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# Form and function of the feeding apparatus of Amphiuma tridactylum.

Susan E. Erdman

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# FORM AND FUNCTION OF THE FEEDING APPARATUS OF AMPHIUMA TRIDACTYLUM

by

Susan E. Erdman

A Thesis
Presented to the Graduate Committee
of Lehigh University
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Master of Science

in
Biology
Lehigh University
1983

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May 13, 1983
(date)

Professor in Charge

Accepted May 13, 1983
(date)

Committee directing the Master's
work of Susan E. Erdman

(Chairman)

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# FORM AND FUNCTION OF THE FEEDING APPARATUS OF AMPHIUMA TRIDACTYLUM

by

Susan E. Erdman

## ABSTRACT

Detailed anatomical descriptions of the form of the cranial bones, muscles, and connective tissues provide precise origins and insertions of the cephalic musculature in *A. tridactylum*. Cinegraphic and high speed videographic analysis investigating potential displacements of the jaws and hyoid apparatus demonstrate that *A. tridactylum* utilizes two distinct types of suction feeding. During stationary capture, which is elicited by small or inactive prey, the head of the salamander does not advance and buccal expansion is delayed until mouth closure. Whereas the strike, seen in capture of large active prey, involves a rapid lunge toward the prey and synchronous buccal expansion and mouth opening. Differences between these types of feeding may be attributable to differences in timing of contraction of the rectus cervicis. Delayed buccal expansion may be due to asynchronous contraction of the rectus cervicis and depressor mandibulae, whereas the strike may involve synchronous contraction of the rectus cervicis and mandibular depressors. Similar patterns of synchronous and asynchronous muscle activity associated with high and low velocity suctions during prey capture are seen in some cichlid fishes.

# INTRODUCTION

Previous accounts of feeding in aquatic salamanders indicate that prey is captured by a "Saugschnappen" or "gape and suck" mechanism (Drüner, '01; Matthes, '34; Özeti and Wake, '69). During prey capture, the salamander reportedly remains stationary while the prey and surrounding water are sucked into the buccal cavity. This mechanism is dependent on expansion of the buccal cavity by movements of a relatively rigid but mobile hyoid apparatus (Özeti and Wake, '69). In most aquatic salamanders, the mouth is relatively small and, during prey capture, the size of the mouth opening may be further reduced by labial folds that partially occlude the mouth opening (Matthes, '34). Although the precise mechanism of capture was not examined in these studies, it was assumed to resemble that utilized by other suction feeding vertebrates, and to involve simultaneous excursions of the hyoid and mandible (Özeti and Wake, '69).

Examination of the suction feeding mechanism in aquatic salamanders poses a number of problems. First, because most aquatic salamanders are very small, the study of the feeding mechanism is technically difficult. Second, there is an extraordinary diversity of structure both in general body form and in specific features of cephalic and branchial anatomy, and it does not appear that a single species will adequately represent the potential range of suction feeding mechanisms in aquatic salamanders. *Amphiuma tridactylum* was chosen for study because 1) initial observations indicated that it displays most features of suction feeding described for other salamanders (Matthes, '34; Özeti and Wake, '69), and 2) it is large and easy to work with, offering potential for a variety of studies of its feeding mechanics.

Amphiuma, unlike most other aquatic salamanders, has a relatively narrow head (Hay, 1890; Davison, 1895; Baker, '45), an elongated mouth opening that extends midway between the snout and spiracle (Bishop, '43), and a pair of spiracles instead of gill slits (Bruner, '14; Regal, '66; Guimond and Hutchison, '76). Features of cranial anatomy pertinent to feeding in Amphiuma have been examined by a number of previous workers. Hay (1890) and Kingsley (1898) described the embryonic skull, whereas Wiedersheim (1877), Davison (1895) and Hilton ('47) illustrated and briefly described the adult skull and branchial apparatus. Development and homologies of the cranial musculature of Amphiuma have been considered by Edgeworth ('20,'35). Detailed accounts of the trigeminal (Luther, '14) and laryngeal (Druner, '04) musculature have not been supported by similarly detailed accounts of the remaining cephalic muscles for which only brief and incomplete descriptions are available (Davison, 1895; Hilton, '59). None of the myological treatments of Amphiuma describe the precise form or position of muscle attachment points. This study re-examines the cephalic bones and associated muscles and connective tissues in Amphiuma from the point of view of their functional interrelationships during feeding. In particular, it describes the temporal relationships of skeletal displacements and suggests mechanisms by which the various cephalic muscles could produce such displacements. Finally, it examines functional similarities between Amphiuma and other aquatic, suction-feeding vertebrates.

# METHODS AND MATERIALS

The cephalic muscles, bones and associated connective tissues were examined by dissection of eight preserved specimens (Lehigh Univ. 1271-76; two specimens accidentally destroyed) of *Amphiuma tridactylum* obtained from a commercial supplier. One of these specimens (LU 1273) had been preserved with the buccal cavity expanded to permit more detailed examination of the hyoid relationships. Additional information on skeletal relationships was obtained from a series of dried skulls of both *A. tridactylum* (CM 6264; LSUMZ 10494; FMNH 31040) and *A. means* (MCZ 939, 85166; FMNH 196098, 196143). Fiber arrangement in some of the more complex muscles was determined by nitric acid maceration (Gans and Gorniak, '82). Illustrations of the skull, hyoid, and associated muscles were made by coordinate transposition using an ocular grid micrometer in a stereo dissecting microscope.

Feeding behavior was examined in three live specimens of *A. tridactylum* (68-72 cm snout-vent length) obtained from Waubun Laboratories, Schriever, Louisiana. These animals were maintained in 120 l aquaria and fed crayfish, worms, fish, and mice between filming sessions. Feeding was recorded on Super 8 ASA 160 film with a Canon 1014XLS camera at 24 or 36 fps with strobe illumination, or on videotape using a dual camera Instar Video system with dual strobe illumination at 120 fps. Thirty lateral, two anterior and ten ventral sequences were recorded at 24 fps. Five lateral sequences were filmed at 36 fps. Two lateral/anterior and eleven lateral/ventral sequences were filmed at 120 fps.

During filming of lateral or anterior sequences, the animal was fed in a small open-ended plexiglass chamber (15 x 7 x 7cm) immersed in the aquarium. Ventral views were filmed using a longer open-ended chamber (30 x 7 x 7cm) supported above a mirror placed at 45° to the horizontal base of the chamber. Food items were placed in the approximate middle of the filming chamber, some being loosely restrained by a thread that passed through a hole in the roof of the filming chamber. Film or video records were obtained of _A_. _tridactylum_ feeding on worms (8-15cm), small crayfish (1-3cm rostrum to telson length), large crayfish (3-6cm), and whole or dismembered dead mice. Preliminary examination of the major patterns of fluid flow were made by injecting India ink into the water immediately surrounding the prey. Six lateral sequences recorded using this technique permitted visualization of some fluid flow patterns during closure.

Films were analyzed frame by frame and displacements were determined by tracing the projected image on graph paper. Because protruding elements were generally visible as lighter areas on the skin and recessed regions generally produced shadows that were noticably darker than the surrounding areas, it was possible to determine the approximate positions of the various bones and muscles during feeding. To gain an estimate of the time course and extent of bone excursions, measurements were made of displacement velocities ignoring rate changes at the beginning and end of the capture sequence. In addition, inflow velocity was estimated by dividing the change in volume of the head per unit time by the area of the mouth opening (Osse, '69). Volumetric changes of the head were calculated by averaging the distance between the dorsal and ventral surfaces every 0.5 cm from the spiracle to the tip of the snout. This averaged distance was used as the diameter of a cylinder whose length was the distance between the spiracle and the snout. Resting volumes derived by this technique were compared with direct volumetric measurements of the head made by water displacement techniques. Some additional measurements and manipulations were performed on two live, anesthetized _A. tridactylum_. In particular, potential displacements of the hyoid apparatus were measured and the effects of particular displacements on surface topography noted for comparisons with the film and video records.

# RESULTS

## Anatomy

### Skull

Most features of the skull have been clearly described and illustrated in previous accounts. Therefore, the following descriptions emphasize those aspects of cranial osteology that serve as muscle attachment surfaces or that are otherwise pertinent to the feeding mechanism. The nomenclature used here is derived from Wiedersheim (1877) unless otherwise indicated.

The tip of the snout is supported by a single stout premaxilla with posteriorly directed processes that extend between the rostral prongs of the parasphenoid ventrally and between the anterior halves of the paired frontals dorsally. These processes firmly anchor the premaxilla to the braincase (Figs. 1 and 2). The 11 peglike teeth of the premaxilla slant caudally and overlap the anterior teeth of the mandible. The robust maxillae are directed posteriorly and slightly laterally. Each maxilla supports approximately 22 teeth and is attached to the braincase by complex amphiarthrodial joints with the prefrontal and the vomeropalatine (Figs. 1 and 2). Manipulations of anesthetized,

Figure 1. Dorsal view of the skull of *Amphiuma* with mandible and hyoid apparatus removed; pterygoid cartilage not shown. This and subsequent figures of the skull represent composite views incorporating features of a number of specimens. The skull features illustrated are similar in *A. means* and *A. tridactylum*. Abbreviations: CEF, cervical epaxial fossa; DLF, dorsal levator fossa; EX, exoccipital; FR, frontal; MX, maxilla; NA, nasal; PA, parietal; PFR, prefrontal; PMX, premaxilla; PRO, prootic; PT, pterygoid; QU, quadrate; SQ, squamosal; TC, temporal crest.

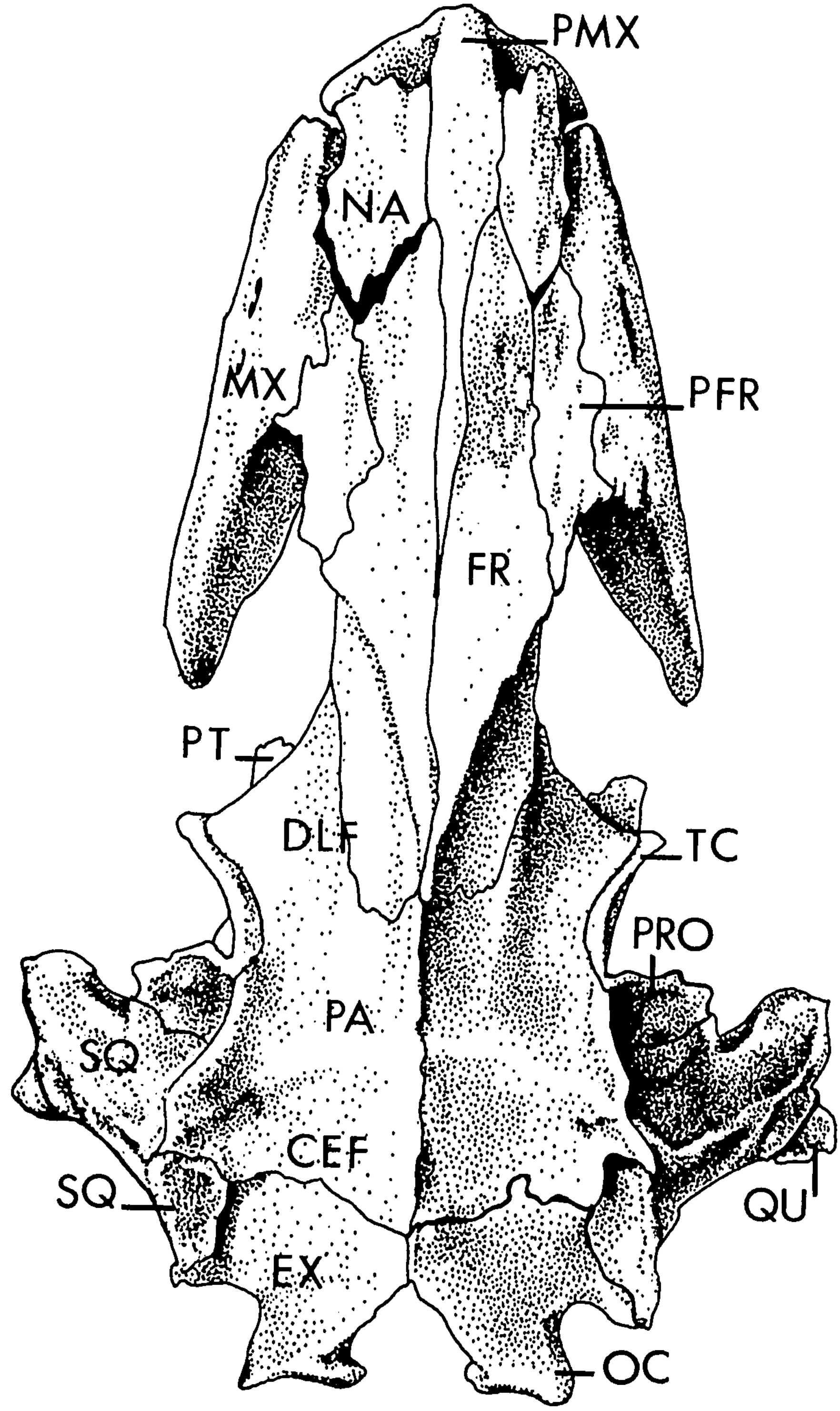
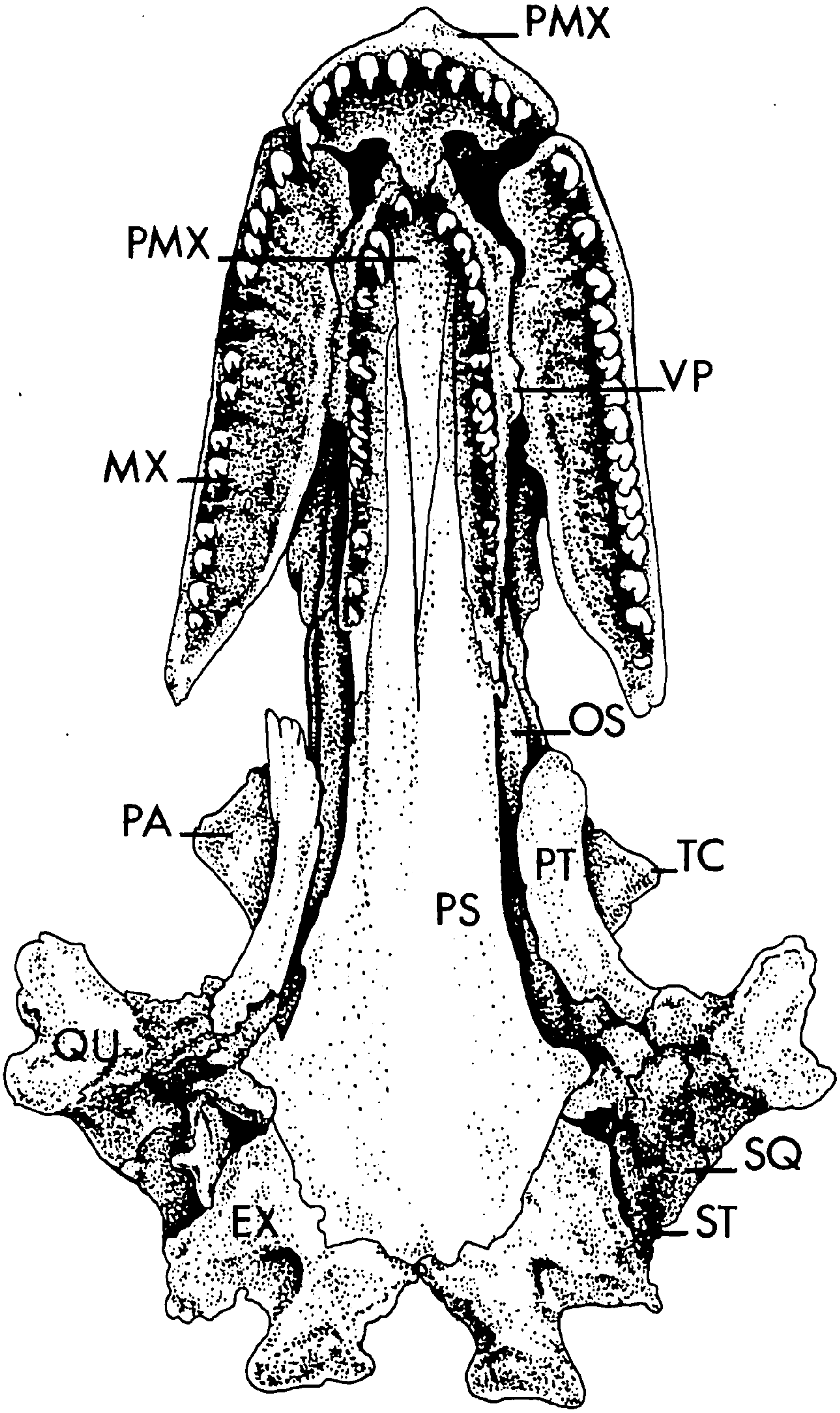

