FUNCTIONAL ANATOMY
AND MOVEMENT CO-ORDINATION OF THE RESPIRATORY
PUMP OF THE CARP (CYPRINUS CARPIO L.)

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INTRODUCTION

The evaluation of the movement co-ordination of fish respiratory systems has
attracted many investigators (Baglioni, 1907, 1910; van Dobben, 1935; Kirchhoff,
1958; Willem, 1931, 1940, 1947; Woskoboinikoff, 1932). For a long time the theories
of the functioning of the system were only based upon anatomical data. It is hardly
surprising that this has led to conflicting theories in many cases where the function of
a muscle was deduced from its origin and insertion only, without knowledge of the
timing of its activity, although a general and superficial picture of course may be
gained in this way. An exact analysis of muscle activity can be made nowadays with
electrophysiological techniques (Ballintijn, 1965, 1969a, b; Ballintijn & Hughes, 1965;
Hughes & Ballintijn, 1965; Hughes & Shelton, 1962) with which the exact timing of
muscular contraction can be recorded.

However, to understand the movement co-ordination as a whole a complete
knowledge of the functional anatomy of the respiratory system remains indispensable.
The visceral skeleton, which performs the respiratory movements under influence of
the contraction of a varying number of head muscles, is a very complicated structure.
It consists of bone arches and of bones which in many places articulate and influence
each other by lever action and by ligaments. Through this the effect of the contraction
of a muscle spreads much farther than at first sight would be expected.

In the present paper an anatomical description of the muscular and skeletal system
of the carp head, as far as it has a respiratory function, will be given. Further, an
outline of the action of the muscles based upon the anatomical data will be presented.
Finally, the coupling possibilities of the visceral skeleton by which movements spread
far over the system will be analysed in detail. This analysis will serve as the basis for a
subsequent paper on the muscle co-ordination of carp respiration (Ballintijn, 1969a).

MATERIALS AND METHODS

The carp used were obtained from hatcheries of the Nederlandse Heidemaatschappij and later from the Organisatie tot verbetering van de Binnenvisserij. They
were kept in concrete tanks supplied with running well-water in the basement of the
laboratory and in a stock pond outside the building.

For the experiments involving electrical stimulation in which the fishes had to be
motionless but alive they were anaesthetized in water containing 50–100 mg./l. MS 222 (Sandoz, Basel).

Muscles were stimulated with stainless-steel electrodes of 250 µ diameter, varnished with Araldite AW.106 except for a tip of about 0.5 mm. Two of these electrodes were inserted into a muscle as far apart as possible.

The electrical stimulus consisted of trains of pulses of up to 10 V. and 3 msec. duration, obtained from a Tektronix 160 series generator (two waveform generators and two pulse generators). The pulses were applied to the muscle electrodes through a simple R-C integrator circuit.

![Fig. 1. The head skeleton of the carp after removal of the opercular and circumorbital bones. (For meaning of abbreviations, see page 564.)](image)

RESULTS

Skeleton

The visceral skeleton of fishes in general supports the walls of the buccal and opercular cavities (Ballintijn & Hughes, 1965; van Dobben, 1935; Gregory, 1959; Henschel, 1939, 1941; Kirchhoff, 1958). Its components articulate in a complicated way so that it can perform the complex movements necessary to pump water across the respiratory epithelium. It is built up of seven bone arches (Fig. 1). Four of these arches have more or less the same shape; the others—the first, the second and the seventh—are different.

The first arch, the palatal arch, is modified and bears the jaws. The next, the hyoid arch, is very well developed and plays a central role in the respiratory system. Then
follow the five gill arches, the first four of which resemble the hyoid arch in construction. They support the gills. The last gill arch is reduced.

The hyoid arch plays a central role in respiration because all the other skeletal elements important for respiration are connected to it and consequently are influenced by its movements (van Dobben, 1935; Henschel, 1939, 1941). Therefore it will be described first.

The most dorsal bone of the hyoid arch, the hyomandibula, articulates with the otic capsule, forming a long, hinge-like joint. It bears, dorsally on its posterior edge, the condyle for the articulation with the operculum. The tapering ventral end of the hyomandibula comes into contact with the symplectic, a part of the palatal arch and through an intermediate bone, the interhyal or stylohyal, with the ventral part of the hyoid arch, often called the hyoid. The connexions of hyomandibula with symplectic and of stylohyal with hyomandibula and hyoid are flexible.

The hyoid is made up of several bones. These are from posterior to anterior: the epihyal, the ceratohyal and the hypohyal. These bones are firmly grown together. The hypohyals of both sides meet in the mid-line, forming a flexible connexion. Here the glossohyal, which is connected to a copula arrangement, formed by the ventral parts of the gill arches, lies dorsally upon the hypohyals. The urohyal—a bone plate with a big median ridge for muscle insertion—is a ventral appendix of the hyoid arch. The connexions with both glossohyal and urohyal are flexible.

Along the hyoid the branchiostegal rays are implants. They are slender, slightly curved bones reinforcing the branchiostegal membrane, which is a cutaneous flap, running from the ventral mid-line of the head to the operculum, along which it continues as the opercular valve.

The branchial arches emerge from the base of the neurocranium. The arches of each side, initially running latero-caudad, curve to the ventral median, where they meet forming a copula plate that is connected to the base of the hyoid arch. As a result of their curvature, and because each following arch is smaller than the previous one, the gills of a fish obtain their characteristic, basket-like appearance. The reduction in size of the succeeding arches is partly a result of a decreasing number of components, as is described below.

