PHILOSOPHICAL TRANSACTIONS.

I. *The Croonian Lecture on the Arrangement and mechanical Action of the Muscles of Fishes.* *By* Anthony Carlisle, *Esq.* *F. R. S. F. L. S.*

Read November 7, 1805.

It was my intention to have continued my physiological inquiries on the phenomena of muscular motion, by a series of chemical experiments; and to have communicated the result, when duly matured, to the Royal Society. But an unexpected request, made at a late period, for the Lecture of the present year, obliges me to defer those researches, and to limit the investigation of the subject I have chosen.

The application of the motive organs of animals has already furnished examples of general utility by increasing our knowledge of mechanical powers; and the cultivation of this study promises still further improvement.

The muscles of fishes are of a very different construction from those of the other natural classes. The medium in which these animals reside, the form of their bodies, and the

instruments employed for their progressive motion, give them a character peculiarly distinct from the rest of the creation. The frame-work of bones or cartilages, called the Skeleton, is simple; the limbs are not formed for complicated motions, and the proportion of muscular flesh is remarkably large. The muscles of fishes have no tendinous chords, their insertions being always fleshy. There are, however, semi-transparent, pearly tendons placed between the plates of muscles, which give origin to a series of short muscular fibres passing nearly at right angles between the surfaces of the adjoining plates. LEWENHOECK* appears to have overlooked these tendons, and the numerous vessels, which he describes in the interstices of the muscular flakes, I have not been able to discern.

The motion of a round shaped fish, independent of its fins, is simple; and as it is chiefly effected by the lateral flexure of the spine and tail, upon which the great mass of its muscular flesh is employed, whilst the fins are moved by small muscles, and those, from their position, comparatively but of little power, I shall only describe in detail the arrangement and application of those masses, which constitute the principal moving organs.

For this purpose a well known fish, the cod,† has been selected as a standard of comparison for the muscles of other fishes, there being a conspicuous resemblance among them all.

The pairs of fins have been considered as analogous to feet, but they are only employed for the purposes of turning, stopping, altering the position of the fish towards the horizon,

* Phil. Trans. Vol. XXXI. p. 190. † *Gadus Morhua* of LINNÆUS.

and for keeping the back upwards. The single fins appear to prevent the rolling of the body, whilst the tail is employed to impel it forward.

Each of those fins, which are in pairs, is capable of four motions, *viz.* of flexion and extension, like oars, and of expanding the rays, and closing them.

The extension of the whole fin is performed by a single radiated muscle, which is often supplied with red blood: the antagonist is of a similar character. The great power of the extensor muscle *(Vide* Plate I. *a, a,)* shews how strongly it is required to act when employed to stop suddenly the progressive motion. A series of intervening muscles expand and close the rays.

In the act of extending the fin the interosseal muscles are passive. It is advanced forward edgeways and closed; but during its flexion, the rays are expanded, striking the water with its broadest surface: this action assists the tail in turning the fish. In the effort to stop, these fins are strongly retained at right angles with the body, by the force of the extensor muscles, the rays are expanded, and the effect is assisted by the tail turning laterally with its broadest surface forward.

The single fins, for the expansion and contraction of their rays, are furnished with two sets of muscles; one of which is situated at their roots, and lies oblique; *(bbbbb)* the other, parallel with the spines, to which the rays are articulated *(cc.)* The fin has also a lateral motion, by which it is occasionally drawn out of a straight line; and by the co-operation of these muscles on both sides, it is kept steady whilst the body of the fish is turned oblique in swift motion, or in eddies.

When placed near the tail, the single fins seem also to aid the effect of that instrument by increasing its breadth.

The tail is the principal organ of progressive motion, and its actions are performed by the great mass of lateral muscles. There are a series of short muscles for the purpose of changing the figure of the tail fin, which arise from the spine and *coccyx*, and are attached to the rays immediately beyond their joints: *(dd)*: their action is to expand the rays, and by partial contractions to alter the lateral position of the fin. Slender muscles are placed between the several rays, *(ee,)* whose office is to converge them previous to the stroke of the tail.

The muscles situated on the head are those, which act on the *membrana branchiostega*, the under jaw, *os hyoides*, *fauces*, and the globe of the eye.

In order to determine the effect of the fins on the motions of fishes, a number of living dace,* of an equal size, were put into a large vessel of water. The pectoral fins of one of these fishes were cut off, and it was replaced with the others. Its progressive motion was not at all impeded; but the head inclined downwards, and when it attempted to ascend, the effort was accomplished with difficulty.

