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Wiesława SUSŁOWSKA

# A comparative study on the muscles of the head of *Aspius aspius* (LINNAEUS, 1758) and *Esox lucius* LINNAEUS, 1758

[Pp. 695—714, with 9 text-figs.]

**Badania porównawcze mięśni głowy bolenia *Aspius aspius* (L.) i szczupaka *Esox lucius* L.**

**Сравнительные исследования мышц головы жереха, *Aspius aspius* (L.) и шуки, *Esox lucius* L.**

Abstract. A description of the structure and topographic relations of the muscles which partake in the process of food ingestion in the pike *Esox lucius* L., a typical flesh-eater, and in *Aspius aspius* (L.), a carnivorous cyprinid, is given. In order to compare the muscles and to demonstrate to what extent the predatory ways of living of *Aspius aspius* have influenced the structure and nature of its muscles co-working with the mouth apparatus, the data concerning the muscles of the carp *Cyprinus carpio* L., an omnivorous cyprinid, have also been used.

## I. INTRODUCTION

The work presented in this paper is a continuation of the myological studies which I started with an investigation of the carp (SUSŁOWSKA, 1960). As in that case, now I have confined myself to an analysis of the group of muscles that are functionally closely associated with food ingestion. The pike, a typical flesh-eater, and *Aspius aspius*, a carnivorous cyprinid, have been chosen for the present study. Special attention was given to the structure and topographic relations of the corresponding muscles in the above-mentioned fish species, because the comparison of these relations in fishes leading a similar mode of life and belonging to remote groups, as regards systematics, seems to be interesting from both the anatomical and the biological point of view.

As I mentioned in the paper on the muscles of the carp, no myological studies of fishes had been carried out in Poland before. The pike musculature was investigated to a various extent by VETTER (1878), then LUBOSCH (1929) and SOUCHÉ (1932). This last author gave only a short description of two muscles of the head. The second species, *Aspius aspius*, has not hitherto been used as the object of a study, as shown by available literature, though some authors, e. g., TAKAHASI (1925) and MATTHES (1963), dealt with the muscles of other cyprinids.

## II. MATERIAL AND METHODS

The study material consisted of 8 heads of *Aspius aspius* and 5 heads of the pike. All the pike and one specimen of *Aspius aspius* were caught by Assoc. Prof. Dr T. PENCZAK in the rivers of the Łódź Province and the other specimens of *Aspius aspius* were caught in the Wisła and received from the Włocławek Station of the Institute of Inland Fisheries. Immediately after the catch, the heads were cut off behind the pectoral girdle and fixed. The preservation of whole big fishes and their transport in the fresh state to the laboratory was impossible for technical reasons.

The head lengths of the specimens of both species, measured from the snout tip to the posteroinferior margin of the operculum, are as follows:

| *Aspius aspius* | *Esox lucius* |
|---|---|
| 1. 10·5 cm | 1. 22·0 cm |
| 2. 11·2 „ | 2. 16·5 „ |
| 3. 9·4 „ | 3. 10·7 „ |
| 4. 11·0 „ | 4. 11·4 „ |
| 5. 10·3 „ | 5. 10·3 „ |
| 6. 8·2 „ | |
| 7. 8·7 „ | |
| 8. 9·7 „ | |

Some heads were fixed in 75% alcohol and the others in 4% formalin. Staining with alizarin was also used (BERTIN, 1941) when the material had been kept rather long in a fixative and the colour differentiation of tissues was indispensable to the identification of some elements. Attempts were also made, as reported by OLIVA (1966), to keep material, fixed previously in formalin, in 5% trichloroacetic acid, but this method causes marked osteomalacia, which does not always favour investigation. Some muscles, situated deep and, therefore, difficult of access, were analysed on heads dissected in a sagittal plane or approached from the side of the oral cavity vault, after the removal of the mucosa.

The following muscles have been included in this study: m. adductor mandibulae, m. articulo-dentalis, m. levator arcus palatini, m. adductor arcus palatini, m. adductor hyomandibularis, m. dila-

tator operculi, m. adductor operculi, m. levator operculi. These muscles are connected with the function of food ingestion to a various degree. Some of them co-work directly with the bony elements of the mouth, the others make the adduction and abduction of the gill opercle possible.

## III. RESULTS

### M. adductor mandibulae

This muscle adducts the lower jaw. Its position is similar in both species. It fills the buccal depression formed by the pterygoid, symplectic and quadrate bones. The essential difference in the structure of this muscle between *Aspius aspius* and the pike mainly concerns its stratification, the occurrence of tendinous elements and the place of attachment.

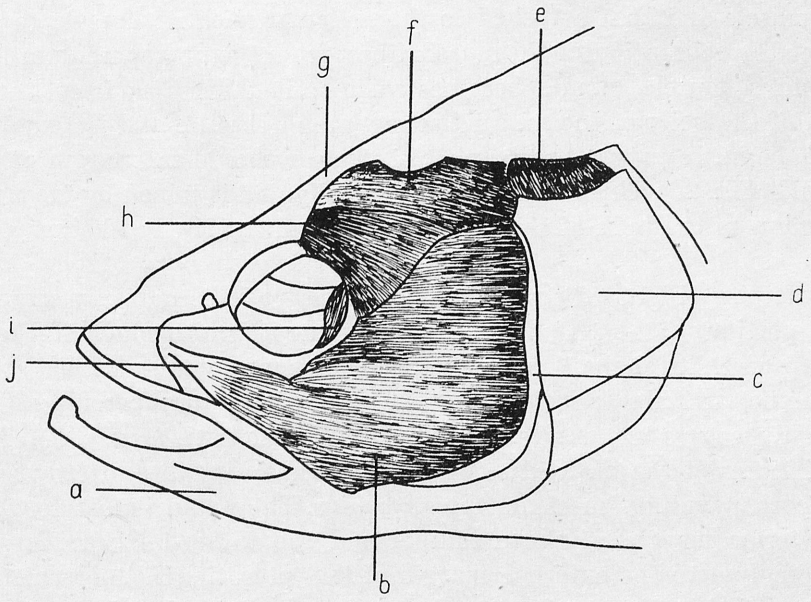


Fig. 1. Side view of the head of *Aspius aspius* (L.), with the skin and orbital bones removed: a — dentary, b — m. adductor mandibulae, c — praeoperculum, d — operculum, e — m. adductor operculi and m. levator operculi, f — m. dilatator operculi, g — frontal, h — m. levator arcus palatini, i — m. adductor arcus palatini, j — tendon of m. adductor mandibulae attached to maxilla