The dorsal part of the first four gill arches, the latero-caudad running epibranchials, together with three small bones, the pharyngobranchials, are loosely anchored in connective tissue on each side at the base of the neurocranium.

The epibranchials are connected to the ventro-mediad running ceratobranchials through a thick, flexible ring of cartilage.

The most ventral parts of the first three arches are the hypobranchials. These are small bones, diminishing in size from the first to the third branchial arch. In the fourth pair of gill arches they are altogether absent. The hypobranchials, together with the copulae or basibranchials, which are small intermediate bones, form the more or less flexible copula plate, which interconnects the branchial arches and together with the glossohyal joins them to the hypohyals of the hyoid arch.

The fifth gill arch is very much reduced. It has no epibranchial but consists solely of a ceratobranchial. It carries the oesophageal teeth and has no respiratory function but is used during food intake.

The palatal arch, the first arch of the visceral skeleton, is very different in construc-
Fig. 2. The palatal complex. The thick black line is cartilage.
(For meaning of abbreviations, see page 564.)

Fig. 3. The head skeleton of the carp after removal of the circumorbital bones.
(For meaning of abbreviations, see page 564.)
tion, compared with the others. Between species of teleosts there is also a considerable variation in the shape, and interconnexion of its components: the palatine, ectopterygoid, entopterygoid, quadrate, symplectic and metapterygoid.

The palatal arch has no posterior articulation with the neurocranium but makes contact with the hyomandibula, which forms the interconnexion with the otic capsule. Palatal arch and hyomandibula thus form together a functional unit, called the palatal complex (Fig. 2), which supports the sides of the buccal cavity and bears the lower jaw.

The symplectic, quadrate, ectopterygoid, entopterygoid and metapterygoid together form an almost square bone-plate of which the first three bones are rigidly grown together, as are the last two. The connexion between both groups, however, is a flexible strip of cartilage. The symplectic is joined to the hyomandibula with connective tissue.

The anterior articulation of the palatal arch with the ethmoidal region of the skull is a double one: the entopterygoid articulates with the parietomoid-prefrontal processus of the neurocranium and the palatine with the forks of the vomer which together with the pre-ethmoid bones form a condylus. The connexion between palatine and entopterygoid is articulate.

The flexible connexions between hyomandibula and symplectic, between symplectic, metapterygoid and entopterygoid on one side and quadrate and ectopterygoid on the other side and between entopterygoid and palatine serve to avoid the stresses which would develop during abduction because the axes of the joints of the hyomandibula, the entopterygoid and the palatine with the skull are not quite parallel.

The mandible articulates with the quadrate. It is built up of three bones on each side (Fig. 3). The articular forms the articulation with the quadrate. Ventral to it is a small bone, the angular. Both bones are grown together with the dentary, the major part of the mandible. The dentaries of both sides are connected flexibly in the mid-line. The upper jaw of the carp has a specialized shape. It is protrusile and can be extended during feeding to suck in material from the bottom. Because its movements are not important in respiration only a superficial description will be given here. More detailed accounts of its functioning are published by van Dobben (1937), Edwards (1926) and Fiebiger (1931). The most important elements of the upper jaw are maxillae and premaxillae. The maxillae articulate dorsally with two short, thick, partly ossified bony pillars, the submaxillary cartilages or cartilagineous rods, which can slide along the same pre-ethmoid-vomer condylus with which the palatine articulates. Ligaments interconnect the maxillae and connect them to projections of the palatines.

The premaxillae are grown together in the mid-line and with their ventro-lateral tip are flexibly connected to the maxillae. The middle of the premaxillae is connected with a ligament to a slender bone, the rostral bone, which in turn has a ligamentous connexion with the mesethmoid.

In the resting position the rostral bone and ligaments are folded up against the vomer.

The opercula have a double function: they protect the gills and they are also an active part of the opercular pumping mechanism. They are built up of four bones (Fig. 3). The largest, the opercular bone, articulates with the hyomandibula. Ventrally the opercular bone partly overlies the subopercular bone. Rostral to that is the inter-
opercular bone, which, with a ridge on its inner surface, articulates with the epihyal-stylohyal junction. The opening between the ventral part of the hyomandibula and the opercular and interopercular bones is filled by the preopercular bone, which comes into close contact with all three.

Caudally the opercula closely follow the shape of the cleithral girdle, which forms the posterior border of the opercular cavities. This close fit is extremely important for the opercular pumping action. The flexible rim of the opercula, the opercular valve, makes a water-tight seal against the cleithra. Ventrally the opercular valves continue as the branchiostegal membranes, which, reinforced by the earlier-mentioned branchiostegal rays, meet in the mid-line, closing the ventral parts of the opercular slits.

**MUSCLES**

Between teleosts, although a common structural plan can be recognized, there are considerable interspecific differences in number, shape and place of origin and insertion of the head muscles. Also many variations in muscle co-ordination pattern exist. These differences represent adaptations of the feeding and respiratory apparatus of the species to its life habits and environment.

Several authors (Ballintijn & Hughes, 1965; Deganello, 1908; Dietz, 1912; van Dobben, 1935, Fiebiger, 1931; Henschel, 1939; Holmquist, 1910, 1912; Kirchhoff, 1958) have published more or less extensive descriptions of the head muscles of different fishes, some with theories on their function, based on anatomical observations. Moreover Vetter, (1878) in a much cited classical work, among other fishes describes the muscles of the carp, and Takahasi (1925) devotes an extensive paper to the cranial muscles of the cypriniform fishes alone.