PMX
NA
MX
PFR
FR
PT
DLF
TC
PRO
SQ
PA
SQ
CEF
QU
EX
OC

Figure 2. Ventral view of the skull of Amphiuma with mandible and hyoid apparatus removed; pterygoid cartilage not shown. Abbreviations: EX, exoccipital; MX, maxilla; OC, occipital condyle; OS, orbitosphenoid; PA, parietal; PMX, premaxilla; PS, parasphenoid; PT, pterygoid; QU, quadrate; SQ, squamosal; ST, stapes; TC, temporal crest; VP, vomeropalatine.


PMX
PMX
VP
MX
OS
PA
TC
PT
PS
QU
SQ
EX
ST

freshly killed and preserved specimens all indicate that the resting position of the maxilla lies at its point of maximum dorsolateral displacement. The prefrontomaxillary joint therefore permits only slight ventromedial excursion of the maxilla. The maxilla slightly overlaps the vomeropalatine ventrally and has a fibrous attachment to the premaxilla and the nasal.

The palate is formed by the vomeropalatines and the parasphenoid. Two anterior prongs of the parasphenoid extend on either side of the ventral process of the premaxilla and attach laterally to the vomeropalatines. Each vomeropalatine supports 24 teeth that are arranged in a row parallel to the maxillary tooth row (Fig. 2). The vomeropalatine teeth are similar to but smaller than the maxillary teeth.

The frontals form the anterior roof of the braincase and the dorsomedial walls of the fossae (dorsal levator fossa) that contain the superficial anterior portion of the levator mandibulae muscle (Fig. 1). Anteriorly, the dorsolateral edge of the frontal is loosely attached to the nasal but tightly attached to the prefrontal. A prominent dorsolateral crest extends from the orbital region to the dorsal midline. The parietal forms the remainder of the elongate dorsal levator fossa. The fossa is separated from the region of the parietal devoted to the attachment of the cervical epaxial muscles (cervical epaxial fossa) by a transverse ridge. The parietal has a sagittal crest that is always more prominent anterior to the transverse crests. The dorsal levator fossa and cervical epaxial fossa are bounded laterally by a prominent temporal crest (temporal flange; Salthe, '73) formed by the prootic (Davison, 1895), squamosal, and parietal.

The posterior end of the braincase is formed by the paired

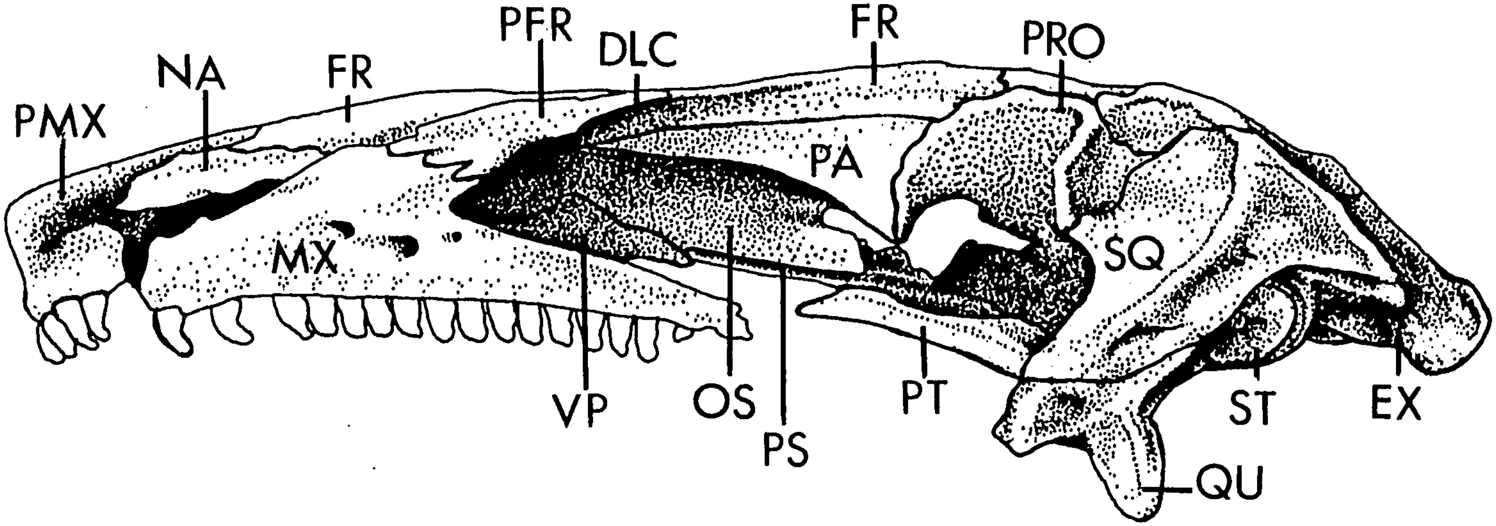
Figure 8: Dorsal muscles of _A_. _tridactylum_ showing superficial musculature on the left and deeper musculature on the right. Abbreviations: adm, anterior depressor mandibulae; dlma, deep levator mandibulae anterior; fcd, fascia cephalodorsalis; FR, frontal; ime, intermyoseptal epaxial muscle; lme, levator mandibulae externus; lr, levator retinaculum; sdm, superficial fibers of depressor mandibulae; slma, superficial levator mandibulae anterior; SQ, squamosal.

exoccipitals (Davison, 1895), each having a large, stalked condylar process lying lateral to the ventral half of the foramen magnum. The condylar surface lies in a transverse plane but curves anteriorly on the ventral aspect.

Extending ventrolaterally from the otic region of the braincase are paired squamosals marked by a prominent lateral crest. Each squamosal articulates with the parietal dorsolaterally and the prootic anteriorly. The prootic forms a large anterolaterally directed crest that separates fossae housing superficial and deep portions of the levator mandibulae externus (Fig. 3). The dorsal region of the squamosal behind the lateral crest overlies the foramen ovale and partially shields the stapedial footplate (stapes; Davison, 1895) from lateral view. The ventromedial surface of the squamosal is firmly sutured to the quadrate (Fig. 2). The quadrate terminates ventrally in a complex sellar joint surface. The joint surface is limited posteromedially by a prominent ridge that extends anterolaterally to a short prong that is convex in the transverse plane and concave in the sagittal plane. A stout anteromedial crest extends ventromedially on the quadrate and is loosely attached to sickle-shaped flexible pterygoids. Each pterygoid is surrounded by a cartilaginous plate that extends anteriorly toward the maxilla.

The two mandibles of the lower jaw are joined by a synarthrosis anteriorly (Fig. 4). The dentary forms the major component of the mandible and supports 22 teeth that are similar in form to the maxillary teeth (Fig. 5). All the teeth slant caudally, although the posterior dentary teeth are shorter and directed caudomedially. A fused angular-articular complex forms both the articulating surface of the mandible

Figure 3. Lateral view of the skull of Amphiuma with mandible and hyoid apparatus removed. Abbreviations: DLC, dorsolateral crest; EX, exoccipital; FR, frontal; MX, maxilla; NA, nasal; OS, orbitosphenoid; PA, parietal; PFR, prefrontal; PMX, premaxilla; PRO, prootic; PS, parasphenoid; PT, pterygoid; QU, quadrate; SQ, squamosal; ST, stapes; VP, vomeropalatine.


PMX
NA
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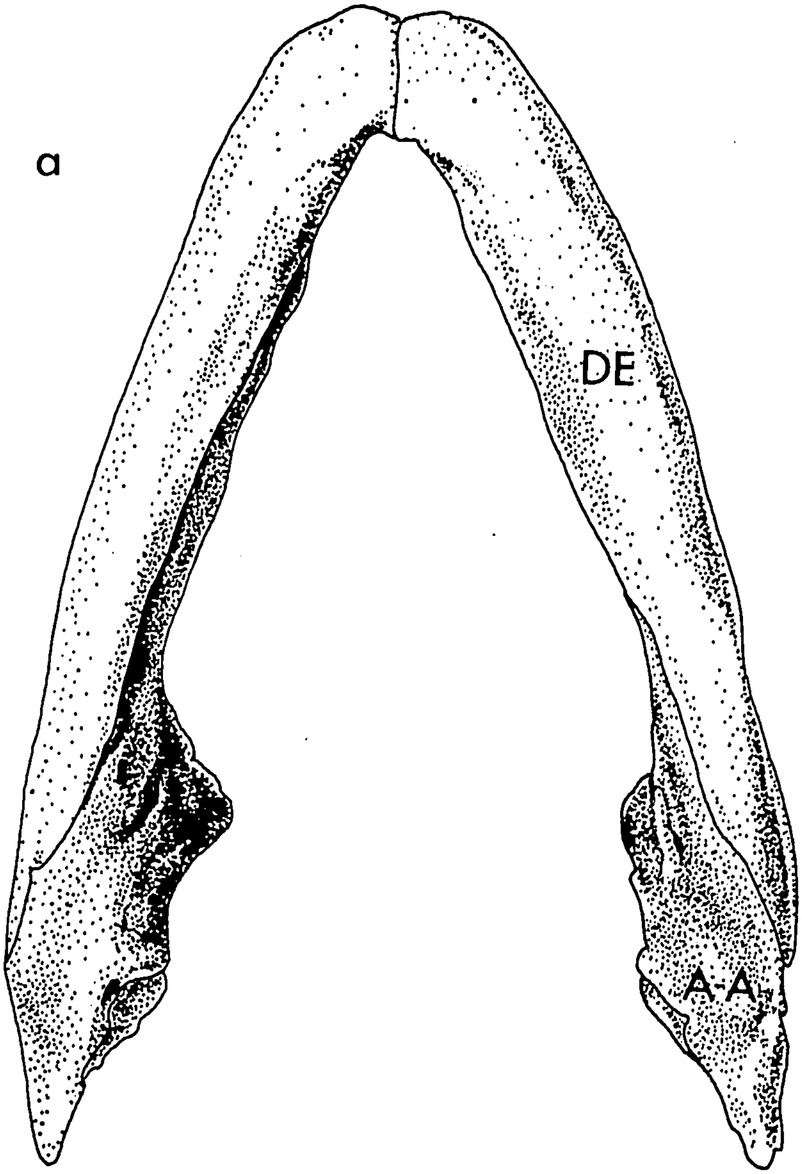
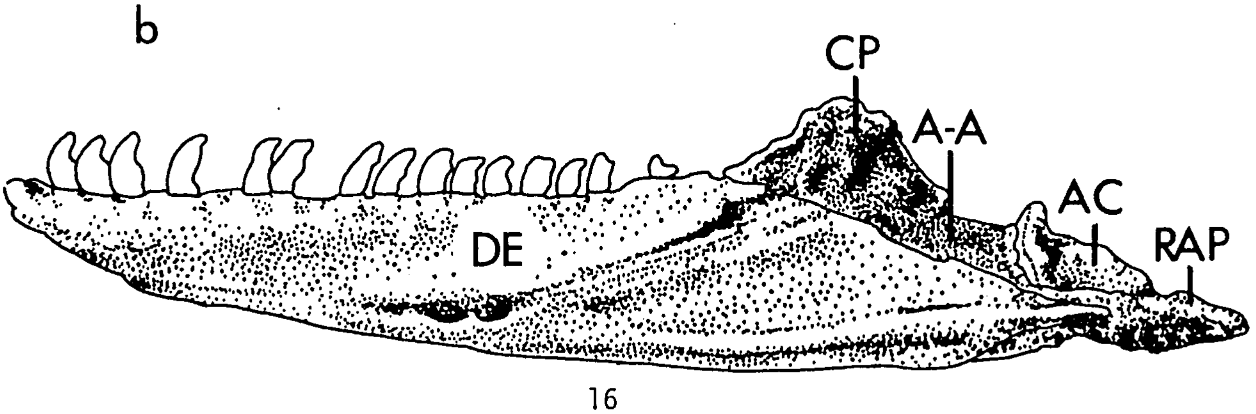
DLC
FR
PRO
PA
MX
SQ
VP
OS
PS
PT
ST
EX
QU

Figure 4. (a) Ventral view, and (b) lateral view of the mandibles. Abbreviations: A-A, angular-articular; AC, articular cartilage; CP, coronoid process; DE, dentary; RAP, retroarticular process.


a
DE
A-A


b
CP
A-A
AC
RAP
DE

and the prominent coronoid process which lies medial to the anterior end of the temporal crest and lateral to the pterygoids when the mouth is closed. The caudodorsal edge of the crest is directed slightly medially. The angular-articular extends anteriorly along the medial edge of the dentary. A short retroarticular process lies posterior to the articulating surface. The entire quadratomandibular joint is enclosed within a fibrous capsule and contains a distinct joint cavity. Manipulations of anesthetized specimens reveal that maximum gape is between 65°-75°.

Aspects of tooth form in Amphiuma have been previously described by Cope (1886), Röse (1895), Hilton ('52) and Rose ('68). Teeth of adult Amphiuma are bicuspid, like those of most adult salamanders, with the cusps arranged so that considerable frictional resistance arises when objects move labially or mesially over the cusps, but little frictional resistance is created by movement in the lingual or distal direction. Details of tooth form and cusp orientation on the premaxillary, maxillary, vomeropalatine, and dentary teeth are illustrated in Fig. 5.

