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THE PROBLEM OF THE RELATIONSHIP BETWEEN AGNATHAN
AND GNATHOSTOME VERTEBRATES

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Materials of the earliest vertebrates: Heterostraci and Thelodonti, were studied and compared with these of sharks. It is concluded that the main features of Heterostraci (olfactory apparatus, brain, lateral line sensory system, gill pouches) are similar with sharks. At the same time sharks display their own distinctive archaic features that bring them close to the Thelodonti. It cannot be excluded that the roots of Elasmobranchii were connected with the Thelodonti.

Key words: Agnatha, Gnathostomata, evolution, phylogeny, morphology.

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The problem of the relationship between Agnatha and Gnathostomata is one of the most obscure in phylogenetics. The hypothesis of the diphyletic origin of Cyclostomata which relates myxinoids (hagfishes) with the Heterostraci, is widely accepted (Stensiö 1932—1968; Berg 1940; Jarvik 1960, 1968; Janvier 1974, etc.). Other workers, however, have criticized either some aspects of the hypothesis or rejected the very idea of such a relationship (Säve-Söderbergh 1941; Obruchev 1945, 1949, 1964; Tarlo 1961; Heintz 1962, 1963; Halstead and Whiting 1965; Halstead 1973). The latter point of view is not confirmed by a system of proofs based on a sufficiently complete morphological analysis of cyclostomes, gnathostomes, and Palaeozoic agnathans.

In the phylogenetic schemes which assume the diphyletic hypothesis and also take into account interpretations of markings of the internal organs, all the Palaeozoic agnathans including the Heterostraci are referred to cyclostomes. The Cyclostomi and the Gnathostomi are in this scheme considered to be two separate branches, which diverged in the Precambrian (Jarvik 1968). It is also assumed that the cyclostome stage could not be the initial one which lead to the Selachii (Jarvik 1960). In the present paper the problem of the relationship between the Heterostraci and myxinoids is analysed. The analysis is based on examination of about 1200

examples of cyathaspid, amphiaspid, and pteraspids (Heterostraci), from the USSR and Spitsbergen. The collections are deposited in the Paleontological Institute of the USSR Academy of Sciences (Moscow) abbreviated as PIN.

It has been established (Novitskaya 1974, 1975) and is now confirmed by a study of the additional material that the Heterostraci are distinguished from the myxinoids by a number of anatomical characters:

1. Structure and disposition of divisions of the brain: the myelencephalon of the Heterostraci does not embrace the other divisions of the brain; unlike the medulla oblongata of myxinoids it is separated from the mesencephalon by a clear isthmus (fig. 1 and 3). These features of