Basically the movable elements of the head skeleton each have their own adductor and abductor muscles. However, in fact the influence of several muscles extends much farther than only the bones they are attached to. It is the aim of this paper to investigate and explain the extent of these interactions.

In the following, the anatomical position of the cranial muscles of the carp and their action on the bones they are attached to directly will be described (Fig. 4). The influence of the resulting movements on a larger part of the visceral system through skeletal couplings will be dealt with in the last section.

The hyomandibula is moved by the palatal complex muscles: the levator hyomandibulae and the adductor arcus palatini. As will be explained later, it plays a central role in almost all movements of the visceral skeleton, and consequently its muscles have a very general influence.

*The levator hyomandibulae* is a powerful muscle. It arises from the sphenotic, runs postero-ventrad and inserts on the outside of the hyomandibula. In other species (e.g. the trout) it can extend along the palatal complex and is then called the levator hyomandibulae et arcus palatini.

The effect of the levator hyomandibulae is abduction of the hyomandibula.

*The adductor arcus palatini*, the antagonist of the levator hyomandibulae, is a continuous strip of muscle arising from the parasphenoid. It is inserted along the entopterygoid, the metapterygoid and the inside of the hyomandibula.

The effect of the adductor arcus palatini of the carp is adduction of the palatal complex.
The operculum is moved by three muscles: the adductor operculi, the levator operculi and the dilator operculi.

The adductor operculi arises in a large hollow in the otic region of the skull, from the underside of the pterotic and the parietal. It is a long, slender muscle, running laterad and inserting on the inside of the operculum, a little below the dorsal border, just behind the articulation of the operculum with the hyomandibula. The effect of the adductor operculi is to close the operculum.

The dilator operculi arises from a groove between frontal, pterotic and sphenotic, and also from the external surface of the dorsal part of hyomandibula. It inserts on a lever-like process of the operculum, dorsal to its articulation with the hyomandibula.
The muscle is fan-shaped, its ventral fibres running almost horizontally from operculum to hyomandibula and its dorsal fibres almost vertically between operculum and pterotic. In the carp it is divided by an aponeurosis into two parts, dorsal and ventral. The effect of the dilator operculi is opercular abduction.

The levator operculi arises mainly from the lateral ridge of the pterotic. A small part, however, has its origin on the dorsocaudal margin of the hyomandibula. It there begins as a strip of short muscle fibres, which inserts along the inside of the upper rim of the operculum just above the insertion of the adductor operculi. More caudally the fibres gradually increase in length and in the posterior part of the muscle they extend for some distance along the inside of the operculum.

The effect of the levator operculi is to lift the operculum, whereby it turns around the articulation with the hyomandibula.

The branchiostegal apparatus can be regarded as a continuation of the operculum and its muscle, the hyohyoideus, even is partly connected to the operculum.

The hyohyoideus can be divided into an inferior and a superior part. The hyohyoideus inferior is very small. Borcea (1906) even considers it absent in the carp. It arises from the inside of the epihyal and runs mesoanteriorly until it meets the muscle from the other side in the mid-line. A tendon connects it with the hypohyal.

The hyohyoideus superior arises from the inner surface of preoperculum, interoperculum and suboperculum. It is a broad sheet of muscle fibres, running mesoanteriorly and interconnecting the branchiostegal rays. In Fig. 5 this part is drawn in broken lines because it runs behind the bones. From the most ventral branchiostegal rays the muscles of both sides run to the ventral mid-line where they meet and also connect to the hypohyal. In Fig. 4 the perspective suggested by the shape of this part of the muscle is deceptive: where it is labelled Hyhy is the ventral mid-line.

The effect of the hyohyoideus is contraction of the branchiostegal apparatus and hyoid and also ventrad rotation of the operculum, so that in this respect it can be regarded as the antagonist of the levator operculi.

The hyoid, apart from the influence the hyohyoideus has on it, is moved by two muscles: the sternohyoideus and the protractor hyoidei.

The sternohyoideus partly arises from the cleithra and partly is a continuation of the ventral body musculature. It inserts on the dorsal side of the urohyal.

The primary effect of the sternohyoideus is abduction of the hyoid.

The protractor hyoidei mainly arises from the ceratohyal and partly from the epihyal. It is divided into a dorsal and a ventral part. The ventral parts of both sides meet in the mid-line, where fibres are exchanged. Both the dorsal and the ventral protractor hyoidei insert on the inside of the dentary in the region of the symphysis of the jaw.

On the function of the protractor hyoidei, different opinions have been expressed. Baglioni (1910) thinks that it serves as abductor of the lower jaw; Deganello (1908), Dietz (1912) and Vetter (1878) even think that it has the double function of adducting the hyoid when the adductor mandibulae keeps the jaw closed, and of abducting the lower jaw when the adductor mandibulae is not active. Holmquist (1912), as a result of extirpation experiments, concluded, however, that it is only active when the mouth is closed, then adducting the hyoid. Although since then some authors (Edgeworth, 1931; Fiebiger, 1931; Henschel, 1941) have maintained the view that the muscle
abducts the lower jaw, recent electromyographic experiments (Ballintijn & Hughes, 1965; Hughes & Shelton, 1962) have shown that for the trout and the tench Holmquist's theory is correct. The same appears now to be the case for the carp (Ballintijn, 1969 a).

