CONTRIBUTIONS TO THE FUNCTIONAL MORPHOLOGY OF FISHES
PART V. THE FEEDING MECHANISM OF *ELOPS SAURUS* LINNAEUS

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INTRODUCTION

Elops saurus, the "Ten-pounder" or "Springer", is a long, slender fish, approximately thirty inches long and thirty pounds in weight. It is a member of the primitive elopiform family Elopidae. This early Cretaceous group possesses the very requisites that place it near the base of modern teleost jaw evolution. Apart from the late Triassic leptolepids and lycopterids, which represent an offshoot of the main line of teleost evolution, the elopids are the oldest known teleosts. This essentially conservative stock of predaceous forms is an early teleost link to fit an important gap in the chain of evolving jaw mechanisms: at or near the base of the explosive teleost evolution.

The head skeleton of *Elops* has been adequately described by Ridewood (1904). Schaeffer and Rosen (1961) mention *Elops* in their discussion of the evolution of the actinopterygian feeding mechanism. Other aspects, such as the musculature and feeding of *Elops*, have, to the author's knowledge, never been described.

MATERIAL AND METHODS

Ten specimens of *Elops saurus* were obtained from the St. Lucia Bay Estuary in Zululand. These were preserved in 10% neutral formalin. In addition four specimens, which were frozen immediately after death, were flown to Cape Town from St. Lucia.

A skull of *Elops* was prepared by boiling a preserved head in antiformin solution (Romeis 1948). The skull served as the basis for osteological study.

The cranial musculature and its innervation were dissected on the preserved specimens of *Elops*. A single preserved specimen of *Megalops cyprinoides* (Broussonet) from St. Lucia and also a member of the Elopiformes, was dissected as a comparison.

The fresh specimens of *Elops* were invaluable in studying the movements of the jaw. This was done by observation, by pulling muscles, ligaments and bones with forceps and also by the use of X-rays. This latter method was used to substantiate the observations in a more definite manner. It is described in detail at a later stage.

Systematic categories have been adopted from the classification proposed by Greenwood et al., 1966. Muscle and nerve nomenclatures are after Edgeworth (1935) and Haller von Hallerstein (1934), respectively. The bone terminology is after Gregory (1933). The following ligaments, to which no reference could be found, were named by the author:

L. palato-maxillare (Fig. 3)
L. praefronto-mandibulare (Fig. 3)
L. abductores radiorum branchiostegalium (Fig. 4)
L. ethmoido et praefronto-palatinus (Fig. 7)

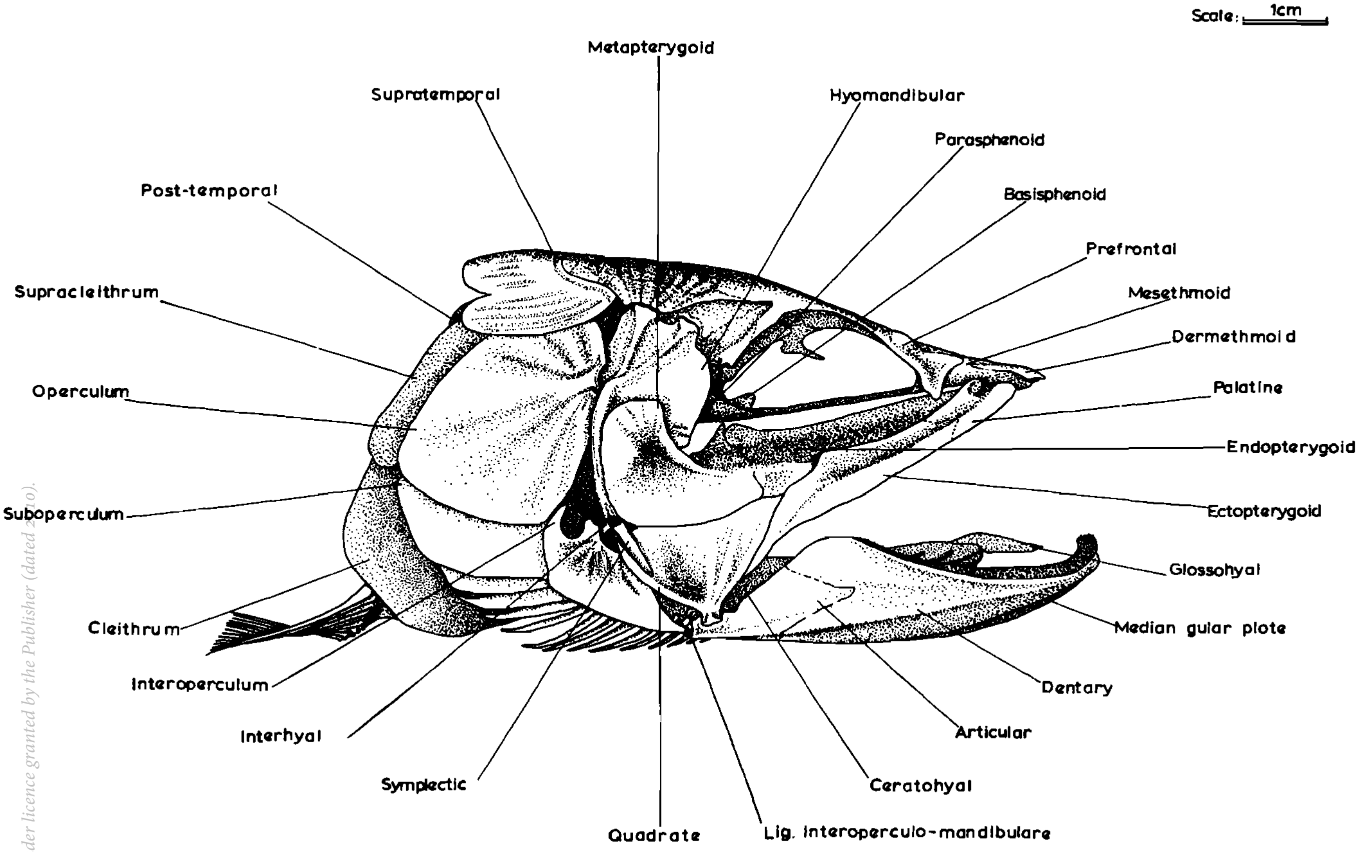

Figure 1. Skull of *Elops saurus* in right lateral view. The maxillary series and infraorbitals have been removed.

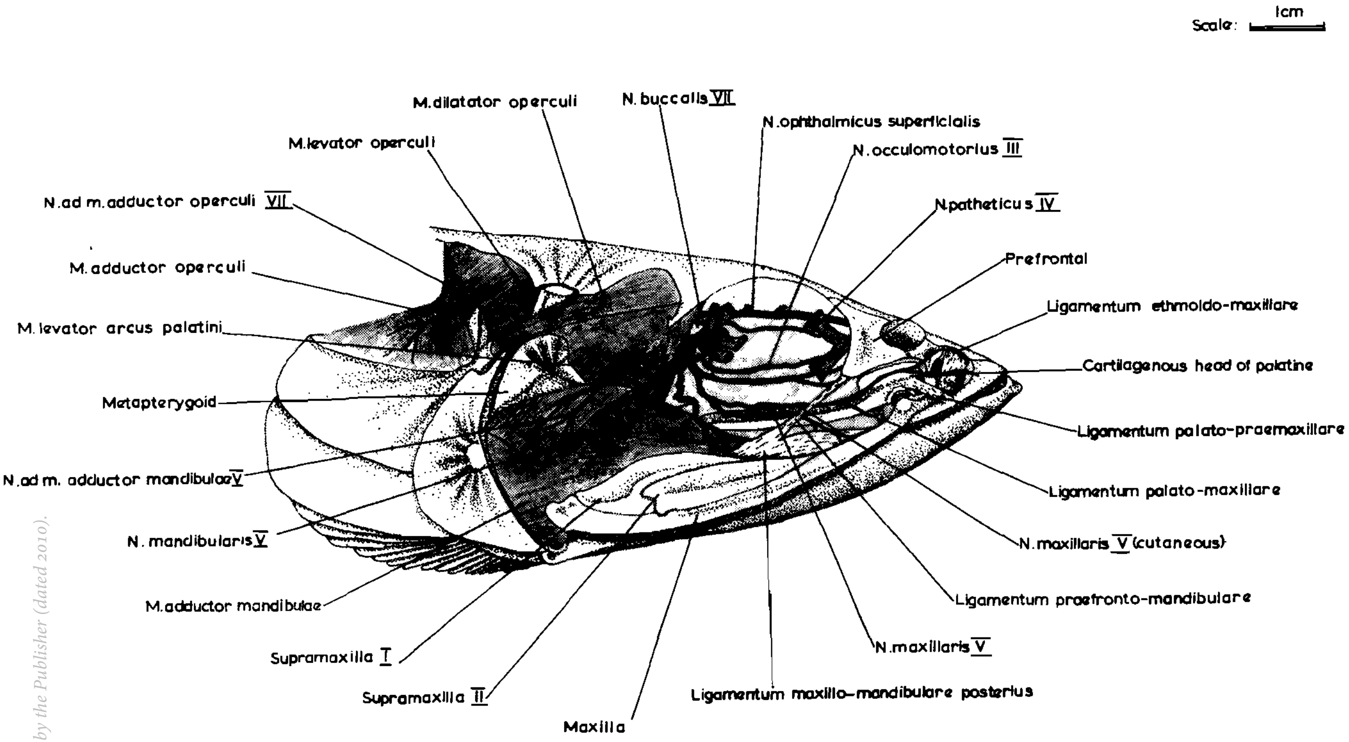

Figure 2. Cranial muscles, nerves and ligaments of *Elops saurus* in right lateral view. The dorsal edge of the operculum has been folded over to expose M. adductor operculi.

