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Myology of the Pectoral, Branchial, and Jaw Regions of the Ratfish *Hydrolagus colliei* (Holocephali)

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Senior Honors Thesis
Biology Department
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ABSTRACT

The musculature of the jaw, branchial, and shoulder regions of the ratfish, *Hydrolagus colliei*, was dissected and described in an effort to determine possible homologous characters shared by the shark, a member of the subclass Elasmobranchii, and the ratfish, a member of the subclass Holocephali. The musculature of the ratfish jaw differs from the morphological pattern found in sharks in that the jaw muscles of the ratfish are located anterior to the orbit, unlike the jaw muscles of sharks, which are posterior to the orbit. It is suggested that this anterior musculature is a character that was shared by fossil ptyctodonts (Class Placodermi) and is not found in any other living fish today. It is further suggested that the labial cartilages of the ratfish may be remnants of the palatoquatrate cartilage which were excluded as the jaw became fused to the braincase. The morphology of the head of the ratfish best supports the hypothesis that ratfish and ptyctodonts are more closely related to each other than either taxon is to sharks or other jawed fishes.

INTRODUCTION

The chimaera (more commonly known as the ratfish) has always been a problem in vertebrate classification. According to Patterson (1965), there are six known genera of chimaeroid fishes one of which is the genus Chimaera, not to be confused with the general usage of chimaera as applied to all members of the order Chimaeriformes. It has generally been accepted that the chimaera, which belongs to the class Holocephali, is most closely related to the class Elasmobranchii, which includes sharks, skates, and rays (Appendix i). In classifying fish, the most primitive condition is characterized by the absence of jaws and paired fins and the presence of a partially cartilaginous skeleton. The agnaths, which include modern lampreys and hagfish, make up what is considered the earliest group of fishes. Traditionally, the agnathans are thought to have given rise to extinct, heavily armored fish known as the class Placodermi. The six groups of placoderms are as follows: arthrodires, ptyctodonts, phyllolepids, petalichthyids, rhenanids, and antiarchs (Romer, 1966). From the placoderms were descended three separate groups of fishes: the extinct fossil group of spiny fish, the Acanthodii; the bony fish or class Osteichthyes; and the cartilaginous fish, class Chondrichthyes (Hildebrand, 1982). The class Chondrichthyes was then further divided into two separate subclasses: Elasmobranchii, which includes as its most familiar member the shark (selachians), and the subclass Holocephali, which has the chimaera as its only member. The Holocephali and Elasmobranchii have long been considered closely related because, unlike other known fishes, each group has a cartilaginous skeleton and unique copulatory organs called claspers. More recently the classification of fish has been revised by Romer and Parsons, 1986 (Appendix ii). In this classification placoderms are no longer grouped as a separate class, but instead are grouped as a subclass of the class Elasmobranchii along with the other subclass, Chondrichthyes. The order Selachii

belongs to the infraclass Elasmobranchii and Holocephali is now a superorder belonging to the infraclass Bradyodonti. This new revised phylogeny in appendix ii implies a closer evolutionary relationship between placoderms and sharks.

Much research attempts to precisely classify the chimaera and determine its relationship to other fishes. Vetter (1878) was one of the first to closely examine the ratfish. His study of Chimaera monstrosa focused on the musculature of the jaw and branchium. Other early work with ratfish was done by Cole (1896); Cole and Dakin (1906) involved study of the cranial nerves of the ratfish. Dean's study of Chimaera colliei (Hyrolagus colliei), Chimaeroid Fishes and Their Development (1906), focused on embryology and included detailed descriptions of various systems of the ratfish.

Most of the work with chimaeras has been on the head region, including the jaw, branchium, and shoulder girdle. The jaw and branchial region are among the key factors in evolution, and research in the anatomy of these regions can provide many valuable clues to the evolution of fish and relationships to other fish. Luther (1909) looked at the musculature of the head region. Allis did work on the circulatory system of Holocephali (cited by Stahl, 1967), as well as studying prechordal portions of the skull (1926). Shann (1919, 1924) examined the musculature of the pectoral region of several fish including the ratfish and drew excellent comparisons between the groups represented. The head anatomy of Callorhynchus antarcticus was closely examined by Kesteven (1933); while Edgeworth (1935) prepared a comprehensive work on vertebrate cranial musculature which includes the Holocephali, focusing mainly on development. More recently, Stahl (1967) examined the holocephalian venous system and researched other systems in an effort to further determine the ancestry of the ratfish. Jollie's (1973) work is another comprehensive study which includes ratfish anatomy especially as it compares to the anatomy of the shark.

Although much work has been done on the anatomy of the jaw and branchium of

the ratfish, no one had completed an examination of the entire region prior to this study. Vetter (1878) and Luther (1909) concentrated on the jaw and Shann (1919) studied only the pectoral region. Little has been done on Holocephali in recent years and less on Hydrolagus colliei in particular. The supposed relationship of Holocephali to elasmobranchs has never been conclusively established.

Three alternative relationships have been proposed based on various studies of holocephalians:

1. The Holocephali are most closely related to sharks including the Bradyodonti, a fossil group of "pavement-toothed sharks" (Romer 1946).

2. The Holocephali are closely related to the Dipnoans, bony fishes with lungs (anonymous, from Stahl 1967).

3. The Holocephali are most closely related to the ptyctodont group of the placoderm fishes (Westoll, 1962; and Romer, 1946).

The purpose of this study is to closely examine the musculature of the jaw, branchial, and pectoral regions of Hydrolagus colliei and by using comparative morphology determine which of these hypotheses is best supported by my evidence.

MATERIALS AND METHODS

Three preserved male specimens of Hydrolagus colliei were obtained from Carolina Biological Supply Co. Over the period of one month the anterior third of the fish were dissected and the musculature of the jaw, branchium and shoulder region was carefully described and drawn. Three specimens were used to check accuracy; however, no comparison could be made between the sexes. A female

Squalus acanthias was also dissected to compare the selachian musculature with that of the holocephalian. It was not possible to obtain a dipnoan representative for dissection and comparison. An extensive literature search for work that has been done relating to the jaw and branchium of lungfishes was conducted in an attempt to accumulate data for comparison between the lungfish and the ratfish.

OBSERVATIONS

I. BRANCHIOMERIC MUSCULATURE

MANDIBULAR MUSCLES innervated by N. V

M. labialis anterior (Fig. 1)

ORIGIN: On the anterior edge of the maxillary cartilage at the junction between the maxillary and prelabial cartilages.

INSERTION: Laterally on the distal end of the prelabial cartilage.

COMMENTS: This muscle is the same as Csd_1 according to Vetter (1878). Edgeworth (1935) refers to a single labialis muscle and does not, as I do here, distinguish separate anterior and posterior muscles.

M. labialis posterior (not illustrated)

ORIGIN: From the medial side of the joint between the maxillary and prelabial cartilages

INSERTION: By tendon, on the center ventral face of Meckel's cartilage and onto its antimere.

COMMENTS: This muscle follows the anterior-most border of the lower lip and is paired. Edgeworth (1935) calls this muscle the intermandibularis anterior. Luther (1909) has also described a very tiny muscle slightly posterior to the labialis posterior which he calls the labialis inferior. Edgeworth distinguishes Luther's labialis posterior as the intermandibularis posterior. This is the only

muscle found in ratfishes that is possibly homologous to the intermandibularis.

M. adductor mandibulae anterior pars nasalis (Fig. 2)

ORIGIN: From the midline ridge of the chondrocranium, anterior to the head clasper and above the rostral process.