The adductor of the mandible of *Aspius aspius* (Fig. 1) resembles a trapezium in shape. Externally it is covered by the suborbitalia and itself covers so large a portion of the praeoperculum that only a narrow strip of this bone is exposed, in which there are the openings of the lateral-line canal. The muscle is characterized by its uniform structure, no stratification being visible within its belly. It stands out fairly distinctly against the m. levator arcus pala-

tini, situated above it, because the fibres of these two muscles run in different direction (Fig. 1h). The fibres of the adductor of the mandible extend horizontally, whereas those of the levator obliquely to it.

The attachments of the m. adductor mandibulae are numerous in *Aspius aspius*. A large number of the fibres are attached to the praeoporculum, to a small portion of the hyomandibula which borders on the praeoperculum, to the metapterygoid and from below to the quadrate. The anterior portion of the muscle is attached to the maxilla. The attachments to the praeoperculum, metapterygoid, hyomandibula and quadrate are muscular and that to the maxilla is tendinous in character (Fig. 1j). After cutting the tendon away from the maxilla and moving aside the anterior part of the muscle, one can see a broad tendon which arises from the middle of the belly of the muscle. It is attached at the border between the dentary and the articular, exactly where there occurs a process on this last bone. Generally speaking, the tendon attached to the maxilla is topographically and functionally associated with the ventral portion of the muscle and that attached to the articular with its dorsal portion.

After the separation of the muscle fibres from the praeoperculum and metapterygoid a muscle bundle becomes visible; it takes rise from the anterior portion of the belly of the m. adductor mandibulae and is attached at the base of the m. levator arcus palatini, near the dorsal margin of the metapterygoid (Fig. 21). This bundle runs diagonally and is joined by means of a narrow tendon to the bulk of the m. adductor mandibulae halfway along the orbit.

In the pike (Fig. 3) the muscle under description is not only stretched over a large portion of the surface of the head, but it is also much thicker than in *Aspius aspius*. Its shape is more or less oval, somewhat broadened at the junction of the articular with the lower part of the praoperculum. It nearly thoroughly covers the m. levator arcus palatini (Fig. 3k). The direction of fibres of the m. adductor mandibulae is quite different from that in the corresponding muscle of *Aspius aspius*. They run almost vertically from the posterior margin of the mandible and the antero-inferior margin of the praeoperculum to the external margin of the pterotic. In the ventral portion of the muscle the fibres are arranged obliquely to each other and scatter to the sides (Fig. 3d). This muscle clings so closely to the skin that the fibres of its superficial layer are sometimes damaged during the removal of the skin. As in *Aspius aspius* the m. adductor mandibulae of the pike presents a uniform muscular mass, undivided externally into smaller elements.

Having cut away some muscle fibres from the praeoperculum, pterotic, metapterygoid and hyomandibula, one uncovers a strong tendon right in the middle of the muscle belly. This tendon is directed towards the articular, as in *Aspius aspius*, and it gives off remifications to the thick outer layer of the muscle, whereas the remaining, also massive part of the tendon runs with numerous muscle fibres upwards to the base of the m. levator arcus palatini, the hyomandibula and the outer surface of the praeoperculum.

The superficial layer of fibres in the adductor muscle of the mandible is chiefly attached to the praeoperculum, only that in the dorsal part of the bone the attachment takes place at its anterior edge and in the ventral part the fibres of the muscle examined penetrate deeper, under the bone, and are attached to its medial surface (Fig. 4t). A small bundle of fibres is also attached to the posterior ramus of the hyomandibula (a depression in the bone is visible at the place of attachment) and to the base of the middle ramus.

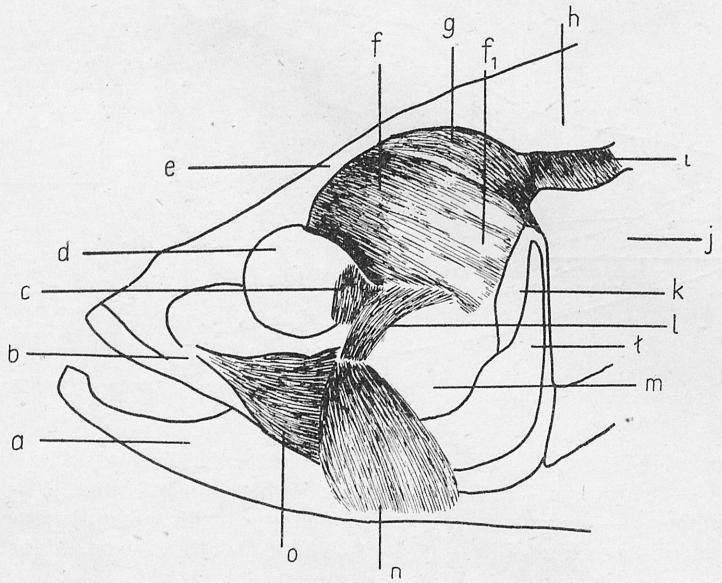


Fig. 2. Side view of the head of *Aspius aspius* (L.), with the outer layer of the m. adductor mandibulae removed: a — dentary, b — maxilla, c — m. adductor arcus palatini, d — orbit, e — frontal, f — m. levator arcus palatini, f′ — tendon of m. levator arcus platini, g — m. dilatator operculi, h — pterotic, i — m. adductor operculi and m. levator operculi, j — operculum, k — hyomandibula, l — bundle of m. adductor mandibulae, ł — praeoperculum, m — metapterygoid, n — outer layer of m. adductor mandibulae moved away, o — part of m. adductor mandibulae attached to maxilla by means of tendon

The outer layer is separated from the deeper one by a broad tendinous membrane which takes origin from the above-mentioned tendon. It has been observed that this membrane is particularly well developed in big specimens.