ACKNOWLEDGEMENTS

I am grateful to the late Dr. D. H. Davies, of the Marine Biological Laboratories in Durban, for having made the fresh material available to me. I wish to thank Mr. and Mrs. A. Brown for their help in carrying out the X-ray method. Mr. Brown, of this department, and Mrs. Brown, a radiographer at the Red Cross Children's Hospital, where the X-rays were taken, not only made possible the whole procedure, but also took the X-rays for me. My thanks are also due to Miss B. Brunhüber of this department for information on the stomach contents of *Elops*. Most of all I am indebted to Dr. N. A. H. Millard, of this department, for her unfailing patience, interest and help with the many problems I brought to her during the course of this project.

OSTEOLOGY

Due to the description of the head skeleton of *Elops* by Ridewood (1904) it will suffice here to remark on a few points only.

The Cranium

Each cartilaginous lateral ethmoid forms a large block which starts at the posterior edge of the prefrontal, runs forward underneath this bone and emerges next to the mesethmoid. Ventrally it offers a broad, smooth, obliquely upward running surface for the cartilaginous head of the palatine (Figs. 1, 2 and 3) to abut against and slide upon.

The Maxillary Series

Together the premaxilla and maxilla, more especially the latter, constitute the upper jaw margin (Figs. 2 and 3). Both bear densely set, minute teeth along their entire lower borders.

The maxilla is an almost straight bone from its posterior margin to the anterior end of the tooth-row (Figs. 1 and 2). Then it curves strongly inwards towards the dermethmoid, its tip being inclined at an angle of approximately 45° with respect to its straight portion. The curved portion bears a pronounced bony knob halfway along its inner dorsal aspect, which fits into a corresponding depression on the palatine (Figs. 2 and 3). On its inner surface this knob forms a hook which hooks over a small strand of connective tissue. This strand attaches to the rest of the connective tissue "jacket" which surrounds this maxillopalatine ball-and-socket hinge.

The anterior tip of the maxilla is expanded and lies against the dermethmoid.

The premaxilla has lost the well-developed dorsal process of holosteans. Instead it has a small pointed backwardly directed process (Fig. 2) that articulates with the ethmoidal cartilage. It is no longer firmly attached as in *Amia*.

There are two supramaxillae, only bound to the maxilla by connective tissue. The larger supramaxilla I has a depression on its antero-ventral border into which overlaps supramaxilla II when the mouth is closed (Figs. 2 and 3).

Ventrally the gape is bounded by the long dentary (Fig. 1), toothed exactly like the upper jaw margin. A large articular borders it posteriorly, forming the nearly horizontal articular facet for the head of the quadrate. Meckel's cartilage lies ventrally in the extensive Meckelian fossa (Fig. 5).

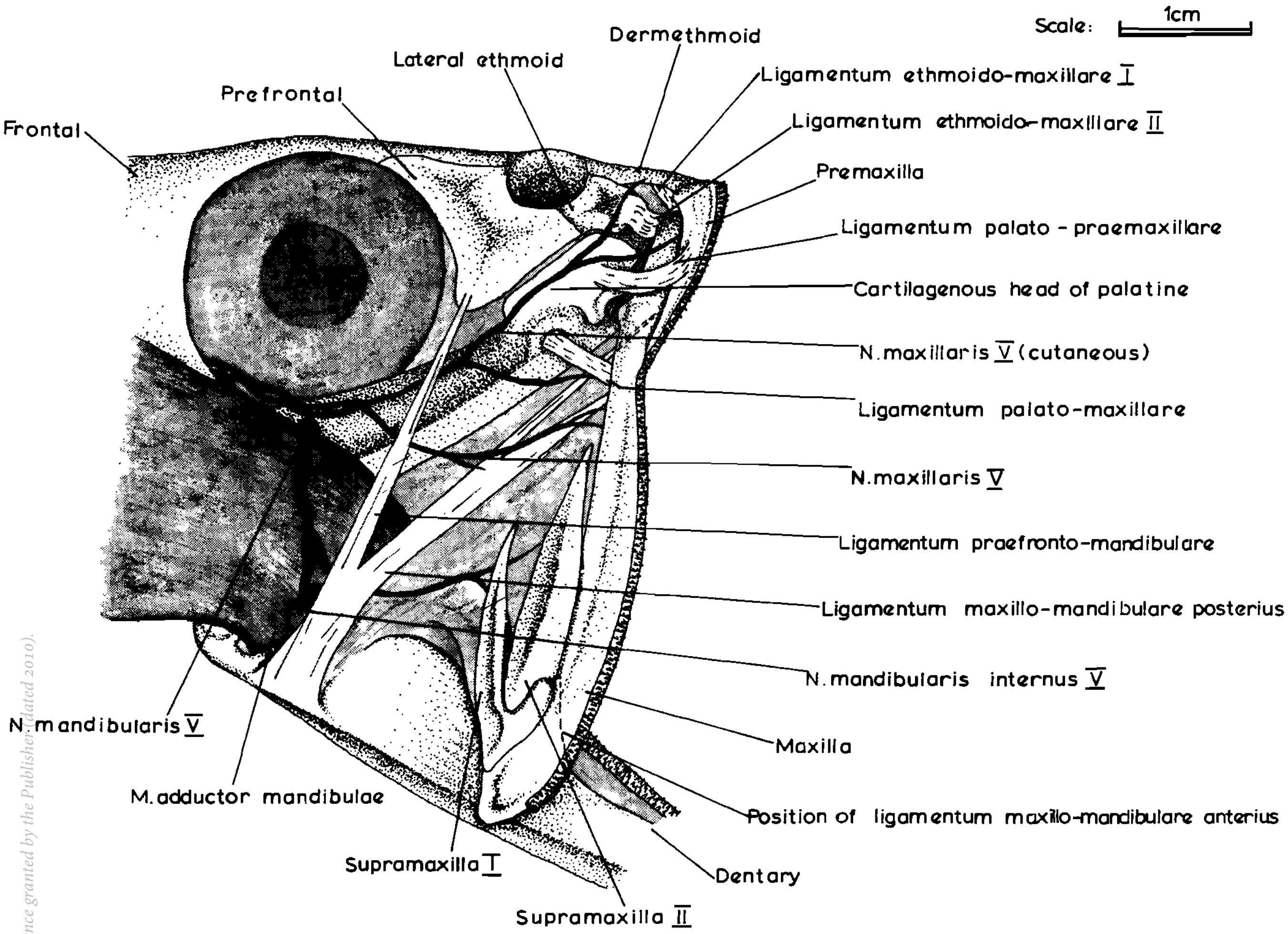

Figure 3. *Elops saurus*. Ligaments of the oral region. Right dorso-lateral view.

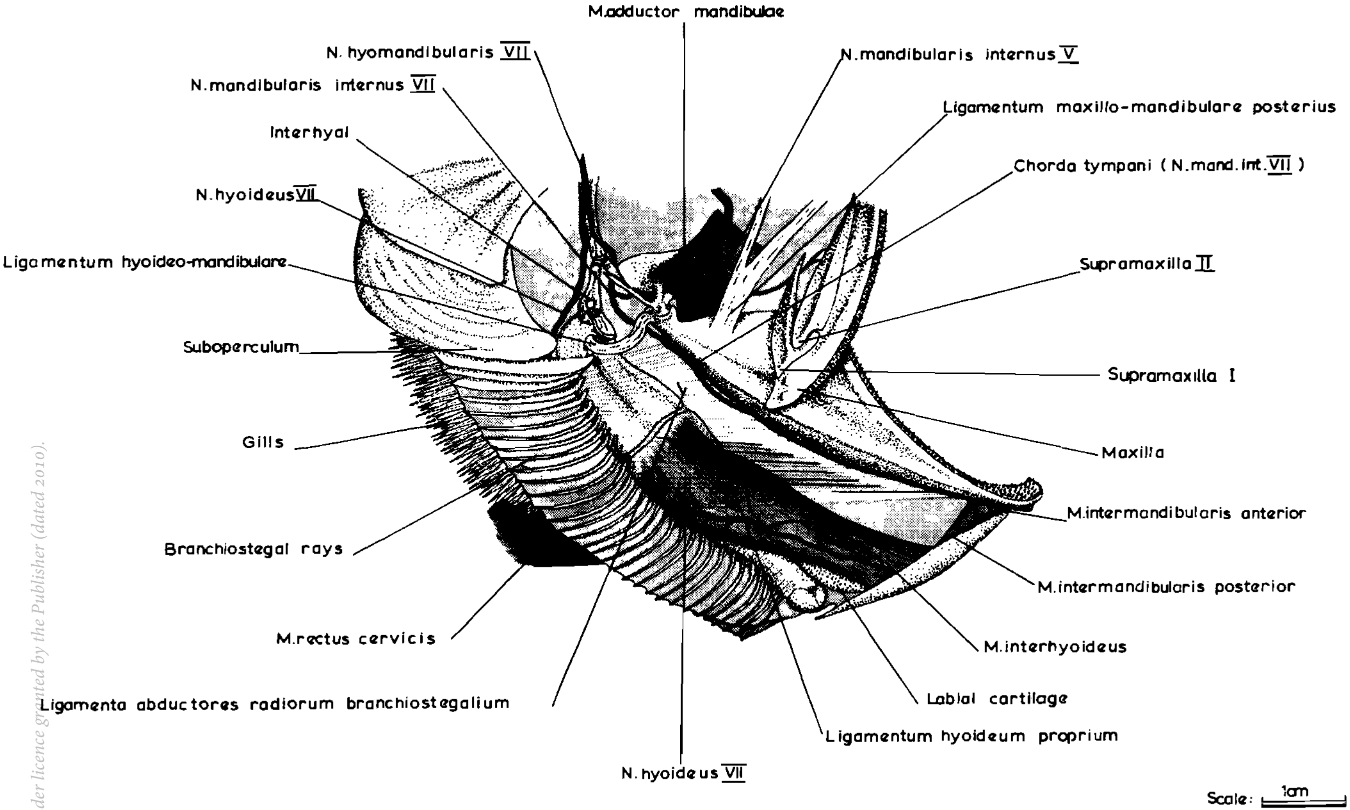

Figure 4. *Elops saurus*. Ventral head region. Right lateral view of fully extended jaw apparatus. The interopercular bone has been removed.