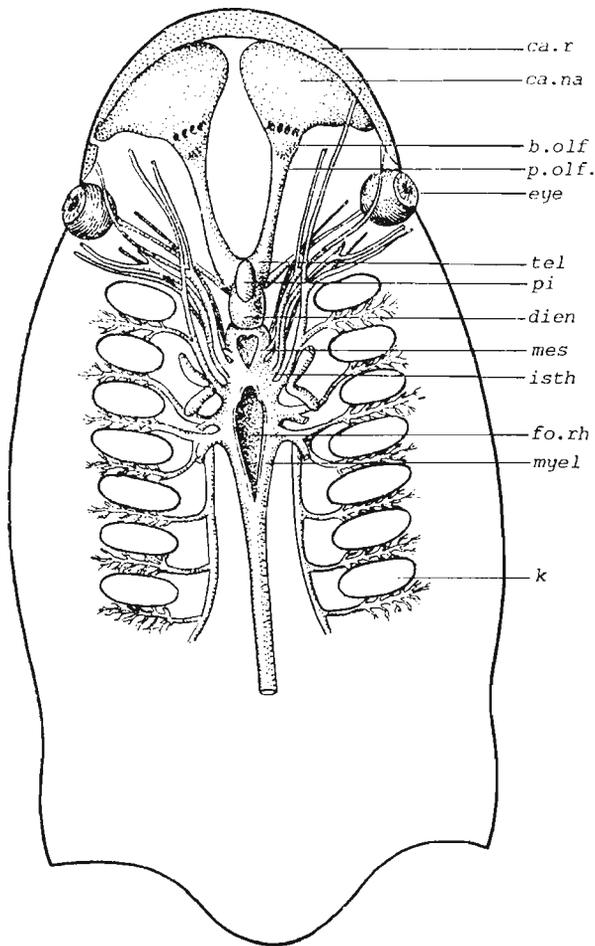


Fig. 1. Reconstruction of nasal sacs, brain and cranial nerves of an heterostracan: cyathaspid, *Poraspis pompeckji* (Brotzen). Abbreviations for figs 1—4: *b. olf*—bulbi olfactorii, *ca. na* capsula nasalis, *ca. r* cartilago rostralis, *corp. cer* corpus cerebelli, *dien* diencephalon, *fo. rh* fossa rhomboidalis, *isth* isthmus, *k* place of gill pouches, *mes* mesencephalon, *myel* myelencephalon, *oc* eye, *p. olf* pedunculi olfactorii, *pi* pineal organ, *s.c* semicircular canals, *tr. olf* tracti olfactorii, *tel* telencephalon.

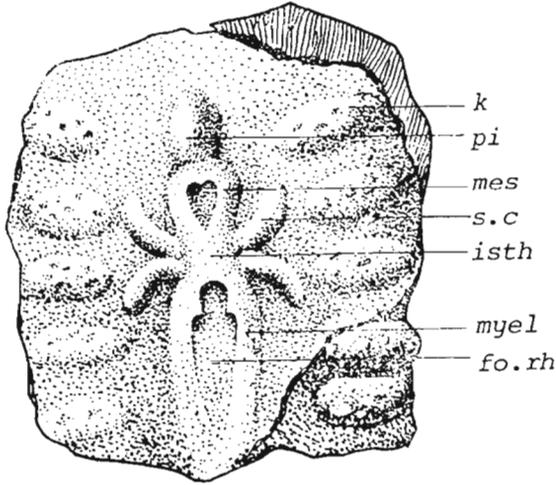


Fig. 2. *Poraspis pompeckji* (Brotzen), dorsal shield showing moulds of brain, pineal organ, semicircular canals and gill pouches. PIN 3592/76. k moulds of gill pouches, other abbreviations as for fig. 1.

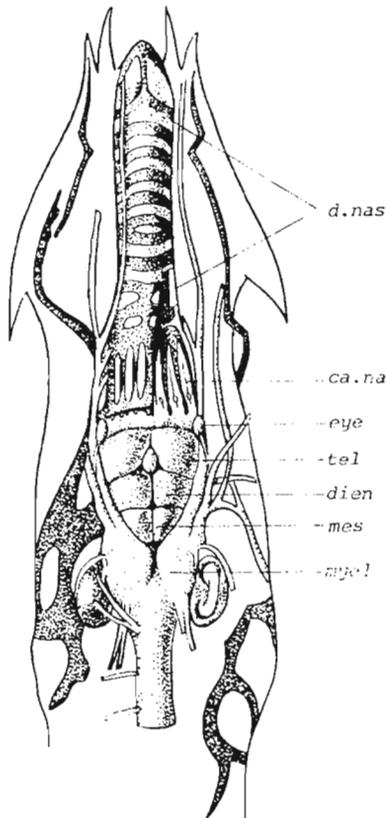


Fig. 3. *Myxine glutinosa* L. Brain and nasal region (after Marinelli and Strenger 1956, with simplifications). Abbreviations as for fig. 1.

brain structure of Heterostraci are clearly visible in some specimens of cyathaspids of Podolia (*Poraspis pompeckji* Brotzen, PIN 3592/76: fig. 2). As is known, the myxinoid brain has unusual features in the structure of the myelencephalon, which distinguish it from the brain of other vertebrates. At the same time, in the earliest stages of embryogenesis it is similar to the lamprey's brain (Conel 1929; Pasteels 1958). These facts favour a relationship between hagfishes and lampreys. It should be mentioned that an indubitable argument in favour of the relationship between these cyclostomes is the similarity of structural type of their head, formed as a result of peculiarities of ontogenesis (enlargement of the upper lip), different from that in gnathostomes and the Heterostraci.

2. In different groups of Heterostraci, it is stated that there is no prenasal sinus (Heintz 1962; Novitskaya 1973, 1974). On the other hand the homology of the prenasal sinus (nasal tube) of myxinoids and the prenasal sinus of the Cephalaspidomorphi (extracephalic space, according to Stensiö 1968) allows one to unite the myxinoids with the cephalaspidomorph branch of the vertebrates.