## Hyoid Apparatus

The hyoid elements are embedded in the throat musculature and fill most of the anterior space between the mandibles. Anteriorly, there are a series of 12 paired and 2 unpaired cartilaginous nodules embedded in tough fibrous connective tissue that have been collectively referred to by Wiedersheim (1877) as the basihyal and hypohyal elements (Fig. 6). An elongate posteromedial pair of typically calcified bodies protrude through the ventral surface of the fibrous capsule and lie immediately lateral to the unpaired, medial basibranchial. The anterior tip of the

Figure 5. (a) Palatal view of right half of the skull illustrating cusp orientation of the various tooth rows. (b) Dorsal view of the mandible showing cusp orientation along the dentary tooth row. (c) Mesiolingual view of a representative tooth of *A. tridactylum*.

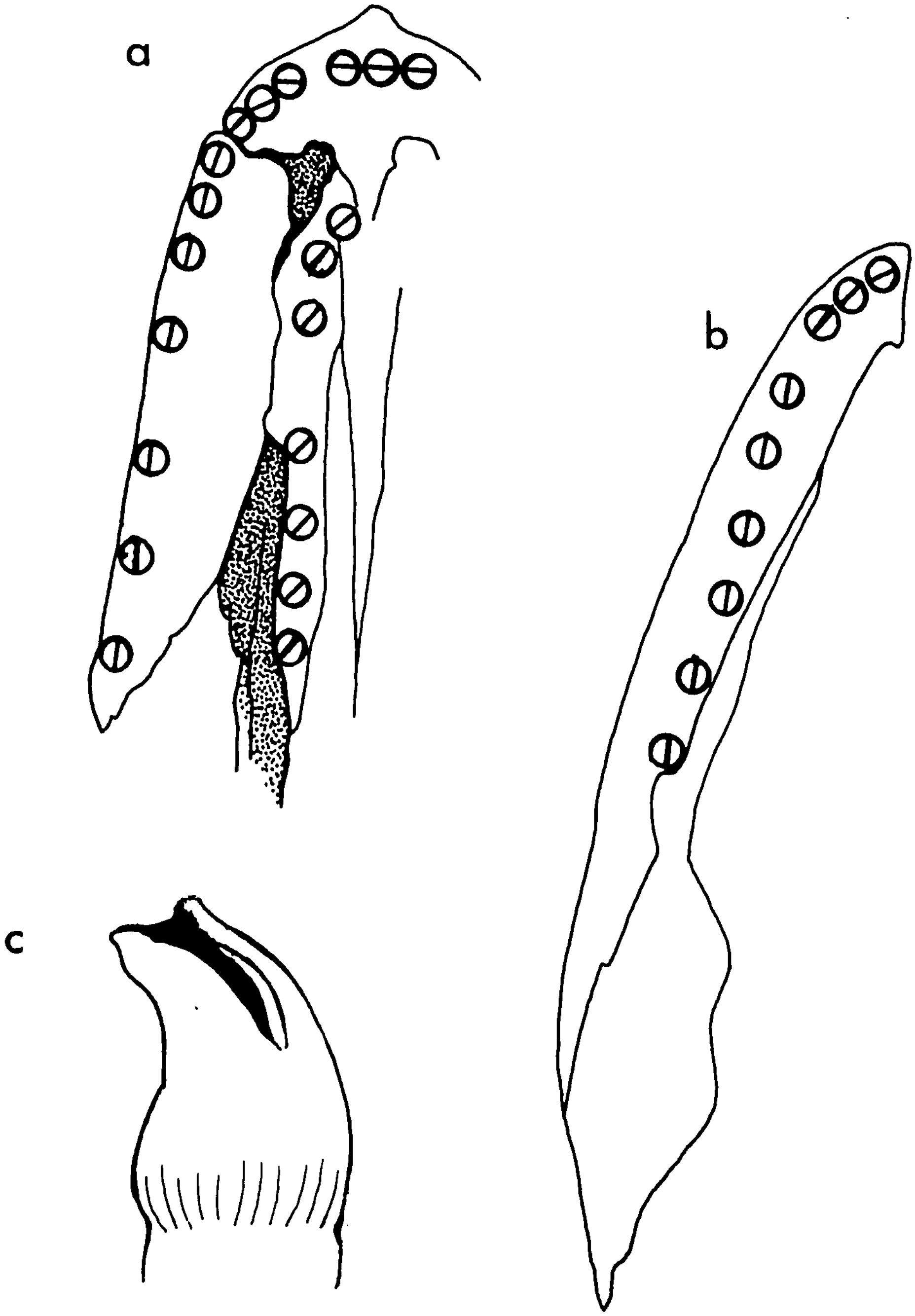
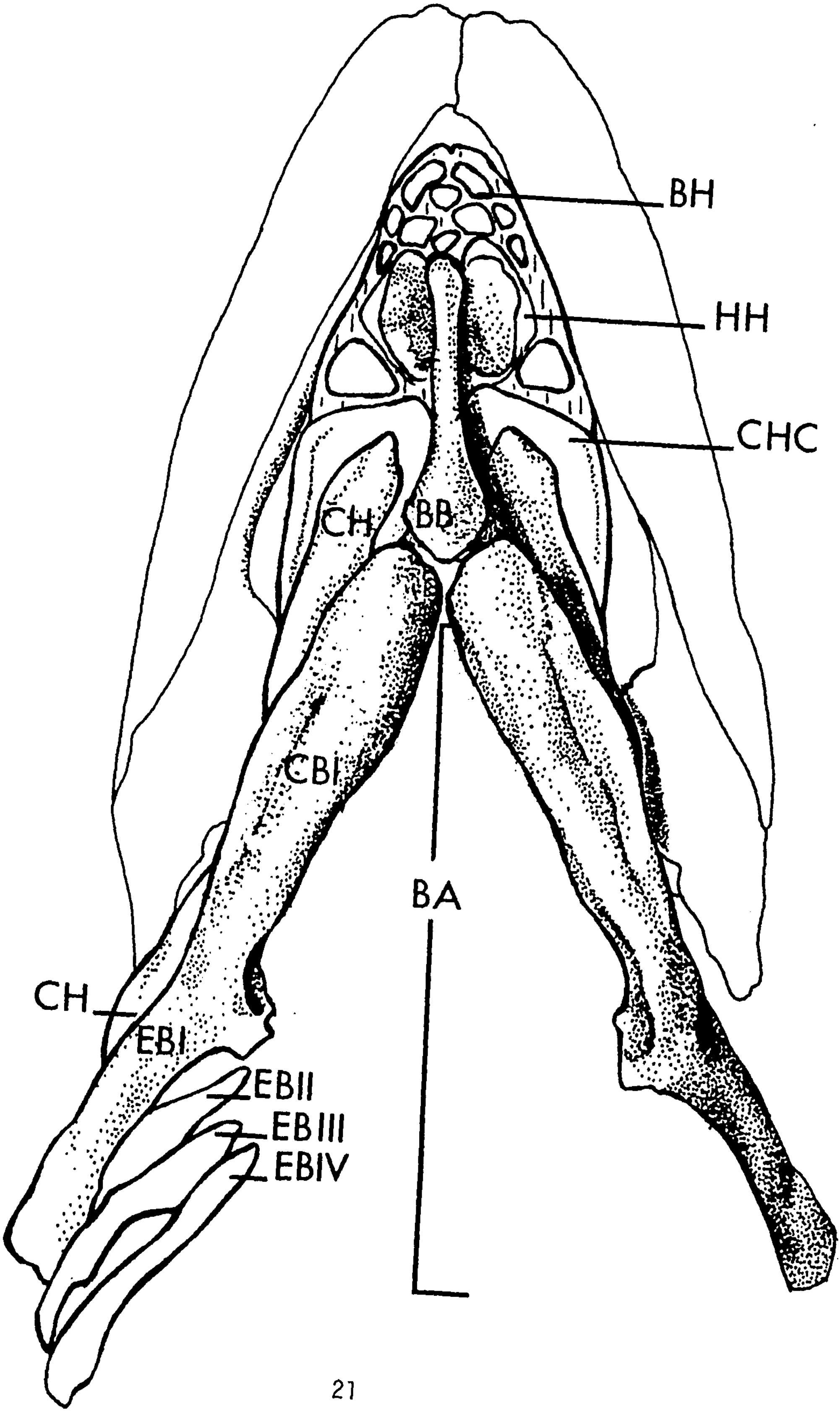

a
b
c

Figure 6. Ventral view of the hyoid apparatus in resting position between the mandibles, ligaments removed. Abbreviations: BA, branchial arm; BB, basibranchial; BH, basihyal; CBI, ceratobranchial I; CH, ceratohyal; CHC, ceratohyal cartilage; EBI, II, III, IV, epibranchial I, II, III, IV; HH, hypohyal.


BH
HH
CHC
CH
BB
CBI
BA
CH
EBI
EBII
EBIII
EBIV

basibranchial is embedded in the dense connective tissue. Dorsolateral to the basibranchial are paired ceratohyals with a narrow elongate shaft that curves dorsolaterally as it extends caudally. The anterior region of each ceratohyal forms a broad cartilaginous shelf marked by a ridge along the ventrolateral border. This shelf is embedded anteriorly in the connective tissue surrounding the basihyal and hypohyal elements and continues posteriorly as a narrow strip of cartilage along the lateral and medial surfaces of the largely ossified shaft (Figs. 6 and 7).

Elongate, osseus branchial arms (Özeti and Wake, '69) lie posterior to the ceratohyals and represent the fusion of ceratobranchial I and epibranchial I. Although previous authors (Wiedersheim, 1877; Hay, 1890; Hilton, '47) have referred to these as separate elements in Amphiuma, the term branchial arm is adopted here because the elements are fused and a single term simplifies functional analysis of the system. The ceratobranchial (anterior) segment is broad with a flat ventral surface and a rounded dorsal surface (Fig. 7). The anterior tip of each branchial arm is cartilaginous and is attached by a band of collagenous fibers to the ipsilateral side of the posterior basibranchial. The branchial arm is capable of angular rotations around the basibranchial of up to 90° in any plane in a fresh, unfixed hyoid preparation. The epibranchial segment is tubular, elongate, and directed caudolaterally. At the point of fusion with the ceratobranchial there is no discontinuity in the ventral surface of the branchial arm, although there is a prominent posteromedial projection near the junction of the elements. Three cartilaginous epibranchials lie parallel and caudal to the epibranchial I, epibranchials III and IV being more curved than the anterior elements.

Figure 7. Lateral view of the hyoid apparatus in Amphiuma. The surrounding skeletal elements indicate the resting position of the apparatus. Abbreviations: BB, basibranchial; CBI, ceratobranchial I; CH, ceratohyal; EBI, II, III, IV, epibranchials I, II, III, IV.

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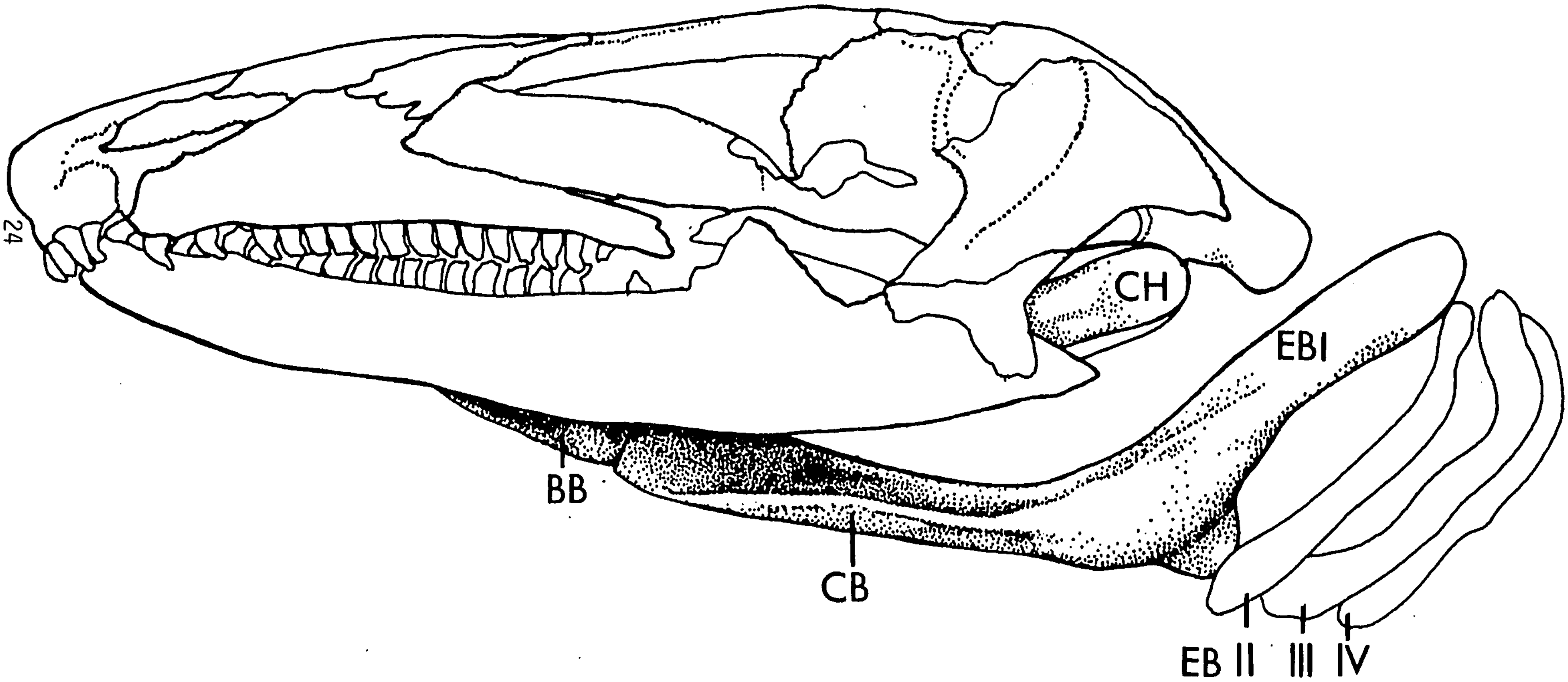


## Ligaments

There have been no previous detailed descriptions of the ligaments associated with the cranium or hyoid apparatus in *Amphiuma*. Ligaments associated exclusively with the cranium include 1) a levator retinaculum extending from the anterior edge of the temporal crest (prootic) to the prefrontal over the lateral surface of the levator mandibulae (Fig.8), and 2) a pterygomaxillary ligament extending from the anterior edges of the quadrate and the squamosal to the lateral edge of the parasphenoid and the medial edge of the maxilla (Fig. 9). This ligament surrounds the osseus and cartilaginous pterygoid. A hyomandibular ligament attaches along the postero-ventral surface of the mandible (angular-articular) and extends to the ventrolateral crest of the anterior ceratohyal (Fig. 10). A broad hyoquadrate ligament (Edgeworth, '35) attaches along the posterior edge of the quadrate and squamosal and extends to the anteromedial edge of the ceratohyal. Finally, a spiracular ligament passes laterally from an inscription in the lateral spinal musculature to the distal tip of the ceratohyal and also to a capsule surrounding the dorsal tip of the branchial arm. From the branchial arm it extends to each epibranchial and passes dorsal to the spiracle to attach to the minute pectoral girdle (Figs. 10 and 11). None of the specimens examined had a ligament extending from the atlas across the parietal to the coronoid process (Salthe, '73).

