



PHYLOGENETIC RELATIONS BETWEEN FOSSIL AND RECENT AGNATHA

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ABSTRACT

The investigation of the structure of Heterostraci has shown that their structural pattern is not stable. This permits them to evolve both towards Cyclostomata and Gnathostomata. In a number of features Heterostraci were much more closer to Osteostraci than it has been previously thought. From the latter recent cyclostomes originated whereas Heterostraci seem to be connected with gnathostomes.

A series of brilliant works of E. Stensiö (1927-1968), who has suggested the hypothesis of the diphyletic origin of recent cyclostomes, has given the way to a many-year discussion centered round the morphology and phylogenetic relations of Heterostraci. Two points of view are especially popular in interpreting Agnatha's affinities. According to one of them Heterostraci are ancestors of myxines (Stensiö, 1927, 1958, 1964, 1968; Lehman, 1959; Jarvik, 1960, 1968; Janvier, 1974, 1975), supporters of other interpretation do not relate them to myxines, considering Heterostraci as a blind branch (Obruchev, 1945, 1966; Balabaj, 1956) or as a possible initial group of gnathostomes (Nikol'sky, 1954; Bystrow, 1957; Tarlo, 1961). Unfortunately, the latter point of view is practically unsupported by proofs. At the same time, lampreys and myxines are considered as a monophyletic group (Severtzov, 1939; Obruchev, 1945; Balabaj, 1956; Romer, 1966, and others), tracing its origin from primitive Cephalaspidomorphi or as a diphyletic group where lampreys are believed to originate from Cephalaspidomorphi, and myxines from Heterostraci (Stensiö, 1927-1968; Jarvik, 1968, and others). According to the supporters of the independent origin of cyclostomes, the structural pattern of cephalaspids and heterostracans already corresponds in the main to that of lampreys and myxines.

The material we have studied (mainly the orders of Amphiaspidiformes and Cyathaspidiformes) provides no evidence that Heterostraci have developed certain specialization typical of myxines (Novitskaya, 1973 a, b; 1974). At the same time, certain features in Heterostraci's organization resemble those of primitive gnathostomes. The conclusions we arrived at were reported to the first European Ichthyological Congress in Yugo-

slavia in 1973, and with some omissions are given in the present article.

In Heterostraci's cranial morphology the most problematic question is connected with the existence in them of homologue of the myxine's nasohypophyseal duct (nasal tube). Paired convexities on the anterior end of Heterostraci's head are sometimes interpreted as the traces of such a structure which is called also a prenasal sinus (Stensiö, 1964, 1968). If Heterostraci really had a prenasal sinus of myxine's type then they had to have the similar morphogenesis of the anterior part of the head, responsible for the appearance of the most important traits of myxine's organization (pronounced expansion of the prenasal zone of the head, ventral position of anterior visceral elements, compressed brain). But explanation of Heterostraci's inner structure in accordance with the structural pattern of myxines, as many authors have noted, appears to be dubious, and there are some facts contradictory to it (Tarlo, 1961; Heintz, 1962; Denison, 1964; Obruchev, 1968; Novitskaya, 1973a, b; 1974). Some researchers believe that the paired convexities are the traces of nasal capsules (Kiaer, 1932; Kiaer and Heintz, 1935; Denison, 1964, Tarlo, 1964, and others). This alters drastically the possibility of phylogenetic approach of Heterostraci. Recent observations made the latter interpretation, at least for part of Heterostraci, more convincing. Let us consider certain facts. Several early Devonian genera of amphiaspids (order of Amphiaspidiformes) from Siberia were found to have traces of nasal capsules (Novitskaya, 1971). The capsules are situated at the anterior edge of the dorsal shield and not near the pineal tubercule as in the case if a prenasal sinus were present. Morphologically the nasal capsules proved to be very different, they either

fuse with anterior edge to form an extremely short nasal duct (*Hibernaspis*) or diverge as in gnathostomes (*Olbiaspis*) (Fig. 1). In the latter case the absence of cyclostome specializations in the rostral zone structure is evident. In the former case the olfactory apparatus is of cyclostome type, but is more similar to that in the initial stages of the ontogenesis of lampreys than of myxines.