The pectoral and abdominal fins were then removed from a second fish. It remained at the bottom of the vessel, and could not be made to ascend. Its progressive motion was not perceptibly more slow; but when the tail acted, the body shewed a tendency to roll, and the single fins were widely expanded, as if to counteract this effect.

From a third fish, the single fins were taken off. This

* *Cyprinus leuciscus.*

produced an evident tendency to turn round, and the pectoral fins were kept constantly extended to obviate that motion.

From a fourth fish, the pectoral and abdominal fins were cut off on one side, and it immediately lost the power of keeping the back upwards. The single fins were expanded, but the fish swam obliquely on its side with the remaining pectoral and abdominal fins downwards.

From a fifth fish, all the fins were removed. Its back was kept in a vertical position, whilst at rest, by the expansion of the tail, but it rolled half round at every attempt to move.

From a sixth fish, the tail was cut off close to the body. Its progressive motion was considerably impeded, and the flexions of the spine were much increased during the endeavour to advance: but neither the pectoral nor abdominal fins seemed to be more actively employed.

From a seventh fish, all the fins and the tail were removed. It remained almost without motion, floating near the surface of the water, with its belly upward.

These experiments were repeated on the roach,* the gudgeon,† and the minnow,‡ with similar results.

The muscles of fishes differ materially in their texture from those of other animals: they are apparently more homogeneous, their fibres are not so much fasciculated, but run more parallel to each other, and are always comparatively shorter. They become corrugated at the temperature of 156° of FAHRENHEIT, when their tendinous and ligamentous attachments are dissolved, and their serous juices coagulated. Under those circumstances the muscles lose their transparency, and the lateral cohesion of their fibres is lessened.

* *Cyprinus rutilus.* † *Cyprinus gobio.* ‡ *Cyprinus phoxinus.*

But the mechanical arrangement and physiology of the lateral muscles of the body of fishes constitute my present object. These parts have already been described in a general way by Professor CAMPER, M. VICQ-D-AZYR, and M. CUVIER, to whom I am indebted for much useful information. They have been denominated "*couches musculaires*" by M. VICQ-D-AZYR,* and "*muscles laterals*" by M. CUVIER.† The term used by M. CUVIER seems very appropriate for the general division or class. But, as the flakes are arranged in distinct longitudinal rows, these rows must be considered as orders. And, as "*couches*" appears objectionable, I shall adopt *series* in its stead; distinguishing each by a word referring to its situation in the animal, *viz.* the dorsal, vertebral, abdominal, and ventral series.

These series are composed of thin masses of muscle, or, as they are commonly called, flakes; which for the most part are thicker upon their outward edges, and become wedge-shaped towards their interior attachments. Each series is separated from the next adjoining by a membraneous partition, which is most apparent between the vertebral and abdominal series.

The dorsal series *(ff)* arises from the back of the head. In its course it is terminated on the upper edge by the bones, which support the single fins, and a membranous *septum:* at this part the flakes are thin. Its lower margin is bounded by the vertebral series, where the flakes become gradually thicker. The first flake is composed of longer fibres than the rest, and possesses more red blood. Those succeeding it

* *Mem. étrangers de l'Académ. des Sci. de Paris.* Tom. VII. p. 18, et 223.

† *Leçons d'Anatomie Comparée.* Vol. I. p. 196.

range obliquely backwards. They are all joined together by cellular membrane, and shining fasciæ, which resemble the tendinous expansions in quadrupeds.

Towards the middle of the fish the flakes are thicker, and stand more perpendicular to the surface, becoming oblique and thin as they approach the tail; whilst the intervening fasciæ are most dense at each extremity. This series consists of forty-five flakes, a number corresponding with that of the spinous processes to which they are attached, and which does not vary with the growth of the fish.

The muscular fibres constituting each flake, run nearly at right angles with its anterior and posterior surfaces, and parallel to the length and surface of the fish; except that their posterior extremities incline somewhat inwards.

As the skull affords the ultimate fixed attachment of this series, and its moveable insertions are on the vertebræ, and the tail, it follows, that its combined action is to bend the whole body and tail towards one side; or, if the flakes contract partially, to give it a serpentine motion. To produce these effects all the other series co-operate.