## Musculature

The cephalic muscles of *A. tridactylum* are remarkably robust. The jaw levators and depressors are particularly massive and originate dorsomedially on the elaborate otic and suspensorial region of the skull.

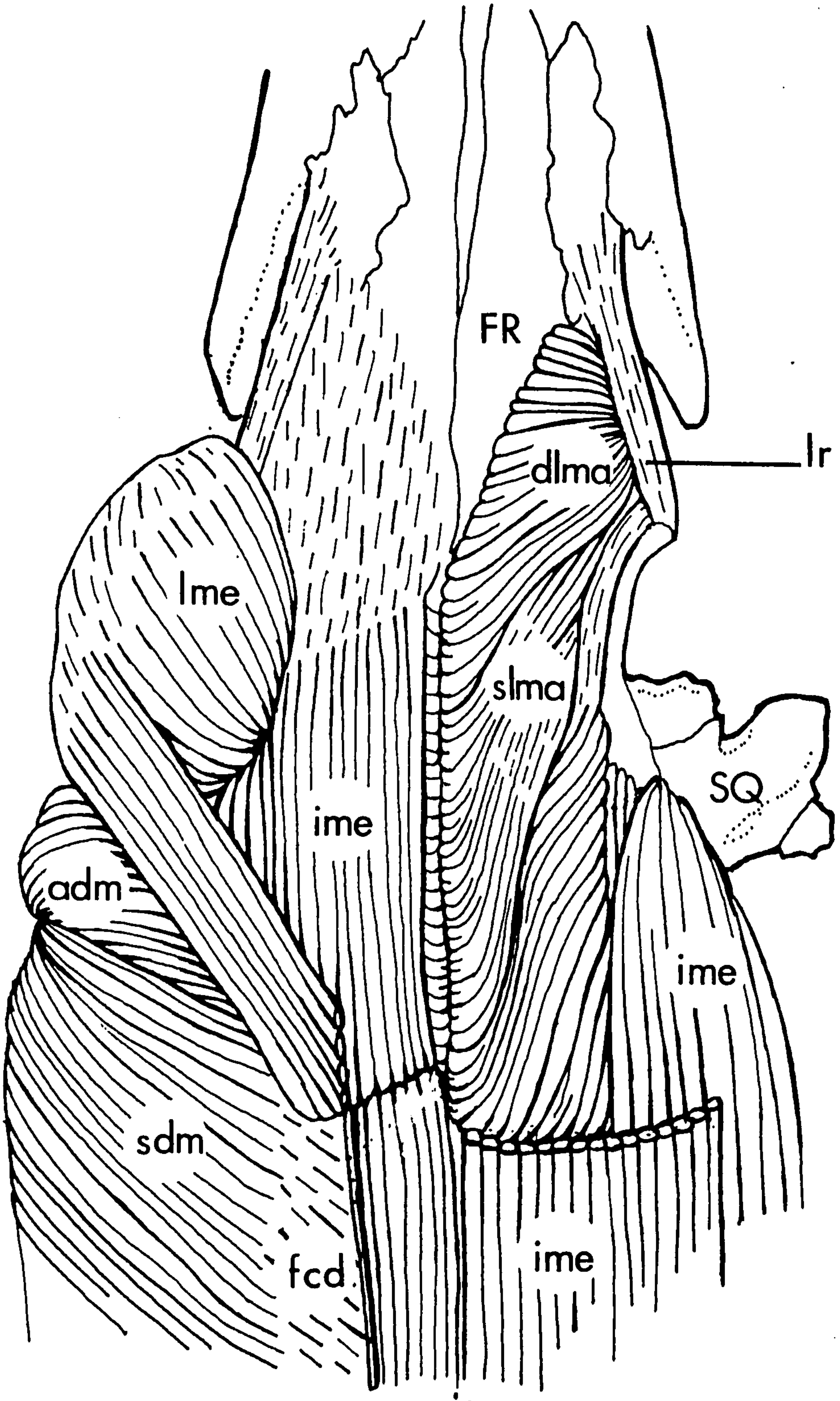

FR
lr
dlma
lme
slma
SQ
ime
adm
ime
sdm
fcd
ime

Figure 9. Cervical hypaxial musculature of A. tridactylum with mandible and hyoid apparatus removed. Abbreviations: EX, exoccipital; lsv, lateral subvertebralis; msv, medial subvertebralis; pml, pterygomaxillary ligament; PTC, pterygoid cartilage.

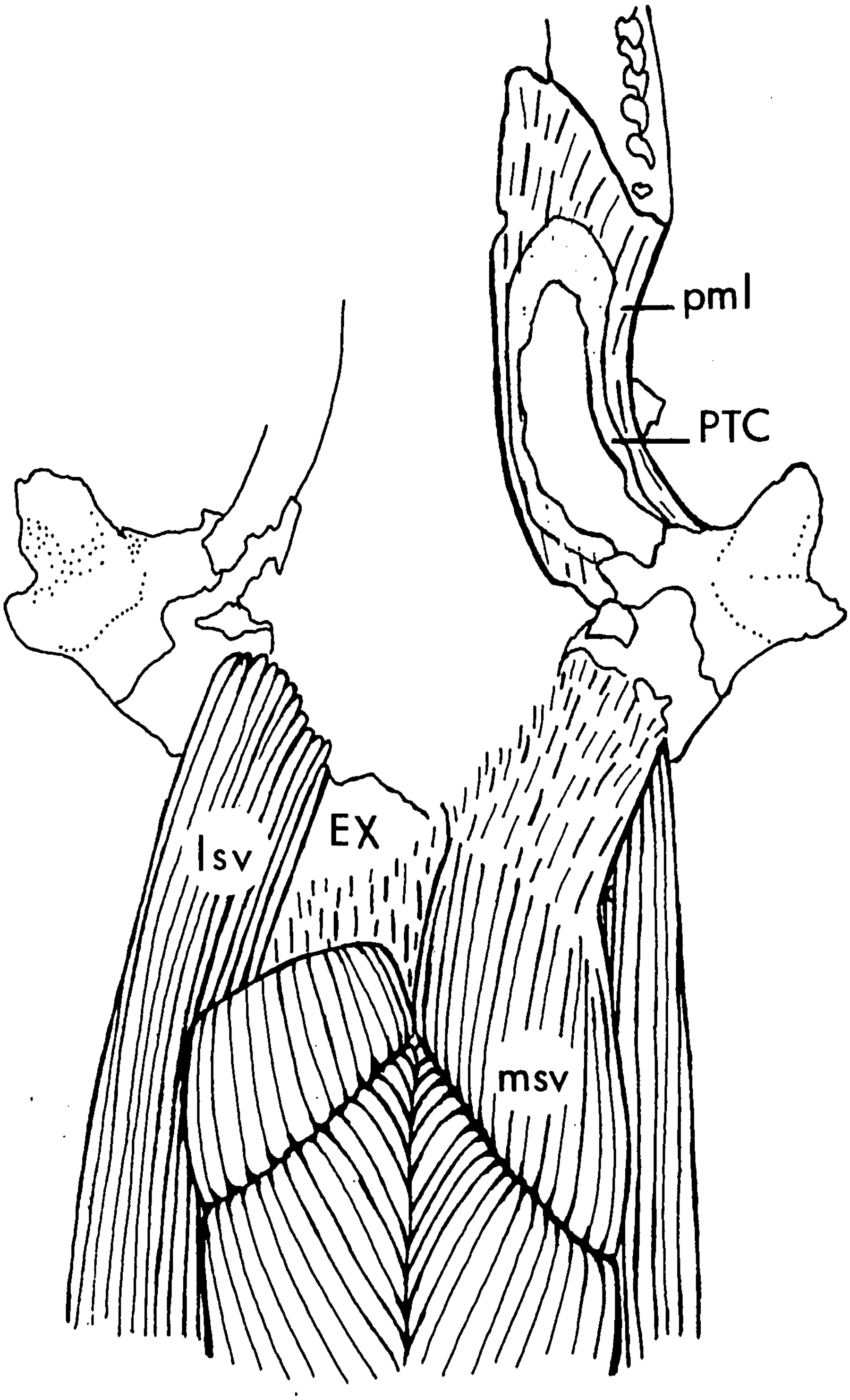
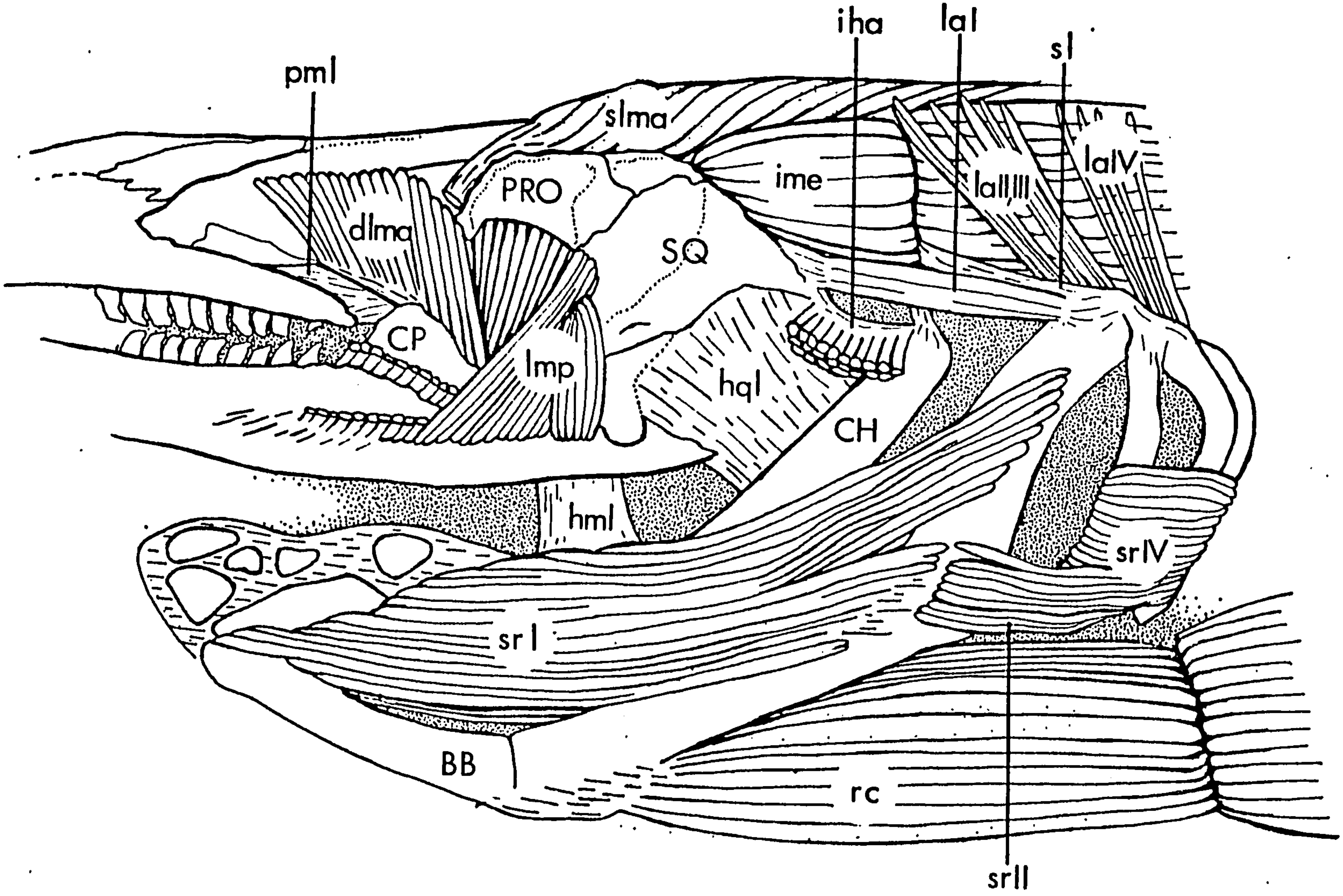

pml
PTC
EX
lsv
msv

Figure 10. Intermediate lateral musculature in A. tridactylum with buccal cavity artificially expanded prior to preservation. The subvertebralis is not shown. Abbreviations: BA, branchial arm; BB, basibranchial; CH, ceratohyal; CP, coronoid process; dlma, deep levator mandibulae anterior; hml, hyomandibular ligament; hql, hyoquadrate ligament; iha, interhyoideus anterior; ime, intermyoseptal epaxial; laI, II, III, IV, levatores arcuum I, II, III, IV; lmp, levator mandibulae posterior; pml, pterygomaxillary ligament; PRO, prootic; rc, rectus cervicis; sl, spiracular ligament; slma, superficial levator mandibulae anterior; SQ, squamosal; srI, subarcualis rectus I; srIV, subarcualis rectus IV.