The fibres of the deep layer run more horizontally and, beginning at the strong tendon attached to the articular (Fig. 5c). and over a distance common to this and the outer layer, they scatter to the sides and to the front. The fibres of the deep layer border on the adductor and levator muscles of the palatine arch and are joined to the dorsal edge of the metapterygoid and next to the hyomandibula and praeoperculum.

In addition to the deep layer, a small, fairly compact bundle of fibres can be distinguished. This bundle runs from the tendon mentioned above and is attached to the dentary (Fig. 5d). It limits the orbit from behind and probably belongs to the adductor muscle of the mandible.

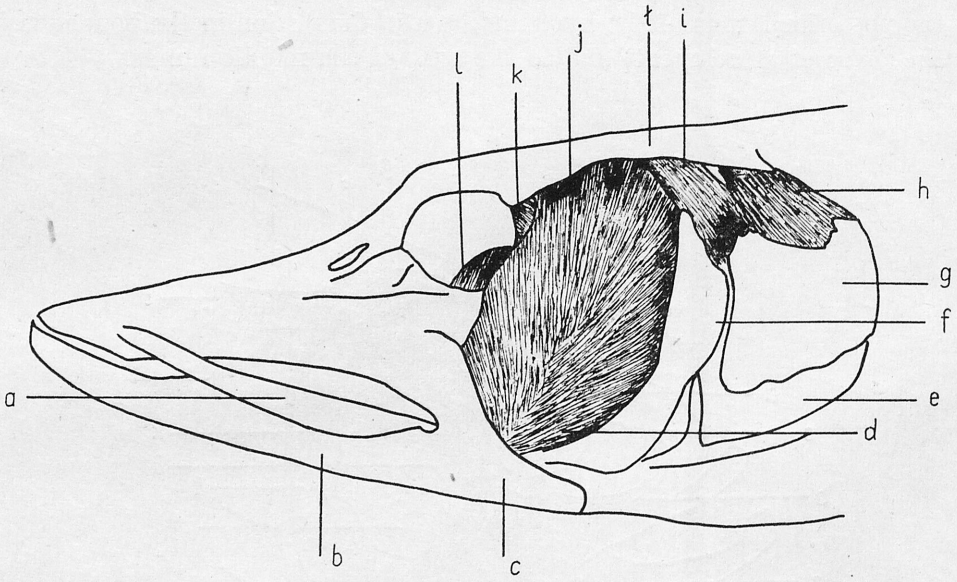


Fig. 3. Side view of the head of the pike *Esox lucius* L., with the skin and orbital bones removed: a — maxilla, b — dentary, c — articular, d — m. adductor mandibulae, e — suboperculum, f — praeoperculum, g — operculum, h — m. adductor operculi and m. levator operculi, i — m. dilatator operculi, j — frontal, k — m. levator arcus palatini, l — m. adductor arcus palatini, ł — pterotic

M. articulo-dentalis

In both species the m. articulo-dentalis is directly connected with the m. adductor mandibulae in respect of topography and function performed. It is particularly well developed in the pike (Fig. 5a), in which it is situated on the medial surface of the dentary so that only a third part of the bone remains exposed. The m. articulo-dentalis fills a depression which extends along the dentary and next reaches the lower edge of this bone and the base of the ridge in which the teeth are set. Some of the muscle fibres enter the fissure of the dentary, in which they have their attachment. A tendinous bundle arises from the main bulk of fibres and it is attached above the base of the articular surface of the articular bone (Fig. 5e).

The same muscle in *Aspius aspius* (Fig. 6h) is markedly worse developed. It spreads on the dorsal portion of the inner surface of the dentary and, farther to the back, passes into a tendinous membrane, joined by means of a broad huge tendon to the m. adductor mandibulae, which itself is attached to the bone at the border between the dentary and the articular.

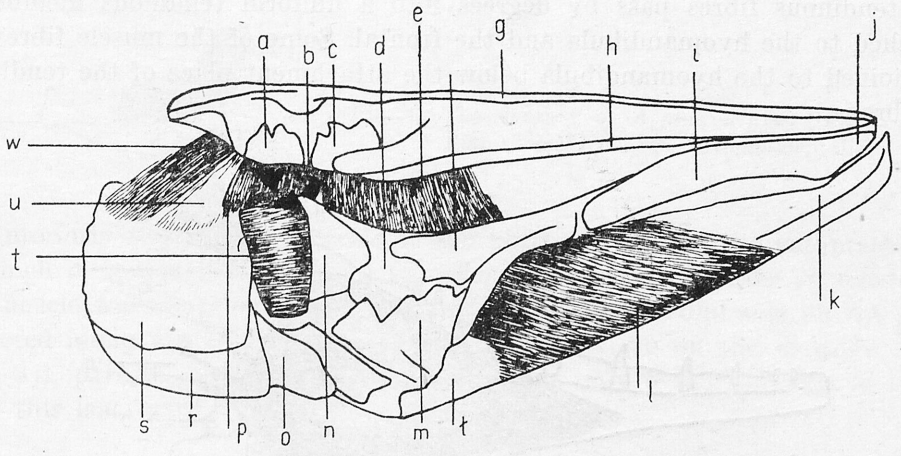


Fig. 4. The head of a pike *Esox lucius* L., cut sagittally and viewed from the medial side: a — basioccipital, b — m. adductor hyomandibularis, c — pro-otic, d — metapterygoid, e — m. adductor arcus palatini, f — entopterygoid, g — frontal, h — parasphenoid, i — palatine, j — vomer, k — dentary, l — m. articulo-dentalis, ł — articular, m — quadrate, n — hyomandibula, o — interoperculum, p — m. dilatator operculi, r — suboperculum, s — operculum, t — m. adductor mandibulae — fibres attached to inner surface of praeoperculum, u — m. dilatator operculi, w — m. levator operculi