The Hyopalatine Series (Fig. 1)

The hyomandibular articulates with the cranium by two heads. The articular plane is nearly horizontal and only slightly inclined downwards anteriorly.

The palatine, bony posteriorly, slides anteriorly along the smooth lateral ethmoid by a cartilaginous, dorsally flat head.

The quadrate-metapterygoid line, and next to it the symplectic-hyomandibular line, both extend upwards nearly vertically (Fig. 1).

The Opercular Series

This series is shown in Fig. 1. A few points deserve special mention. The rays numbered from twenty-six in the smallest specimen to thirty-three in the largest. The last few rays become progressively larger and flatter. Their anterior ends extend further forward over the hyoid arch, until the last ray nears the suspensorium (Fig. 4). It is so large as to resemble the branchio-operculum of *Amia*. The anterior rays are attached to the edge of the hyoid arch. The attachments of the interhyal are referred to in detail in the discussion of the jaw mechanism.

The interopercular is joined medially to the ceratohyal (epihyal of Gregory (1933)).

The median gular plate (Figs. 4 and 6) lies between the ventral margins of the dentaries.

LIGAMENTS AND CONNECTIVE TISSUE

Elops not only possesses numerous ligaments, of vital importance to its jaw mechanism, but also aggregations of connective tissue fibres, so disposed as to have direct influence on bone movements.

1. *L. maxillo-mandibulare anterius* (Fig. 3) stretches from both external and internal dorsal margins of the dentary to the inner maxillary and supramaxillary surfaces.
2. *L. maxillo-mandibulare posterius* (Fig. 3) originates on the external posterior surface of the dentary. It divides into two sections, the anterior of which attaches to the inner surface of the maxilla.
3. *L. praefronto-mandibulare*, the posterior section, is attached to the ventral tip of the prefrontal.
4. *L. ethmoido-maxillare I* (Fig. 3) is a thick connective tissue sheet stretching from the dermethmoid to the expanded maxillary tip.
5. *L. ethmoido-maxillare II* is a similar sheet stretching from the lateral ethmoid to the maxillary tip.
6. *L. palato-praemaxillare* stretches from the cartilaginous head of the palatine to the median posterior border of the premaxillary ramus. The ligament lies in a groove-like depression between the "ball", of the ball-and-socket hinge, and the club-shaped maxillary tip.
7. *L. palato-maxillare* stretches from a depression on the palatine to the inner border of the maxilla.
8. *L. hyoideo-mandibulare* (Figs. 4 and 5) is a large (approximately three millimetres in diameter), round ligament, stretching from the angle of the lower jaw to the posterior ossification of the ceratohyal.
9. *L. interoperculo-mandibulare* (Fig. 1) connects the interopercular and the angle of the jaw.

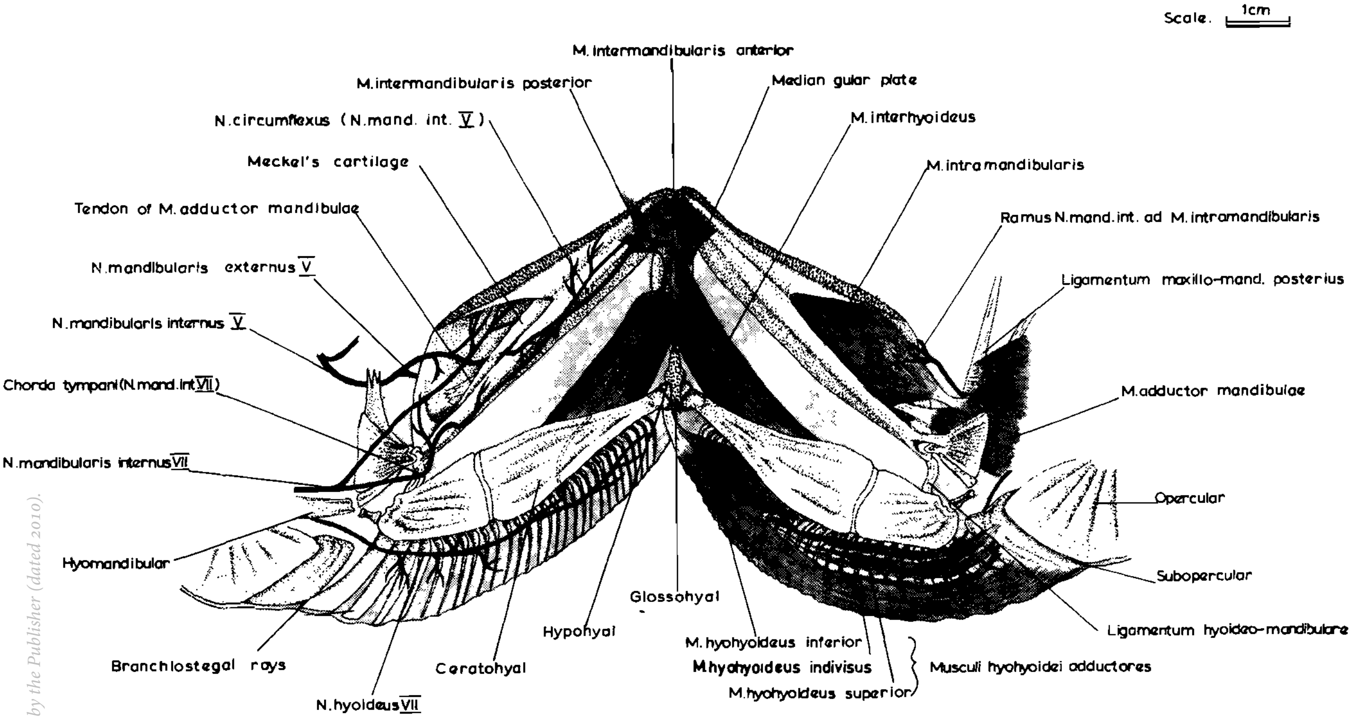

Figure 5. *Elops saurus*. Nerves and muscles of the lower jaw. Dorsal view. On the left side M. adductor mandibulae, M. intramandibularis and Mm. hyohyoidei have been removed. The posterior gular plate insertion of M. intermandibularis posterior has been turned up. The anterior gular plate origin of M. interhyoideus has been turned up. The labial cartilage has been removed.

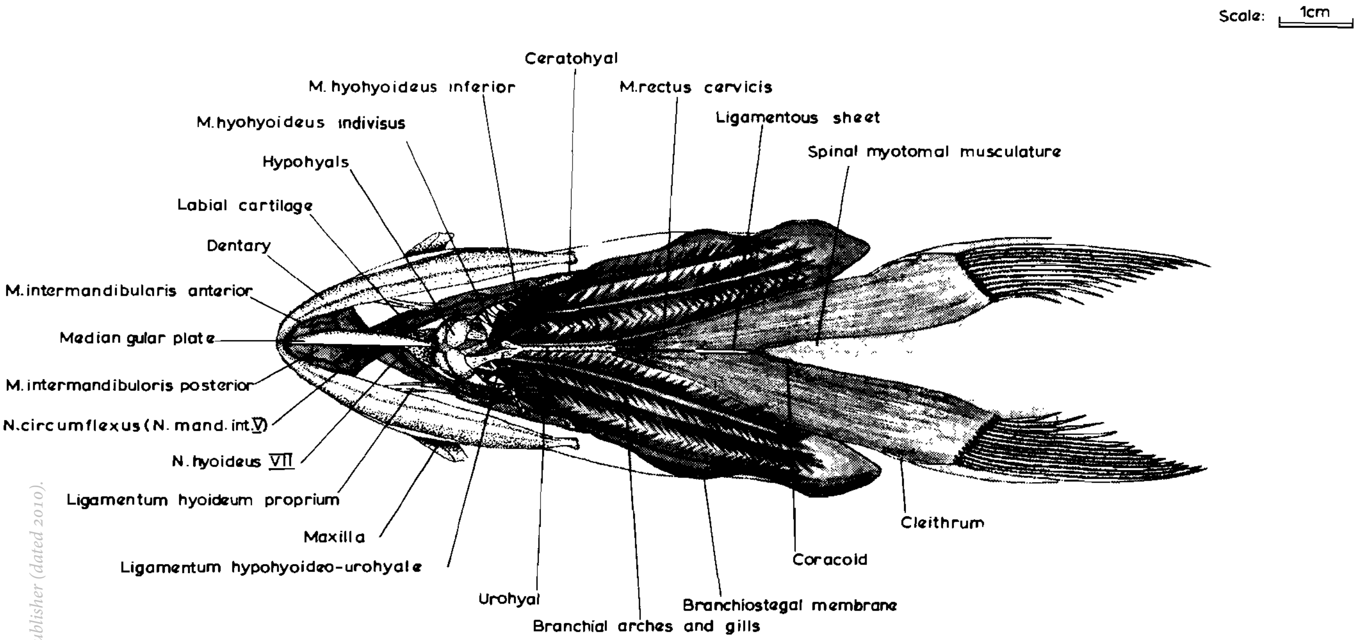

Figure 6. *Elops saurus*. Ventral view of anterior region. The right half of the gular plate has been removed. The ligamentous insertions of the right Mm. hyohyoidei have been severed from the lower left hypohyal and turned backwards.