Instead of protractor hyoidei, the name geniohyoideus is sometimes used. According to Edgeworth (1931) and Holmquist (1910) this name is incorrect, because the protractor hyoidei is not homologous with the geniohyoideus of the tetrapods on ontogenetical grounds. The use of the name 'geniohyoideus' moreover creates confusion because that muscle in tetrapods abducts the lower jaw, whereas the protractor hyoidei adducts the hyoid. For these reasons the name protractor hyoidei is preferable.

The jaws of the carp are served by the intermandibularis muscle and the adductor mandibulae complex.

*The intermandibularis* is a very small muscle, interconnecting the rami of the lower jaw across the symphysis. It lies between the protractor hyoidei superior and inferior.

The effect of the intermandibularis is to contract the rami of the lower jaw, but because it is almost rudimentary in the carp its influence is not great. It is not shown in Fig. 5.

*The adductor mandibulae* consists of several muscles, which can be divided into two sets: the maxillaris group moving the upper jaw and the mandibularis group moving the lower jaw.

Two muscles, A 1α and A 1β (or A 1' and A 1 of van Dobben) form the maxillaris group. A 1α arises from the preoperculum and the symplectic. It runs almost horizontally and inserts on the maxilla with a slender tendon. A 1β lies anterior to A 1α with which it is somewhat continuous at the base. It arises from preoperculum, quadrate, symplectic and mandible and runs in an anteriodorsad direction, inserting on the dorsal margin of the maxilla with a slender tendon which crosses over the tendon of A 1α.

On the effect of the maxillaris muscles, different opinions are held. Vetter (1878) supposes both muscles to pull the maxilla back when the mouth is closed. According to Fiebiger (1931) A 1β and A 1α are antagonists, the first extending the upper jaw and the second pulling it back. Van Dobben (1935) ascribes the same functions to these muscles, but in addition he mentions the possibility that, when A 1β is extending the upper jaw, additional activity in A 1α could reinforce this movement. It is one of the present investigations in our laboratory to analyse the co-ordination of the maxillaris muscles of the carp during feeding, with the aid of electrophysiological methods. For the present paper only the mandibularis group is regarded.

To the mandibularis group belong the muscles A 2, A 3 and A ω. A 2 is a thin, broad muscle arising from quadrate, symplectic, preoperculum and hyomandibula. It inserts with a short, plate-like tendon on the processes of the dentary and on the articular.

A 3 is partly fused with A 2. It arises from the hyomandibula and the metapterygoid in two parts, one external and one internal to the levator hyomandibulæ. Both parts insert together with a flat, tapering tendon on the articular. The mentalis or A ω muscle is attached to the tendon of A 3 and inserts on the inside of the mandible on Meckels cartilage.

The effect of the mandibularis muscles is lifting of the lower jaw.
Fig. 5a and b. For legend see facing page.
Mechanics of carp respiration

There is no special muscle for abduction of the mandible attached to it directly. A slight abduction will be due to gravity when the jaw is not actively held adducted, and besides that the action of muscles inserted on other parts of the system, as will be shown later, results in lowering of the jaw.

Couplings

In the anatomical description, the visceral skeleton of fishes was shown to consist of a number of bone arches and bones, joined by articulations. This articulate construction results in a considerable flexibility.

From the description of the muscular system it appeared that the visceral apparatus is equipped with numerous muscles, inserting at various places. Obviously such a highly flexible system, in which a number of forces can be applied at different places, is capable of intricate movements. The complexity of the system is even greater, because some bone arches are interconnected by ligaments or have articulations placed in a special way so that a force on one element, through a kind of lever action, also affects other parts. It is through these mechanical couplings that the effect of the contraction of a given muscle not only affects the parts it is directly attached to, but spreads over a larger part of the system, and also that various different muscle co-ordination patterns encountered in one and the same fish at different times all produce a satisfactory respiratory pumping action.

The anatomical configuration and the activity pattern of the respiratory muscles can vary considerably between different teleosts species. In the coupling possibilities of the skeleton, however, the same plan is easily recognized in many teleosts. In the past several authors have published separate descriptions of parts of these couplings in different fishes. The first more complete survey of the mechanical properties in one fish species, the trout, was published in 1965 by Ballintijn & Hughes.

The couplings in the carp (Fig. 5) now prove to be comparable and a detailed description will be given in the following.

The findings of the authors mentioned above, which will of course be cited at the appropriate places, partly served as a basis for the account. The following experimental procedures were used to obtain a complete picture of the couplings in the head of the carp.

In the first place the anatomical position and relationship of the skeletal elements, which for this purpose was established by dissection, suggested the interaction of certain movements. The possibilities of movement thus predicted were checked on intact animals which had died shortly before or were made motionless with a heavy dose of anaesthetic. The procedure consisted of artificially moving separate skeletal elements and noting the spread of the motion.