3. The Heterostraci, as well as some myxinoids, have in their visceral apparatus one pair of exhalant gill openings. However, this common character is not the result of a profound similarity in the visceral system. In the Heterostraci there is no *ductus pharyngocutaneous* typical of myxinoids; the gill pouches of the Heterostraci are much larger and are not surrounded by peribranchial sinuses. The latter is proved by the presence of the markings of blood vessels on the gill pouch surface. The number of pouches (up to 15 pairs) in some myxinoids is close to that of the Osteostraci which have 10—11 pairs of pouches.

4. In the Heterostraci the roof of the mouth cavity is composed of the visceral constituent of the endoskeleton (premandibular arches). In this respect they are similar to all vertebrates, myxinoids included. But the absence of a respiratory duct (prenasal sinus, after Stensiö 1964) between the visceral part of the roof of the stomodeal invagination and the dorsal surface of the head does not make the Heterostraci close to the myxinoids.

5. The mouth apparatus of the Heterostraci, consisting of oral plates placed in the skin folds on the lower margin of the mouth, cannot be compared to the mouth apparatus of myxinoids.

The above characters show that the Heterostraci and myxinoids are markedly different in the major features of their organization. Points 1—3, however, show close similarities between the myxinoids and the Cephalaspidomorphi. The roots of the myxinoids were undoubtedly connected with vertebrates evolving in the same direction which gave rise to the Cephalaspidomorphi, though at present it is hardly possible to determine among the Cephalaspidomorphi a definite ancestral group from which the Myxinoidea could have been derived. *Jamoytius*, which is sometimes mentioned as a form ancestral to myxinoids, has a dorsally dis-

posed naso-hypophyseal opening which in itself excludes it from the possible ancestors of myxinoids (Novitskaya 1976).

From the above characters it is clear that there is to some degree a morphological similarity between the Heterostraci and the most archaic gnathostomes. A more detailed analysis can distinguish some of the main characters bearing on the solution of the relationships problem.

1. The telencephalon of the Heterostraci and the lower Gnathostomes is differentiated into *tracti* and *bulbi olfactorii* (figs 1, 4). In this respect the brain of the Heterostraci is particularly similar to that of sharks. This differentiation is one of the main differences in organization of the gnathostomes and the cephalaspidomorph vertebrates.

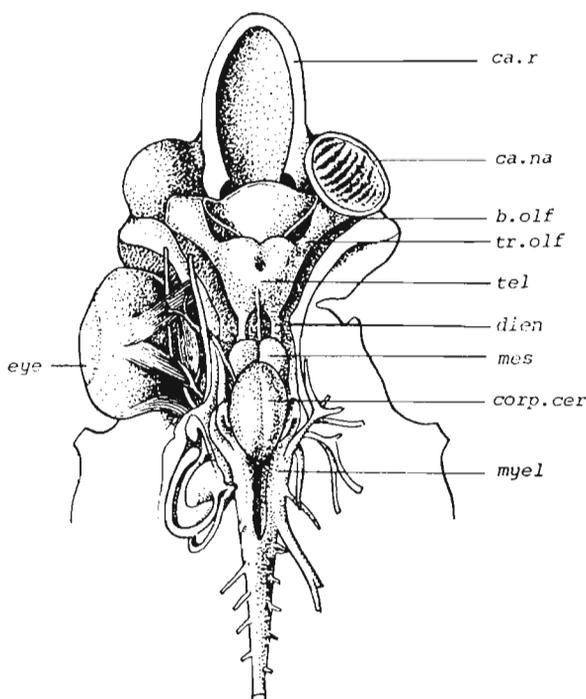


Fig. 4. *Squalus acanthias* L. Brain and nasal region (after Marinelli and Strenger 1959, simplified). Abbreviations as for fig. 1.

2. Nasal sacs of the Heterostraci are not displaced on the dorsal side of the head by the enlargement of the upper lip (post-hypophyseal fold). The absence of this enlargement indicates a similarity of morphogenetic processes, which have determined the development of the head at the earliest stages of ontogenesis in both Heterostraci and gnathostomes. At the same time these processes were radically different from those forming the structural plan of the head in the cephalaspidomorph-cyclostome group.