INSERTION: On the ventro-lateral surface of Meckel's cartilage just ventral to the insertion of the levator anguli oris posterior.

COMMENTS: This muscle appears as a large muscle mass with a dense connective tissue dividing the muscle into two distinct parts. The parts do not separate easily, but the fibers run in distinctly different directions and insert together by a large tendon (two tendons according to Edgeworth). Vetter (1878) has named the entire muscle the adductor mandibulae and the nasalis portion the levator labii superior. Luther (1909) has named this muscle, the adductor mandibulae anterior pars nasalis the preorbitalis. Edgeworth (1935) does not distinguish it as a separate part of what he calls the levator mandibulae anterior.

M. adductor mandibulae anterior pars orbitalis (Fig. 2)

ORIGIN: From connective tissue at anteroventral edge of the orbit with some fibers extending higher dorsally to originate from cartilage at the anterodorsal edge of the orbit.

INSERTION: By tendon to the lateral face of Meckel's cartilage, just medial to the maxillary cartilage. Inserts with the adductor mandibulae pars nasalis.

COMMENTS: The adductor mandibulae anterior has not previously been described as having two parts.

M. adductor mandibulae posterior (Fig.3)

ORIGIN: On the cartilage of the chondrocranium below the orbit extending from the region of the post-orbital ridge to the posterior edge of the nasal capsule.

INSERTION: By several tendons to the ventro-lateral face of Meckel's cartilage slightly dorsal to the insertion of the levator anguli oris.

COMMENTS: This flat muscle lies in a depression on the chondrocranium. It is almost entirely covered by the two parts of the adductor mandibulae anterior. According to Vetter (1878) the entire adductor mandibulae (pars nasalis, pars orbitalis, and the posterior portion) of the ratfish is homologous to the adductor of the selachian. According to Edgeworth (1935), it is homologous to the levatores mandibular anterior and posterior in Dipnoi.

M. levator cartilaginous prelabialis (Fig. 1)

ORIGIN: By tendon from the cartilage plate at the anterior base of the head clasper.

INSERTION: Center of the medial face of the prelabial cartilage.

COMMENTS: Described by Luther (1909) as distinct from the levator anguli oris anterior as its insertion seems to indicate; however, fibers of this muscle coalesce with the levator anguli oris anterior near the origin.

M. levator anguli oris anterior (Fig. 1)

ORIGIN: With M. levator cartilaginous prelabialis from the cartilaginous plate at the anterior base of the head clasper.

INSERTION: Onto the distal edge of the maxillary cartilage at the junction between the maxillary and prelabial cartilages.

COMMENTS: Vetter (1878) suggests this is homologous with the levator

maxilla superior (levator palatoquadrate) of the selachian, or perhaps is part of the adductor mandibulae.

M. levator anguli oris posterior (Fig. 1)

ORIGIN: Connective tissue of the anterior ventral edge of the orbit.

INSERTION: By tendon ventrally to the skin of the lower lip.

COMMENTS: Some fibers of this muscle join with the levator anguli oris anterior near its origin. Together the levator cartilaginous prelabialis and the levators anguli oris anterior and posterior form a complex coalesced muscle that lies directly over the anterior portion of the mandibular adductor. These three muscles are unique to holocephalians.

HYOID MUSCLES innervated by N. VII

M. constrictor ventralis (Fig. 1)

ORIGIN: From the ventral mid-line fascia (linea alba) with some fibers originating from a small part of the ventral edge of Meckel's cartilage near the corner of the mouth.

INSERTION: Along the ventral edge of the tough fibrous operculum.

COMMENTS: The fibers of this muscle run dorsoventrally with a few fibers that originate on the lower jaw running in an anterior-to-posterior direction and becoming completely fused with the dorsoventral fibers. Vetter (1878) described this muscle as composed of six fused constrictor muscles. The constrictor ventralis pars anterior makes up the anterior portion of the constrictor ventralis. Edgeworth (1935) named the constrictor ventralis the constrictor hyoideus.

M. constrictor dorsalis (Fig. 1)

ORIGIN: By a fibrous connection to the ventral edge of the cartilaginous

post-cranial ridge ventral to the first dorsal fin, with some fibers originating from part of the post-orbital ridge.

INSERTION: On the dorsal edge of the tough fibrous operculum.

COMMENTS: This muscle is also described by Vetter (1878) as a series of fused constrictors. Vetter (1878) does not distinguish the dorsal constrictor and ventral constrictor as two separate muscle masses.

M. constrictor operculi (Fig. 1)

ORIGIN: From a small area on the anterior lateral edge of the pectoral girdle just below the insertion of the trapezius superior.

INSERTION: Fused into the posterior edge of the ventral constrictor where the fibers run together.

COMMENTS: This muscle forms the lateral edge of the opercular opening. It has not been described as a separate muscle and is considered by Vetter (1878) to be part of the constrictor muscles. It appears to originate from the pectoral girdle, and the fact that it is easily separated from the ventral constrictor would distinguish it as a separate muscle.

M. hyoideus superior (Fig. 2)

ORIGIN: From deep medial surface of the post-orbital ridge at the posterior edge of the orbit.

INSERTION: On the anterior edge of the fused hyoid rays.

COMMENTS: This small flat muscle lies on the dorsal surface of the entire branchial apparatus. Edgeworth (1935) calls this muscle the levator hyomandibulae.

M. hyoideus inferior (Fig. 2)

ORIGIN: On the medial face of the ventral-most part of Meckel's cartilage.

INSERTION: On the lateral face of the proximal end of the ceratohyal just ventral to the articulation with the epihyal.

COMMENTS: Edgeworth (1935) has named this muscle the interhyoideus. According to Vetter (1878) both hyoid muscles of the holocephalian are homologous to the second dorsal and ventral constrictors of the selachian.

TRAPEZIUS GROUP innervated by the vagus

M. trapezius superficialis (Fig.1)

ORIGIN: From the post-orbital ridge with some fibers originating from dorsal fascia.

INSERTION: On the posterior edge of the pectoral girdle just dorsal to the origin of the constrictor operculi.

COMMENTS: This muscle is identified as the M. levator pectoralis by Shann (1919), and as the M. trapezius externus by Stahl (1967). Vetter (1878) and Edgeworth (1935) describe two muscles in the trapezius group. Edgeworth calls the trapezius superficialis the cucullaris superficialis; like Vetter I call it the trapezius superficialis. According to Shann (1919) this muscle is derived from the mesio-ventral portion of the lateral muscle and is homologous to the levator pectoralis (or trapezius) in the shark and the sterno-cleidomastoid in the Dipnoi.

M. trapezius profundus (Fig. 2)

ORIGIN: From the post-orbital ridge medial to the trapezius superficialis.

INSERTION: On the last epibranchial.

COMMENTS: This muscle is fused anteriorly to the trapezius superficialis. Fibers pass underneath the pectoral girdle to insert on the posterior dorsal part of the branchium. Edgeworth has named this the cucullaris profundus.

II. MYOTOMIC MUSCULATURE innervated by spinal nerves (I, II)

M. coracomandibularis (Fig. 4,5)

ORIGIN: On the anterior edge of the ventral-most portion of the pectoral girdle.

INSERTION: On the posterior edge of the posteroventral edge of Meckel's cartilage.