Fig. 5. Three-dimensional diagram of the couplings in the respiratory system of the carp (a) during expansion and (b) during contraction. (Thick black lines are ligaments.) See Figs. 1–3 for the names of the bones. 1, Levator hyomandibulae; 1a–d, effect of the levator hyomandibulae. 2, Dilator operculi; 2a, effect of the dilator operculi. 3, Levator operculi; 3a–d, effect of the levator operculi. 4, Sternohyoideus; 4a–h, effect of the sternohyoideus. 5, Adductor arcus palatini; 5a–d, effect of the adductor arcus palatini. 6, Adductor operculi; 6a–c, effect of the adductor operculi. 7, Adductor mandibulae; 7a, effect of the adductor mandibulae. 8, Protractor hyoidei; 8a–f, effect of the protractor hyoidei. 9, Hyohyoideus; 9a–c, effect of the hyohyoideus.
Latterly this type of experiment was much refined; separate muscles of such a motionless fish were stimulated electrically with trains of integrated square-wave pulses. In this way the spread of the movement caused by the contraction of each individual muscle as a result of the couplings could be ascertained.

A. The hyoid arch

The hyoid arch is the most important coupling element because it affects the whole respiratory system; the volumes of the buccal and opercular pumps, the position of the opercula and even the position of the lower jaw are changed by its movements. This can easily be demonstrated as follows; if in a deeply narcotized fish the floor of the buccal cavity is pushed down with a probe entering through the mouth, the ventral part of the hyoid arch, which lies there, is abducted. This results in wide opening of the mouth through lower jaw abduction, lateral expansion of the sides of the mouth cavity, opercular abduction and expansion of the branchiostegal system.

Functionally the hyoid arch can be divided into two parts: the hyomandibula and the hyoid.

(a) The hyomandibula

*Abduction of the hyomandibula.* Contraction of the levator hyomandibulae abducts the hyomandibula. This results in the first place in abduction of the palatal complex, formed by the hyomandibula and the palatal arch, and consequently in a considerable increase in volume of the mouth cavity, the sides of which are supported by the palatal complex.

The lower jaw articulates with the quadrate, one of the palatal arch bones, and because the medial connexion of its rami is flexible it also expands laterally, increasing the cross-sectional area of the mouth opening. Obviously this is more important for food intake than for respiration.

The operculum is connected to the hyomandibula and therefore expands also, increasing the volume of the opercular cavity. As the connexion between operculum and hyomandibula is articulately, opening of the opercular slit is not a necessary consequence of opercular expansion caused by hyomandibula abduction, but depends on other forces acting at the same time.

The laterad movement of the ventral tip of the hyomandibula during abduction is transmitted to the epihyals (the dorsal bones of the hyoid) through mediation of the stylohyal (Henschel, 1939, 1941). This results in laterad expansion of the hyoid, the rami of which have a flexible connexion mid-ventrally. The epihyals are also connected to the inside of the interopercula and thus through their laterad movements reinforce the opercular expansion, already produced by the direct connexion between hyomandibula and operculum.

The hyoid can be regarded as an isosceles triangle, the base of which is formed by the line connecting the articulations of the epihyals with the stylohyals on both sides. Lateral displacement of the epihyals increases the length of the base of this triangle and consequently decreases its height. Thus the ventral tip of the hyoid moves caudad and takes with it the basal copula arrangement to which the branchial arches are flexibly connected. This caudad movement, as a consequence of the curved shape of the gill arches, results in expansion of the branchial basket.
Electrical stimulation of the levator hyomandibulae indeed shows an over-all lateral expansion of the sides of the head from palatal arch to operculum.

Adduction of the hyomandibula. The hyomandibula is adducted by the adductor arcus palatini. This muscle, contrary to its antagonist, the levator hyomandibulae, is inserted not only on the hyomandibula but partly also on the palatal arch. It thus directly adducts the whole palatal complex and decreases the volume of the mouth cavity.

Its secondary effects are opposite to those of the levator hyomandibula:

(i) The rami of the lower jaw are compressed laterally through mediad movements of the ventral tips of the hyomandibulae and the quadrates.

(ii) The opercula are adducted through their connexion with the hyomandibulae, decreasing the volume of the opercular cavities. The mediad movement of the hyomandibula tips via the stylohyals is transmitted to the epihyals, so that the rami of the hyoid are compressed and opercular adduction is reinforced because of the epihyal-interopercular connexion.

(iii) Mediad movement of the epihyals also shortens the base of the hyoid triangle, moving forward its apex, the mid-ventral tip of the hyoid and copula, and consequently contracting the branchial basket.

(b) The hyoid

From the resting state the hyoid can be abducted, retracted and expanded as a result of sternohyoideus contraction. These three movements are, however, independent in so far as prevention of one does not hamper the execution of the others.

Abduction of the hyoid. When the hyoid is abducted it rotates around the articulation with the stylohyal, its tip moving in a ventrocaudad direction. Through this movement the floor of the mouth cavity in which the glossohyal extends is lowered, thus increasing the buccal volume.

Further, with the anterior tip of the hyoid the copula plate of the branchial arches moves ventrocaudad, expanding the branchial basket, as a consequence of the curvature of the gill arches.

Extreme hyoid abduction stretches the mandibulo-hyoid ligament, the protractor hyoidei (passively) and the skin between hyoid and mandible and so reinforces lower jaw abduction.

Retraction of the hyoid. Contraction of the sternohyoideus results in a force along the bones of the hyoid because the muscle is not orientated perpendicular to them. Under influence of this force the stylohyal, which articulates with the hyoid and the hyomandibula, describes an arc around the latter articulation, enabling the hyoid to move in a caudad direction. This retraction of the hyoid results in abduction of the lower jaw in two ways.