10. *Ll. abductores radiorum branchiostegalium* are extremely important ligamentous structures lying between the dentary and hyoid arch. These thin but continuous fibrous strands can be seen (Fig. 4) to connect the outer upper portion of approximately the last twenty rays, to the mandible. Those strands from the more anterior rays extend only a short distance upwards to merge with the connective tissue lining.
11. *L. hyoideum proprium* is an obliquely forward-running thickening (consisting of the same strands) in the Ll. abductores. Although its strands are orientated from the rays to the dentary, this thickening as a whole, is orientated from the lateral midpoint of the hyoid arch, where it is attached by connective tissue, to the anterior mandible (Fig. 4). The name of this ligament has been adopted from Holmquist (1910) who found similar ligamentous conformations in various species. Some he described as strong ligaments, e.g. in *Gadus;* others were weaker and more diffuse, constituting merely a thickening of the connective tissue, e.g. in *Gaidropsarus mustela.*
12. *A L. hypohyoideo-urohyale* (Fig. 6) stretches obliquely forward from the anterior tip of the urohyal to the lower hypohyal on each side.

In addition more diffuse fibrous tissue, which hardly warrants the name of ligament, occurs in the following situations:

The gular plate is strongly attached by ligamentous tissue to the mandibular symphysis.

The anterior tip of the last and broadest branchiostegal ray is connected by fibrous tissue to the angle of the jaw.

Between the urohyal and the coracoids there is an extensive ligamentous sheet on which insert the two halves of M. rectus cervicis.

MUSCLES

THE MANDIBULAR MUSCLES

Mm. adductores mandibulae et intramandibularis

The adductor of *Elops* is not the simple, completely undivided muscle sheet which occurs in *Lepidosteus.* Neither has it the complex subdivisions present in later teleosts. *Elops,* in fact, exhibits the first stage of differentiation, namely the separation of the intramandibular.

The adductor originates as a single sheet on the entire external surface of the metapterygoid, as well as on the anterior margins of the preopercular and the long ventral process of the hyomandibular. It inserts by three tendons (Fig. 5). The most dorsal of these is a short, thin, but broad band of fibres, inserting on the inner surface of L. maxillo-mandibulare posterius, internal to L. preafronto-mandibulare. More ventrally a stronger tendon links the adductor to its derivative, M. intra-mandibularis (Fig. 5). The latter broadens considerably and inserts on the inner surface of Meckel's cartilage, as well as on the surfaces of the Meckelian fossa. The most ventral tendon is the longest of the three, and inserts on the inner surface of the dentary between it and the intramandibular.

The muscle is innervated by a branch of N. mandibularis V (Fig. 2) arising close to the origin of the latter from the trigeminal. The main trunk of the mandibular then continues over the external surface of the adductor to dive inwards between the first two tendons mentioned above. At this stage a small twig is given off to the intramandibular.

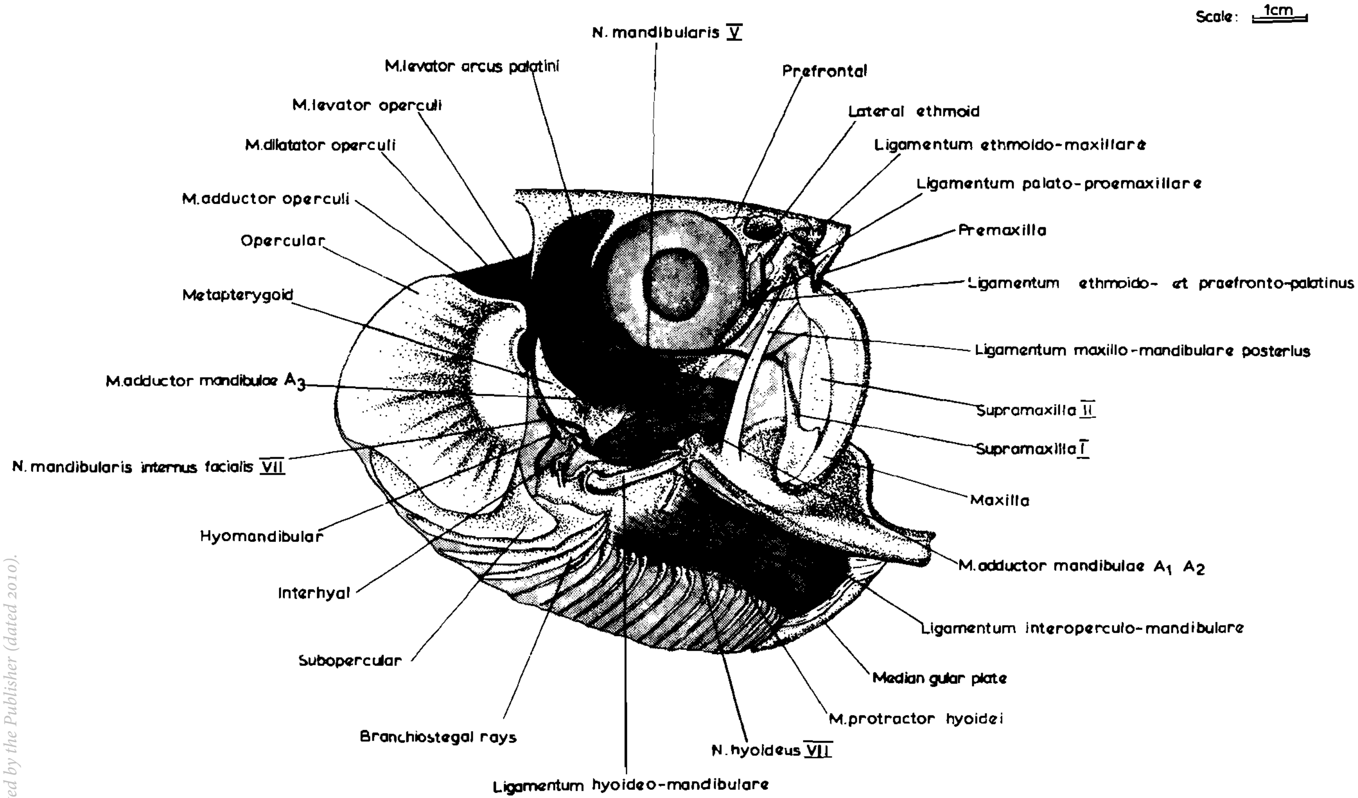

Figure 7. *Megalops cyprinoides*. Abducted cranial region. Right lateral view. The interopercular has been removed.

M. intermandibularis (Fig. 5)
Immediately behind the mandibular symphysis muscle fibres stretch transversely from one dentary to the other, without interruption. This is M. intermandibularis anterior. More posteriorly the fibres from either side insert on a median raphé and on the gular plate. This is M. intermandibularis posterior. As one progresses in a posterior direction along this muscle, the fibres become orientated more and more obliquely backwards, until the posterior margin of the muscle is at an angle of 45° to the anterior margin (Fig. 4). The posterior fibres of the intermandibularis posterior are dorsally overlapped by the anterior fibres of M. interhyoideus. The fibres of the two muscles cross and interweave before inserting together on the gular plate. The muscle is innervated by branches of N. mandibularis internus V (Fig. 5).

M. levator arcus palatini
This muscle originates on the postfrontal and in the lateral temporal groove behind it (Figs. 1 and 2). It inserts on the inner face of the metapterygoid and along the hyomandibular, below the ridge formed by its anterior articular head. The muscle is innervated by a branch of N. mandibularis V (Fig. 2).

M. dilatator operculi originates on the pterotic bone and on the hyomandibular dorsal to the ridge of the anterior articular head (Figs. 1 and 2). Its fibres converge onto a very strong tendon, which inserts on the outer rim of the cup-shaped opercular articular facet. This muscle is not distinctly demarcated from the levator arcus palatini.

The muscle is innervated by a branch of N. mandibularis V which passes internal to the levator arcus palatini.

THE HYOID MUSCLES

M. adductor hyomandibulae
This muscle originates over the entire breadth of the prootic and inserts on part of the dorsal hyomandibular. Although the posterior muscle fibres stretch obliquely forward and would retract the hyomandibular, the bulk of the muscle fibres run straight outwards and adduct it. Accordingly, it is named M. adductor hyomandibulae.

Mm. levator et adductor operculi
These muscles have a common origin on the opisthotic and pterotic and in the subtemporal fossa. The insertions of the two are more or less distinct, that of the levator on the anterior margin of the opercular bone and that of the adductor on the inner dorsal margin (Fig. 2). These muscles are innervated by two branches of N. hyoideus VII.

M. interhyoideus
This muscle originates on the outer surface of the ceratohyal and inserts with its fellow in the midline of the gular plate. Here it overlies and partly weaves its fibres through the posterior part of M. intermandibularis posterior (Figs. 4 and 5). The fibres of the two muscles never fuse and there is no development of a protractor hyoidei in *Elops*. The interhyoideus is innervated by N. hyoideus VII which passes over its ventral surface.

