fig. 3. Interpretative scheme of head part of specimen DVGI 2007 Tz-59-1/95 from Polar Urals, Russia (anterior to right): 1, mouth opening; 2, food sac; 3, food sac boundary; 4, putative gut boundaries; 5, putative opening for water outlet; 6, H skeletal elements; 7, tentacles.

particles were filtered and moved towards the P elements, where they were pressed up to form the food clot that with the help of muscles moved to the pharynx and farther along the gut channel. In our opinion, water came out from the food sac through the paired openings located on the sides of the animal head. On the Ural imprint, in the back of the food sac, one can observe openings on both left and right sides of the head, through which the filtered water went out. The statement that the clearly visible tissue on this imprint, surrounding the openings of the food sac, may be relevant to the operculum, has no reason, because the openings in the sac are small-sized and do not have any skeletal supporting structures. It could be supposed that the comparatively small size of these openings were needed to keep food particles and small animals in the food accumulating sac.

DISCUSSION

The detailed study of the arrangement pattern of the head structures on the euconodont animal imprints from the Polar Urals and Lower Carboniferous deposits of Granton established that their tooth apparatuses in many imprints are placed beyond the body not by accident. They were found in the accumulating food sac situated on the outer ventral side of the animal body below the longitudinal axial line. The ramiform S and M elements were, most likely, adopted to filter the food fine particles and were situated in the food sac frontal part obliquely to the animal axis. P elements were arranged perpendicular to the axis nearer to the pharynx (Aldridge & Purnell, 1996). P elements helped to structurise the food clot and to move it into the pharynx and farther into the gut for digestion. All tooth elements, including S, M, and P ones, could move within the food sac due to the muscles attached to them, depending on the animal physiological state. Only the entity of the food sac correctly explains the position of the tooth elements in the fossilised state in imprints from Granton as well as their occurrence as if beyond the body. In fact, they do not lie in the body of the euconodont animal. All tooth elements are in the food sac situated on the body outer side. In the sac, the food particles were filtered from water, water was removed through the openings, and the food clot was formed and moves into the feeding canal (gut). Depending of the head position in a individual euconodont animal in the fossilised state, the details of the head structure and the outer tooth elements of the apparatus, placed in the food sac, might coincide. Existence of the food sac is not a unique phenomenon in the animal world. The mechanism of the function of accumulating organ in the form of a sac under beak (pelicans) or cheek poaches (hamsters) is well known in different groups. New data obtained on the head structure of the euconodont animal allow new interpretation of their behavior and nutrient habits. The head segment of euconodonts occupies rather large part of the body (about 18%). This may testify that they were, probably, the filter feeders in contrast to animals, for example, in protoconodonts (Chaetognaths), which had the length of the head segment not more than 5–8% of the total body length (Kassatkina & Stolyarova, 2010). They were adapted to the near-bottom dwelling over substrates in water layers rich with small food items available for filtration. The established specific features of the head region can be the main argument to substantiate the phylogeny and, probably, the taphology of the euconodont animals under study.

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