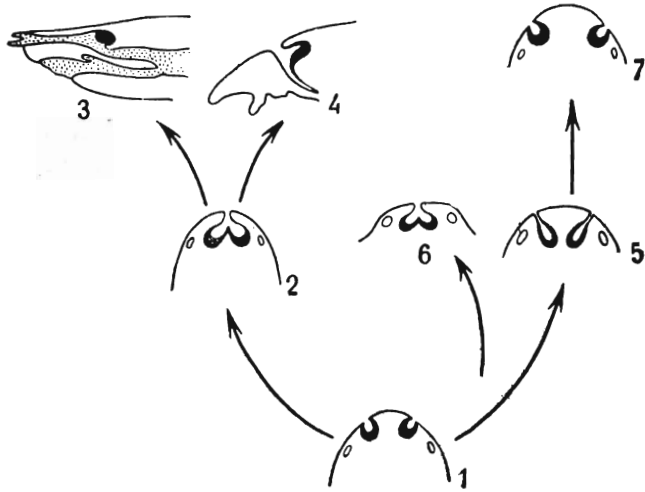


Fig. 1. Scheme of the olfactory organs transformation in the evolution of cyclostomes (on the left) and gnathostomes (on the right) (Novitskaya, 1973).

- 1—primitive type of the olfactory organ in the ancestral group;
- 2—pre-specialized stage in the cyclostomes development (nasohypophyseal sack is not shifted backwards and is open terminally);
- 3—nasal organ of myxines;
- 4—cephalaspiumorphous type of the nasal organ (cephalaspids, anaspids, lampreys);
- 5—structure of the nasal organ in Heterostraci of *Olbiaspis* type and at earlier stage of gnathostomes evolution;
- 6—olfactory apparatus of cyclostomes type and that of certain Heterostraci (*Hibernaspis*);
- 7—typical gnathostome scheme.

Myxinoid specialization in the head structure is absent also in amphiaspids possessing praespiracula (Novitskaya, 1973 a, b). Praespiracula are always situated on the dorsal side of the head, laterally to the orbits. This means that the rostrum of such Heterostraci was of a mixed origin, i.e. it consisted of a ethmoid and visceral components (epitrematic parts of premandibular visceral arches) that were situated dorsally and not ventrally as in myxines. All the above-said makes it possible to suggest the existence among Heterostraci of such forms which did not have not only myxinoid but even cyclostomes specialization as far as the structure of the anterior part of the head is concerned. Besides amphiaspids, they seem to include cythaspids and, perhaps, certain forms of pteraspids, whose rostral zone speaks, as Tarlo (1961) and Heintz (1962) have demonstrated, against the hypothesis about the existence of prenasal sinus.

From morphological point of view Heterostraci are

more diversified and more widely adapted to the environments than Osteostraci (cephalaspids). Unlike cephalaspids represented by bottom forms only, Heterostraci include benthic and benthopelagic species, benthophages, planktonophages and also highly specialized forms with oral apparatus of a tube-like type which functionally appears to be similar to the oral apparatus of recent syngnathids.

The origin of Heterostraci from ancestors common with Osteostraci is generally acknowledged, though the time of their divergence is controversial. Jarvik (1968) believes that these two subclasses differ drastically in the structural plan and therefore their common roots should be sought to start from the early Precambrian. Nevertheless, as the morphology of amphiaspids has shown, in a number of anatomic features previously thought to be very different in Heterostraci and Osteostraci, these two groups have proved to be similar. Thus, both groups have premandibular branchial sack, posterior gemibranch on the premandibular visceral arch, and premandibular branchial nerve. The oral cavity in both Heterostraci and Osteostraci is short and formed by a stomodeal invagination. The fact that there is no complete morphological break between Heterostraci and Osteostraci is also supported by the discovery in China of early Devonian polybranchiaspids (order Polybranchiaspidiformes) that combine in their organization features both of Heterostraci and Osteostraci (Liu-Yu-hai, 1965). Virtually, polybranchiaspids are Heterostraci from dorsal side and Osteostraci from ventral side. Their morphology, like that of amphiaspids, makes us to conclude that (1) Heterostraci and Osteostraci possess much more common inherited features than it was previously believed (to a certain degree this observation speaks in favour of their possible divergency not in Precambrian but later), and that (2) early Devonian *Agnatha* had not yet been formed completely in their structural plan. To a greater extent it is true for Heterostraci. Judging from the structure of the rostro-nasal zone, they developed in two directions, towards acquiring gnathostomic features and to cyclostomes (Fig. 1). In the latter case Heterostraci show certain affinity with the initial stage of ontogenesis of lamprey (Novitskaya, 1973a). Certain structural traits of Heterostraci (common branchial opening, reduction of eyes in some forms) were acquired by them in parallel to the evolutionary line of myxines.