M. hyohyoideus
As in *Polypterus* this muscle forms an almost continuous sheet on the inner surfaces of the branchiostegal rays (Fig. 5). It can be divided into three parts.

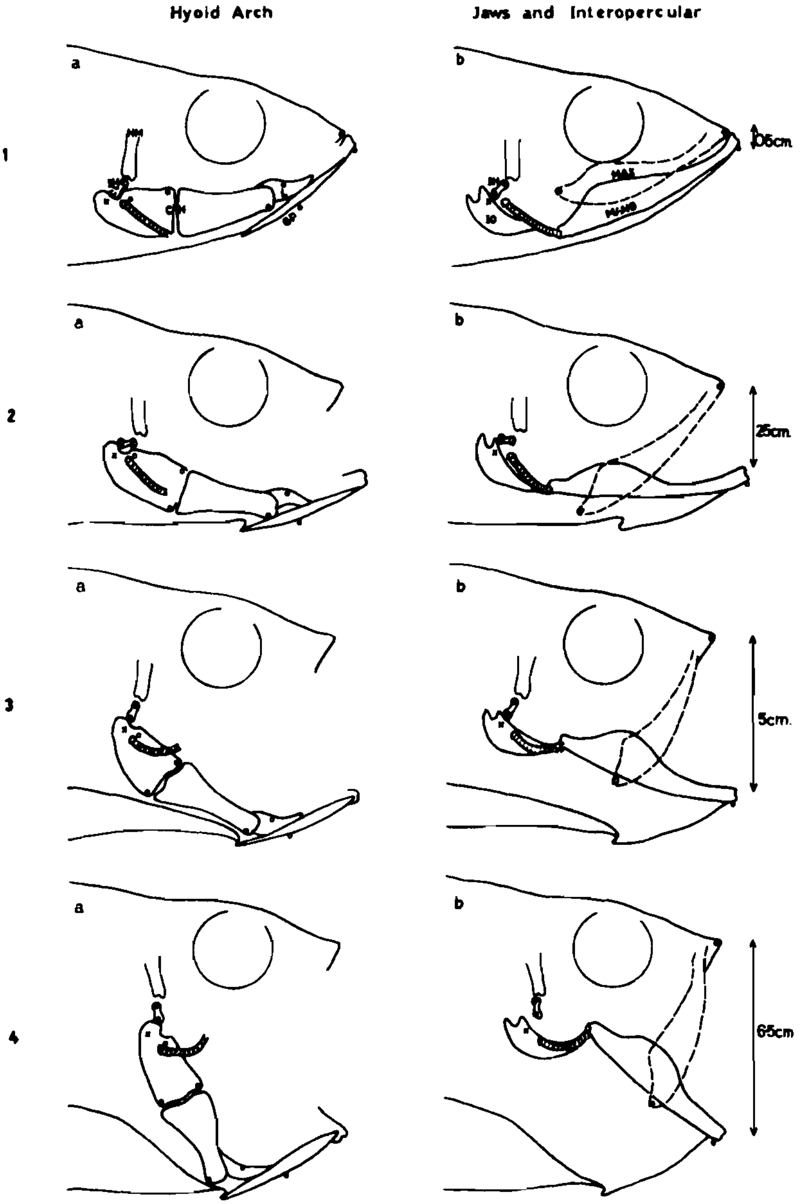

Figure 8. Tracings of x-ray negatives showing positions of bones during four progressive stages of jaw opening, from "mouth closed" to "mouth fully open". The elements of the hyoid arch are shown on the left and the jaws and interopercular bone on the right. The marker pins are shown by small circles. L. hyoideo-mandibulare is indicated by coarse hatching and L. interoperculo-mandibulare by solid black. x marks the point of attachment between the external surface of the ceratohyal and the internal surface of the interopercular.
CH, ceratohyal. *GP*, gular plate. *HM*, hyomandibular. *IH*, interhyal. *IO*, interopercular. *L*, labial cartilage. *MAND*, mandible. *MAX*, maxilla.

a) M. hyohyoideus superior originates on the anterior part of the suboperculum and consists of approximately four separate fibre bundles. These stretch forward, to insert on successive rays near the middle of the branchiostegal series (Fig. 5).

b) M. hyohyoideus inferior originates on the anterior half of the ventral margin of the ceratohyal. It passes obliquely forward to insert by a thick tendon on the lower hypohyal of the opposite side.

c) M. hyohyoideus indivisus, a flat sheet of fibres which originates on the posterior part of the subopercular, passes over the entire ventral margin of the ray series. It inserts by the same tendon as (*b*) on the lower hypohyal of the opposite side (Figs. 5 and 6).

In *Elops* the hyohyoid muscle seems to be in its first stage of differentiation from the primitive ventral constrictor, (as seen in *Polypterus*, Edgeworth 1935). The anterior components have already differentiated into Mm. hyohyoideus superior and inferior. The posterior part has remained a primitively undifferentiated sheet and is here termed M. hyohyoideus indivisus (Fig. 5). The muscle is innervated by branches of N. hyoideus VII, given off as the latter crosses the internal surface of the branchiostegal rays.

M. rectus cervicis

This muscle originates on the pectoral girdle and meets its fellow in the midline to insert on a ligamentous sheet and on the urohyal (Fig. 6). Being myotomal in origin, this muscle is supplied by a number of ventral root nerves, united to form the hypoglossal nerve.

Anastomoses between nerves V and VII (Fig. 5)

As it passes along the inner surface of the dentary, N. mandibularis internus V undergoes exchange of fibres with N. mandibularis VII (the chorda tympani) by a few anastomoses. More anteriorly N. mandibularis internus V gives off a branch innervating the intermandibularis posterior. This branch forms an anastomosis with R. hyoideus VII, after the latter has innervated M. interhyoideus.

MECHANISM OF THE JAW AS DETERMINED BY THE USE OF X-RAYS

Method: A fresh *Elops* was firmly tied onto a wooden board. The head, as far back as the posterior edge of the opercular bone, overlapped one edge of the board, so as to give it complete freedom of movement. Pinheads, cut off just below the head, were pressed into the bones at numerous salient positions. Three nails were driven into the board to serve as markers. It was then possible to hold the jaw open in different positions by the use of wooden sticks of various lengths, placed between the glossohyal bone ventrally and the palatine bones dorsally. For each position one X-ray was taken, showing up the nails as markers and the pinheads on the bone (Fig. 9). Finally the X-ray negatives were traced onto architect's tracing paper and the tracings superimposed on one another. The exact relative movements of the pinheads, as the jaw opened, could thus be clearly seen.

Results: In all, X-rays of thirteen positions were taken from "mouth closed" to "mouth fully open". Of these, four have been selected for the construction of Fig. 8.

It is recognised that this method has certain drawbacks. For instance the rectus cervicis muscle, which in life initiates jaw opening, is fixed and constricted by the cords holding the fish in place. Furthermore, the glossohyal is probably abnormally depressed by the stick resting on it. However, experiments on the fresh fish indicate that pulling on the rectus cervicis causes no difference in the movement of the bones relative to one another.

The apparent inaccuracy of the bones in Fig. 8 is a natural consequence of the fact that tracings were made of negatives representing three-dimensional movement.

In Fig. 8, 1a and b, where the mouth is completely closed, the interhyal rests in a semicircular depression on the ceratohyal. The two ligaments involved in the movement are taut, namely the hyoideo-mandibulare and the interoperculo-mandibulare. In Fig. 8, 2, the hyoid arch has been rotated. Its posterior part is in a postero-dorsal position, with the interhyal twisted accordingly. Point X, the interopercular-hyoid connection, has moved similarly. The two ligaments have consequently exerted a pull on the posterior part of the mandible, causing it to drop anteriorly. The anterior part of the hyoid arch has rotated ventrally, carrying the gular plate and mandible with it. The drop of the mandible has caused antero-ventral motion of the broad maxillary ramus, to which it is attached by ligaments (Fig. 3). Fig. 8, 3, shows further depression and a backward rotation of the ceratohyal. This has the effect of pressing down the gular plate, thus enlarging the cavity of the mouth and further depressing the mandible. The latter has carried the maxilla with it. The movement of the posterior ceratohyal, interopercular and consequently the posterior attachments of both ligaments, is no longer backward but anterodorsal. As a result the ligaments are slack, yet the mandible continues to drop. The interhyal returns to a more vertical position. In Fig. 8, 4, all tendencies of the previous figure are intensified.

The normal closing mechanism, as observable by this method, is a step by step reversal of stages 1-4, Fig. 8. It was not established whether the alveolar end of the maxilla could remain depressed during mouth-closing as has been shown to occur in the Acanthopterygii by Alexander in 1967, whose paper had not appeared at the time when these experiments were conducted (1965). However, it is unlikely that this situation exists in *Elops*, due to the comparative immobility of the maxilla and premaxilla and the tautness of L. maxillo-mandibulare anterius.