COMMENTS: This muscle was named the geniocoracoid by Edgeworth (1935). According to Shann (1919) it is homologous to the geniocoracoid of Dipnoi and the coracomandibularis of Selachii, a mesio-ventral derivative. From a v-shaped septum, described by Shann, fibers extend dorsally into the body splitting just before inserting on the anterior edge (the glenoid border) of the pectoral girdle dorsal to the pectoral fin. According to Edgeworth, Vetter calls this posterior portion of the coracomandibularis the posterior part of the coraco-hyoideus.

M. coracobranchialis (Fig. 3,5)

ORIGIN: From the anterior edge of the ventral one-third of the pectoral girdle.

INSERTION: On the posterior edge of the ceratobranchial cartilages and at the junction between the adjacent ceratobranchials of arches four and five.

COMMENTS: This muscle is a large, flat, sheet-like muscle mass that makes up most of the postero-lateral border of the branchium. Homologous to the coracobranchialis of selachians (Shann, 1919).

Mm. adductores arcuum branchialium (4) (Fig. 3)

ORIGIN: On the medial face of the epibranchials.

INSERTION: On the posterior edge of the ceratobranchials.

COMMENTS: Edgeworth (1935) calls these muscles the constrictors branchiales.

M. coracohyoideus (not illustrated)

ORIGIN: On the posterior edge of the basihyal.

INSERTION: On the anterior edge of the pectoral girdle dorsal to the glenoid surface. Fibers attach to the v-shaped septum of the coracomandibularis.

COMMENTS: This muscle runs partially underneath the coracomandibularis and forms a furrow into which the deepest portion of the coracomandibularis runs. Along with the coracomandibularis this muscle is homologous to the coraco-arcualis communis of Selachii (Shann, 1919). Edgeworth calls this muscle the rectus cervicus.

M. retractor dorsalis pectoralis (Fig. 3)

ORIGIN: From the lateral epaxial muscle above the lateral line.

INSERTION: On the posterior edge of the scapular process of the pectoral girdle.

COMMENTS: According to Shann (1919) this muscle comprises part of the mesio-dorsal and all of the latero-dorsal portion of posterior muscles. This muscle would then correspond to the retractor mesio-dorsalis pectoralis and retractor latero-dorsalis pectoralis in selachians.

M. retractor latero-ventralis pectoralis externus (Fig. 2)

ORIGIN: The latero-ventral muscle mass.

INSERTION: On the lateral surface of the pectoral girdle ventral to the retractor dorsalis pectoralis.

COMMENTS: Originates from the latero-ventral portion of lateral muscle. Homologous to the retactor latero-ventralis pectoralis of selachians (Shann,

1919). This muscle exists as a two part muscle in Holocephali, it is also homologous to the serratus in Dipnoi (Shann 1919).

M. retractor latero-ventralis pectoralis internus (not illustrated)

ORIGIN: The latero-ventral muscle mass.

INSERTION: On the medial surface of the pectoral girdle deep to the externus.

COMMENTS: This muscle is fused to the retractor latero-ventralis pectoralis externus.

M. retractor mesio-ventralis pectoralis superior (Fig. 2)

ORIGIN: Fascia immediately below the lateral line extending posteriorly and gradually fusing to the lateral muscle mass.

INSERTION: Posterior edge of the pectoral girdle, ventral to the retractor latero-ventralis pecotralis externus.

COMMENTS: Shann also describes retractors mesio-ventralis pectoralis medius and inferior. These are shown, but not described, in this paper. They are homologous to the same muscles in Selachii and the three are homologous to the latissimus dorsi pectoralis in dipnoans (Shann 1919).

M. protractor dorsalis pectoralis lateralis (Fig. 3)

ORIGIN: On the post orbital ridge deep to the trapezius profundus.

INSERTION: On the anterior edge of the scapular process.

COMMENTS: According to Shann (1919), this muscle arises from the latero-dorsal portion.

M. protractor dorsalis pectoralis medialis (Fig. 3)

ORIGIN: From the post orbital ridge slightly medial to the origin of the

protractor dorsalis pecoralis lateralis and extending further dorsally.

INSERTION: On the medial face of the scapular process.

COMMENTS: This muscle has not previously been described as having lateral and medial parts; however, the origin does obviously differ and the difference in the insertions is indicative of a division in this muscle mass.

M. adductor superficialis (Fig. 1)

ORIGIN: From the posterior border of the scapula and from fascia of the retractor latero-ventralis pectoralis at the lateral line.

INSERTION: On the propterygial radial of the pectoral fin.

COMMENTS: This muscle is described by Shann (1919, pp.554) and acts to raise the pectoral fin.

M. abductor superficialis (Fig. 4)

ORIGIN: On the anterior edge of the ventral region of the pectoral girdle.

INSERTION: On the propterygium and the propterygial radial with deep fibers inserting on the metapterygium.

COMMENTS: Described by Shann (1919, pp. 555) and acts to lower the pectoral fin.

M. latero-ventralis

ORIGIN: Lateral muscle of the body wall.

INSERTION: By tendon at the bifurcation of the post-orbital ridge.

COMMENTS: Appears as a thick columnar muscle mass that runs anterior to posterior and makes up much of the lateral body wall. This muscle is shown, but not described, by Stahl (1967).

DISCUSSION

There is much disagreement today as to the systematic relationships of Holocephali. Romer (1946) states that although there seem to be many characters that are shared by the Holocephali and the fossil ptyctodonts, he supports the hypothesis linking chimaeras to the fossil group Bradyodonti, or "pavement-toothed sharks," based on their shared characteristic dentition. Bradyodonts and chimaeras possess a plate-like dental apparatus and slow tooth succession, apparently an adaptation for eating molluscs. Of course, the apparent similarity of this shared characteristic dentition could be due to convergence. Alternatively, Westoll (1962) refers to work done by Orvig which strengthens the case for ptyctodont ancestry based on skull morphology. Stahl (1967) indicates that the most attractive hypothesis favors a ptyctodont ancestor, yet stresses that this relationship is still unproven. Stahl also refers to an attempt (anonymous) to relate Holocephali to Dipnoi based on the shared characteristics of an autostylic jaw (one in which the hyoid does not support the jaw) and an operculum; however, work done by DeBeer and Moy-Thomas (1935) indicates that the autostyly exhibited in Holocephali differs from other forms of autostyly and, based on cartilaginous fusion of the jaw to the braincase and a non-suspensorial hyoid arch, should more correctly be termed "holostyly." Because there is no concensus of opinion, most scientists today support a relationship between sharks and ratfish based on the shared cartilaginous skeleton and the peculiar copulatory organs.

A typical branchial arch should exhibit a levator muscle, a dorsal constrictor muscle, and a ventral constrictor muscle. For the first modified arch, or jaw arch, of the ratfish, the levator may be absent. Alternatively, the levator may be represented by the levators anguli oris anterior and posterior,

along with the levator cartilaginous prelabialis. If these three muscles are not a modified levator, then they must be part of the adductor mandibulae that has broken away from the main muscle mass. The first dorsal constrictor is almost certainly represented in the ratfish by the adductor mandibulae anterior and posterior. The anterior adductor is unusual in that it has two bellies. The ventral constrictor should be a ventral muscle with transverse fibers. In the ratfish there do not appear to be any ventral muscles associated with the jaw that run in a transverse direction with the possible exception of the labialis posterior. This muscle may be the sole remnant in the ratfish of the ventral constrictor.