First, because the mandibulo-hyoid ligament connects the dorsal part of the epihyal (near the articulation with the stylohyal) to the angular bone of the lower jaw. Stretching of the ligament through hyoid retraction abducts the lower jaw as it inserts below the articulation with the quadrade.

Secondly, because the epihyal is connected to the interoperculum, and this with the mandibulo-interopercular ligament is connected to the angular bone near the insertion of the mandibulo-hyoid ligament. Hyoid retraction moves the interoperculum dorso-
Caudad and stretches the mandibulo-interopercular ligament, which then also abducts the lower jaw because it inserts below the articulation with the quadrate (van Dobben, 1935; Henschel, 1939, 1941; Holmquist, 1910; Woskoboinikoff, 1932).

Expansion of the hyoid. The force along the bones of the hyoid, apart from the caudad component resulting in retraction, also has a laterad component because the sternohyoideus makes an oblique angle with the bone. As the halves of the hyoid midventrally have a flexible connexion, this laterad force expands the hyoid. This hyoid expansion through the connexion of the epiphyal with the interoperculum is mediated to the opercular bones (van Dobben, 1935).

Further, the hyomandibula is abducted because the stylohyal connects it to the expanding epiphyal. The hyomandibula, because it articulates with the operculum, also reinforces the opercular abduction already produced by the hyoid-interopercular connexion, and besides that, because it is part of the palatal complex, extends the expansion to the sides of the buccal cavity. Electrical stimulation of the sternohyoideus indeed shows abduction of the lower jaw, lowering of the floor of the buccal cavity and over-all lateral expansion.

Adduction protraction and contraction of the hyoid. The protractor hyoidei can, at least in its respiratory function, be regarded as the antagonist of the sternohyoideus. The electromyographic experiments reported in another paper (Ballintijn 1969a), show that this is true because when it contracts, activity in a part of the adductor mandibulae complex keeps the lower jaw, on which the protractor hyoidei originates, fixed. Thus the action of the protractor hyoidei results in adduction, protraction and narrowing of the hyoid, on which it is inserted. The effects are opposite to those of sternohyoideus contraction, which are as follows.

The hyoid and through it the floor of the mouth is raised, decreasing the buccal volume.
The basal copula of the gill arches moves dorso-frontad, contracting the branchial basket.
The epiphyals move forward and with them the opercular bones, taking tension off the mandibulo-interopercular ligament. The mandibulo-hyoid ligament also becomes slack.
The hyoid contracts laterally and adducts the hyomandibula (and with it the operculum) through mediation of the stylohyal.

Electrical stimulation if combined with electrical stimulation of adductor mandibulae produces the above mentioned effects. If the adductor mandibulae is not stimulated at the same time, the jaw is abducted and the other effects seem of a lower intensity.

B. The operculum

Abduction of the operculum is caused by the dilator operculi muscle. The movement has no secondary effect. This is supported by electrical stimulation of the muscle.

Adduction of the operculum

The operculum is adducted by the adductor operculi. Because the muscle inserts close to the articulation of operculum and hyomandibula, the latter will also be adducted by it. In some teleost species, among which is the trout, the adductor operculi
is not even a separate muscle, but part of the adductor arcus palatini (Ballintijn & Hughes, 1965; Dietz, 1912).

Because, owing to its small size, it is difficult to stimulate this muscle without at the same time stimulating the levator operculi, the results of these experiments were not regarded as conclusive.

**Fig. 6. Abduction of the lower jaw through opercular levation. Slight displacement of opercular bones, hyoid and stylohyal, through lever action results in appreciable lower jaw abduction. (L is ligament.)**

**Levation of the operculum**

The levator operculi lifts the complex of opercular bones, turning it around the condyle of the articulation with the hyomandibula. The result is a dorsocaudad movement of the ventral elements, the sub- and the inter-opercula. Van Dobben (1937), Henschel (1939-41), and Holmquist (1910) already recognized that this movement may serve to lower the jaw. The mechanism is as follows (Fig. 6). Through levator operculi action the operculum complex rotates around its articulation with the hyomandibula. Its ventral components (especially the interoperculum) consequently move in a dorsocaudad direction. This stretches the mandibulo-interopercular ligament, which connects the interoperculum with the angular bone of the lower jaw, behind and below its articulation with the quadrate. The result of the traction on this ligament is lower jaw abduction.

The interoperculum, although connected to the hyoid, can perform the dorsocaudad movement because the stylohyal connects epihyal and hyomandibula and, articulating with both, makes retraction of the hyoid possible. The retraction of the hyoid, as the movement is small, is of little consequence for the volume of the respiratory cavities, but reinforces the lower jaw abduction because the mandibulo-hyoid ligament, which inserts on the angular near the mandibulo-interopercular ligament, is stretched. Electrical stimulation of the levator operculi indeed results in opercular levation and lower jaw abduction.
C. The branchiostegal system

Abduction of the branchiostegal system is not active in the carp, in contrast to the flat fishes and other bottom fishes where the system plays an important role in respiration (Borcea, 1906; Henschel, 1939, 1941; Holmquist, 1912). It is only passively stretched as a secondary effect of the abduction of the opercular bones and the abduction and expansion of the hyoid.

Adduction of the branchiostegal system, however, is active and brought about by contraction of the hyohyoideus, which because of its origin on the opercular bones, also exerts an adducting, ventromediad traction on the operculum. In addition, because the muscles of both sides meet in the ventral mid-line, it adducts the hyoid.