Hypothesis of jaw mechanism based on results:

I) *The effect of the muscles involved in jaw opening:*

The opening of the jaw is initiated by the contraction of the rectus cervicis (sternohyoideus of Allis (1897)). This exerts a pull on the urohyal, which is directly transmitted to the hypohyals, via the two hypohyoideo-urohyal ligaments (Fig. 6). The latter force is probably intensified by the hypaxial body musculature, which retracts the pectoral girdle at every inspirational phase (Van Dobben 1935). The backward movement of the hyoid arch is limited posteriorly by the extent of the arc which the loosely attached interhyal can describe. Therefore the pull of the rectus cervicis is translated into downward, and eventually backward, motion of the anterior hyoid arch (Figs. 8, 2-4). The median gular plate allows this movement to take place relatively unimpeded due to extremely loose connective tissue connections between it and the anterior hypobranchial complex. The gular plate itself is carried downwards by the pressure of the hypohyals. It is finally pulled backwards, when the connective tissue is stretched to a maximum, exerting a pull on the mandibular symphysis. Such a pull would only occur during maximum mouth opening.

The strong L. hyoideum proprium (Fig. 4) becomes taut soon after mouth opening. While exerting a certain pull on the mandible, it also exerts tension on the median part of the ceratohyal. The posterior end of the latter can swivel upwards, its anterior end downwards about this point.

The large size and strength of the hyoideo-mandibular ligament (Fig. 4) give reason to name it as the most important jaw depressor. Its effect has been observed: it is stretched in the closed-mouth position. Any further backward and/or upward movement of the ceratohyal must exert an immediate strong pull on the angle of the jaw (Fig. 8), causing it to drop.

The interopecular is attached to the angle of the jaw by the interoperculo-mandibular ligament (Fig. 1) anteriorly. Posteriorly it is rigidly attached to the opercular bones by thick connective tissue. Medially it is anchored to the ceratohyal (at point X, Fig. 8). Any backward or upward movement of the interopercular (whether by the agency of its hyoid arch or opercular connections) would have a lesser but similar effect on the mandible to the hyoideo-mandibular ligament.

Water enters the opened mouth and is sucked in by the expansion of the whole mouth cavity. This is achieved as follows: The levator arcus palatini (Fig. 2) contracts, lifting the hyopalatine complex. This swivels outwards laterally on the articular heads of the hyomandibular, while the palatine slides on the lateral ethmoid. A further effect of the hyoid bar aids the suction: while the hypohyals move postero-ventrally, the backward and upward motion of the ceratohyal reaches the limit allowed by the interhyal attachment. The hyomandibular rami respond to continued backward force by swinging laterally. They carry the interoperculum and consequently to some extent the opercular complex outwards as well. The outward movement of the opercular complex by the dilatator operculi expands the opercular chamber. The considerable concomitant reduction of pressure causes water to flow through the gill slits into this chamber, the "suction-pump" of Hughes (1960). Some authors (Van Dobben 1935; Holmquist 1910) believed that the levator operculi lifts the operculum synchronously with its abduction by the dilatator operculi, with a concomitant added pull on the angle of the jaw via L. interoperculo-mandibulare. However, Ballantijn and Hughes (1965) proved conclusively by electromyographic recordings that in the trout, at least, the activity in adductor and levator operculi is synchronous and alternates with that of the dilatator operculi. It seems likely that this condition exists in other fishes as well. Certainly in *Elops* adductor and levator operculi form a continuous muscle strip difficult to separate. However, the persistent presence of the interopercular-mandibular ligament in teleosts suggests that a pull on the angle cf the jaw via this ligament during jaw opening does exist, being transmitted from the dilatator operculi and hyoid arch movement (Fig. 8).

When the anterior hyoid arch drops, the Ll. abductores radiorum branchiostegalium become taut, expanding the branchiostegal rays (Fig. 4). These ligaments have the function of the hyohyoidei abductor muscles of other fishes.

If the suction pump is to operate effectively, water must be prevented from entering past the expanded rays through the opercular opening. It is widely accepted that the branchiostegal membrane acts as a passive valve, being pressed against the body by inrushing water. A hypothesis more likely to ensure the efficiency of the suction pump and based on the anatomy of the hyohyoid muscles in *Elops* is presented here: The hyohyoideus indivisus of fig. 5 consists of fine fibres and extends from the suboperculum, along the rays, to the opposite hypohyal. Although it is innervated by the same nerve as the other hyohyoid muscles, its motor fibres could come separately from the brain centre and allow its independant contraction during inspiration. Such contraction would cause an inward curving of the rays, which are soft enough at their tapering ends. The whole branchiostegal membrane would curve towards the body wall and make an active opercular valve possible, while allowing the rest of the opercular complex to maintain full extension.

During extreme mouth opening, the anterior tip of the hyoid arch would move further down. This time the hyoid arch also moves down as a whole (compare Figs. 8, 2 and 3). The hyoideo-mandibular and interoperculo-mandibular ligaments become slack. Their initial action is completed. (This was actually observed on the fresh specimens and substantiated by the X-rays). Now the orobranchial and opercular chambers are completely extended, laterally and ventrally, and the opercular suction pump has reached its climax and its conclusion.

The mechanism outlined above deals with the total range of possible jaw opening movements. It must be stressed that any actual movement of the living fish lies somewhere in that range. Unfortunately a live *Elops* could not be observed, but its respiratory movements are assumed to be similar to those of other fish observed by the author, in that they only involve slight jaw opening during normal conditions. In this connection Ballantijn and Hughes (1965) had interesting results in their investigation of the trout. During normal respiration only a few muscles come into play. During feeding or deeper ventilation such as would occur during lack of oxygen, fast movement, or the "coughing" described by Baglioni (1908), the full range of described muscles and movements would be involved.

II) *Movements of the upper jaw during mouth opening:*

As the dentary is lowered, so the lower end of the maxilla moves progressively forward (Fig. 8). It is carried along by the folds of L. maxillo-mandibularis anterius (Fig. 3). This ligament stretches from the dentary to the postero-dorsal margin of the maxilla, in actual fact more to the supramaxillae. The resistance encountered by the curved anterior part of the maxilla on this forward path tends to push its broad posterior part away from the head. Owing to the position of the above-mentioned ligament, only the anterior maxillary margin bearing the toothrow is free to do this. It twists forward and outward. This in turn causes the curved maxillary head to push forwards and downwards underneath the premaxilla (Fig. 3). The latter is lifted anteriorly as far as its relatively loose posterior connective tissue connection will allow.

Movement of the maxillary head and the premaxilla is controlled by a series of ligaments.

The palato-praemaxillary ligament (Figs. 2 and 3) runs across the groove formed between the "ball" of the ball and socket joint, and the club-shaped maxillary tip (Fig. 2). It holds the curved maxillary head firmly against the skull while allowing it to rotate.

The strong palato-maxillary ligament attached on the inner surface of the maxilla (Figs. 2 and 3) not only endorses this effect, but it is also antagonistic to outward rotation of the toothrow. It allows rotation up to a certain point and no further.

The Ll. ethmoido-maxillare I and II (Fig. 3) fix the anterior tip of the maxilla posteriorly and dorsally.

The L. maxillo-mandibulare posterius, inserted on the inner anterior maxillary surface (Fig. 3) provides a further antagonist to outward rotation as well as a swivel point about which the curved part rotates and the long expanded part of the maxilla swings forward.

The praefronto-mandibular ligament binds the prefrontal to the dentary. Both last-mentioned ligaments act as antagonists to excessive jaw opening.

As the jaw opens, the supramaxillae fold out as from a fan, providing some firmness to the unprotected lateral wall of the mouth.

III) *The jaw closing and constricting mechanism:*

The closing of the jaw commences with the contraction of the massive adductor mandibulae as it does in the trout (Ballantijn and Hughes 1965).

The adductor tendon to Meckel's cartilage lifts the mandible. The tendon to the dentary transmits the force of the adductor via the intramandibular to this bone. This is an important differentiation of the adductor. The mandible can be thought of as a third class lever (Gregory 1933) with its fulcrum at the angle of the jaw. In forms such as *Lepidosteus*, with a single adductor insertion on Meckel's cartilage, the effort arm (between the tendinous insertion and the angle of the jaw) is short. By the development of the intramandibular in *Amia* and Elopiformes, the effort arm is lengthened to comprise over half of the mandibular length (Fig. 5).

The adductor tendon to the L. maxillo-mandibulare posterius withdraws the maxilla and causes inward rotation of the toothrow. This in turn rotates the maxillary head to its original position and allows the premaxilla to subside into place.

The withdrawal of the maxilla is aided by the retreat of the hyopalatine arch which had moved forward during jaw expansion. The palato-maxillary ligament (Fig. 3) retreats with it and pulls the maxillary ramus in a posterior direction.

The mandible being fixed by the adductor muscle, contraction of the interhyoideus-intermandibularis posterior complex now protracts the hyoid arch, from a posterior, nearly vertical position to its original anterior one in a horizontal plane.

The levator arcus palatini has relaxed and the hyopalatine complex is pulled inwards and backwards by the adductor hyomandibulae.

The interhyal transmits this inward and backward motion to the hyoid arch. Concomitantly the anterior end of the latter moves upwards and forwards, sliding along the median gular plate. All this time it pulls the interopercular backwards with it.

The intermandibular has also contracted to firmly adduct the gular plate.

There are no buccal valves in *Elops* and the mouth presumably has to close completely, which is in fact made possible by the small teeth, to ensure the full effect of a buccal force pump. The buccal volume is now much reduced and water is forced backwards.

As also found by Ballantijn and Hughes (1965) in the trout, the relaxation of the dilatator operculi precedes the simultaneous contraction of the levator and adductor operculi. The progressive constriction of the orobranchial and opercular chambers in an antero-posterior direction forces the water out of the opercular cavity. The Ll. abductores radiorum branchiostegalium (Fig. 4) are slack and all the hyohyoid muscles contract to drive the last water out. This too is in agreement with the findings of Ballantijn and Hughes (1965) in the trout.