3. Gill pouches are large in the most ancient Heterostraci (cyathaspids) and gnathostomes (sharks). Their number is similar in both groups. There are obvious differences in their position concerning visceral arches, though the transition from one state to another is possible (see below).

4. Sensory canals of the head are, in their length and mutual position, similar in the Heterostraci and in shark embryonic stages. The similarity in certain features of organization is also noticeable in the lateral line sensory system of the Heterostraci and other gnathostome fishes: acanthodians, crossopterygians and palaeoniscides. (This problem is considered in more detail in a special chapter of a monograph being prepared by the author).

5. The histological composition of the exoskeleton is similar in non-cephalaspidomorph Palaeozoic agnathans (the Heterostraci, Thelodonti) and in archaic gnathostomes (Chondrichthyes). In both groups it is formed by dentine, an enamel-like layer and non-cellular bone. The presence of placoid scales is one of the most typical characters of cartilaginous fishes and thelodonts.

The first, second and fourth characters discussed above show that the Heterostraci were evolving in the same direction as the Gnathostomata, but not in the direction of cephalaspidomorphs which gave rise to the Cyclostomata. Point 3 (first part) and 5 indicate the similarity with sharks. Stratigraphically non-cephalaspidomorph agnathans (the Heterostraci and Thelodonti) appeared earlier than gnathostomes. They also have a lower level of organization. In such temporary and morphological correlations the probability is too low that the Gnathostomata acquired the same fundamental structural features independently of the agnathans. Although a direct relationship between the Agnatha and Gnathostomata is obvious, it is difficult to define more precisely the connections between them because of the complete absence of data on thelodont internal structure. Certain difficulties are connected with the recognition of criteria of primitiveness within the Gnathostomata and distinguishing among their ancient groups the most primitive, i.e. which is the closest to the probable ancestral state. I suggest that for criterion of primitiveness of groups of gnathostomes there is a degree of similarity with Palaeozoic agnathans. Among them only the Heterostraci can be considered to be a group suitable for such comparisons. Firstly, they are one of the most ancient vertebrate groups, which evolved in the same direction as the true gnathostomes. Secondly, they have been known well enough for comparison with other fishes in their main organ systems.

The author's comparison of the Heterostraci with Placodermi which are usually placed at the base of the gnathostomes, and the comparison with elasmobranchs have shown that the Elasmobranchii possess the greatest similarity with the former. The similarity between the Heterostraci

and placoderms is marked only in three characters, which are also common for Heterostraci and sharks: brain structure, the general pattern of sensory lines, shape and position of nasal sacs. At the same time the differences between placoderms and Heterostraci are so great (the pattern of plates in the armour, histological composition of the exoskeleton, ossification in endocranium of the most ancient placoderms, the dorsal position of their nostrils, etc.) that, proceeding from the now known palaeontological material, it is not possible to reconstruct the transition in the level of organization from Heterostraci to Placodermi.

The sharks belong to a group whose morphology combines advanced features, which accounts for their flourishing in both the Recent and Palaeozoic fauna, with rather archaic characters showing their closeness to the Agnatha. The archaic characters include the presence of gill pouches, a large number of gill openings (up to seven), the absence of gill covers, the presence of large spiracles, placoid scales and the absence of any essential difference between the body scales and teeth in the mouth cavity, the preservation of the arrangement of teeth in rows similar to those of scales and the structure of the telencephalon and the neurocranium which is a single and very simply organized box. The view that the endocranium of sharks is less primitive than in crossopterygians (Bjerring 1968; Jarvik 1968) is unlikely to be correct. The endocranium of sharks is devoid of the intracranial articulation typical of crossopterygians. The articulation is treated by the above mentioned authors as a primitive feature. This view is based on the opinion that the intracranial joint is a homologue of intervertebral articulations. However, if we survey vertebrate evolution with regard to its most ancient stages, the absence of the intracranial joint should be recognized as a more primitive feature than its presence. The absence of this articulation in the neurocranium of sharks is a feature typical also of the most ancient vertebrates — early Palaeozoic agnathans, which were at an evolutionary stage when vertebrae had not yet arisen.

The idea that placoid scales are highly specialized (Stensiö 1962) has also not been proved. The typical placoid scales of thelodonts are undoubtedly primitive. In sharks they are also primarily primitive, not secondarily simplified. A more detailed discussion of this problem is given in a monograph on the Heterostraci now in preparation.