## M. levator arcus palatini

This muscle raises a complex of bones composed of the hyomandibula, quadrate and palatine in a dorsolateral direction. This occurs in connection with the action of opening the mouth. In the pike the muscle has the characteristic shape of a pyramid directed with its wide base towards the metapterygoid and with its top towards the sphenotic. One of the sides of the pyramid forms the posterior edge of the orbit and the other borders on the muscle delatating the opercle. The anterior portion of the base of the m. levator arcus palatini covers the m. adductor arcus palatini. The former muscle is nearly completely built of muscle fibres. A small tendon departing dorsalwards from the middle of its belly is attached to the anterior edge of the hyomandibula. In addition, the m. levator arcus palatini is attached to the inner surface of the frontal, where this bone is thickest and has a rough surface, which ends in a crest on the medial side. The attachment to the frontal is formed only by muscle fibres. The m. levator arcus palatini joins the dorsal edge and the inner surface of the metapterygoid from below. The surface of this bone is provided with a crest, which is the place of attachment. It should be added that the muscle fibres are also attached lower and deeper, namely, to the alisphenoid and the anterior part of the pro-otic.

The corresponding muscle of *Aspius aspius* (Fig. 2f) is particularly well developed, especially in the posterior portion of the orbit. It is attached to the metapterygoid and hyomandibula, and its large part is tendinous in character (Fig. 2f), which can be clearly seen after removing a thin outer layer of the muscle.

The tendinous fibres pass by degrees into a uniform tendinous membrane, attached to the hyomandibula and the frontal. Some of the muscle fibres are also joined to the hyomandibula below the attachment place of the tendinous membrane.

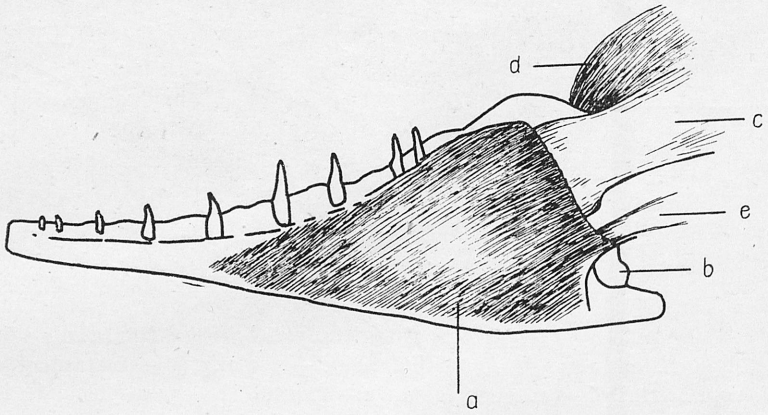


Fig. 5. The dentary of a pike *Esox lucius* L., seen from the medial side: a — m. articulo-dentalis, b — articular surface for quadrate, c — tendon of m. adductor mandibulae, d — bundle of m. adductor mandibulae limiting the orbit posteriorly, e — tendinous bundle

## M. adductor arcus palatini

This is the antagonist of the m. levator arcus palatini and therefore it adducts the palatine arch medially. In the pike this muscle (Figs. 3l, 4e) is not visible until the m. adductor mandibulae has been removed and the m. levator arcus palatini cut away thoroughly. The m. adductor arcus palatini is very well developed, markedly elongated and oriented somewhat obliquely to the long axis of the skull (Fig. 7). It runs from the midlength of the orbit (this part of the muscle is situated most ventrally) up to the hyomandibula (the part situated dorsally). Its attachments occur on the antero-superior edge of the metapterygoid and hyomandibula (Fig. 7a, b). Here, this muscle is joined to the inner surface of the body of the hyomandibula and covers the there existing foramen for the seventh (facial) pair of nerves. The adductor muscle has not been found to reach the palatine. Instead, it comes to the entopterygoid, to which it is attached (Fig. 7d). A small tendon is, besides, attached to a crest situated at the base of the lower ramus of the hyomandibula. A large number of the fibres are attached to the parasphenoid and a small bundle to the pro-otic, below the attachment place of the m. levator arcus palatini (Fig. 4c, h).

As in the pike, the m. adductor arcus palatini of *Aspius aspius* is situated in the postero-inferior part of the orbit, and also as in that fish, it whole becomes visible only after the removal of the m. levator arcus palatini (Figs. 2c, 8h). Its lower edge is joined to the metapterygoid process and to the postero-superior part of this bone, shaped into a ridge.

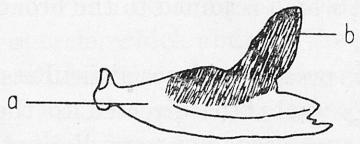


Fig. 6. The dentary of *Aspius aspius* (L.): a — medial surface, b — m. articulo-dentalis

Anteriorly this muscle extends to the posterior edge of the entopterygoid, to which it is attached (Fig. 8i). In order to observe the other attachments, the muscle was examined from the inside, from the medial side on the skull dissected along the parasphenoid. Its attachments are on the metapterygoid (Fig. 8j), parasphenoid and hyomandibula, but only a small bundle of fibres joins this last bone.