Already the rectus cervicis has started to contract again for the next mouth-opening phase.

FEEDING

Feeding in fishes involves essentially the same mechanisms as does breathing. It seems likely that *Elops*, in catching prey of the size described below, would open its jaws as widely as possible, using the extreme jaw opening mechanism described previously (see also Figs. 3, 4 and 8).

The stomach contents of *Elops*, as investigated by B. S. Brunhüber, of this department, comprised the following:

Fishes of the genera *Ctenotrypauchen* and *Microcephalus*;
Johnius belengerii ranging from 12 to 19.5 centimetres and 34 to 59 grams;
Small mullet and *Gobius*;
The remains of a larger unidentified fish over 14 centimetres;
Crustacea including *Penaeus japonicus* and *Hymenosoma orbiculare*;
Polychaets;
Weeds and sand.

The streamlined form of *Elops* suggests a fast swimmer, and its diet a good hunter. Judging by the crabs and the sand, it must be a benthic as well as a pelagic feeder.

In one fresh specimen a hook, baited by a prawn, was found attached to the anterior part of the oesophagus. This must have reached its position in one snap of the fish's jaw. It probably swims at considerable speed towards its prey, jerks open its mouth to maximum expansion and engulfs the prey. The latter process would, in the case of smaller prey at least, be aided by the current of water set up by the suction and force pumps. To actually bring the prey to a position suitable for swallowing would necessitate a series of gulps. Between gulps the teeth could hold the struggling prey.

The sudden violent opening of the mouth would necessitate the retraction of the pectoral girdle by the hypaxial muscles, aiding the rapid contraction of the rectus cervicis. Also the epi-axial musculature inserted in the posterior temporal fossa, would, by violent contraction, aid in jerking up the cranium and snout.

The impact of the jaws snapping shut could be taken up by the extremely movable ethmopalatine sliding articulation and the systems of snout ligaments. Together they could act as a shock absorber.

The support of the anterior lateral buccal walls, afforded by the supramaxillaries and ligaments, aids in protecting the mouth cavity. (In later evolutionary forms the maxilla, lying behind the premaxillary jaw margin, strengthens this vulnerable connective tissue area).

On the whole *Elops* probably fits into the category of fishes, using both suction and biting in their feeding, outlined by Alexander (1967a). The varied stomach contents, the well-developed opercular suction pump and the absence of special adaptations characterising strong bite force (e.g. shortened mandible, large coronoid process, oblique suspensorium: see Schaeffer and Rosen 1961), lead to the conclusion that suction feeding predominates in *Elops*. However, as Alexander (1967a) points out, the relatively fixed premaxillae are probably suitable for biting. Such biting is visualized as the holding of prey between successive swallowing movements as outlined above.

THE CRANIAL ANATOMY OF MEGALOPS CYPRINOIDES

This section includes a brief outline of those anatomical features of *Megalops cyprinoides* which are of interest in a discussion of the jaw mechanism of *Elops*. In most features the two fishes are essentially similar. *Megalops* is a larger, sturdier fish. It is shorter and more compact in relation to its size than the snake-like *Elops*.

Osteology and ligaments

The cranium is deeper and the gape smaller than that of *Elops* (Fig. 7). The mandible is notably higher in proportion to its length. The suspensorium has a considerable backward slope.

The L. maxillo-mandibulare posterius forms a single thick band from mandible to maxilla. The premaxilla possesses a slight process where L. palato-praemaxillare joins it.

In place of L. praefronto-mandibulare of *Elops* (Fig. 3), a ligament stretches from the lateral ethmoid and prefrontal to the palatine. It has been named L. ethmoido- et praefronto-palatinus.

The L. palato-maxillare, which was exceptionally strong in *Elops*, is absent.

The gular plate is strongly reduced. It is narrower than that of *Elops* and its lateral borders are replaced by a strong connective tissue fold (Fig. 7). (In *Albula*, of the closely related elopomorph family Albulidae, the bone has disappeared leaving only an intergular fold (Hubbs 1919)).

Musculature

In the musculature there are certain fundamental differences from *Elops*.

Mm. adductor mandibulae et intramandibularis:

The adductor mandibulae is divided into two main parts. Superficially, an unbroken muscle sheet originates exactly like the adductor of *Elops*, but inserts by only two tendons. The dorsal tendon inserts solely on L. maxillo-mandibulare posterius. The ventral tendon is continuous with the large intramandibular. This muscle sheet is considered to represent M. adductor mandibulae A_1 A_2, following Vetter's terminology (Fig. 7).

Internal to this muscle lies M. adductor mandibulae A_3. It originates on the metapterygoid and inserts on the ventral tendon of A_1 A_2, i.e. the tendon continuous with the intramandibularis.

N. mandibularis V passes between adductors A_1 A_2 and A_3.

M. protractor hyoidei:

In *Megalops* the interhyoideus and intermandibularis posterior are represented by a single muscle band stretching from the hyoid arch, to insert on the gular plate posteriorly and by ligamentous fibres on the midline of the mandible anteriorly. The posterior section is innervated by R. hyoideus VII and the anterior section by R. mandibularis internus V. It was not possible to ascertain on the single specimen available whether these two nerves were connected by an anastomosis or not. This muscle, retaining its double innervation, undoubtedly represents the protractor hyoidei of Holmquist (1910), often cited as a classmark of the teleosts. In this respect *Megalops* seems to be more advanced than *Elops*, where the two components remain separate.

DISCUSSION

It has been pointed out that *Elops saurus* occupies a unique position near the base of teleostean evolution. Many of its features, whether seen in a purely anatomical and/or functional light, provide an interesting link in actinopterygian evolution.

A study of the literature on the evolution of the protractor hyoidei yielded the following facts: in the holostean *Lepidosteus*, the ventral hyoid constrictor grows forwards and inserts on the midline. It is still one large undifferentiated muscle which by each contraction pulls together the whole ventral hyoid and opercular apparatus.

In *Polypterus* (Edgeworth 1933, Fig. 245) the intermandibularis slants backwards towards the midline and the interhyoideus forwards. This is almost exactly the condition in *Elops*.

In *Amia* the protractor hyoidei is complete; i.e. a single muscle with attachments to hyoid arch and mandible as well as double innervation, although in its ontogeny it undergoes a stage where it still inserts on the ventral midline (Allis 1897). The condition in *Megalops* is roughly comparable to this. With respect to the development of the protractor hyoidei, the Elopidae appear to be more primitive than *Amia*. With respect to other features, however, *Amia* seems to be the immediate precursor of the Elopomorpha.

The purely expirational nature of the developmental stages of the protractor hyoidei, as gleaned from literature available to the author, strengthens the belief that the muscle has remained throughout a purely expirational muscle which it has been shown to be in the trout by Ballantijn and Hughes (1965).

The interhyoideus-intermandibularis posterior system of *Elops* is thus on the brink of becoming one muscle. Moreover, the motor nerves supplying its two elements have established an anastomosis between them (Fig. 5). It is possible that the anastomosis arose initially as did the better-known ones between the internal mandibular branch of V and the chorda tympani for the passage of visceral sensory fibres. Later, motor fibres from the hyoidean nerve, already supplying the interhyoideus, could cross the anastomosis to supply the intermandibularis posterior as well. Alternatively motor fibres from nerve V could innervate both muscles via the anastomosis, or both conditions could occur together. In one of these ways better co-ordination between the two elements of the muscle could be achieved. It is conceivable that in more advanced teleosts the anastomosis could be lost and the single protractor hyoidei retain innervation from one source only.

A jaw opening mechanism, whether muscular or otherwise in nature, must have existed and evolved alongside the ventral constrictors. In ganoids the hypobranchial muscles extend forward beyond the hyoid arch to form genio-hyoids or genio-branchials which could open the jaw (Edgeworth 1935). In teleosts such muscles are absent and an alternative arrangement is necessary. There is evidence that the essential ligaments as found in *Elops* and later teleosts are already present in some preteleosts.

Pollard (1892, quoted by Holmquist 1910) mentioned a L. hyoideo-mandibulare in *Polypterus*. Allis (1897) described such a ligament in *Amia*, with essentially the same attachments as in *Elops*. Holmquist (1910) depicts *Lepidosteus* as possessing a L. hyoideo-operculare.

The hyoideo-mandibular ligament of *Amia* and *Polypterus* has become the chief jaw opener in *Elops*. It appears to be more primitive than the interoperculo-mandibular ligament, which in later teleosts completely replaces it.

As Hubbs (1919), Gregory (1933) and Ridewood (1904) point out, in no extant teleost is it more clearly seen than in the primitive Elopomorpha (and thus *Elops* and *Megalops*) that the opercular and subopercular are the two terminal elements of the series of branchiostegal rays. This is clearly shown in Figs. 4 and 7.

In both *Elops* and *Megalops* the last rays have definite connective tissue connections with the angle of the jaw. In *Amia* the first branchiostegal rays are connected to the mandible by a ligament. In *Lepidosteus* even the preopercular has such a connection with the angle of the jaw (Gregory 1933). It appears that the participation of opercular lift, due to the dilatator operculi and hyoid arch movements, in mandibular depression is not merely a late teleost arrangement, but plays a part throughout the Actinopterygii. It seems reasonable to suggest that the interopercular, peculiar to the teleosts, owes its existence to this arrangement. It was only by the differentiation of this bone from the branchiostegal series, that opercular lift in its full strength could be focussed onto the mandible.