For the second modified arch, the hyoid arch, the dorsal and ventral constrictors of the ratfish are named as such. The dorsoventral direction of the fibers, as well as innervation by the seventh cranial nerve, are evidence in favor of this assumption. Because of its position and apparent function, the modified levator is most likely the hyoideus superior. It runs from the posterior chondrocranium to the dorsal elements of the hyoid arch and apparently functions to levate, or lift, the arch.

The five arches posterior to the hyoid arch do not appear to have a dorsal or ventral constrictor. The two parts of the trapezius almost certainly represent one or more fused levators for the arches.

These interpretation of homology are based on the observation that in the holocephalian as compared to the selachian condition, the muscles of the jaw arch are shifted anteriorly. If the mandibular adductor has shifted anterior to the orbit in ratfish, the levators may have shifted from a posterior position also. They could have gone from originating on the otic capsule and inserting on the dorsal palatoquadrate cartilage to a position originating from parts of the chondrocranium anterior to the orbit and inserting on the cartilage that would be homologous to the palatoquadrate of other fishes. If this is true, then the

labial cartilages (the maxillary and prelabial cartilages) may be homologous to the palatoquadrate cartilage of the jaw of an hyostylic or an amphistylic ancestor. This would seem to indicate that the condition of autostyly in Holocephali arose independently of autostyly in Osteichthyian fish. In Holocephali, the lower jaw would have attached directly to the braincase, with the exclusion of elements of the palatoquadrate cartilage as separate labial cartilages instead of becoming incorporated into the chondrocranium as the jaw became autostylic. This would support the hypothesis that based on the type of autostyly exhibited, Holocephali are not related to Dipnoi or any other bony fish groups.

Alternatively, the levators anguli oris anterior and posterior and the levator cartilaginous prelabialis are not the levators of the first modified arch. Instead, they represent muscles that have broken off of the adductor mandibulae and become associated with the labial cartilages. Therefore, the homology between the labial cartilages and the palatoquadrate cartilage would be an incorrect assumption. However, the anterior shift of the mandibular adductors would still argue against a close relationship between Osteichthyes and Holocephali. Bemis and Lauder (1986) described and illustrated the jaw and branchial apparatus and the superficial musculature of the lungfish Lepidosiren paradoxa (Dipnoi). The adductor mandibulae is posterior to the orbit, and the morphology is more similar to the generalized tetrapod morphology than to the morphology of holocephalians, as would be expected. There is a large, two-part adductor mandibulae that inserts by a single tendon, two lip retractors, and a large, well-developed intermandibularis muscle. As discussed above, ratfishes either lack the intermandibularis, or have reduced it to the small labialis posterior muscle. The three bellies of the two-part ratfish adductor are very differently arranged than the two parts of the single adductor of dipnoians. Finally, the dipnoian lip retractors, though superficially similar to the

levators anguli oris of ratfishes, do not insert or originate in the same fashion. In sum, there is no compelling evidence of a close relationship between dipnoi and holocephalians and the difference in jaw suspension argues against such a relationship.

Romer's (1946) hypothesis of a close relationship between pavement-toothed sharks (Bradyodonti) and ratfishes is a tenuous one. It is based entirely on the similarities of ratfish teeth to isolated bradyodont teeth from the Carboniferous and Permian; very few conplete specimens of bradyodonts are known and those few are badly fossilized. It is impossible to ascertain from the few badly preserved specimens of bradyodonts (illustrated in Romer, 1966) whether there has been an anterior shift of the jaw musculature similar to that of the ratfishes. Certainly none of the ratfish adaptations examined in this study are evident in the modern sharks. Bradyodonts may be ratfish ancestors, or both bradyodonts and ratfishes may be descended from ptyctodonts, but given the nature of evidence available, both hypotheses must be regarded as being only weakly supported at best.

In the ratfish an extensive amount of cartilage anterior to the orbit functions as a point of origin for the forward-shifted adductor mandibulae. This interesting feature seems to be unique to the ratfish among living fish. It appears to be present in reconstructions of fossil ptyctodonts (see Fig. 7), further suggesting a possible relationship between the two groups. Ptyctodonts were a line of placoderms that were in the process of losing the dermal outer layer of the skull (see Fig. 7) while retaining the inner chondrocranium. It is interesting that the shape of the ptyctodont chondrocranium is similar to that of the ratfish chondrocranium (compare Figs. 3 and 7). There is relatively little cartilage posterior to the orbit in either group, there is a considerable extent of cartilage anterior to the orbit, and the overall shape of the jaws and teeth

are similar. I suggest that it would only be necessary to continue the already evident trend of loss of dermal elements to go from a ptyctodont ancestor to a ratfish descendant. Ptyctodonts would seem to share with ratfishes the derived character of the forward shift of the jaw muscles to a position anterior to the orbit. This character, unknown among other living fishes, may be unique to ratfishes and ptyctodonts. It is impossible to determine whether there are small cartilages present lateral to the jaw of ptyctodonts as in ratfish. Romer (1966) has drawn what appears to be a palatoquadrate cartilage in his reconstruction of a ptyctodont (see Fig. 7). It would be useful to examine the real fossil to see if the palatoquadrate showed any evidence of being excluded from the jaw joint.

In summary, there are two lines of evidence that support a relationship between ptyctodonts and ratfish. The first would be the anterior expansion of the chondrocranium, presumably to support the origin of the adductor mandibulae. The second would be the remarkable similarity in the morphology of the jaw indicating the possible fusion of the lower jaw directly to the chondrocranium with the exclusion of the upper jaw elements. If my hypothesis is correct, it would represent a unique type of autostyly shared by these two groups. The two characters seem to show that there is not a close relationship between sharks and ratfishes or between dipnoian lungfishes and ratfishes.

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APPENDIX i
From Hildebrand, M. 1982. PP. 38-39.

Kingdom Animalia

Phylum Chordata- notochord, presence of gill slits at some time in development, dorsal, hollow nerve cord

Subphylum Vertebrata- articulated vertebrae, cephalization

Class Agnatha- jawless fish

*Class Placodermi- dermal head shield

Class Chondrichthyes- cartilaginous fish

Subclass Elasmobranchii- sharks, skates, and rays

Subclass Holocephali- chimaeras

*Class Acanthodii- spiny fish

Class Osteichthyes- bony fish

Subclass Actinopterygii- ray-finned fishes

Superorder Chondrostei- sturgeon

Superorder Holostei- bowfin, gar pike

Superorder Teleosti- most modern bony fish

Subclass Sarcopterygii- lobe-finned fishes

Superorder Crossopterygii- group that gave rise to amphibian line

Superorder Dipnoi- lungfishes

*=extinct

APPENDIX ii
From Romer, S. and T. Parsons, 1986. pp. 619-622.