In the transition from the Agnatha to Gnathostomata, the explanation of transformations in the visceral and oral apparatus is particularly difficult to envisage. The hypothesis given below suggests a way leading to the transformation of visceral structures. Before outlining the hypothesis, it should be emphasized that the position of gill pouches inside the visceral skeleton is generally considered to be one of the main characters distinguishing Cyclostomi from Gnathostomi. In fact it is not a specializa-

tion of Cyclostomi only. A study of fossil vertebrates shows that such positions of pouches inside the visceral skeleton is typical of all ancient groups: Heterostraci, Osteostraci, Anaspida, Turiniida and Thelodonti. This is evidence that this state is archaic in the evolution of vertebrates. The presence of gill pouches is also a primitive character. Apparently in Palaeozoic vertebrates, as well as in modern ones, they had a mixed ento-ectodermal origin. It seems quite probable that gill filaments in Palaeozoic forms were developed in both parts of the pouch. In this case the transition from such pouches to the ectodermal ones of gnathostomes could take place in the presence of some hypothetical elements, i.e. a series of internal postmandibular cartilaginous arches, placed on the border of the ento- and ectodermal parts of the pouch. The transition from pouches to the gnathostome condition in this case includes comparatively few transformations: 1) reduction of external gill arches, equivalent remains of the latter are the extrabranchialia of sharks, 2) the growing importance of the role of the internal cartilaginous arches and their further differentiation. The existence of the internal and external gill arches in myxinoid embryos (Holmgren 1942) supports our hypothesis, though it certainly does not mean that myxinoids are related to the Heterostraci. The presence of internal arches in myxinoids demonstrates only preservation of the most ancient states in their ontogenesis. The above transition scheme is obviously simplified if the individual openings of gill pouches were present. Among non-cephalaspidomorph vertebrates such a state is typical of thelodonts.

The palaeontological material so far studied yields no data on the origin of jaws. Evidently it must have started at a fairly primitive level, perhaps among Ordovician agnathans.

The material studied suggests that the Heterostraci evolved in the same direction that gave rise to the Gnathostomata and have no bearing on the origin of the cyclostomes. The undoubted similarity in heterostracan structures to those in the gnathostomes (Elasmobranchii) can be explained as having been inherited by the sharks from the morphological level of agnathans. Some morphological peculiarities of thelodonts permit to suppose that they are an ancestral group for the Elasmobranchii. These peculiarities are as follows: placoid scales with a histological composition similar to that in sharks, exhalant openings of each gill pouch, epicercal caudal fin, the presence of primitive paired and unpaired fins. The Placodermi, also an archaic group of Palaeozoic fishes, evolved separately from the other Gnathostomata, possibly forming divergent lines with the most ancient sharks.

In general, the above groups show that the distribution in time of the main stems of both agnathans and gnathostomes constituted a group of branches which can be traced back to non-cyclostome vertebrates.

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O POWIĄZANIACH FILOGENETYCZNYCH MIĘDZY AGNATHA
i GNATHOSTOMATA, VERTEBRATA

Streszczenie

W niniejszej pracy przeprowadzono analizę morfologiczno-porównawczą wczesnych kręgowców, zwłaszcza Heterostraci i rekinów. Stwierdzono, że w głównych rysach budowy (aparatus węchowy, mózg, system linii bocznej, oddzielne worki skrzelowe) grupy te są do siebie podobne. Rekiny wykazują jednocześnie archaiczne cechy zbliżające je do Thelodontia. Na tej podstawie można przypuszczać, że Elasmobranchia wywodzą się z Thelodontia.

ЛАРИСА И. НОВИЦКАЯ

ПРОБЛЕМА РОДСТВЕННЫХ СВЯЗЕЙ МЕЖДУ БЕСЧЕЛЮСТНЫМИ
И ЧЕЛЮСТНОРОТЫМИ ПОЗВОНОЧНЫМИ

Резюме

В сравнительно-морфологическом аспекте были изучены древнейшие позвоночные (главным образом гетеростраки) и акулы. Установлено, что в основных чертах организации (обонятельный аппарата, головной мозг, система боковой линии, отдельные жаберные мешки) гетеростраки сходны с акулами. В то же время акулы имеют архаичные признаки строения, сближающие их с телодонтами. Возможно, что эласмобранхии берут начало от телодонтов.