In a pre-interopercular stage the upper branchiostegal rays probably lay across the hyoid arch and were connected to the angle of the jaw, as they are today in *Elops* and *Megalops*. Above the rays were those opercular bones, already differentiated from the series of rays in response to a new breathing mechanism (Gregory 1933). The force of the dilatator operculi would be transmitted most effectively by the most dorsal, i.e. the last ray.

Its connection with the angle of the jaw would thicken into a ligament, and it would move across the hyoid arch and upwards. Becoming stronger and broader, it acquires an anchorage on the hyoid arch. From this stage onwards the interopercular can transmit the force of the hyoid arch, as well as that of the opercular complex, to the angle of the jaw. This is the stage encountered in *Elops* and *Megalops* where L. interoperculo-mandibulare is beginning to rival L. hyoideo-mandibulare as the chief jaw opener.

It is only at a later stage, when the interopercular connection with the hyoid arch shifts onto the interhyal, that the bone attains the full functional versatility seen in modern teleosts. Van Dobben (1935) explains how the amount of jaw opening depends directly on the position of the interopercular connection along the interhyal. This connection, the suspensorial angle and length of the mandible (Schaeffer and Rosen 1961), the position of the quadrate articulation and other factors, combine in many permutations to exploit the versatility of the interopercular action. L. hyoideo-mandibulare becomes redundant and disappears.

The differentiation of the adductor mandibulae in *Elops* and *Megalops* is of interest. In Chondrostei the adductor is a single muscle sheet, situated internal to R. mandibularis V. In *Lepidosteus* it inserts by a single tendon on Meckel's cartilage (Edgeworth 1933). *Elops* differs in the possession of an extra section, the intramandibularis, and in the sub-divisions of the tendinous insertions. Only the dorsal part of the muscle is internal to R. mandibularis V, since the nerve dives inwards below the tendinous insertion on L. maxillo-mandibulare posterius (Fig. 5).

In *Megalops* the muscle sheet has divided into a superficial and a deep section. The superficial section (A_1A_2) is external to R. mandibularis V. Its dorsal part inserts on L. maxillo-mandibulare posterius by a tendon comparable to the one in *Elops* and appears to be the precursor of A_1. Its ventral part is continuous with the ventral part of the intramandibularis and appears to be the precursor of A_2. The deep section of the muscle is internal to R. mandibularis V and, from its position, origin and insertion, clearly represents A_3 of higher teleosts.

It is thus clear that in these two members of the Elopidae the adductor has differentiated in different ways. That part inserting on L. maxillo-mandibulare posterius (the forerunner of A_1) appears to be comparable in the two, yet it is internal to the nerve in *Elops* and external to it in *Megalops*. This casts doubts on Kesteven's assertions (1942; see also Millard 1966) on the constancy of the relationship between the nerve and the muscle sections and on the possibility of homologizing muscles in teleosts with those in tetrapods.

With respect to jaw protrusibility *Elops* and *Megalops* stand near the base of teleost evolution. In the Elopoidei the upper jaw is not protrusible in the accepted sense, although free to rotate on the palatine and ethmoid region of the skull. The ligaments controlling this movement are such that they could have evolved into the "crossed-ligament" arrangement (Eaton 1935) in percomorphs with protrusible jaws.

The maxillary head and the premaxilla of Elopoidei are held in position mainly by Ll. ethmoido-maxillare and L. palato-praemaxillare respectively. In *Megalops* a special process on the premaxilla is present for the attachment of the latter. In later evolutionary stages the loosening of the median symphysis between the premaxillae and the greater mobility of the alveolar rami would require the controlling force to be closer to the midline. L. palato-praemaxillare would thus tend to be more median and would come to lie over L. ethmoido-maxillare II.

As Schaeffer and Rosen (1961) have pointed out, the ball and socket joint between the maxilla and palatine appeared *de novo* in Elopidae, but became reversed in later evolution with the withdrawal of the maxilla from the gape. This has already been partly achieved in *Megalops*, where the anterior head of the palatine fits into a socket in front of the "ball" of the maxilla.

Thus the tendency in the Elopoidei is towards greater mobility in the snout region and the organization of bones and ligaments into a more efficient feeding and breathing system. This trend can be seen to develop amongst later teleosts, to culminate in the specialised, highly protrusible mechanisms of recent forms, such as *Idus* and *Gobio* (Alexander 1966).

Elops, from the same protospondylous line that gave rise to *Amia*, has in every feature remained completely generalised. However, in its very generalisation are evident the potential beginnings of the subsequent evolution which gave teleosts dominance among fishes.

SUMMARY

1. The osteology and ligaments of the skull of *Elops saurus* are described.
2. A study is made of the cranial muscles: their structure, function and innervation.
3. The mechanism of the jaw was determined by the use of X-rays.

4. In the light of the results obtained from the X-rays and from the anatomical investigations, the mechanism of respiration and action of the jaw during feeding are discussed. *Elops* possesses the forerunner of a protractor hyoidei, which is considered to function in protracting the hyoid arch and not in depressing the mandible. An unusual anastomosis between nerves V and VII is thought to participate in the co-ordination of this incomplete protractor hyoidei.
5. The cranial anatomy of *Megalops cyprinoides*, an allied species, was investigated. In a comparison with *Elops* it was found to be more advanced, notably in the possession of a protractor hyoidei.
6. It is concluded that *Elops*, due to its primitive predatory habits, has in most features of its jaw mechanism remained generalised. It is this lack of specialisation which provides the suitable primitive condition from which the various teleost jaw mechanisms may have evolved.

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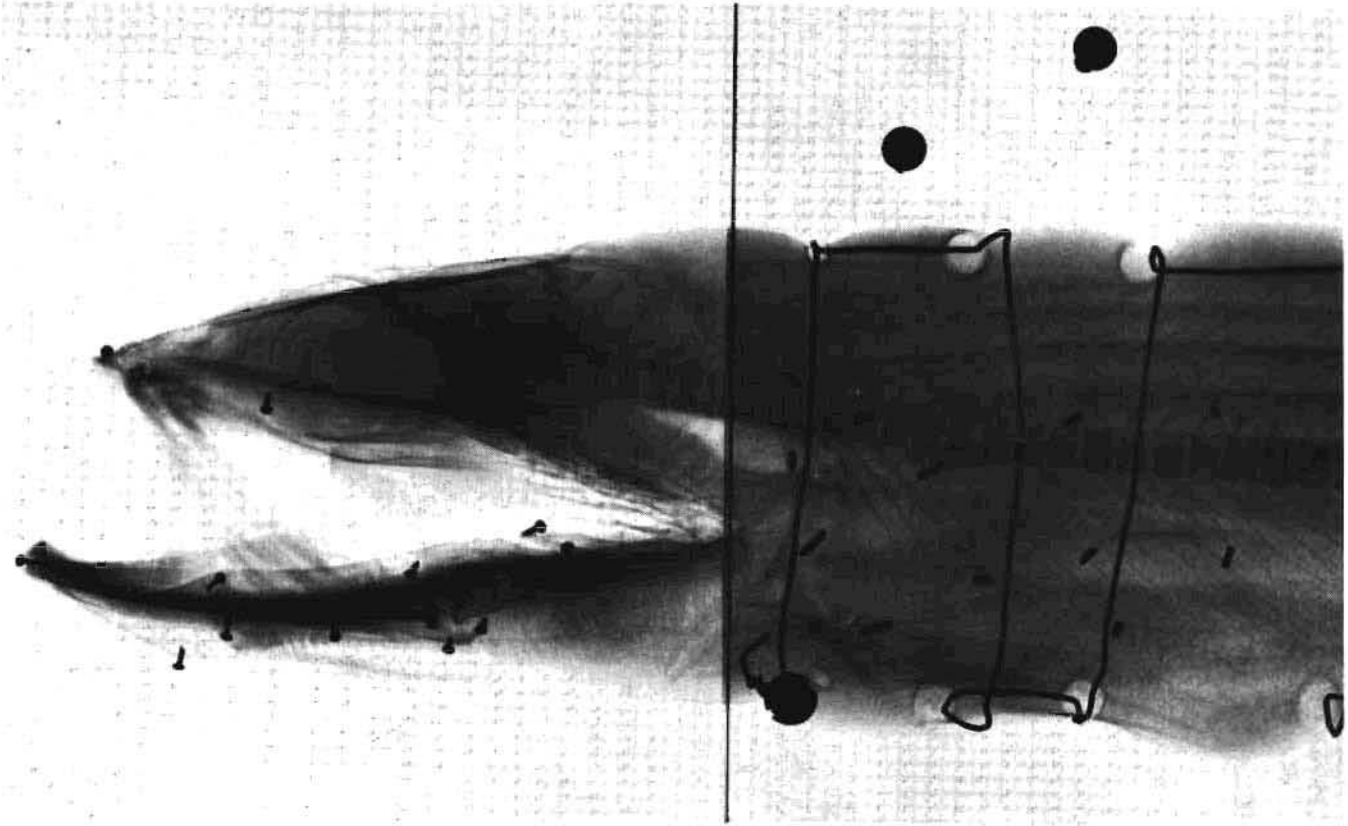

Figure 9: An example of an x-ray photograph of the head of *Elops saurus*, with the jaw opened 3.5 cm., *i.e.*, intermediate between stages 2 and 3 in fig. 8. Three nails and various "marker"pinheads are shown. The front edge of the supporting board is indicated by a vertical line.

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ABBREVIATIONS USED IN THE FIGURES

Lig. = Ligamentum
M. = Musculus
N. = Nervus
N. ad m. = Nervus ad musculus
N. mand. int. = Nervus mandibularis internus