M. adductor hyomandibularis

This muscle adducts the hyomandibula medially and thus it works together with the m. adductor arcus palatini. Both in the pike and in *Aspius aspius* it is visible on the dissected skull only from below after the removal of the mucosa which covers the vault of the oral cavity. Anteriorly this muscle touches the m. adductor arcus palatini and at the back the m. dilatator operculi, from which it is quite sharply discriminated.

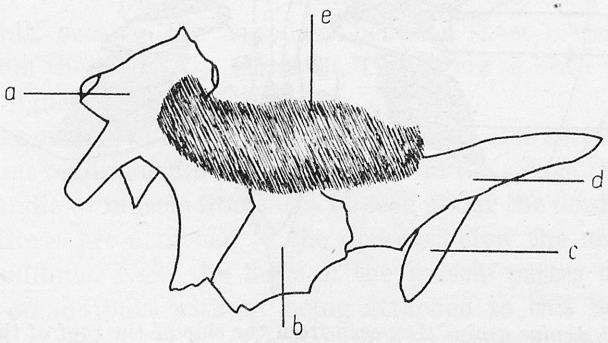


Fig. 7. M. adductor arcus palatini of a pike *Esox lucius* L.: a — hyomandibula, b — metapterygoid, c — ectopterygoid, d — entopterygoid, e — m. adductor arcus palatini

In *Aspius aspius* (Fig. 8f) the adductor muscle of the hyomandibula is attached by means of a broad tendon to the inner surface of the dorsal portion of this bone (Fig. 8k). Its attachment to the cerebral cranium is fairly extensive and located where the pro-otic adheres to the alisphenoid, between the depression in the bone and the foramen for the fifth pair of the cranial nerves (trigeminal), and next it extends as far backwards as the temporal fossa. The attachment of the m. adductor hyomandibularis to the cranium is performed not

only by means of muscle fibres but also by a tendon, which is joined to the broad tendon inserted into the hyomandibula.

The identification of this muscle in the pike presents some difficulties, for it is an extension of the m. adductor arcus palatini directed to the rear (Fig. 4b) and the boundary between these two muscles is not very distinct. It may be stated in general that the m. adductor hyomandibularis of the pike is poorly developed, much more poorly than it is in *Aspius aspius*.

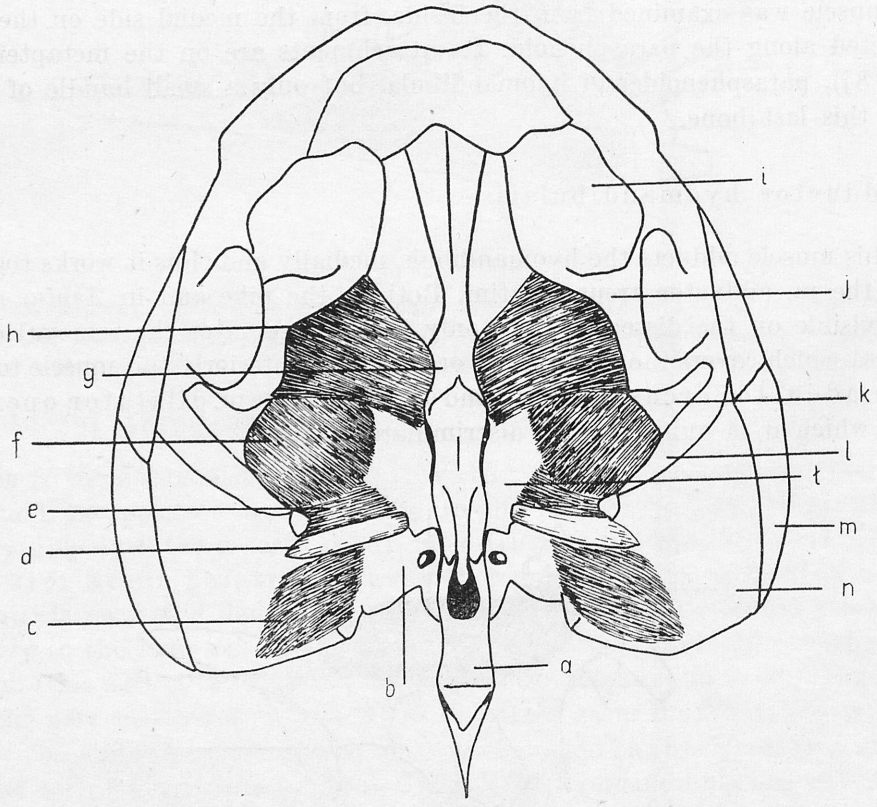


Fig. 8. The head of *Aspius aspius* (L.), seen from the side of the roof of the oral cavity, with the skin removed: a — basioccipital, b — lateral occipital, c — m. levator operculi d — m. adductor operculi, e — m. dilatator operculi, f — m. adductor hyomandibularis, g — parasphenoid, h — m. adductor arcus palatini, i — entopterygoid, j — metapterygoid, k — hyomandibula, l — praeoperculum, ł — pro-otic, m — suboperculum, o — operculum

One of its attachments, formed by means of both muscle fibres and tendinous elements, occurs on the medial side of the hyomandibula, above the foramen for the seventh pair of nerves, and the other one is situated within the cerebral cranium, on the pro-otic (Fig. 4c).

The group of muscles remaining to be discussed is closely associated with the activity of the gill opercle. They are stretched between the opercle and the lateral edge of the cerebral cranium, at the height of the otic bones.

The first muscle of this group that I shall describe is the dilatator of the opercle, which abducts the gill opercle and, as a results, exerts a direct influence on the dilatation of the gill slit.