Kingdom Animalia

Phylum Chordata

Subphylum Vertebrata

Class Agnatha

Class Elasmobranchiomorphi- cartilaginous fish and certain primitive and bony relatives

Subclass Placodermi- jawed fish with bony armor

Subclass Chondrichthyes- cartilaginous fish

Infraclass Elasmobranchi- sharks, skates, and rays; hyostylic jaw gill slits, teeth rapidly replaced

Order Selachii- sharks

Infraclass Bradyodonti- chimaeras and related forms; operculum, teeth replaced slowly

Superorder Paraselachii- extinct, poorly known; jaw attachment varies

Superorder Holocephali- autostylic jaw, tooth plates

Order Chimaeriformes- ratfish

Class Osteichthyes- bony fish

Subclass Acanthodii- extinct, "spiny sharks"

Subclass Actinopterygii- ray-finned fish

Superorder Chondrostei

Superorder Teleosti

Superorder Holostei

Subclass Sarcopterygii- fleshy-finned fish

Order Crossopterygii- hyostylic jaw

Suborder Rhipidistia- ancestral to tetrapods

Suborder Coelacanthiformes- aberrant marine forms

Order Dipnoi- lungfish; autostylic jaw, tooth plates

Appendix iii

MUSCLE NAMES-SYNONYMS (adapted from Edgeworth. 1935. p. 255)

labialis anterior	Csd_1 (Vetter)
	labialis (Edgeworth)
labialis posterior	intermandibularis anterior (Edgeworth)
adductor mandibulae ant.	levator mandibulae ant. (Edgeworth)
	preorbitalis (Luther)
	levator labii superior (Vetter)
adductor mandibulae post.	adductor mandibulae (Luther)
	levator manidibulae post. (Edgeworth)
levator cart. prelabialis	sic Luther
levator anguli oris ant.	sic Luther
	levator anguli oris i (Vetter)
levator anguli oris post.	sic Luther
	levator anguli oris ii (Vetter)
constrictor ventralis	constrictor hyoideus (Edgeworth)
	Cs_{1-6} (Vetter)
constrictor dorsalis	constrictor hyoideus (Edgeworth)
	Cs_{1-6} (Vetter)
hyoideus superior	levator hyomandibulae (Edgeworth)
hyoideus inferior	interhyoideus (Edgeworth)
trapezius superficialis	cucullaris superficialis (Edgeworth)
	trapezius externus (Stahl)
	levator pectoralis (Shann)
trapezius profundus	cucullaris profundus (Edgeworth)
coracomandibularis	geniocoracoid (Edgeworth)
coracobranchialis	sic Vetter
	coracobranchialis (Shann)
coracohyoideus	rectus cervicus (Edgeworth)
	coracohyoideus (Shann)
adductors arcuum branch.	sic Vetter

Fig. 1

Right lateral view of head and shoulder region showing superficial muscles.

scale: bar=1 cm

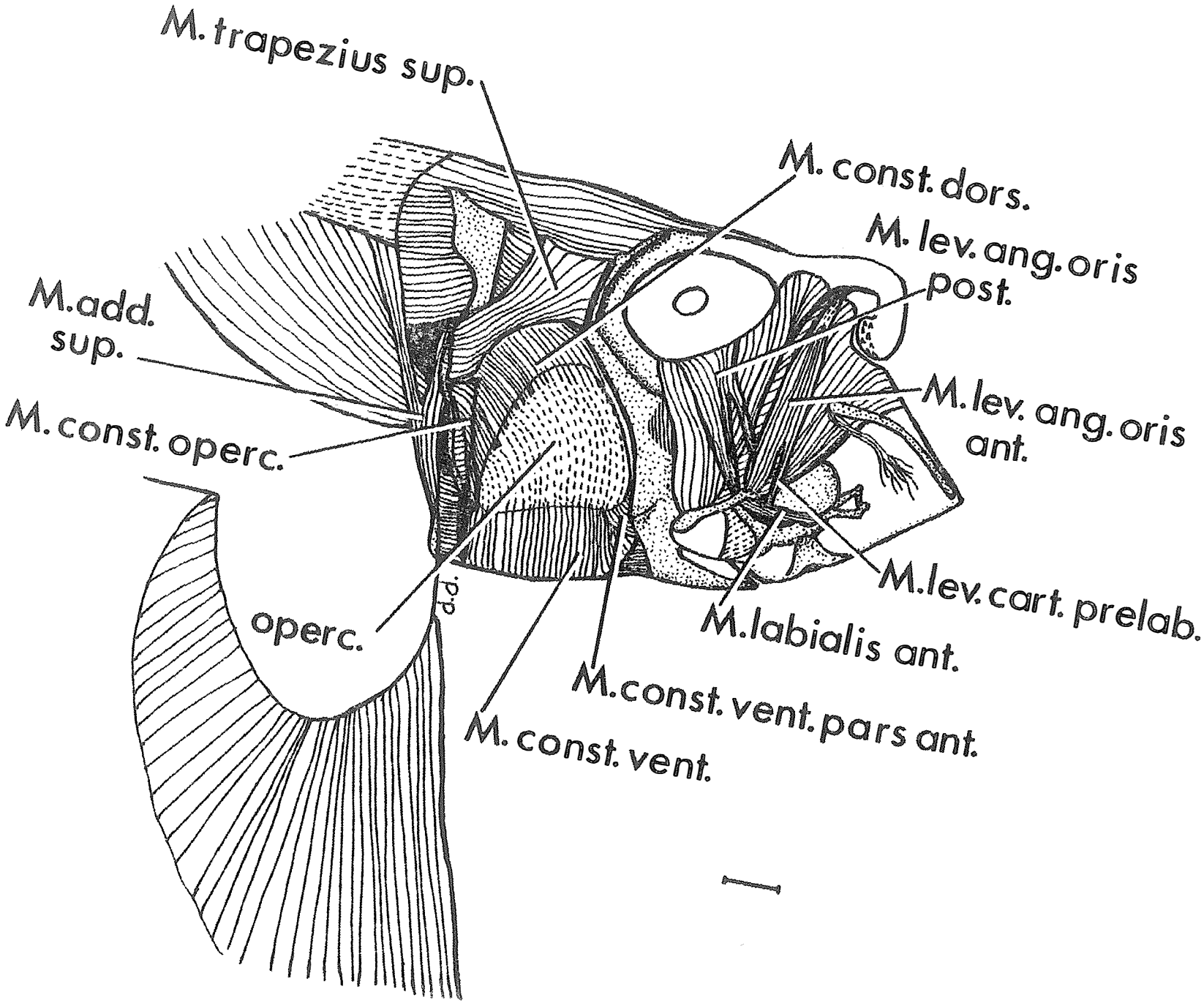

M. trapezius sup.
M. const. dors.
M. lev. ang. oris post.
M. add. sup.
M. const. operc.
M. lev. ang. oris ant.
operc.
d.d.
M. lev. cart. prelab.
M. labialis ant.
M. const. vent. pars ant.
M. const. vent.

Fig. 2

Right lateral view of head and shoulder region with superficial muscles and operculum removed.