iha
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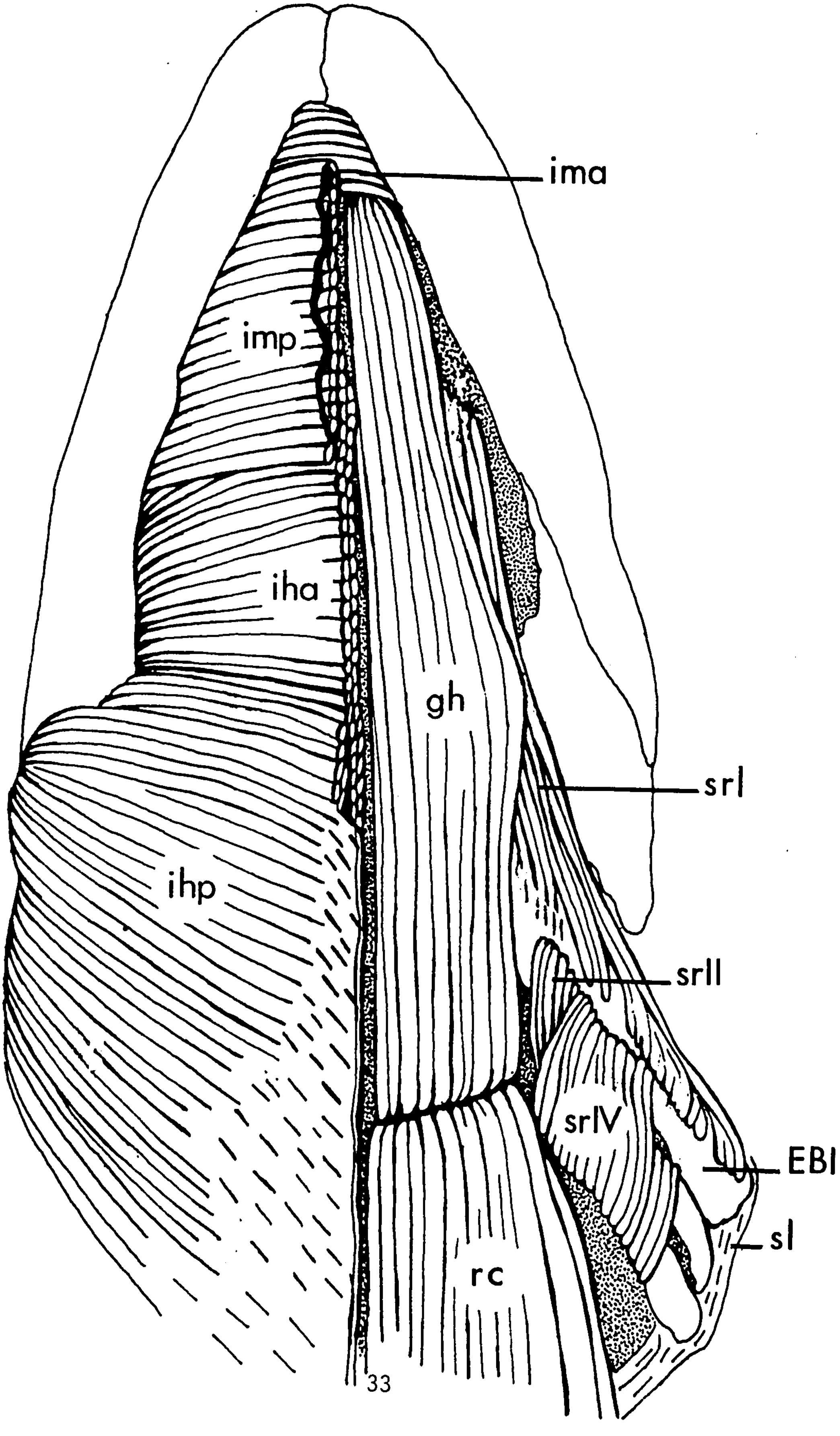
laIV
dlma
SQ
CP
lmp
hql
CH
hml
srIV
srI
BB
rc
srII

Figure 11. Ventral muscles of A. tridactylum showing superficial muscles on the left and deeper muscles on the right. Abbreviations: EBI, epibranchial I; gh, geniohyoideus; iha, interhyoideus anterior; ihp, interhyoideus posterior; ima, intermandibularis anterior; imp, intermandibularis posterior; rc, rectus cervicis; sl, spiracular ligament; srI, II, IV, subarcualis rectus I, II, IV.



33

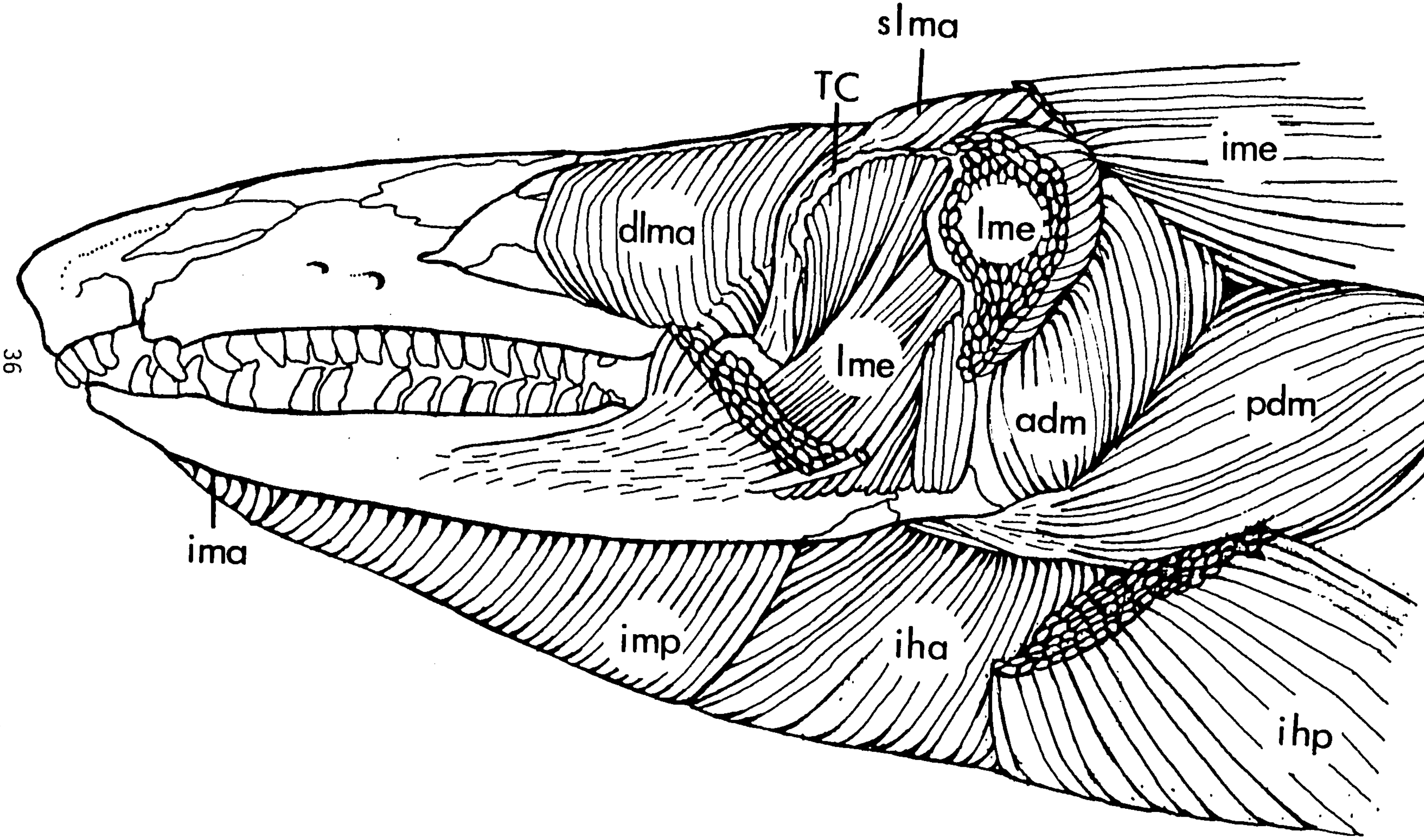
Several portions of the levator have a unipinnate arrangement, while the depressor mandibulae is bipinnate, an arrangement seen only in Amphiuma and Siren (Edgeworth, '35). Although there are few anatomically distinct muscles in A. tridactylum, many of the muscles are subdivided and exhibit several different heads or slips or multiple inscriptions. In the following account, the cranial muscles are arranged in groups according to their proposed functions. The nomenclature is taken from Edgeworth ('35). Although muscles were examined only in A. tridactylum, the descriptive section refers to Amphiuma for simplicity. It should be recognized that interspecific differences may exist.

### Mandibular depressors and elevators

The depressor mandibulae is a thick complex pinnate muscle (Fig. 12). In Amphiuma, the muscle is divided into anterior and posterior parts. Most of the fibers of both parts insert on a tendinous sheet (raphe) that attaches to the posterior tip of the retroarticular process. The anterior depressor mandibulae originates along the lateral edge and face of the temporal crest and the posterolateral surface of the squamosal. The lateral fibers run caudoventrally to insert on the raphe and the dorsolateral surface of the retroarticular, whereas the medial fibers insert on the medial surface of the retroarticular process.

The posterior depressor mandibulae is massive. Most of the fibers arise from the fibrous capsule around the distal tip and dorsolateral surface of epibranchial I (Fig. 12). The fibers run anterolaterally to insert on both the raphe and ventrolateral surface of the retroarticular process. Superficial fibers of both the anterior and posterior depressor

Figure 12. Lateral superficial musculature of _A_. _tridactylum_, with portions of several superficial muscles and the levator retinaculum removed. Abbreviations: adm, anterior depressor mandibulae; CP, coronoid process; dlma, deep levator mandibulae anterior; ima, intermandibularis anterior; ime, intermyoseptal epaxial muscle; imp, intermandibularis posterior; iha, interhyoideus anterior; ihp, interhyoideus posterior; lme, levator mandibulae externus; pdm, posterior depressor mandibulae; slma, superficial levator mandibulae anterior; TC, temporal crest.


slma
TC
ime
dlma
lme
lme
adm
pdm
ima
imp
iha
ihp

originate from the fascia cephalodorsalis (Druner, '04), a tough fibrous sheet overlying the dorsal musculature (Fig. 8), and insert on the raphe.

The levator mandibulae complex (Figs. 10 and 12) consists of several anatomically separate muscles in Amphiuma. These include a large anterior group lying in the dorsal levator fossa and arising from the anterolateral cranium, a levator mandibulae externus arising primarily from the temporal crest, and a small levator mandibulae posterior lying in the angle of the jaws. The levator anterior is divided into superficial and deep parts on the basis of similarity to the condition in Salamandra (Francis, '34).

The superficial levator mandibulae anterior forms a thick cylindrical belly that originates on the neural spines of the atlas and anterior vertebrae. The muscle runs anterolaterally to insert on a thick tendon that passes along a fibrous pad adherent to the skin of the anguli oris to attach to the dorsomedial surface of the coronoid process. Additional fibers arise from both the parietal and a tendinous sheet along the dorsal midline and insert into smaller tendons that run adjacent to the primary tendon (Fig. 8). The deep section arises along the dorsolateral crest and the lateral surface of the frontals. The fibers run posterolaterally and form a unipinnate attachment to a sheet that attaches to the medial surface of the coronoid process. The deepest fibers of this muscle arise from the lateral and ventral surface of the parietal and some fibers may also arise from the ventral edge of the prootic (Figs. 10 and 12). These fibers insert directly on the medial surface of the coronoid process, caudal to the insertion of the more superficial fibers.

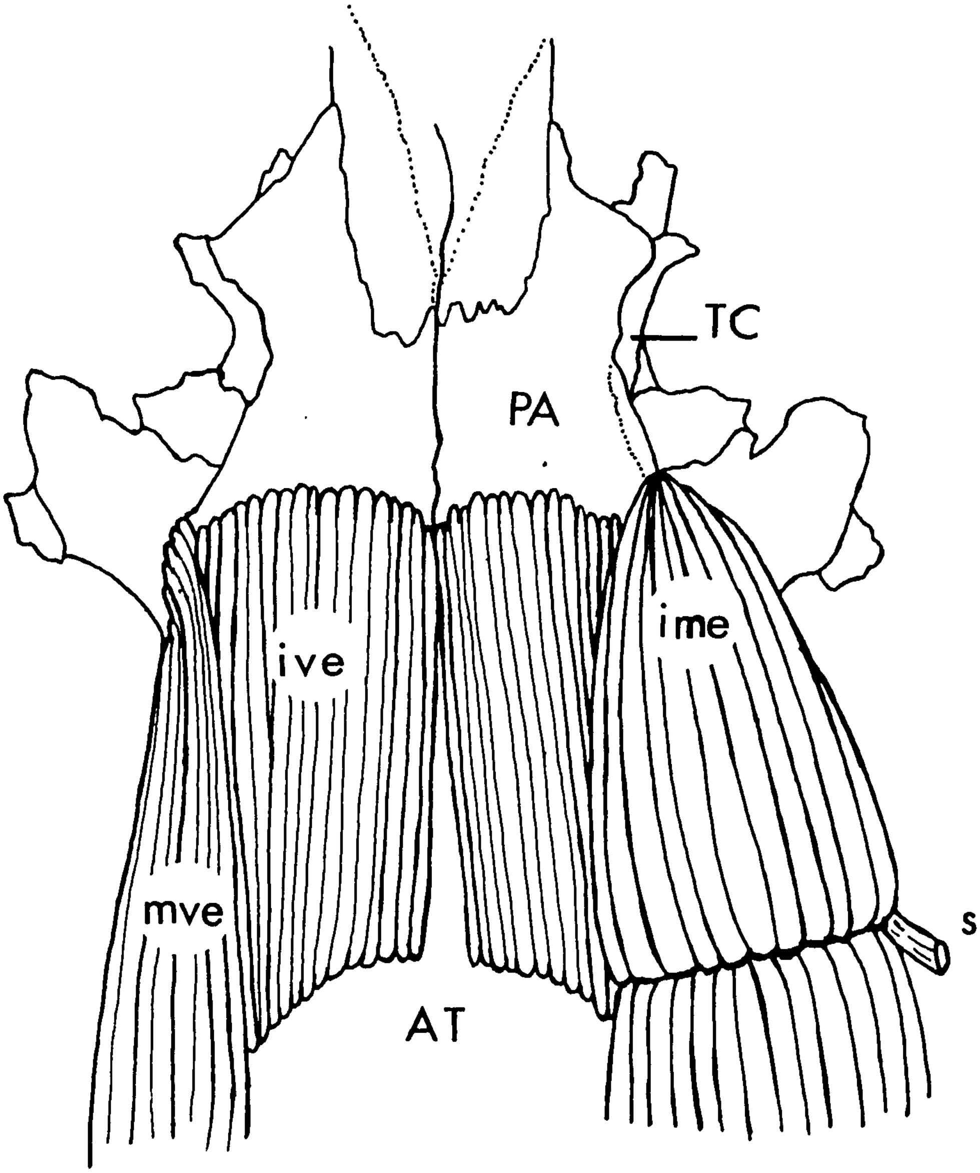
The levator mandibulae externus is a large, primarily superficial muscle (Fig. 12). Its superficial fibers originate on the temporal crest in the vicinity of the junction of the prootic, squamosal and parietal. An additional narrow band of fibers originates from the fascia cephalodorsalis. Both insert on a thick tendon that passes anterolaterally over the primary tendon, fuses with the fibrous pad of the anguli oris, and continues ventrally to insert on the lateral surface of the dentary. The deeper fibers originate from the lateral surface of the prootic and both the lateral ridge and the anterior face of the squamosal. The fibers run anterolaterally and insert along the dorsal edge of the dentary.

The levator mandibulae posterior is a small triangular muscle in the angle of the jaws. The entire muscle lies posterior to the mandibular branch of nerve V (Edgeworth, '35). It originates on the anterior face of the quadrate. The fibers run anteroventrally to insert in the mandibular fossa and the lateral edge of the dentary.

Spinal musculature

Auffenberg ('59) described three major components in the epaxial musculature of Amphiuma, including intermyoseptal, myoseptal-vertebral, and intervertebral fiber tracts. Although Auffenberg ('59) did not examine the relationships of the cervical epaxial muscles, all the tracts have some attachments to the braincase in the specimens examined here. The intermyoseptal fibers are extensive and cover most of the dorsal part of the body. These fibers are continuous anteriorly and insert on the medial surface of the temporal crest, medial to the origin of the levator mandibulae externus (Fig. 13). A superficial sheet inserts into an aponeurosis attached to the dorsolateral edge of the

Figure 13. Cervical epaxial musculature in _A_. _tridactylum_. Intermyoseptal epaxial muscle removed on left. Abbreviations: AT, atlas; EBI, epibranchial I; ime, intermyoseptal epaxial muscle; ive, intervertebral epaxial muscle; mve, myoseptal-vertebral epaxial muscle; PA, parietal; TC, temporal crest.