It proved difficult to stimulate the hyohyoideus as a whole. However, the branchiostegal rays between the stimulating electrodes invariably came closer to each other during electrical stimulation. Expansion was never obtained.

D. The lower jaw

Abduction of the lower jaw

The lower jaw has no abductor muscle inserted on it. Active opening exclusively takes place through the action of muscles inserting on other bones (e.g. the levator operculi and the sternohyoideus) by way of the couplings described above.

The results of electromyographic experiments (Ballintijn, 1969b) shows that the most important muscle for lowering of the jaw during respiration is the levator operculi.

It works as described above under Levation of the operculum (p. 561).

The sternohyoideus also can abduct the lower jaw as described above under Abduction of the hyoid and retraction of the hyoid (p. 559).

Finally, contractions of the ventral and dorsal body musculature influence opening of the mouth. The former, through retraction of the cleithra from which the sternohyoideus arises, reinforces the action of this muscle. The latter moves the cranium, and with it the upper jaw, slightly dorsad (Holmquist, 1910).

DISCUSSION

In 1910 Holmquist was already aware of the important role couplings can play in the mechanism of the visceral system. He concluded from his extirpation experiments, for instance, that different muscles could lower the mandible through mechanical interaction. After that more couplings were proposed on anatomical grounds.

The demonstration in this paper of the extensive interaction of elements throughout the whole respiratory system of the carp on anatomical grounds, and on the evidence of movement and muscle stimulation analyses, is supported also by the results of electromyographic experiments (Ballintijn, 1969b).

Because of the integrative effect due to the spread of the respiratory movements by way of the couplings, the result of the contraction of almost every individual head muscle is ultimately a rather complete respiratory movement. Thus a contraction of any of the muscles producing a laterad movement of the element they are inserted upon, such as the levator hyomandibulæ, the adductor arcus palatini and the adductor
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operculi, results in a laterad movement of the wall of both the buccal and the opercular cavities. There is only one exception: the dilator operculi which abducts the operculum only. Further, the hypobranchial muscles, sternohyoides, protractor hyoidei and hyohyoides, which produce dorsoventrad hyoid movements, besides influencing the volumes of buccal and opercular cavities in a dorsoventrad direction, give rise to laterad movements of the side walls of all the cavities as well. Finally the lower jaw, which has no abductor muscle inserted upon it directly, is abducted by the levator operculi. Lower jaw abduction also is one of the effects of sternohyoides contraction.

The integrative effect of this interaction of all the movements of the respiratory pump is functionally very important for the following reasons. The energetic efficiency of muscular contraction has been shown to increase with increasing activity in the muscle under observation (Bronck, 1930). A consequence of this is that it is more efficient to obtain a low-intensity movement with high activity in a few muscles than with low activity in many.

In the respiratory system low-intensity respiration indeed appears to be brought about mainly in this, from the viewpoint of contraction energy the most efficient way, namely by reducing the number of muscles taking part (Ballintijn, 1960a). However, the switching on or off of whole muscles causes the number of forces driving the respiratory pumps as well as their point of application to change with ventilation intensity. This could lead to a less efficient performance because of a changed movement pattern, were it not that the movements as a result of the integration due to the mechanical couplings remain virtually unaltered, changing in amplitude and frequency only. Consequently the hydrodynamic efficiency of the pumps is the same from high to low respiration intensity, regardless of the number of muscles active.

SUMMARY

1. An anatomical description of the head skeleton of the carp (Cyprinus carpio) is given. The description is limited to what is relevant for the functioning of the respiratory pumps.

2. An anatomical description of the head muscles of the carp is given.

3. The result of the contraction of most of the head muscles through coupling of skeletal elements spreads farther over the respiratory system than only to the bones to which the muscles are attached directly. It is through this that in the first place all the muscles producing laterad movements, with the exception only of the dilator operculi, influence the volume of both the buccal and opercular cavities, and in the second place that contraction of the hypobranchial muscles not only results in vertical movements of the floor of all the respiratory cavities, but also in laterad movements of their side walls. The hyoid arch plays a central role in the coupling system because it interconnects almost all the other elements.

4. The functional significance of the interaction through couplings is integration of the respiratory movements through which during low-intensity breathing whole muscles can cease to be active and during high-intensity respiration whole muscles can be recruited without seriously affecting the co-ordination of the movements and hence the hydrodynamic efficiency of the pumps.
LIST OF ABBREVIATIONS

Add arc pal  adductor arcus palatini
Add md     adductor mandibulae
Add op     adductor operculi
An         angular
Ar         articular
Chr        ceratobranchial
Chy        ceratohyal
Cl         cleithrum
Cop        copula
D          dentary
Dil op     dilator operculi
Eb         epibranchial
Ecp        ectopterygoid
Ehy        epihyal
Exp        entopterygoid
Ghy        glossohyal
Hb         hypobranchial
Hky        hypohyal
Hmd        hypomandibula
Hy         hyoid
Hyhy       hyohyoideus
Iop        interoperculum
Lev kyom   levator hyomandibulae
Lev op     levator operculi
Mtp        metapterygoid
Ms         maxilla
Op         operculum
Pal        palatine
Pb         pharyngobranchial
Pmx        premaxilla
Pop        preoperculum
Prot hy    protractor hyoid
Qu         quadrate
R          rostral
R br       branchiostegal rays
Smc        submaxillary cartilage
Sop        suboperculum
St hy      sternohyoideus
Sth        stylohyal
Sy         symplectic
Uhy        urohyal
Vo         vomer

REFERENCES


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APPENDIX

(The numbering corresponds with that of Fig. 5.)