scale: bar=1 cm

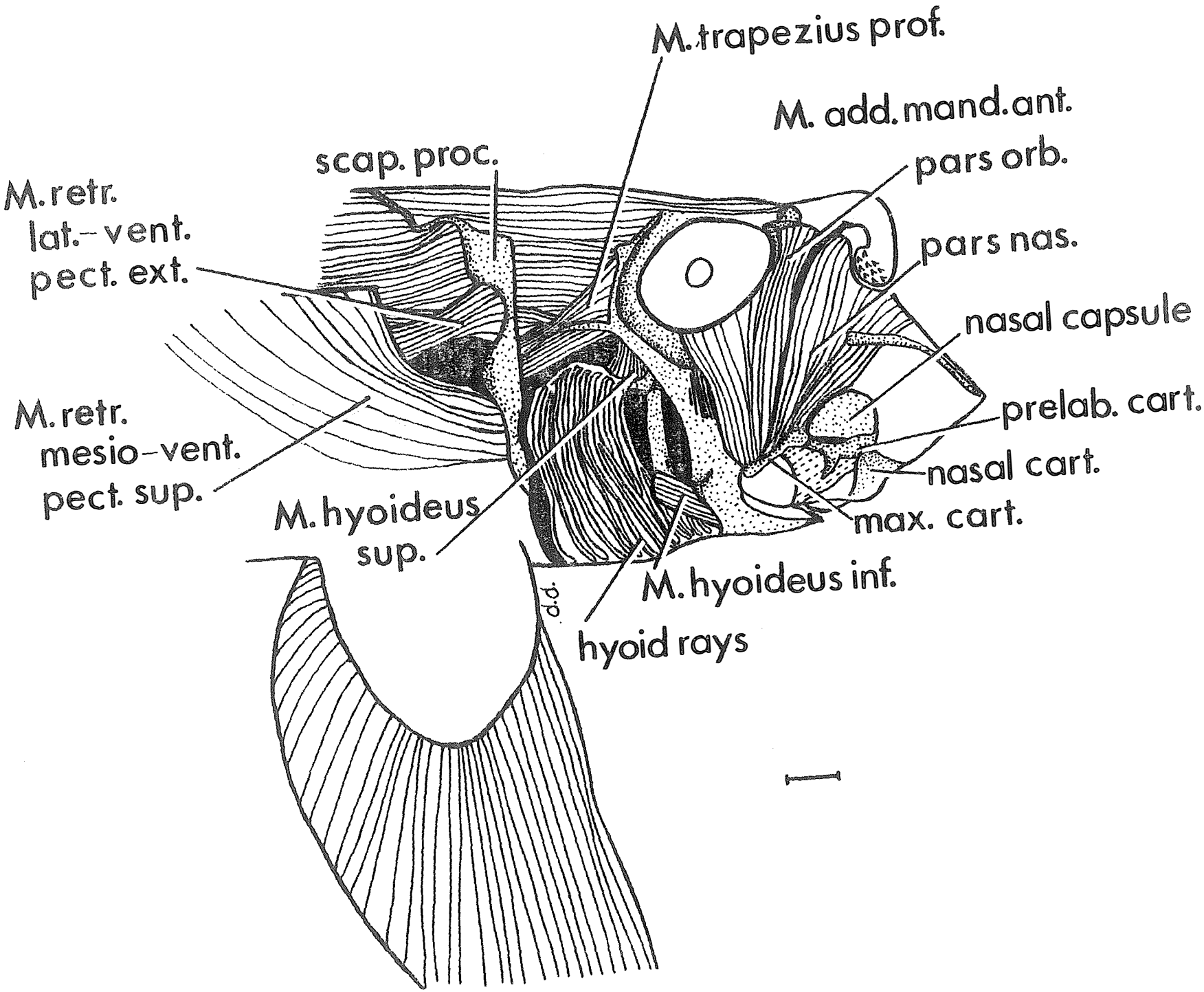

M. trapezius prof.
M. add. mand. ant.
pars orb.
pars nas.
nasal capsule
prelab. cart.
nasal cart.
max. cart.
scap. proc.
M. retr.
lat.-vent.
pect. ext.
M. retr.
mesio-vent.
pect. sup.
M. hyoideus
sup.
M. hyoideus inf.
hyoid rays
d.d.

Fig. 3

Right lateral view of head and shoulder region with deep muscles exposed.

scale: bar=1 cm

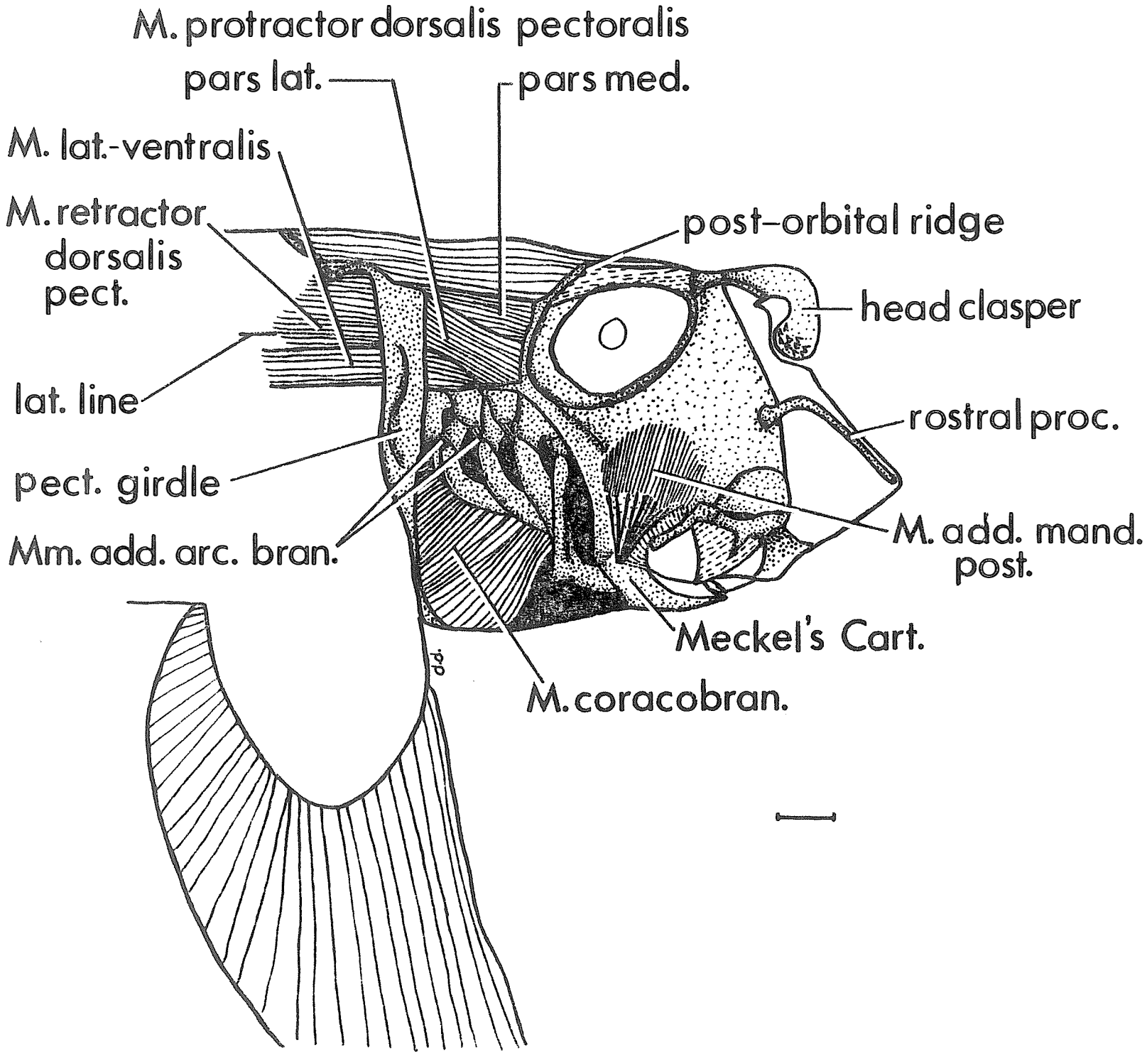

M. protractor dorsalis pectoralis
pars lat.
pars med.
M. lat.-ventralis
M. retractor dorsalis pect.
post-orbital ridge
head clasper
lat. line
rostral proc.
pect. girdle
Mm. add. arc. bran.
M. add. mand. post.
Meckel's Cart.
M. coracobran.
pp

Fig. 4

Ventral view of head, branchium, and pectoral region showing superficial musculature.