TC
PA
ive
ime
mve
sl
AT

frontal (Fig. 8). Anterior myoseptal-vertebral fibers originate on a transverse septum attached to the atlas and run anterodorsally to insert on the medial surface of the temporal crest, caudal to the insertion of the intermyoseptal fibers (Fig. 13). The deep intervertebral fibers originate on the anterior face of the atlas and run anteriorly to insert in the cervical epaxial fossa and along the transverse ridge.

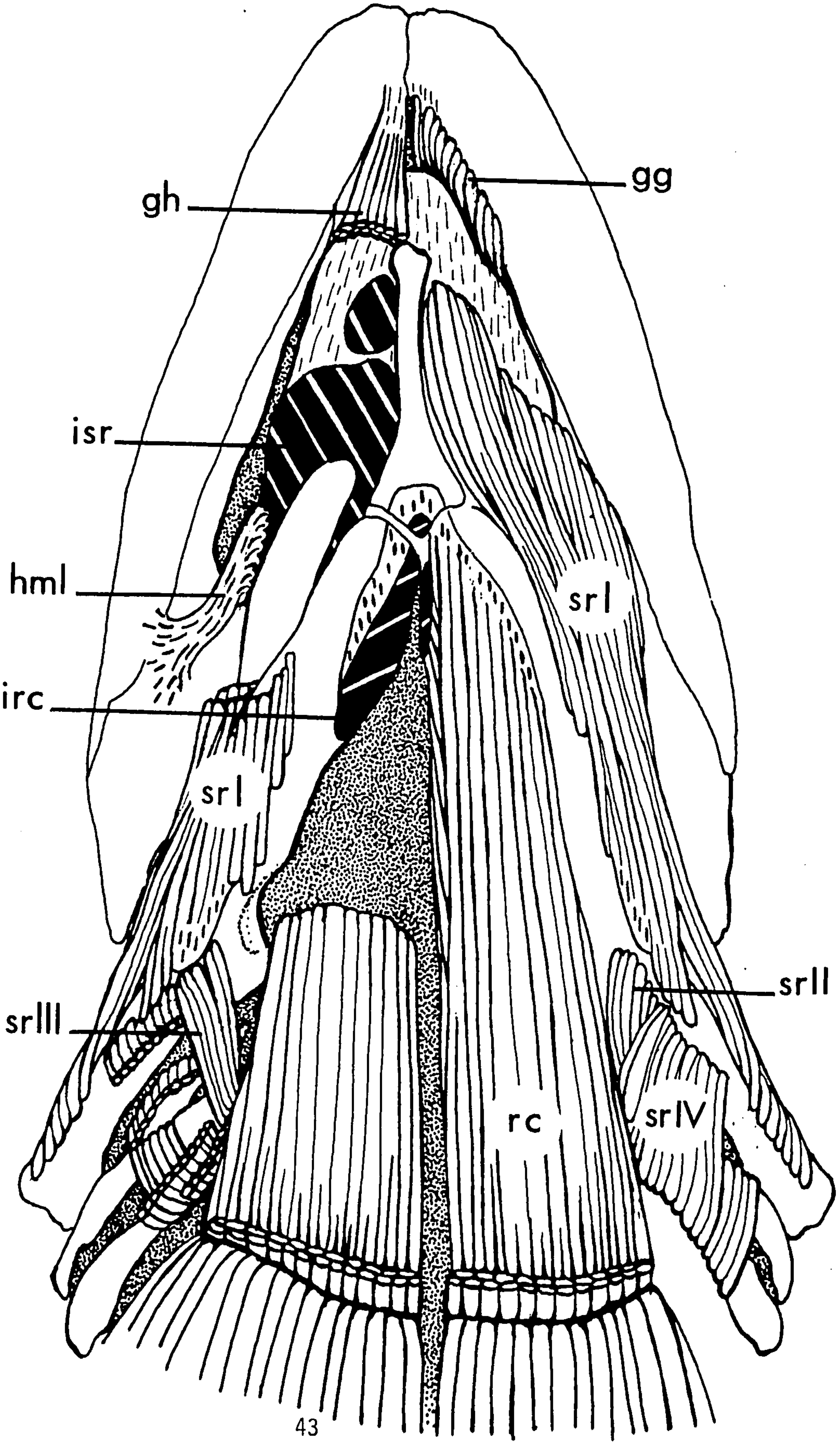
The cranial subvertebralis (Auffenberg, '59) is divided into two sections in _Amphiuma_, lateral fibers which are continuous with the subvertebralis lateralis and medial fibers which originate from the ventral surface of the cotylar process of the atlas. The deeper medial fibers insert on the surface of the exoccipital, and the superficial lateral fibers insert on an aponeurosis that passes superficial to the deep fibers and attaches to the cranial edge of the exoccipital and the caudal edge of the parasphenoid.

### Hyoid Musculature

Muscles that attach directly to the hyoid in adult _Amphiuma_ include the rectus cervicis of the hyobranchial-spinal group and the subarcualis recti and levatores arcuum of the branchiomeric musculature (Edgeworth, '35).

The rectus cervicis is a massive ventral muscle that is continuous posteriorly with the rectus abdominus and runs anteriorly to insert on the anterior half of the medial surface of ceratobranchial I and the posterior tip of the basibranchial. Its superficial fibers attach via an aponeurosis to the corresponding ventral portions of the ceratobranchial and basibranchial (Figs. 10 and 14). The most medial fibers of the rectus cervicis converge on a ventral raphe near the junction

Figure 14. Deep ventral musculature of *A. tridactylum* to show insertions of the subarcualis rectus I and rectus cervicis. Abbreviations: gg, genioglossus; gh, geniohyoideus; hml, hyomandibular ligament; irc, insertion of rectus cervicis; isr, insertion of subarcualis rectus I; srI, II, IV, subarcualis recti I, II, IV.


gg
gh
isr
hml
irc
srI
srI
srII
srIII
rc
srIV

of the posterior elements of the hyoid. The posterior portion of this muscle, caudal to the origin of the geniohyoideus (see below), is subdivided by transverse inscriptions.

Four subarcualis recti are present in adult Amphiuma. Subarcualis rectus I is a large muscle extending from the ceratohyal to the branchial arm. The lateral fibers arise from the anterior and lateral face of epibranchial I and form a thin sheet that inserts along the ventrolateral edge of the cartilaginous part of the ceratohyal (Fig. 14). The ventral fibers originate from an aponeurosis attached to an elongate ventral ridge on the ceratobranchial, and run anteriorly to insert by a series of slender tendons onto the calcified hypohyal cartilage. The remaining deep fibers arise from the anterolateral surface of the ceratobranchial and proximal epibranchial I, and run cranially to attach to the posteroventral surfaces of the ceratohyal and hypohyal. Subarcualis recti II and III originate from the lateral surface of epibranchial I and insert on the posterolateral surface of epibranchial III. The muscles are separated by a longitudinal inscription. Subarcualis rectus IV originates on the posterolateral face of epibranchial IV. A small bundle of deep fibers passes anteriorly and inserts on epibranchial III, a more superficial bundle extends to epibranchial II and the most superficial and ventral fibers extend to the ventrolateral face of epibranchial I. The entire complex is ventral to the spiracle.

Adult Amphiuma also retain a series of small branchial levators, the levatores arcuum, that are associated with the dorsal tips of the epibranchials. Levator I is a narrow band of fibers that arises by a small tendon from the posterolateral edge of the temporal crest (Fig. 10). It runs posteriorly and inserts on the medial surface of the dorsal tip of epibranchial I. Levators II, III, and IV arise from the fascia cephalodorsalis, and in some cases the inscriptions of the cervical epaxial musculature, pass posteroventrally and insert on the dorsal tips of epibranchials II, III, and IV respectively.

### Buccal Constrictors

Functional constrictors of the buccal cavity include the intermandibularis and interhyoideus muscles (derivatives of the ventral constrictor plate), both of which have separate anterior and posterior muscles in adult Amphiuma, and the geniohyoideus,a hyobranchial-spinal muscle that indirectly ties the hyoid to the mandible via its attachment to the rectus cervicis.

The intermandibularis anterior is a small triangular sheet in the angle formed by the anterior tips of the mandibles (Fig. 11). The fibers arise from the ventromedial surface of the dentaries and run uninterrupted across the midline. The caudal edge of the muscle lies deep to the intermandibularis posterior.

The intermandibularis posterior is a thin sheet lying superficial to the hypohyal, basihyal and anterior ceratohyal (Figs. 11 and 12). It arises along a narrow band on the medial surface of the posterior two-thirds of the dentaries and the anterior angular-articular. The fibers run medially to insert on a sinuous raphe along the ventral midline.

The interhyoideus anterior (interhyoideus of Edgeworth, '35) originates along the dorsal edge of the hyoquadrate ligament (Fig. 10). As noted by Edgeworth ('35), additional scattered fibers originate from the quadrate and the squamosal. The fibers run ventrally, medial to the mandible and lateral to the ceratohyal and the ceratobranchial, then curve medially to fan across the ventrum (Fig. 11). The anterior fibers, which lie at the level of the anterior tip of the basibranchial, are deep to the intermandibularis posterior and the posterior fibers are deep to the interhyoideus posterior. All of the fibers insert into a raphe along the ventral midline.

The interhyoideus posterior is considerably more massive than the other ventral constrictors (Fig. 11). This triangular muscle originates from a thick tendon attached to the posterolateral surfaces of the quadrate and squamosal, the quadratoarticular joint capsule, and the lateral surface of the mandible. The fibers fan postermedially, superficial to the ventral part of the branchial arm,and insert primarily on the midventral pectoral fascia, a few lateral fibers reaching the pectoral girdle.

The geniohyoideus is a paired, parallel, longitudinal muscle lying along the ventrum, deep to the superficial buccal constrictors (Fig. 11). It originates from the anterior inscription of the rectus cervicis. The fibers converge anteriorly and insert on a narrow aponeurosis that attaches to the ventromedial surface of the dentary near the mandibular symphysis. A band of connective tissue extends from the anterolateral geniohyoideus to the ventrolateral crest of the ceratohyal.

### Tongue Musculature

The tongue in Amphiuma, as noted by Baker ('45) and Regal ('66), is only a slightly elevated glandular bed in the floor of the mouth. The only muscle associated with the tongue is the genioglossus (Fig.

14) which is comprised of fibers that originate on the medial surface of the mandible in the region of the mandibular symphysis, deep to the geniohyoideus. These fibers insert into the mucosa of the floor of the mouth.

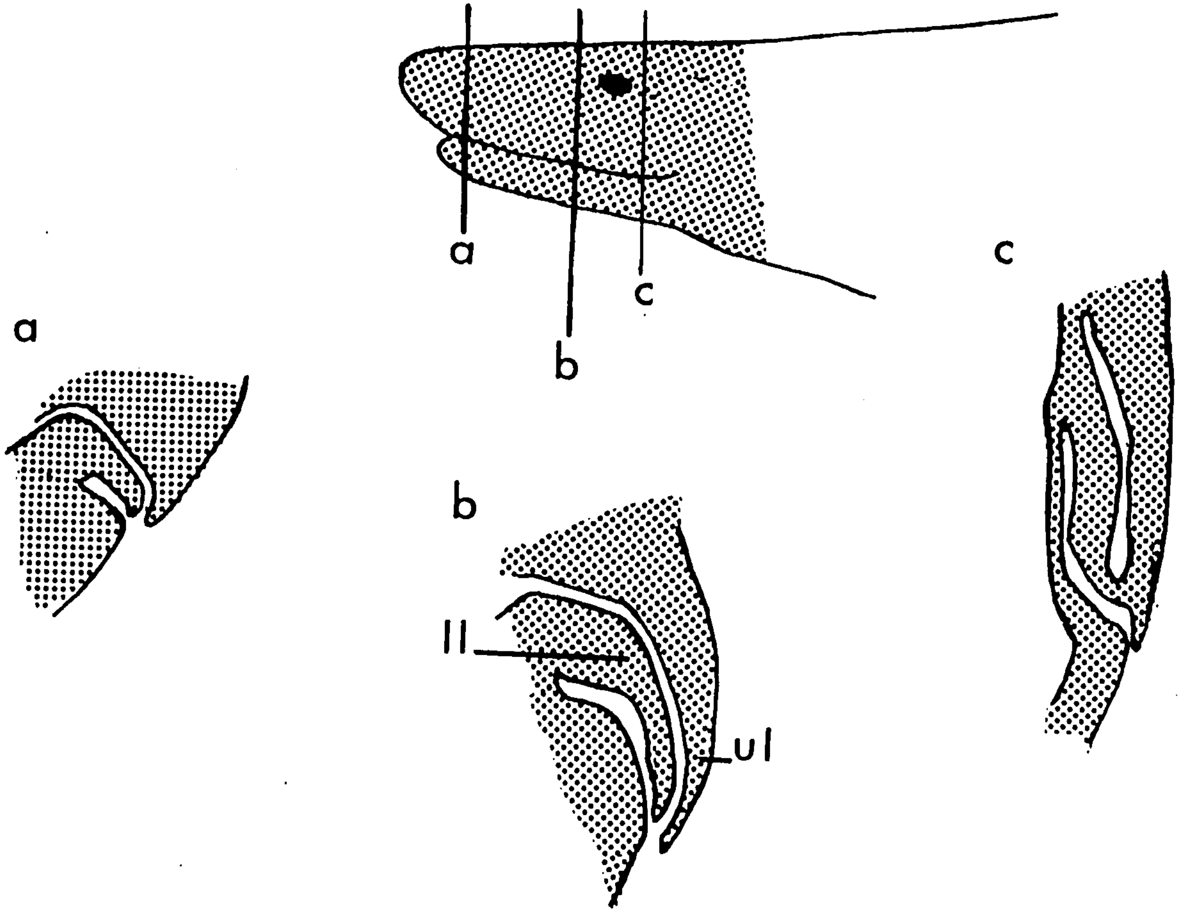
### Labial Lobes

The labial lobes are stiff folds of skin lying along the lateral edges of the mouth (Fig. 15). The upper lobe extends ventrally beyond the edge of the maxilla, and overlies the mandible and its associated lower lobe when the mouth is closed. The lower lobe is composed of a large lateral flap that covers the edge of the mandible when the mouth is closed. The free edge of the flap is directed outward and lies medial and parallel to the upper lobe. The upper and lower lobes are approximately equal in size and terminate anteriorly at the level of the rostral end of the maxilla.