In the pike this muscle is very clearly distinguishable (Fig. 3i) and to a high degree covered by the outer layer of the m. adductor mandibulae. The fibres of the m. dilatator operculi run from the opercle towards the cerebral cranium. Its attachment to the opercle, being mostly tendinous, is confined to a small area situated on the outer side of the bone, above the articular depression. The muscle fibres, which are attached to the sphenotic and pterotic, just above the articular facet for the hyomandibula, radiate from the above-mentioned tendon towards the cranium.

In *Aspius aspius* this muscle is greatly elongated but, as in the pike, it is not very well developed, being composed of a thin layer of fibres (Figs. 2g, 9b). It extends slantingly from the process of the opercular bone to the posterior edge of the orbit. The attachment of this muscle is extensive; on the vault of the cranium it is attached not only to the inner surface of the frontal but also to the sphenotic and reaches up to the anterior edge of the pterotic, above the articular facet for the hyomandibula. The other end of this muscle has its insertions in the hyomandibula and the process of the inner surface of the opercle (Fig. 9b, c, e).

The m. adductor operculi, which adducts the gill opercle, works in opposition to the dilatator of this organ. It lies in the close neighbourhood of the m. levator operculi. The separation of the adductor from the levator is rather difficult, because the boundary between these muscles is not visible, especially so from the outside of the skull. This refers to both the species discussed, but in a higher degree to the pike.

The m. adductor operculi of *Aspius aspius* is characterized by the occurrence of numerous tendinous fibres, especially from the side of the oral cavity (Fig. 8d). A small bundle of muscle fibres can be seen under the tendinous fibres. Both sorts of these fibres are attached to the opercle below the articular depression for the hyomandibula. Next the belly of the muscle passes over the posterior edge of the hyomandibula without being attached to this bone and is joined to the cerebral cranium. It is attached at the same height as the adductor of the hyomandibula but deeper, as far as the temporal fossa, on its anterior wall, formed by the pro-otic.

As has already been mentioned, the m. adductor operculi is difficult to separate from the levator. No distinct demarcation line is visible between the fibres of these muscles in the pike (Fig. 3h, i), whereas both of them differ somewhat in fibre direction from the dilatator of the opercle. The fibres of this last muscle radiate from the base of the articular surface of the opercle, and those of the adductor and levator radiate downwards from the lateral edge of the skull. The attachment to the cerebral cranium is stronger than it is in *Aspius aspius*, because the muscular and tendinous fibres are intertwined in it. It is displaced to the rear of the skull and situated on the lateral occipital bone,

at its border with the pterotic. A depression which is the place of attachment is visible in the lateral occipital.

The last muscle of this group, the m. levator operculi, lies directly behind the adductor and raises the gill opercle.

In *Aspius aspius* (Fig. 8c) this muscle is characterized by the complete lack of tendinous elements, being made up of muscle fibres only. It is poorly developed and forms a relatively thin and delicate layer attached to the inner surface of the caudodorsal portion of the opercle at one end and to the cerebral cranium at the other end. This muscle can be seen from the outside of the skull after the removal of the skin from it (Figs. 8c, 9f). The attachment to the cerebral cranium is situated on the pterotic, in the place of the extension of the articular surface for the hyomandibula.

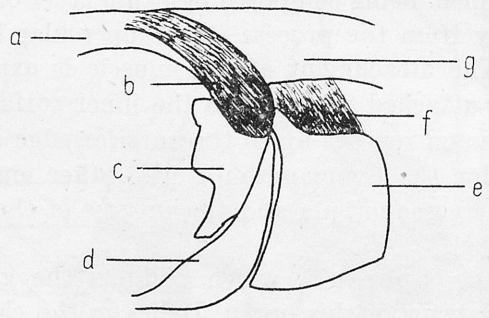


Fig. 9. M. dilatator operculi of *Aspius aspius* (L.): a — frontal, b — m. dilatator operculi, c — hyomandibula, d — praeoperculum, e — operculum, f — m. levator operculi and m. adductor operculi, g — vault of skull

In the pike this muscle is well developed and formed of a thick layer of fibres (Figs. 3h, 4w). At one end it is inserted by means of tendinous fibres into the opercle, close behind the insertion of the adductor on the inner side of the bone, and by means of muscle fibres on its outer side. The other end has its attachment on the pterotic within the cerebral cranium. It is situated along the caudolateral edge of this bone and next in a depression formed by the dorsocaudal part of the pterotic.

## IV. DISCUSSION

The cephalic muscles of *Aspius aspius* and the pike were used as material for the present study. The data obtained in the course of the study of the carp muscles (Susłowska, 1960) were also used for comparison. A comparison of the musculature of these three species made it possible to demonstrate to what extent the predatory ways of living had influenced the structure and character of the muscles associated with the mouth apparatus. Attention was focused chiefly on the general build of the muscles, their stratification and the localization of attachments.

The terminological divergencies found in some publications (VETTER, 1878; TAKAHASI, 1925; SOUCHÉ, 1932; YEREMEYEVA, 1948) have been passed over in silence, since they are discussed rather at length in the paper on the carp.