The superior external edges of the flakes of the vertebral series *(gg)* form acute angles with the inferior external edges of those of the dorsal series, the apices of which point towards the tail: the flakes are larger, but their number is the same. The lower margin of this series is bounded by the central membranous partition, which has already been noticed to be more conspicuous than the other longitudinal divisions, and it apparently admits of greater motion.

The abdominal series *(hh)* is composed of flakes similar to the preceding. They range towards the tail, forming an angle

with those of the vertebral series, the apex of which is presented towards the head. They are attached internally to the transverse and inferior spinous processes of the vertebræ. The ribs are placed in the line of the centre partition, and lie between the flakes. This series arises from a bone which borders the opening for the gills, and the pectoral fin, with its scapula and muscles, is situated between its foremost flakes. Wherever this series encloses the viscera, its flakes are shallow, and their thickness internally is not much less than at their external superficies.

Lastly, the flakes of the ventral series *(ii)* form acute angles with the abdominal flakes, the points of which incline to the tail. It is attached anteriorly to the *os hyoides*, and the bones of the lower jaw. In its course it is bounded above by the abdominal series, and below by a membranous *septum*, within which the inferior single fins arise. The flakes, that cover the viscera, are shallow; and they lie more oblique as they approach the tail. Both this, and the last described series, have their muscular fibres arranged according to the length and figure of the fish.

Three large superficial nerves *(kk)* passing longitudinally from the head to the tail, in the course of the membranous partitions, give off fibrils at right angles, which bend inwards between each of the muscular flakes. A larger set of nerves are sent from the *medulla spinalis*, one between each flake, the branches of which seem to enter without ramifying there. Another small nerve passing from the head, and running deep-seated, and close to the dorsal spines, crosses and unites with each of the spinal fibrils, and at the junction a remarkable body appears: it is a loose transparent vesicle, about the

size of a millet-seed, containing a white substance like the carbonate of lime found in the intercostal ganglions of frogs. This vesicle is included within the sheath of the nerve.

The coats of the blood-vessels are of a delicate texture, and easily ruptured. In order, therefore, to secure them from being injured by the violent and sudden actions of the muscles, the principal trunks both of the arteries and veins are inclosed in osseous canals, formed by the bases of the superior and inferior spinous processes; and their first ramifications lie within grooves in the spines. As they pass out to supply the muscles, their branches are immediately subdivided, so that a considerable vessel soon becomes extremely minute.

The rate, at which many fishes move through a medium so dense as water, is very remarkable; their velocity being scarcely surpassed by the flight of the swiftest birds: and although the large proportion of muscles, and their advantageous application, may partly account for the phenomenon, yet the power would be inadequate to the effect, if it were not suddenly enforced; as is evident from the slow progress of eels, and such fishes as are incapable from their length, and flexibility, of giving a sudden lateral stroke.

But the quickness and force of action in the muscles of fishes are counterpoised by the short duration of their powers. Those accustomed to the diversion of angling, are aware how speedily the strength of a fish is exhausted, for if, when hooked, it be kept in constant action, it soon loses even the ability to preserve its balance, and turns upon its side, fatigued and incapable of motion. This has been vulgarly attributed to drowning, in consequence of the mouth being closed upon

the hook; but the same effects take place when the hook is fastened to the side, or tail. This prostration of strength may depend partly on fear, and partly on interrupted respiration, since fishes, when swimming rapidly, keep the *membranæ branchiostegæ* closed, and when nearly exhausted, act violently with their gills.

The shortness of the muscular fibres, and the multiplied ramifications of the blood-vessels, are probably peculiar adaptations for the purpose of gaining velocity of action, which seems to be invariably connected with a very limited duration of it. Such examples form an obvious contrast with the muscular structure of slow-moving animals, and with those partial arrangements where unusual continuance of action is concomitant.

Since my former communications on the subject of cylindrical arteries,* another instance of their supplying slow-moving muscles, which are capable of long continued action, has been pointed out to me by Mr. MACARTNEY. It is in the muscles, which act upon the feet and toes of many birds, and seems to be an adaptation for the long exertion of those muscles while they sleep, and also when they alternately retract one foot under the feathers to preserve it from the effects of cold.

The muscles of the human body, which perform the most sudden actions, have their masses of fibres subdivided by transverse tendons, or are arranged in a penniform direction. The semi-tendinosus, and semi-membranosus of the thigh are thus constructed; the former having its fleshy belly divided by a narrow *fascia*, and the fibres of the latter being ranged

† Phil. Trans. 1800, p. 98.—Also 1804, p. 17.

in a half-penniform manner. The *recti abdominis* are also divided into short masses by transverse tendons, and all these muscles are conjointly employed in the action of leaping.