## Cephalic displacements during feeding

*Amphiuma* utilizes two distinct types of suction feeding during prey capture. These will be referred to subsequently as 1) stationary capture, in which the predator does not advance as the prey is sucked inward, and 2) strike, in which the predator moves toward the prey while it is sucked inward. The following descriptions emphasize the most common conditions for each type of suction feeding although ranges of displacements are given where pertinent.

Figure 15. Cross-sectional view of the labial lobes of *A. tridactylum* at the level of (a) the rostral maxilla, (b) midway along the mouth opening, (c) immediately anterior to the anguli oris. The upper lobe is on the right and the lower lobe is on the left. Abbreviations: ll, lower lobe; ul, upper lobe.


a
b
c
a
b
c
ll
ul

### Stationary capture

Stationary feeding was observed when Amphiuma were offered worms, small crayfish, and whole and dismembered dead mice. During the approach, Amphiuma usually nudge the prey item and then remain stationary for several seconds before feeding. Mouth opening is typically initiated when the prey is within one centimeter of the tip of the snout, and results from depression of the mandible, elevation of the snout, or both, depending upon whether the prey is above or below the level of the snout.

During opening, the buccal floor initially undergoes little ventral displacement. Instead, the skin between the medial hyoid region and the mandible is strongly indented and vertically oriented lateral protrusions become visible below the spiracles due to lateral movement of the dorsal branchial arms. The prey usually is not displaced toward the Amphiuma until the latter stages of mouth opening.

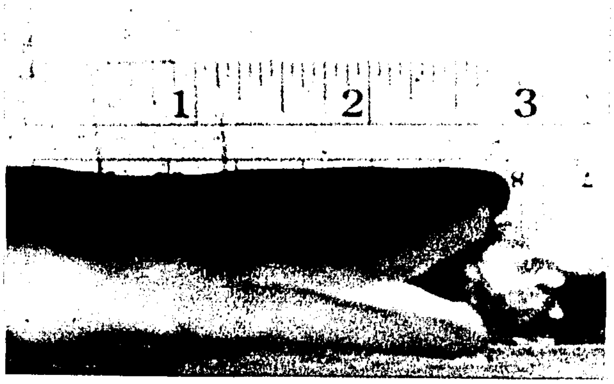
As the jaws part, the dorsal labial lobe obscures the lateral mouth opening. The lower lobe remains unextended and flattened against the mandible. Even when the jaw angle exceeds 50° the lower lobe remains unextended and much of the lateral mouth ventral to the dorsal lobe is open.

At maximum gape for a given capture, jaw angle varies from 8°-65° and part or all of the prey lies between the jaws (Fig. 16a). Only slight ventral displacement of the medial hyoid elements between the posterior tips of the mandibles accompanies maximum gape (Table 1).

The prey completely disappears from lateral view as closure of the jaws and buccal expansion are initiated, 4-12 msec after the mouth

Figure 16. Reproductions of two frames from strobe illuminated Super-8 film showing (a) maximum gape (80 msec after beginning of mouth opening) during stationary capture and (b) approximate middle of mouth closure (120 msec after beginning of mouth opening) during stationary capture. The prey is between the jaws in (a) and has entered the buccal cavity in (b). Note absence of elevation of the lower labial lobe and the limited hyoid displacement characteristic of stationary capture.

a



b

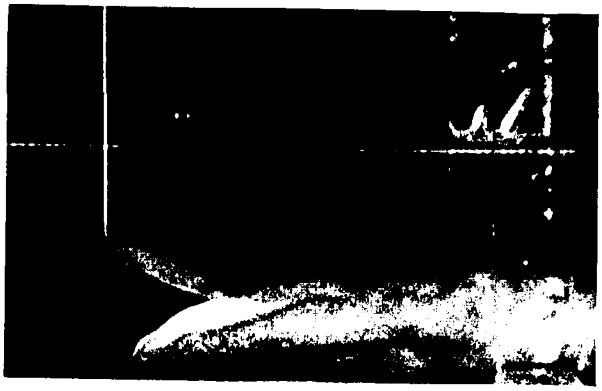


TABLE I. Estimates of Ventral Displacement Midway between Snout and Spiracle

| | Stationary (n=13) | | Strike (n=11) | |
|---|---|---|---|---|
| | mean(cm) | standard deviation | mean(cm) | standard deviation |
| maximum gape | 0.23 | ±0.25 | 1.06 | ±0.26* |
| mouth closure | 1.06 | ±0.58 | 1.62 | ±0.42 |

*the large standard deviations are partially attributable to the low film speed (24 fps) and the rapidity of the displacements.

began to open (Fig. 16b). Buccal expansion is due primarily to ventral displacement of the entire buccal floor anterior to a point approximately midway between the posterior tip of the mandible and the spiracle. Slight lateral expansion of the buccal walls is evident below the spiracles, and as the jaws meet there is additional expansion in the area below and parallel to the mandible. These changes in surface features suggest that the medial hyoid elements move caudoventrally and the branchial arm and ceratohyal swing laterally as the mouth closes. During stationary capture there is considerable variation in the degree and duration of buccal expansion (Table 1). When feeding on worms or whole dead mice,the gape and displacement of the buccal floor are small and only part of the prey enters the oral cavity to be grasped by the teeth. During capture of crayfish or dismembered mice the gape and degree of buccal expansion are greater, frequently resulting in complete engulfment of the prey during capture.

Mouth closure is the result of either depression of the snout and/or elevation of the mandible. Depression of the snout, which is accompanied by marked flexion of the craniovertebral joint, is invariably associated with large depressions of the buccal floor. On the other hand, during elevation of the mandible there is a dorsal shift of the anterior buccal floor apparently due to dorsal shift of the hyoid. Mandibular elevation may be followed by flexion of the craniovertebral joint.

The behavior of the spiracle during stationary capture is variable. Usually, the spiracle opens between maximum gape and the termination of buccal expansion. Introduction of ink around the prey demonstrates that water flows out of the spiracle as it opens.

Following closure, the craniovertebral joint straightens and the entire buccal floor is gradually raised. If the prey remains lodged between the jaws, the rate of buccal contraction is much greater than if the jaws are completely closed. In the latter case, buccal contractions may take as long as 2.0 sec. and evacuation of water occurs primarily through the spiracle.

During stationary capture involving large buccal displacements, the head of *Amphiuma* may move forward a few millimeters. Following capture, *Amphiuma* manipulates the prey by repetitive movements similar to those used in stationary capture. Swallowing appears to occur during a prolonged ventral flexion of the braincase that follows prey manipulation. The extent of processing was not assessed in most cases, but several worms retrieved following MS-222 induced regurgitation (45 min. after swallowing) were still alive and active.

### The Strike

The strike is a qualitatively and quantitatively different mode of capture elicited in these experiments by large crayfish, live mice, and live fish. Only feeding on crayfish was filmed. Prior to capture, *Amphiuma* frequently nudged the prey or pressed it against the wall of the filming box. Frontal, lateral, and dorsal strikes were observed. The frontal strike, which is more common and less variable, will be discussed first.

The first detectable movements during a strike are the simultaneous depression of the mandible and elevation of the snout. Within 10 msec. of these initial movements the buccal floor caudomedial to the mandible moves ventrally, suggesting ventral shift of the medial hyoid, as the entire head begins rapid acceleration toward the prey. The strike is typically initiated when the prey lies 1-2 cm anterodorsal to the tip of the snout. Although the prey may move slightly during the beginning of the strike, it is difficult to determine whether this displacement is due to fluid pressure generated by the strike or by locomotory movements of the prey.

As mouth opening proceeds, the medial hyoid elements drop sharply caudoventrally and a bulge appears on the skin ventral to the mandible. The labial lobes become fully extended and block the lateral opening of the mouth (Fig. 17a). As the jaws of <u>Amphiuma</u> approach maximum gape (55°-65°), the buccal floor shifts further caudoventrally while the lateral elements, the branchial arm and the ceratohyal, swing laterally. Continued forward movement of the head of <u>Amphiuma</u> frequently carries the mouth to the position occupied by the prey prior to the initiation of the strike. During mouth opening, forward displacement of the head ranged from 1.4 to 3.0 cm. with estimated minimum velocities of 35-58 cm $sec^{-1}$. Ignoring initial and terminal acceleration, and based on a calculated change in volume of the buccal region of approximately 43 $cm^3$ in a specimen of 70 cm svl, estimated minimum inflow velocity is 450 cm $sec^{-1}$ assuming equal flow rate at all points across a gape surface of 2.4 $cm^2$. Compared to stationary feeding, there is much less variation in the extent and duration of buccal excursion (Table 1) and the maximum gape angle achieved during the strike. Occasionally slight caudal displacement of the prey is evident as the prey passes between the jaws. Further displacement is obscured by the labial lobes.

Figure 17. Reproductions of two frames from strobe illuminated Super-8 film showing (a) maximum gape (40 msec after beginning of mouth opening) and (b) end of closure (80 msec after beginning of mouth opening) during a strike. Note that the prey has disappeared, the lower labial lobes are elevated, and the buccal region is expanded in (a). Depression of the snout, flexion of the craniovertebral joint and nearly vertical orientation of the lateral hyoid elements characteristic of closure during the strike (see text) are shown in (b).

a

b

As the mouth begins to close, there is little additional forward displacement of the snout, but the craniovertebral joint continues to move anterodorsally carrying the quadratomandibular joint in the same direction. Thus, although it appears that closure is always the result of rapid depression of the snout, frequently it is actually the result of dorsal rotation of the cranium around the tip of the snout (Fig. 17b). As this occurs, the expanded region of the buccal floor moves caudally. The posterior tip of the medial element, the basibranchial, comes to lie in the transverse plane of the spiracle. Simultaneously, the lateral elements swing further ventrally and laterally, indicating lateral swing of the branchial arm and ceratohyal around their dorsal attachments. The branchial arm, which appears curved at the beginning of closure, appears nearly straight as the jaws meet (Fig. 17b). The duration of the frontal strike is approximately 80 msec.

The spiracle opens as the jaws start to close. Unlike stationary capture, in which the spiracle appears elongate and flush with the external body surface, during the strike the spiracle is round and the surrounding tissue bulges outward. During closure the lower labial lobe often remains everted and protrudes beyond the upper lobe following closure (Fig. 5). Large crayfish are usually wedged between the jaws during closure. In such cases the jaws do not meet and evacuation is rapid.

In the lateral and dorsal variation of the strike, the head turns or elevates with the initiation of opening. In the lateral strike, Amphiuma frequently presses the prey against the wall of the filming box with the side of the snout. In both lateral and dorsal strikes the sequence of the jaw and hyoid displacements is similar to that of the frontal strike. However, the lateral strike is more rapid and may last only 40 msec.

Following closure, the craniovertebral joint is gradually extended, and the anterior buccal floor (medial hyoid elements) shifts dorsally. The entire head of Amphiuma may continue to move anteriorly or anterodorsally 2-10 cm. As the craniovertebral joint straightens, the jaws part slightly (less than 0.8 cm), the spiracle closes, and the buccal floor, in particular the region between the posterior tips of the mandibles, shifts dorsally. Manipulations of the prey following evacuation primarily entail rapid snapping movements of the jaws accompanied by only slight buccal displacements. A crayfish retrieved following repeated snapping was inactive and had an extensively fractured exoskeleton.

## Mechanism

The relationships of the cephalic bones and muscles combined with the recorded displacements of these elements permit formulation of a few basic hypotheses regarding the origin, direction and approximate temporal relationships of the muscular forces during feeding. Although electromyographic data are not presently available for Amphiuma, it seems likely that in most cases one of several muscles may be responsible for a particular displacement. Therefore the directional properties attributed here to the contractions of a particular muscle may actually represent the combined effects of several synergists. The following interpretation should be viewed as a preliminary model that must ultimately be tested by more refined functional-anatomical methods.

## Stationary Capture

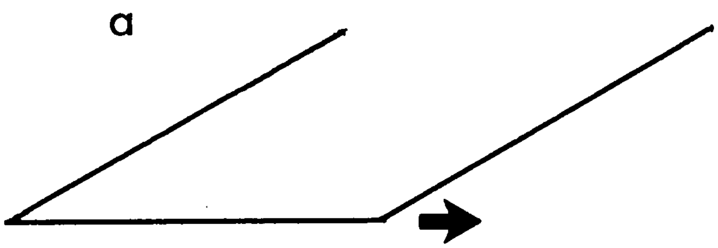
During mouth opening there is a reduction in intraoral pressure that sucks inward the water near the mouth opening. This pressure differential between the oral cavity and the surroundings may result in some indentation of the buccal floor. The depressor mandibulae opens the mouth, but whether the snout is elevated or the mandible is depressed depends on the extent of contraction of the cranial elevators and depressors. The small mass of the mandible relative to the cranium, activity of the posterior depressor (which does not originate on the braincase), and stabilization of the braincase by contraction of the subvertebralis would all contribute to depression of the mandible. On the other hand, elevation of the snout is probably achieved by contraction of the cervical epaxial musculature. Contraction of the posterior depressor, while depressing the mandible, would pull the distal branchial arm anteroventrally. Because the anterior end of the branchial arm is prevented from moving directly rostrally by its attachment to the medial hyoid elements which are wedged between the mandibles, contraction of the posterior depressor actually results in rotation of the branchial arm such that the dorsal end shifts laterally and ventrally. This causes the angle of the branchial arm to shift ventrally without appreciable ventral displacement of its anterior end or the remainder of the hyoid apparatus. Although these excursions appear to be relatively small they would further decrease the internal pressure.

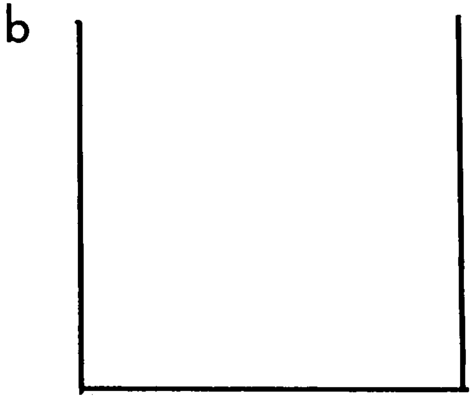
In the latter stages of mouth opening there is increased abduction of the jaws and slight additional displacement of the angle of the branchial arm which further decreases the pressure within the buccal cavity. During this period, the prey is sucked between the jaws. Despite relatively small excursions of the hyoid, inflow velocity may be high as the mouth begins to close because the upper labial lobe occludes much of the lateral mouth opening, particularly when maximum gape is small, effectively reducing the surface area across which inflow is occurring.

As the mouth begins to close the rectus cervicis pulls the basibranchial and anterior end of the branchial arm caudally. Application of a posteriorly directed force on the medial hyoid shifts this entire region of the apparatus caudoventrally (Fig. 18). Similar displacement of the dorsal tips of the hyoid are prevented by the hyoquadrate and spiracular ligaments (Fig. 10) but the dorsal ceratohyal and branchial arm may swing laterally. Simultaneous contractions of the subarcualis rectus could enhance this lateral motion by pulling the dorsal branchial arm anterolaterally and the anterior ceratohyal caudoventrally. These movements rapidly enlarge the buccal cavity, further reducing the internal pressure. As a result, water influx continues and water between the jaws is sucked further caudally. Flow rate through the mouth may still be increasing at this time. This would aid in carrying the prey caudally into the buccal cavity.