scale: bar=1 cm

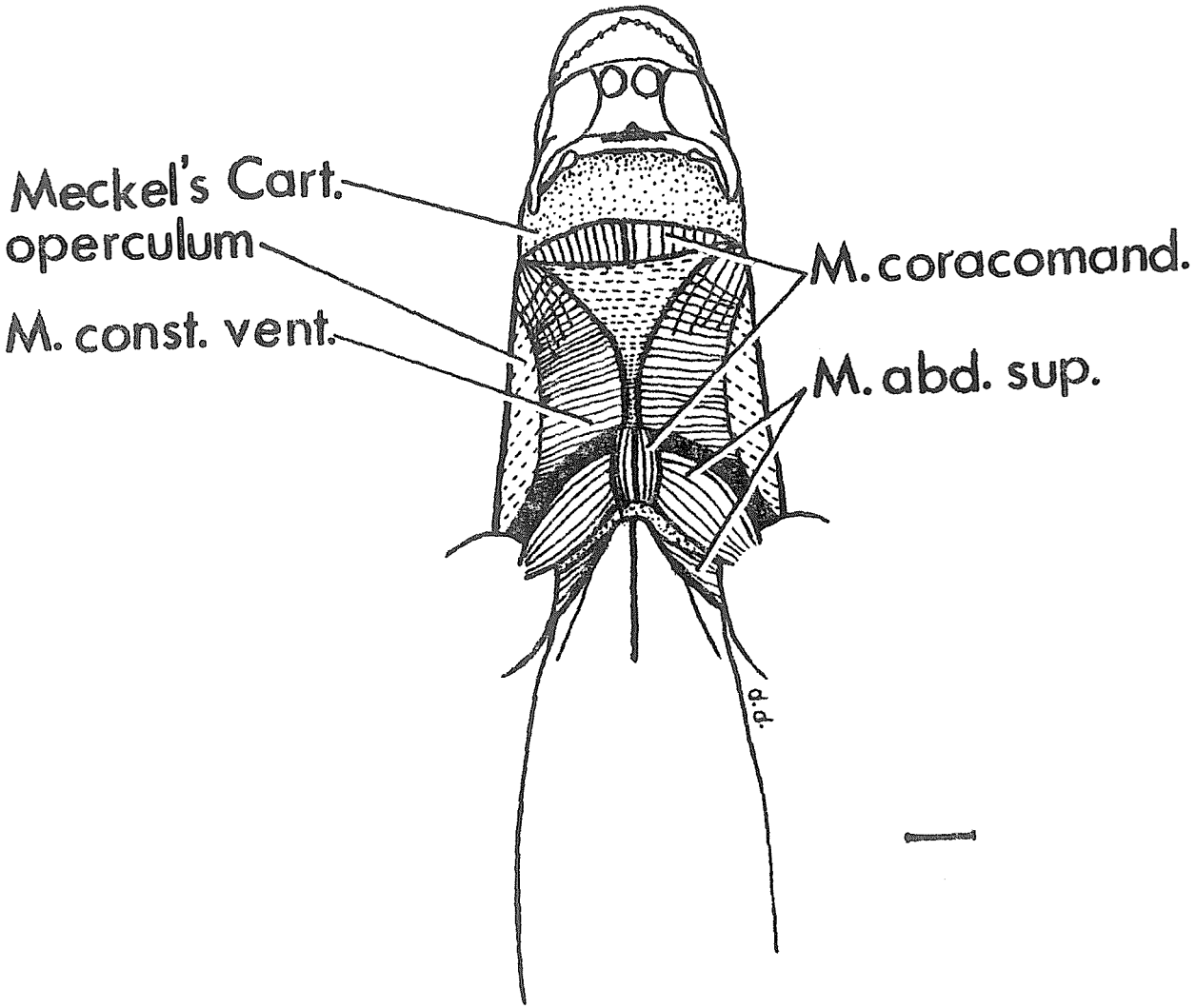

Meckel's Cart.
operculum
M. const. vent.
M. coracomand.
M. abd. sup.
d.p.

Fig. 5

Ventral view of head, branchium, and pectoral girdle with superficial muscles removed.

scale: bar=1 cm

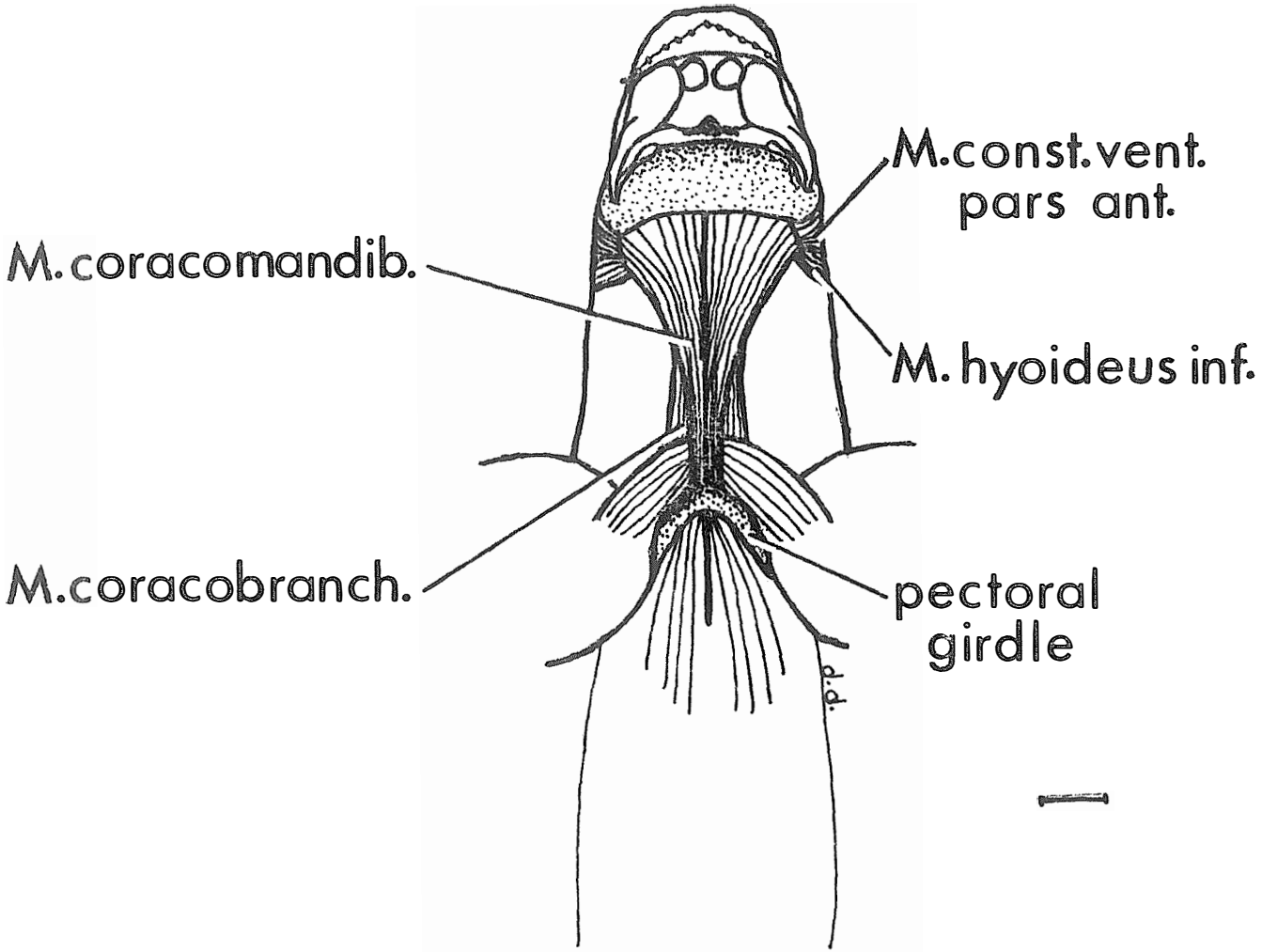

M.const.vent.
pars ant.
M.coracomandib.
M. hyoideus inf.
M.coracobranch.
pectoral
girdle
p.p.