My own observations concerning the characteristics of the structure are presented in the form of a table. As can easily be seen, the differences which occur between the cephalic muscles of the pike and those of the carp are conspicuous and their interpretation is relatively easy. A completely different manner of food ingestion demands a different arrangement and proportions not only between individual muscles but also within each of them. For example, the stratification of the m. adductor mandibulae of the carp and the functional differentiation of its parts (SUSŁOWSKA, 1960) are closely associated with the protrusion and retraction of the snout. In the pike the movements of the jaws which cause the opening and closing of the oral cavity are of decisive importance to the acquisition of food. The muscles partaking in this process must therefore be shaped in a different manner. This is certainly why the structure of the m. adductor mandibulae is massive and uniform. The direction of action of the muscle force is also different in the pike; it is vertical, and probably for this reason the arrangement of the muscle fibres is vertical, too. In the carp the contraction of the muscle fibres which accompanies the retraction or protrusion of the snout takes place in a horizontal plane. *Aspius aspius* as a flesheating cyprinid feeding on small fish holds an intermediate position between these two species. The m. adductor mandibulae of *Aspius aspius* is uniform in structure, its particular layers are not clearly separated as in the pike, but the direction of fibres remains the same as it is in the carp. It is noteworthy that there occurs only one tendinous attachment on the maxilla in *Aspius aspius*. This tendon is topographically and functionally connected with the belly of the muscle. This would indicate a partial change in the function of this muscle in comparison with the carp. In this last species both parts of the outer layer are attached by means of two tendons to the maxilla and their work is connected with the protrusion of the snout in so far as the ventral portion of the muscle is concerned, whereas the contraction of fibres of the dorsal portion causes its retraction. In the pike, a typical flesh-eater, there is no attachment of this muscle at all on the maxilla. It may be supposed that this structural type of the m. adductor mandibulae is characteristic not only of the pike but of other flesh-eating fishes. Some information about this subject, as regards the salmon and perch, can be found in the papers by YEREMEYEVA (1948, 1950).

One may raise some objections to the interpretation of the structure of this muscle in the pike presented by SOUCHÉ (1932), for he divided the m. adductor mandibulae into two superficial parts situated side by side one above the other. Although the structure of this muscle was examined several times in large and smaller specimens and on fresh and fixed material, such a division was never observed. VETTER (1878), who among other problems was concerned in the musculature of the pike did not distinguish the superficial layer at all

Table I

A comparison of structural characteristics of cephalic muscles in *Cyprinus carpio* L., *Aspius aspius* (L.) and *Esox lucius* L.

| | *Cyprinus carpio* L. | *Aspius aspius* (L.) | *Esox lucius* L. |
|---|---|---|---|
| m. adductor mandibulae: | | | |
| shape: | trapezoidal | trapezoidal | oval |
| thickeness: | | | much thicker than in remaining species |
| fibre direction: | horizontal | horizontal | vertical |
| stratification: | superficial layer | uniform structure | structure uniform, |
| | middle layer | undifferentiated | superficial and deep |
| | deep layer | into layers | layers slightly distinguishable |
| attachments | maxilla (2) | maxilla (1) | — |
| | quadrate | quadrate | — |
| | articular | articular | articular |
| | praeoperculum | praeoperculum | praeoperculum |
| | hyomandibula | hyomandibula | hyomandibula |
| | dentary | dentary | dentary |
| | metapterygoid | metapterygoid | metapterygoid |
| | — | — | pterotic |
| m. articulo-dentalis: | | | |
| development: | poorly developed | poorly developed | well-developed |
| attachments: | dentary | dentary | dentary |
| | articular | articular | articular |
| m. levator arcus palatini: | | | |
| development: | well-developed | well-developed | poorly developed |
| attachments: | numerous tendinous | tendinous fibres | muscular fibres |
| | fibres | prevail | prevail |
| | frontal | frontal | frontal |
| | hyomandibula | hyomandibula | hyomandibula |
| | metapterygoid | metapterygoid | metapterygoid |
| | — | — | alisphenoid |
| | — | — | pro-otic |
| m. adductor arcus palatini: | | | |
| attachments: | — | metapterygoid | metapterygoid |
| | — | hyomandibula | hyomandibula |
| | entopterygoid | entopterygoid | entopterygoid |
| | parasphenoid | parasphenoid | parasphenoid |
| | — | — | pro-otic |

Table I (continued)

| | *Cyprinus carpio* L. | *Aspius aspius* (L). | *Esox lucius* L. |
|---|---|---|---|
| m. adductor hyomandibularis: attachments: | parasphenoid<br>hyomandibula<br>pro-otic<br>— | —<br>hyomandibula<br>pro-otic<br>alisphenoid | —<br>hyomandibula<br>pro-otic<br>— |
| m. dilatator operculi: attachments: | operculum<br>sphenotic<br>pterotic<br>frontal<br>hyomandibula | operculum<br>sphenotic<br>—<br>frontal<br>hyomandibula | operculum<br>sphenotic<br>—<br>—<br>— |
| m. adductor operculi: attachments: | pro-otic<br>operculum | pro-otic<br>operculum | lateral occipital<br>operculum |
| m. levator operculi: attachments: | operculum<br>hyomandibula<br>pterotic | operculum<br>—<br>pterotic | operculum<br>—<br>pterotic |

on the assumption that this layer, if it exists, should be attached to the maxilla. There is no such attachment in the pike, which has been confirmed by the results of the present study. In addition, it has been found that the superficial layer of fibres is uniform and separated from the deeper parts of the muscle by a huge tendon.

As has been mentioned above, the m. articulo-dentalis is closely associated with the m. adductor mandibulae. Some authors do not even name it as a distinct muscle but treat it as a part of the m. adductor mandibulae (VETTER, 1878; JUGE, 1899; TAKAHASI, 1925). This opinion seems justified to a great extent and it refers also to the three species under discussion. They resemble each other both in the situation of this muscle and in its close association with the m. adductor mandibulae. The difference boils down to the better development of the m. articulo-dentalis in the pike. A high degree of its development is indicated also by SOUCHÉ (1932), who even distinguishes three separate parts in it.

Comparing the m. levator arcus palatini of the carp, *Aspius aspius* and the pike, one should emphasize a great similarity of the structure of this muscle in the first two species. The similarity concerns especially the well-developed belly, in which the tendinous fibres clearly prevail. The part played by this muscle in the omnivorous cyprinids has been defined by VAN DOBBEN

(1935) and MATTHES (1963). It consists in abducting the palatine arches in a dorsolateral direction so as to increase the capacity of the oral cavity and to produce negative pressure in it, necessary for the mechanism of sucking in. In the case of carp the interdependence between the function and the structure of the m. levator arcus palatini is quite clear. *Aspius aspius* has changed its mode of feeding, which more resembles that of the pike, and yet this fact has not resulted in any visible changes in the shape of this muscle.