Perhaps these observations may indicate the reason for that diversity in the lengths of various muscles, which act together; thus, organs of velocity are joined with those of power, and mutually co-operate to produce a simultaneous effect.

Description of Plate I.

The drawing was made from a cod which had been coagulated by heat, in a case of plaister of Paris, the skin being taken away, and an equal portion of the flakes carefully removed from each series, to exhibit their several directions. The subject was reduced to the present size by accurate measurements.

aa, Muscles which extend the pectoral and jugular fins.

bbbbb, Oblique muscles, which erect the rays of the single fins.

cc, Muscles which depress the rays.

dd, Muscles which extend the rays of the tail.

ee, Interosseal muscles, which close the rays.

ff, The dorsal series of muscular flakes.

gg, The vertebral series.

hh, The abdominal series.

ii, The ventral series.

kkk, Three superficial nerves which run longitudinally between the series of flakes.

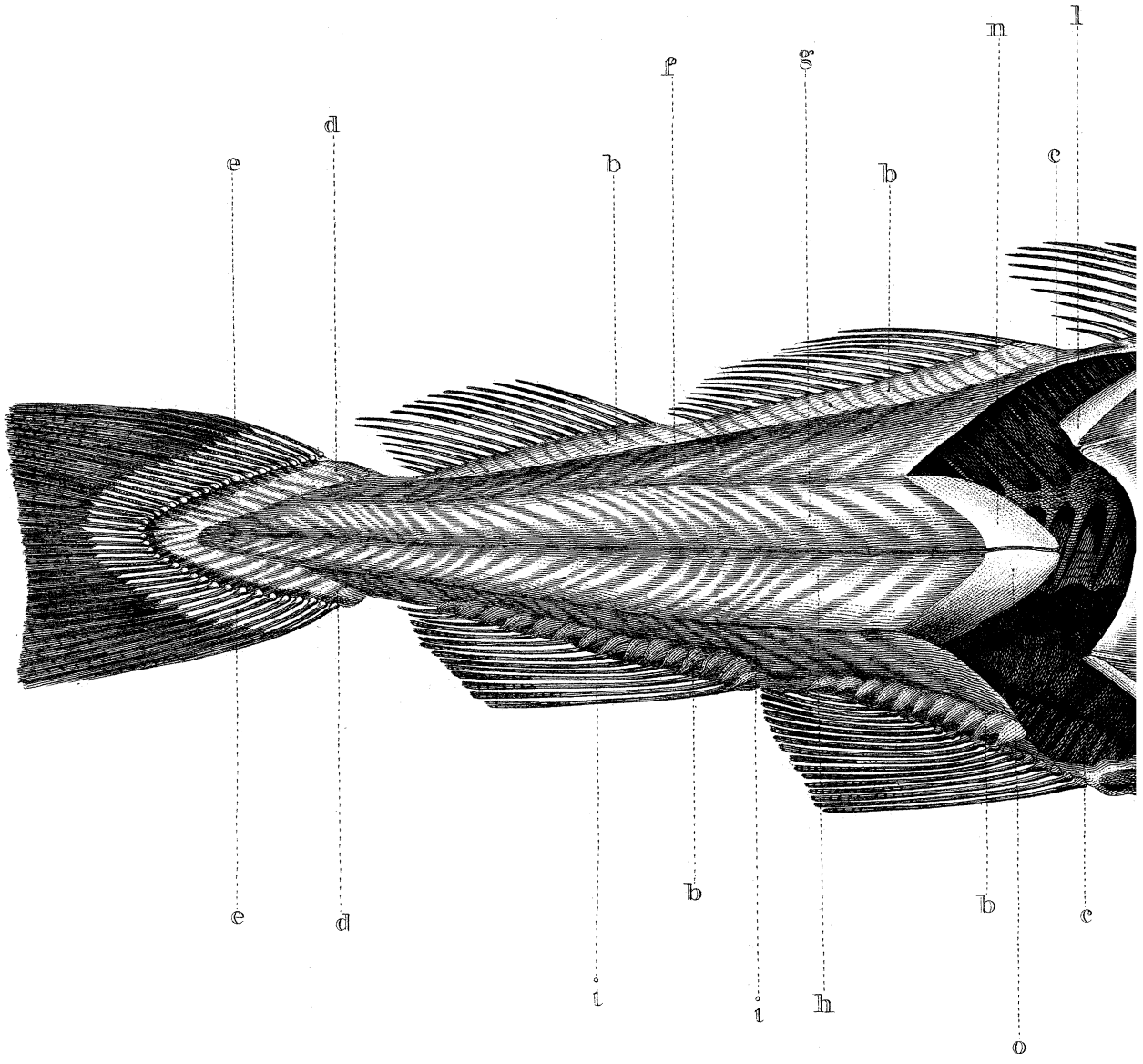
l, Posterior surface of a dorsal flake.