Fig. 6

Right lateral view of head showing nerves as they exit the brain.

scale: bar=1 cm

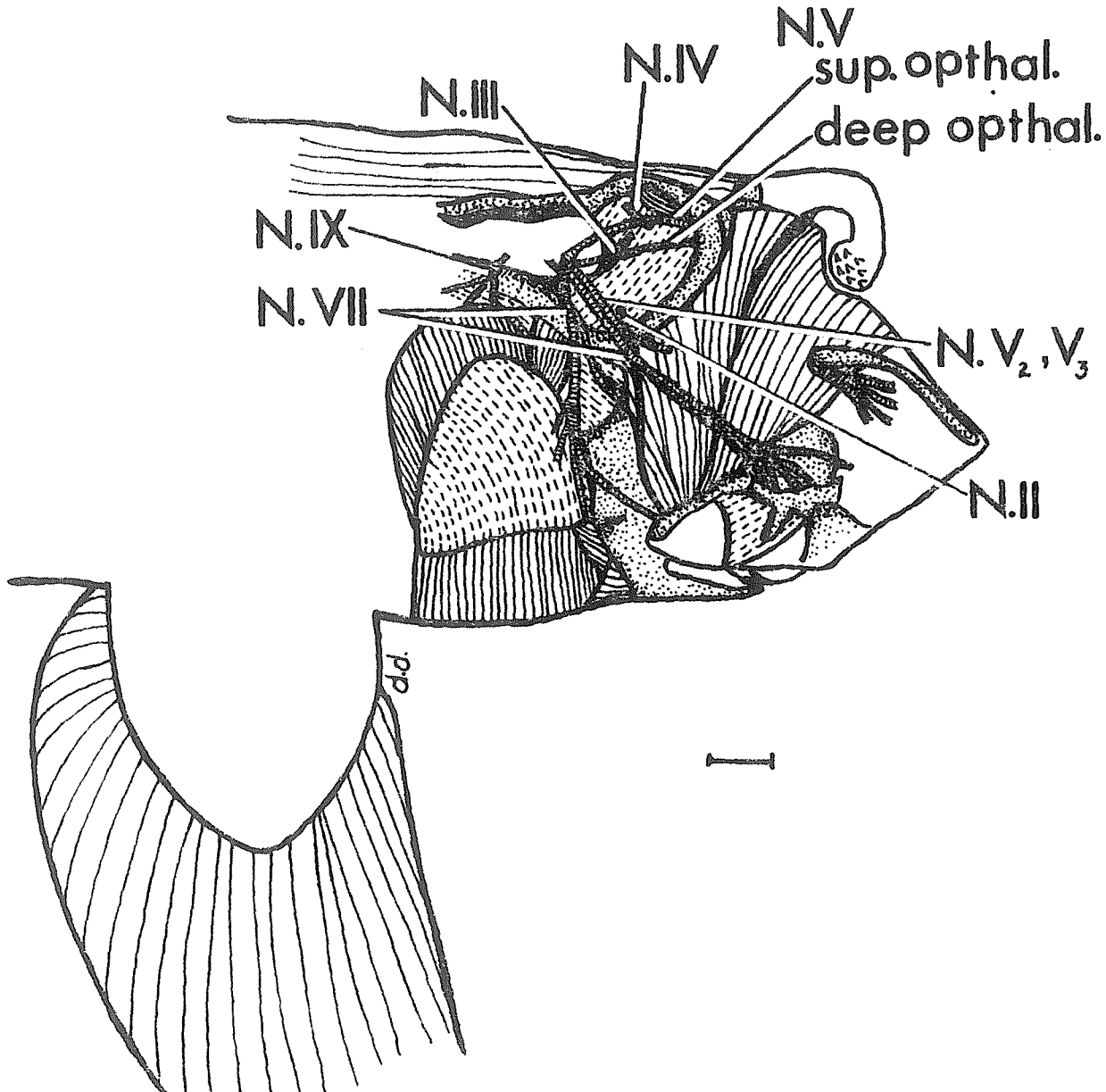
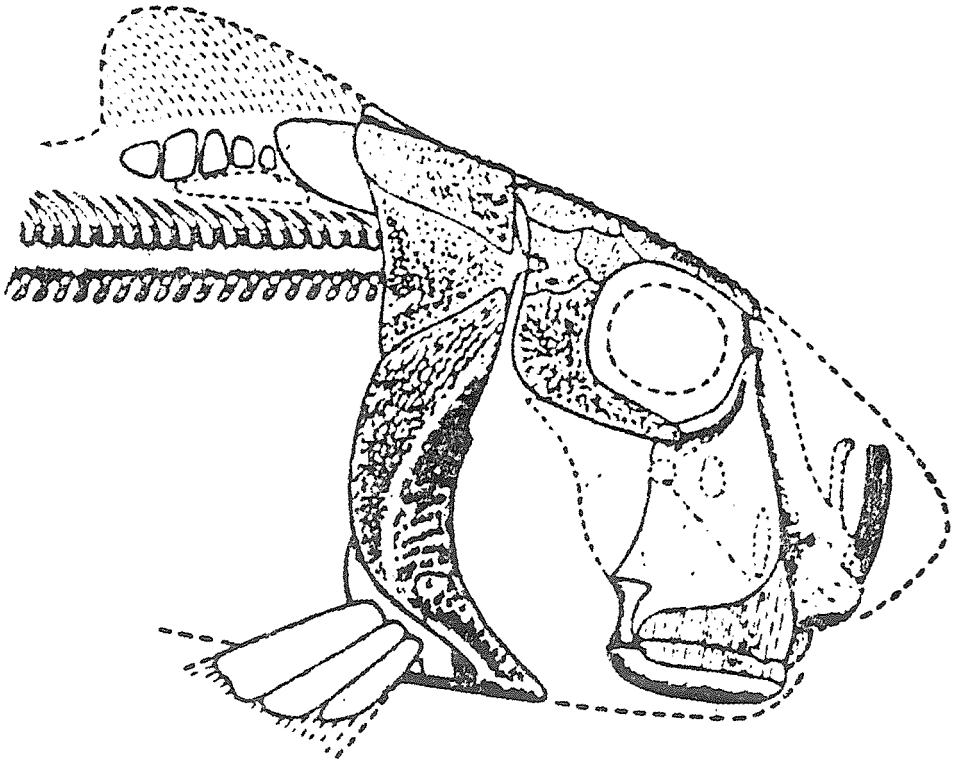

N.III
N.IV
N.V
sup. opthal.
deep opthal.
N.IX
N.VII
N. V_2, V_3
N.II
d.d.

Fig. 7

Restoration of a fossil ptyctodont. Taken from: Romer, A. S. 1966. Vertebrate Paleontology 3rd ed., University of Chicago Press, pg. 30.