It has been found that the fibres of the m. levator arcus palatini may partly unite with the adductor of the hyomandibula. This is probably so because these two muscles are not very sharply demarcated from each other and in all the three species are attached, among other bones, to the hyomandibula. SOUCHÉ (1932) writes that in some fishes the m. levator arcus palatini may also unite with other muscles, e. g., with the dilatator of the opercle. This, however, has not been observed in any of the three species examined in the present study.

An interesting fact is undoubtedly the displacement of the attachment of the m. levator arcus palatini towards the back of the cerebral cranium, which is probably connected with a strong elongation of the skull in this species. The problem of relations between the muscular system and the skeleton in fishes is being worked out and will be presented in another publication.

The attachments of the m. adductor arcus palatini and m. adductor hyomandibularis of *Aspius aspius* are rather characteristic. In the case of the first muscle they agree partly with the corresponding attachments to the entopterygoid and parasphenoid in the carp and partly with those to the metapterygoid, hyomandibula and parasphenoid in the pike. The attachments of the m. adductor hyomandibularis to the hyomandibula and pro-otic are similarly situated in *Aspius aspius* and the pike, there being an additional attachment to the parasphenoid in the carp.

It seems that the task done by these muscles in the species that differ extremely in their mode of food ingestion must be different, too. The swallowing by the pike of a whole big prey is possible only with the palatine-quadrate arches drawn aside to a maximum, which is naturally executed with the help of the m. adductor arcus palatini. This is certainly why this muscle is marked by a remarkable thickness and extensive attachment to the cranium in the pike. On the contrary, in the carp it is poorly developed and its attachments are limited to small areas on the bones. *Aspius aspius* holds an intermediate position in this respect. On the one hand, being a cyprinid, it resembles the carp in the structure of the m. adductor arcus palatini, on the other hand, on account of its predatory ways of living, it shows some similarities in the structure of this muscle to the pike.

Analysing the degree of development of the opercular muscles and their attachments in the species under study, I must state that the greatest differences occur in the muscle abducting the gill opercle (m. dilatator operculi). It will be seen from the studies carried out by WOSKOBOINIKOFF (1932) and YE-

REMEYEVA (1950) that in fishes with a well-developed snout and, consequently, having great sucking possibilities of the mouth the muscles which are directly associated with the dilatation of the gill slit show a particularly great development Flesh-eating fishes, naturally including *Aspius aspius*, are characterized by a different method of food acquisition, which determines the degree of development of the opercle itself and of its musculature. This problem has already been signalled in an earlier paper (SUSŁOWSKA and URBANOWICZ, 1957). Special attention should be given to the manner in which the m. dilatator operculi is attached to the cerebral cranium. In the carp its area of attachment is large and lies on three bones (sphenotic, pterotic and frontal), in *Aspius aspius* this muscle is joined to the cranial bones over a smaller area, whereas in the pike it is evidently limited.

University of Łódź
Departament of Comparative Anatomy and Ecology
Łódź, Nowopołudniowa 12/16

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## STRESZCZENIE

Praca ma charakter porównawczy i dotyczy budowy a także topografii mięśni głowy dwóch gatunków ryb, prowadzących podobny tryb życia a przynależnych do różnych rzędów. Do badań wybrano szczupaka, *Esox lucius* L. — typowego drapieżnika i bolenia, *Aspius aspius* (L.) — drapieżną rybę karpiowatą. Badania ograniczono do grupy mięśni, których rola związana jest ściśle z czynnościami pobierania pokarmu. Niektóre z nich współdziałają bezpośrednio z elementami kostnymi aparatu gębowego (m. adductor mandibulae, m. articulo- dentalis, m. levator arcus palatini, m. adductor arcus palatini, m. adductor hyomandibularis), inne zaś umożliwiają przywodzące i odwodzące ruchy pokrywy skrzelowej (m. dilatator operculi, m. adductor operculi, m. levator operculi).

Do celów porównawczych wykorzystano również dane odnoszące się do mięśni aparatu gębowego ryby wszystkożernej — karpia, *Cyprinus carpio* L. Porównanie umięśnienia tych trzech gatunków pozwoliło wykazać, w jakim stopniu drapieżny tryb życia bolenia wpłynął na budowę mięśni współdziałających z aparatem gębowym.

Wpływ sposobu żerowania bolenia na budowę mięśni bezpośrednio związanych z tą czynnością przejawia się zwłaszcza w ukształtowaniu i lokalizacji przyczepów m. adductor mandibulae.

## РЕЗЮМЕ

В настоящей статье представлено сравнение строения и топографию мышц головы двух видов рыб, ведущих похожий образ жизни и принадлежащих к различным отрядам. Исследования производились на щуке — типичном хищнике и жерехе — хищной рыбе из семейства карповых. Исследования ограничивались к группе мышц, роль которых тесно связана с поглощением корма. Некоторые из них непосредственно взаимодействуют с костными элементами ротового аппарата (m. adductor mandibulae, m. articulo-dentalis, m. levator arcus palatini, m. adductor arcus palatini, m. adductor hyomandibularis), другие же делают возможными приводящие и отводящие движения жаберной крышки (m. dilatator operculi, m. adductor operculi, m. levator operculi).

К сравнительным целям использовано также данные, относящиеся к мышцам ротового аппарата всеядной рыбы — карпа, *Cyprinus carpio* L. Сравнение мускулатуры этих трёх видов позволило выявить в какой степени хищный образ жизни жереха повлиял на строение мышц, взаимодействующих с ротовым аппаратом.

Влияние способа питания жереха на строение мышц непосредственно связанных с этим действием особенно проявляется в образовании и локализации прикрепления мышц m. adductor mandibulae.

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