m, Posterior surface of an abdominal flake.

n, Anterior surface of a vertebral flake.

o, Anterior surface of an abdominal flake.

The middle portion of the fish from whence the flakes have been removed, shews the several directions of them, and also their different thicknesses. The spine appears in the chasm.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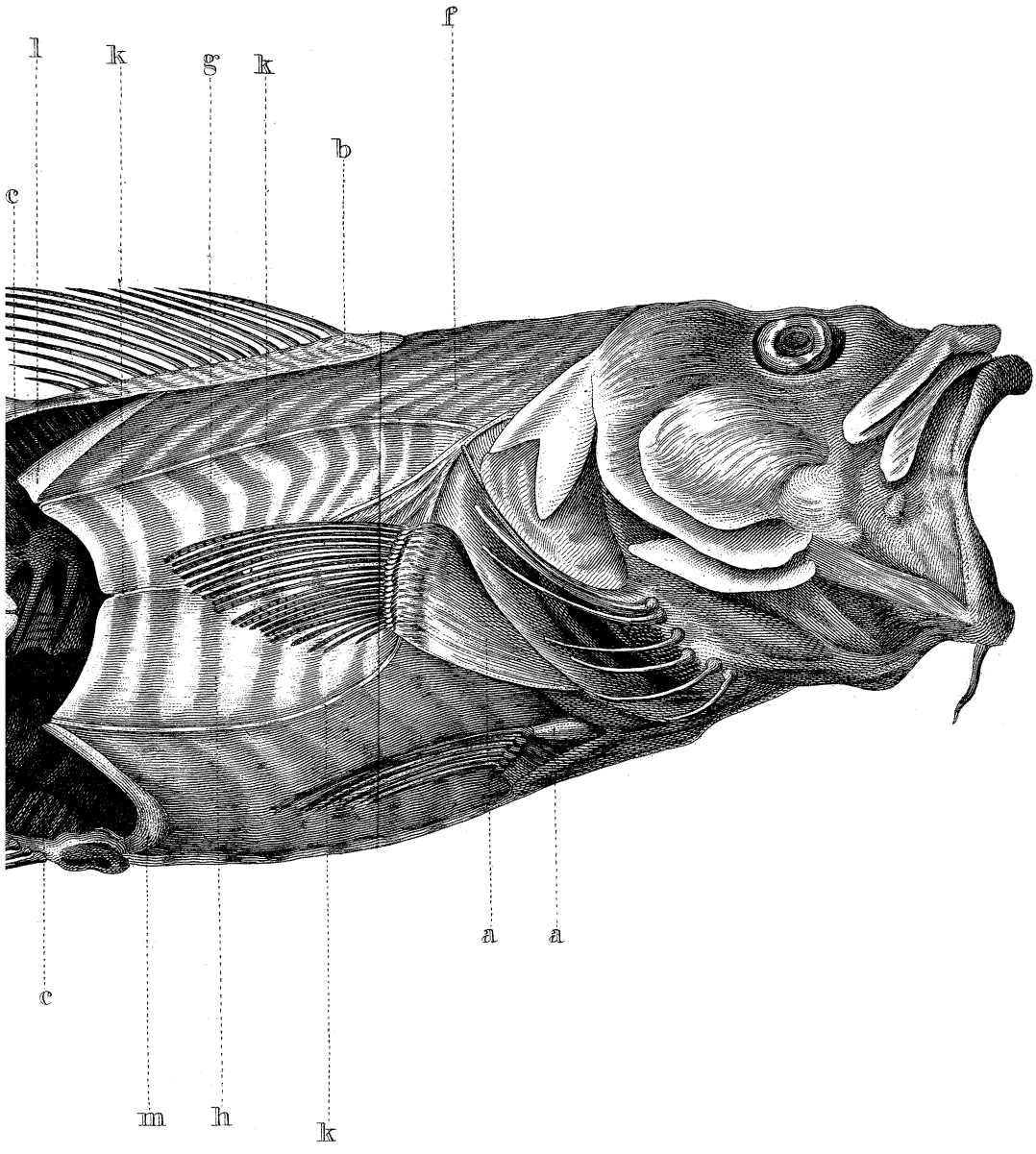