LEVATOR HYOMANDIBULAE (1)

**PRIMARY EFFECT.** Abduction hyomandibula 1 (a).

**EVENTUAL INFLUENCE UPON:**

*Opening of mouth.* Lateral widening of mouth opening via expansion of palatal complex (1 a) and lower jaw (1 d).

*Expansion of buccal cavity.* Lateral expansion sides (palatal arch) (1 a). Lateral expansion floor (hyoid) (1 c).

*Expansion of branchial basket.* Hyomandibular abduction via lateral hyoid expansion gives caudad movement of copula and slight branchial expansion.

*Expansion of opercular cavity.* Abduction operculum and interoperculum (1 b) through hyomandibular abduction (1 a)

ADDUCTOR ARCUS PALATINII (5)

**PRIMARY EFFECT.** Adduction arcus palatinus and hyomandibula (5 a).

**EVENTUAL INFLUENCE UPON:**

*Closing of mouth.* Narrows mouth opening laterally (5 d) through adduction arcus palatini (5 a).

*Contraction of buccal cavity.* Lateral contraction of sides (palatal arch) (5 a); lateral contraction of floor (hyoid) (5 c).

*Contraction of branchial basket.* Hyomandibular adduction (5 a) via lateral contraction of the hyoid (5 c) and craniad movement of the copula gives slight branchial arch contraction.

*Contraction of opercular cavity.* Hyomandibula adduction (5 a) gives opercular and interopercular adduction (5 b).

Sternohyoideus (4)

**PRIMARY EFFECT.** Abduction (4 a), retraction (4 b, c) and expansion (4 g) hyoid.

**EVENTUAL INFLUENCE UPON:**

*Opening of mouth.* Opens mouth through retraction of hyoid (4 b, c) via caudad movement interoperculum and mandibulo-interopercular ligament (4 e) and via mandibulo-hyoid ligament, skin, etc. (4 c).
**Expansion of buccal cavity.** Lowering floor through abduction hyoid (4a). Lateral expansion through expansion hyoid (4g). Lateral expansion sides through expansion hyoid via hyomandibula and palatal arch (4b).

**Expansion of branchial basket.** Hyoid abduction gives caudad movement of copula and branchial expansion.

**Expansion of opercular cavity.** Hyoid expansion causes interopercular abduction (4h) and also via hyomandibular abduction (4g) and opercular abduction (4h).

**Protractor hyoidei (8)**

**PRIMARY effect.** Adduction (8a) and protraction (8b) hyoid.

**EVENTUAL INFLUENCE UPON:**

- **Contraction of buccal cavity.** Raising (8a) and lateral contraction (8d) of floor (hyoid). Lateral contraction through adduction of palatal arch via hyoid and hyomandibula adduction (8e).
- **Contraction of branchial basket.** Hyoid protraction via craniad movement of the copula gives branchial contraction.
- **Contraction of opercular cavity.** Lateral hyoid contraction gives interopercular adduction and via hyomandibula adduction, opercular adduction (8f)

**Hyohyoideus (9)**

**PRIMARY effect.** Contraction of branchiostegal apparatus, adduction hyoid (9a) and ventral opercular border. Downward movement of operculum.

**EVENTUAL INFLUENCES UPON:**

- **Contraction of buccal cavity.** Raising and lateral contraction floor through lateral compression (9c) and adduction (9a) of hyoid.
- **Contraction of branchial basket.** Lateral compression and adduction of hyoid (9c) via craniad movement of the copula gives branchial contraction.
- **Contraction of opercular cavity.** Through contraction of the branchiostegal membrane and consequent adduction of the operculum (9b).

**Dilator operculi (2)**

**PRIMARY effect.** Dilation of operculum.

**EVENTUAL INFLUENCES UPON:**

- **Expansion of opercular cavity.** Abduction of operculum.

**Adductor operculi (6)**

**PRIMARY effect.** Adduction of operculum (6a).

**EVENTUAL INFLUENCES UPON:**

- **Contraction of buccal cavity.** Lateral compression via hyomandibula adduction (6b).
- **Contraction of opercular cavity.** Through adduction of operculum (6a).

**Levator operculi (3)**

**PRIMARY effect.** Levation operculum (3a).

**EVENTUAL INFLUENCES ON:**

- **Opening mouth.** Dorsocaudal movement of interoperculum opens mouth via mandibulo-interopercular ligament (3b) and also via hyoid retraction and mandibulo-hyoid ligament (3c).
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ADDUCTOR MANDIBULAE (7)

**PRIMARY EFFECT.** Adduction mandible is the most important respiratory function (7a).

**EVENTUAL INFLUENCES ON:**

- *Closing of mouth.* Closes mouth (7a).
- *Contraction of buccal cavity.* Serves as anchor for hyoid protraction by fixing the lower jaw in closed position.

DORSAL BODY MUSCULATURE

**PRIMARY EFFECT.** Lifting cranium.

**EVENTUAL INFLUENCE ON:**

- *Opening of mouth.* Opening mouth reinforced through lifting cranium.

VENTRAL BODY MUSCULATURE

**PRIMARY EFFECT.** Retraction of cleithra.

**EVENTUAL INFLUENCE ON:**

- *Opening of mouth.* Opening mouth reinforced through retraction origin sternohyoideus.