Are there reasons to see affinity between Heterostraci and Gnathostomata, or the cyclostomes, as Jarvik believes (Jarvik, 1960, p. 23), really acquired from the time of their appearance "such peculiarities (two semicircular canals, branchial sacks, unpaired olfactoral organ, etc.) which make them impossible to be ancestor of any of the known Gnathostomes?" As far as the above features are concerned, the existence of semicircular canals in

the initial gnathostomes is not known from available paleontological data. At the same time, Heterostraci were likely to possess not only horizontal but vertical semicircular canals, too (Denison, 1964). Branchial sacks are typical both of Agnatha and ancient Gnathostomata (in recent ichthyofauna such sacks are characteristic of sharks). As noted above, the olfactory organ in some of Heterostraci included two separate nasal capsules similar to those of gnathostomes. Thus, in the morphology of Heterostraci we cannot find convincing reasons which could preclude their relationship with gnathostomes. Moreover, Heterostraci bear more resemblance to gnathostomes in a number of features, including (1) existence of long pedunculi olfactorii (Novitskaya, 1974), (2) ventral position of outer nostrils, which is typical of certain Heterostraci and of the most primitive Gnathostomata (sharks), (3) multiple generation of dermal teeth in the exoskeleton. These rather primitive traits could be inherited by initial Gnathostomata from Heterostraci. Ancestors of Gnathostomata are likely to be found among ancient (Ordovician?) Heterostraci when they took the way of progressive differentiation of visceral arches.

As for the origin of recent Gnathostomata, then, in spite of significant differences between lampreys and myxines, embryogenetic data speak in favour of their monophyletic origin. In particular, it follows from the homology of muscles of the lingual piston in the Myxine and Petromyzon embryos (after Lindstrom, 1949). Attempts were made to find ancestors of recent cyclostomes among hypothetical Protocyclostomes (Severtzev, 1939) or "generalized ancestors" common for Cyclostomes, Osteostracans and Anaspids (Balabaj, 1956) as well as among Anaspids (Obruchev, 1945, 1949). Stensio's studies in the morphology of Ostracoderm revealed a fundamental resemblance in the structure of lampreys and cephalaspids. The view on Anaspids as an ancestral group of lampreys contradicts, as shown by Jarvik (1968), to the morphology of their labyrinth. The residual diverticula in the membranous labyrinth of lampreys corresponds to diverticula containing the electric field canals in cephalaspids (Jarvik, 1968). Electric fields in anaspids are absent. For this reason Silurian Jamoytius belonging to the most primitive anaspids and recently redescribed by Ritchie (1968) by well-preserved specimens from Scotland, also can not be considered as possible ancestor of lampreys. The phylogenetic relation between Jamoytius and myxines, admitted by Ritchie (1968), is hardly probable, since judging from the structure of the nasohypophyseal complex this form is already well-specialized towards lampreys (nasohypophyseal opening are situated dorsally). In myxines this opening occupies terminal position and never was found on the dorsal side of the head. If Jamoytius were belonging to the lamprey's

phylogenetic line, the origin of myxines from such a form could be explained by fetalization (negative anaboly) as it is admitted by Obruchev (1971). However, since Jamoytius is probably not related to lampreys, then, in order to imagine the origin of myxines from Jamoytius we have to admit that myxine were developing for a long time towards lamprey pattern, having reached considerable specialization in this direction (i.e. their naso-hypophyseal opening got dorsal position). This evolution should proceed in parallel to the development of true lampreys, what is quite impossible. From above we consider Jamoytius undoubtedly standing in a row of Anaspids' ancestors but having nothing common with ancestors of recent lampreys and myxines. Ancestors of cyclostomes probably should be found among poorly specialized cephalaspids with the nasal sack abutting to the anterior end of the head and opening terminally as it is the case in the early stages of the lamprey's ontogenesis (Fig. 1). The structural level of such forms provides practically equal possibilities for their further evolution both towards recent lampreys and myxines.

The transition of the recent Cyclostoma ancestors to concentrated food rich in calories (tissue and blood of other jawless vertebrates and fishes) posed them into a more favourable, as compared to cephalaspids, condition in their competition with gnathostome vertebrates. At the same time, a gradual transition to crystic mode of life was the only chance to survive by the appearance and intensive distribution of more active and well-armed fishes (elasmobranchiomorphs, crossopterygians) in the Devonian period. Adaptation to new food was accompanied by specialization of the tongue and of the powerful oral apparatus whose evolution served as the major cause of forming the structural type characteristic of recent cyclostomes.

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