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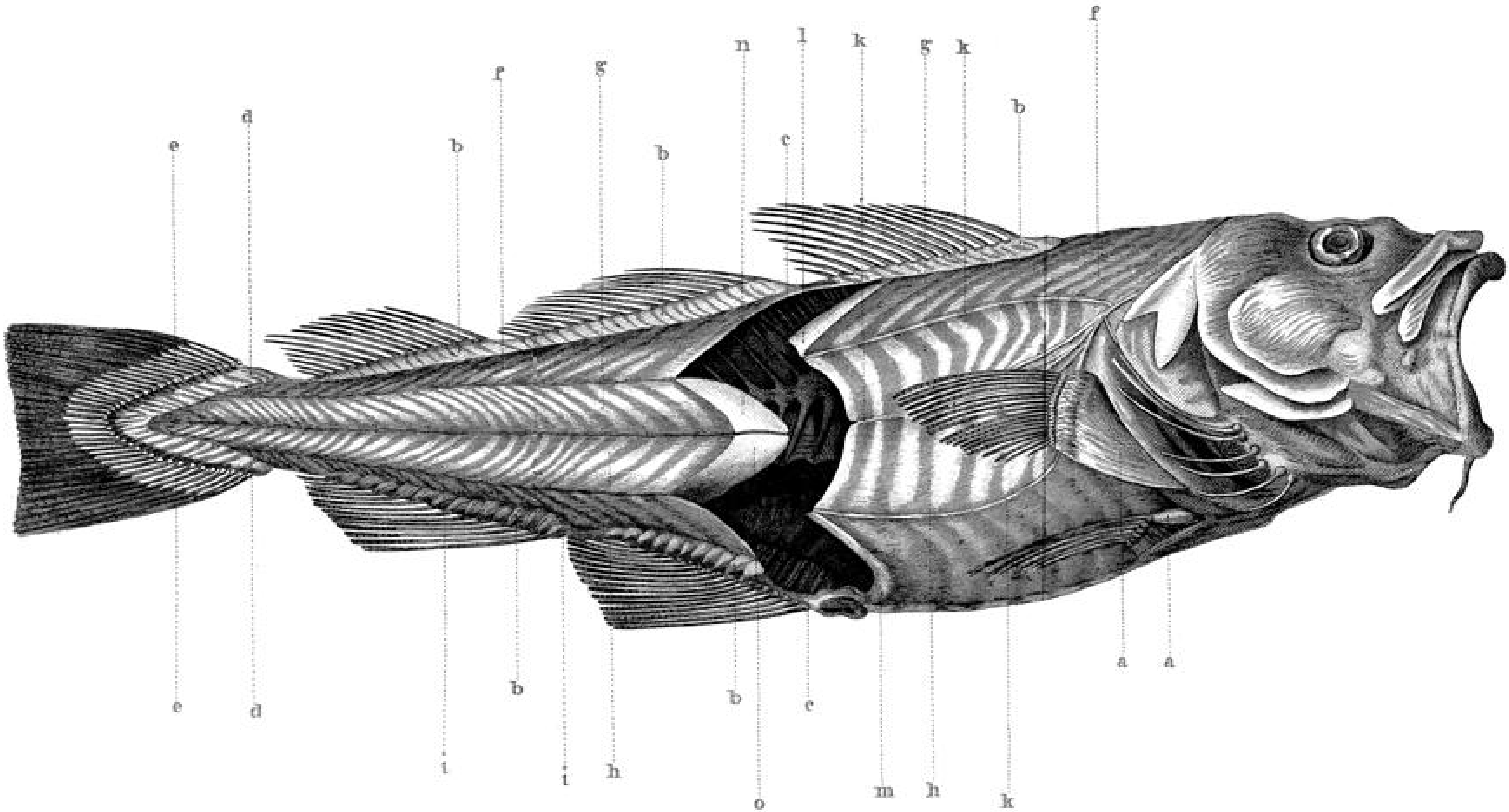

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