The levator mandibulae complex may close the mouth by either elevating the mandible or depressing the snout, again depending on the degree of contraction of the spinal elevators and depressors. The

Figure 18. Modified three bar system representing the hyoid apparatus during (a) resting position and (b) with application of caudal force to the horizontal bar. The horizontal bar represents the basibranchial.


a


b

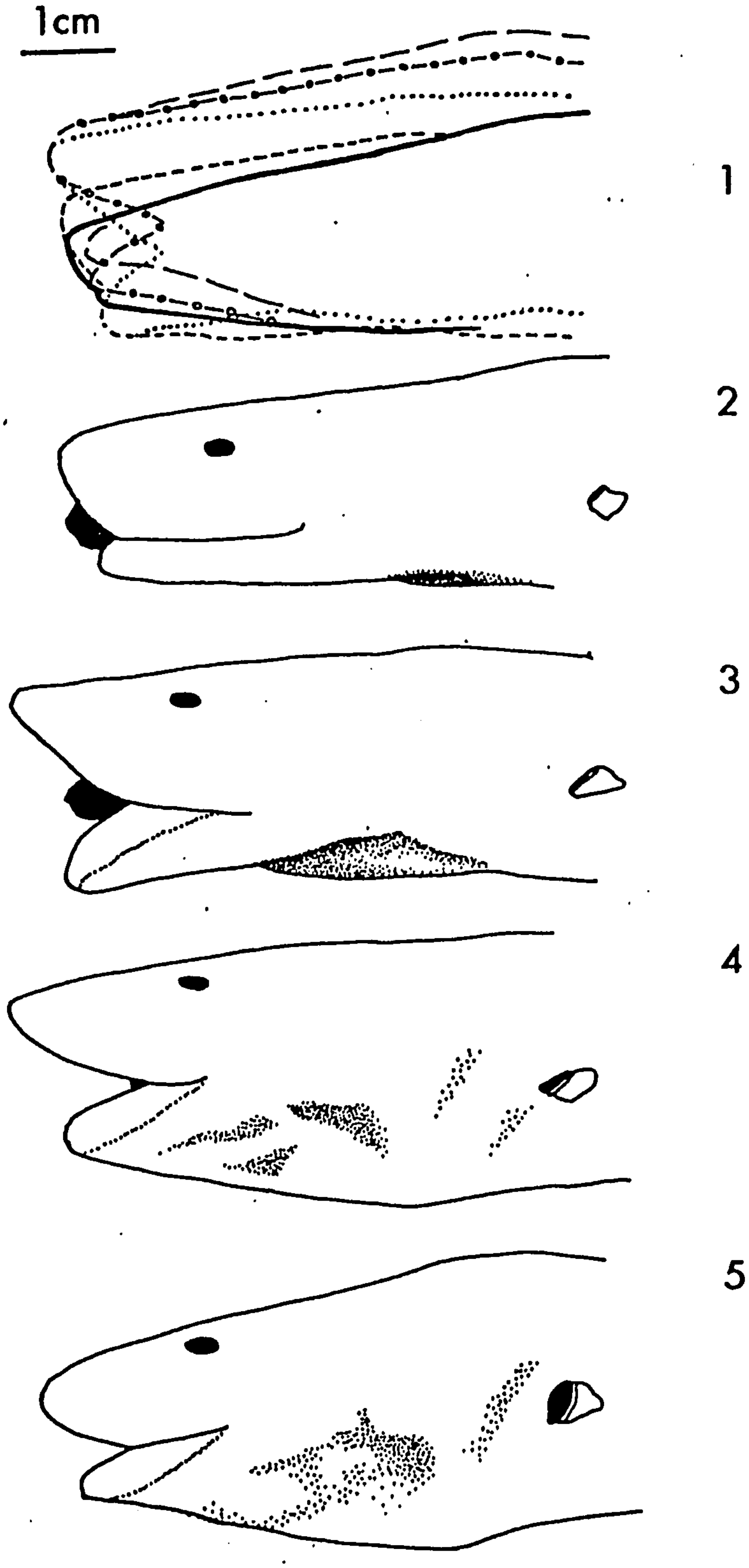
hyomandibular ligament and the geniohyoideus pull the anterior hyoid upward which increases the pressure on the anterior buccal contents. Snout depression, rather than mandibular elevation, usually follows extensive caudoventral displacement of the hyoid apparatus. This suggests that, during closure, the hyoid is pulled caudally by the rectus cervicis and the mandible is prevented from shifting anteriorly by hyomandibular associations. Snout depression may be aided by contraction of the subvertebralis.

As the jaws close the spiracle opens, probably as a result of contractions of subarcualis rectus II and III which would protract epibranchials II and III. Opening the spiracle prevents the development of a large positive intrabuccal pressure during closure and reduces possible efflux between the jaws. Fluid dynamics of capture in which the spiracle opens before closure begins are not clear. Opening of the spiracle prior to filling of the buccal region should result in a flow of water inward through the spiracle which would counteract the development of negative intrabuccal pressure and reduce the rate of inflow through the mouth.

Slight anterior displacement of the entire head of <u>Amphiuma</u> (Fig. 19) during the large buccal shifts in stationary feeding may be attributable to rapid changes in the volume of the buccal cavity (Osse, '69). Such movements should be proportional to the change in buccal volume relative to the weight of the salamander. In large buccal displacements the change is small compared to the volume of whole <u>Amphiuma</u>, but may account for the slight anterior movements recorded in some sequences.

Repeated suctioning that follows engulfment pulls the item further

Figure 19. Tracings of five consecutive frames during a stationary capture sequence filmed at 24 fps.


1cm
1
2
3
4
5

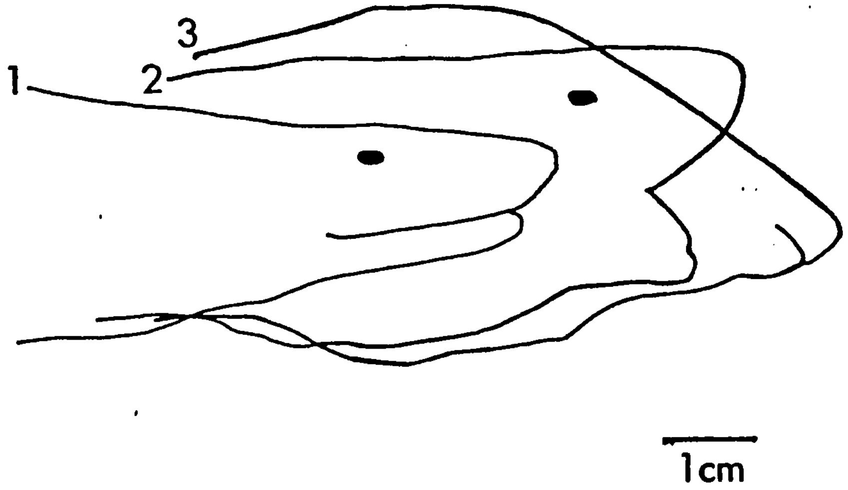
caudally and facilitates swallowing. Following the stationary capture recorded in this study, Amphiuma did not attempt to subdue or macerate the prey prior to swallowing.

### Strike

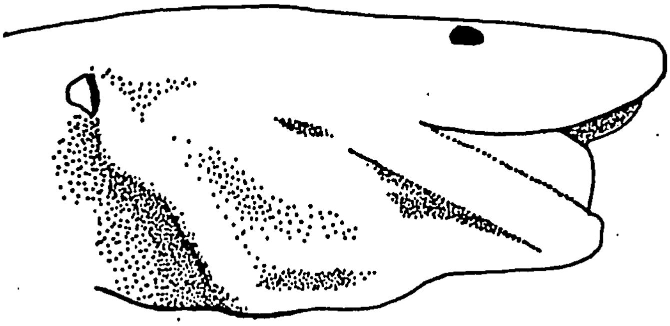
Patterns of displacement during the strike differ from patterns during stationary capture in one important feature. Whereas stationary capture entails a delayed caudal displacement of the medial hyoid, the strike is distinguished by rapid and extensive posterior displacement of the medial hyoid that is synchronous with mouth opening (Figs. 19 and 20). This difference could be generated by advancing the initiation of contraction, and possibly increasing the rate of fiber recruitment of the rectus cervicis and the subarcualis rectus. If the patterns of activity of the remaining cephalic muscles remained similar to those during stationary feeding, the simple advance of hyoid muscle action should generate the movements seen during the strike. Although several features of the strike (immediate displacement of Amphiuma toward the prey as the mouth opens and greatest forward movement correlated with greatest buccal displacement) suggest force-generated displacement of the head, previous consideration of the ratio of buccal volume to body mass suggests that the entire acceleration of the head toward the prey cannot be entirely attributed to inertial reaction to the sudden influx of water. It is therefore proposed that some of the force that shifts Amphiuma forward during the strike is produced by locomotory muscles of the trunk.

Unlike stationary feeding, the strike is characterized by full

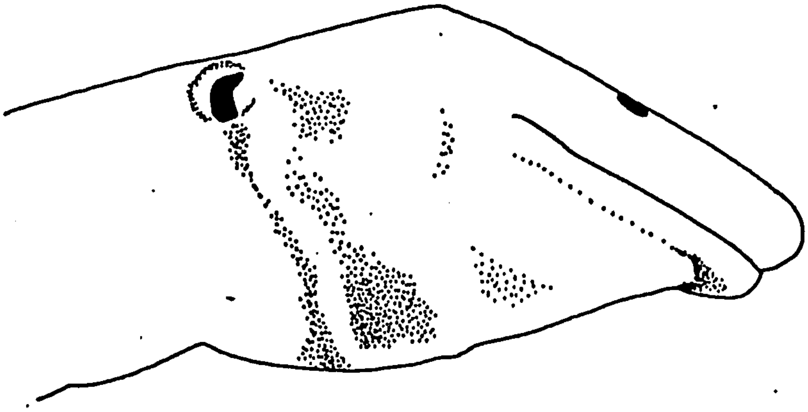
Figure 20. Tracings of three consecutive frames during a strike filmed at 24 fps.



2



3



extension of the lower labial lobe which helps reduce the surface area of the lateral mouth opening. By reducing the total surface area of the mouth opening, the lobes should increase the inflow velocity and limit the peripheral inflow during suction.

As the mouth begins to close the rectus cervicis continues to pull the caudomedial portion of the hyoid caudally while the hyomandibular ligament, possibly with the aid of the geniohyoideus, retains the mandible in its depressed position. As a result, contraction of the levator mandibulae complex depresses the snout while inertia from the strike carries the anterior trunk and craniovertebral joint anterodorsally. Following capture, the spiracle closes and water is forced between the jaws which shifts the prey anteriorly, possibly to the level of the vomeropalatine teeth. The strike is invariably followed by a series of powerful crushing bites combined with hyoid movements that shift the prey along the tooth row. It is possible that this prey movement results in tearing action (Regal, '66), although it seems likely that the major reduction of the prey occurs during a levator power stroke following tooth contact with the prey surface.

## DISCUSSION

### Anatomy

Previous authors have described Amphiuma as a secretive burrowing salamander that prefers habitats with crayfish burrows and have suggested that the stout construction and narrowness of the skull are specializations for burrowing (Hay, 1890; Davison, 1895; Baker, '45; Salthe, '73). However, considering that the form of the head must meet a number of functional demands (Alexander, '67; Dullemeijer, '74) cephalic relationships in Amphiuma must represent a compromise to various activities, including feeding.

The assumption that Amphiuma actively burrows (questioned by Darnell, '48) has led most previous workers to note the rigid construction of the entire skull. It was therefore surprising to find that the perimeter of the snout is capable of appreciable deformation due to the mobility of the maxillae. This mobility would appear to have little advantage during burrowing when force transmission to the medium surrounding the head should be enhanced by rigidity of the peripheral skull elements. Furthermore, apart from the fact that medial displacements of the maxillae would be limited by the dentary tooth row when the mouth is closed, skull width is greatest at the quadratomandibular joints and cannot be decreased by maxillary movements. However, as the mouth opens during feeding, the maxillae may move slightly medially, reducing the width of the mouth opening and increasing inflow velocity. Also, during closure, contraction of the levators would stress the pterygomaxillary ligament and pull the maxillae medially. Such movements appear to occur and may serve several functions. First, the maxillary tooth row is depressed and brought closer to the prey, increasing the probability of maxillary tooth contact should the prey attempt to escape. Second, the elasticity of both the maxilloprefrontal joint and the pterygomaxillary ligament may serve to dampen shock transmission to the braincase during rapid closure.

Salthe ('73) noted that the premaxilla of Amphiuma is co-ossified.

As defined by Trueb ('70), co-ossification involves fusion of ossified regions of the dermis to underlying bone. This is not the case in Amphiuma in which the premaxilla is covered by a thick layer of spongy connective tissue providing considerable mobility of the epidermis relative to the surface of the premaxilla. Therefore, the premaxilla of Amphiuma is not co-ossified and the integument is not modified noticeably for burrowing.

Elongation of the head of Amphiuma has resulted in a concommitent elongation of the various tooth rows (Regal, '66). In most aquatic salamanders, the palatal tooth rows tear the prey as it shifts in and out of the mouth. In Amphiuma, the position of the teeth and the orientation of the cusps may result in a slicing action as the prey is forced along the teeth, as suggested by Baker ('37). Shearing force may be generated by the parallel arrangement of the maxillary and vomeropalatine teeth on either side of the dentary tooth row. However, it seems unlikely that the shape of the tooth rows is solely related to feeding on crayfish, because Cryptobranchus, which also feeds predominantly on crayfish (Nickerson and Mays, '73), has maxillary and vomeropalatine tooth rows that form almost perfect arcs.

Unlike the laterally elongate mouth opening in Amphiuma (Noble, '31; Baker, '45), most aquatic salamanders have a small anterior mouth opening (Özeti and Wake, '69), that is further reduced by labial lobes (Matthes, '34). The angle of the mouth in aquatic larval salamanders actually lies anterior to the eye and migrates caudally during metamorphosis to the terrestrial adult (Ozeti and Wake, '69). Only Cryptobranchus, which also feeds on crayfish (Nickerson and Mays, '73), has a mouth opening as extensive as that in Amphiuma. Considering that most salamanders are carnivorous and will eat anything that fits into their mouth (Noble, '31; Cochran, '52), the elongate opening, by increasing gape size, may permit Amphiuma to consume larger and more diverse prey. The long jaws and their associated tooth rows may also increase the probability of snagging elusive prey, and perhaps facilitate handling of elongate prey. The labial lobes,which occlude much of the lateral aspect of the mouth during opening, are flexible and probably do not prevent the engulfment of larger prey.

Reviewing considerations of head shape, the nature of the integument covering the snout and the flexibility of the maxillae suggest that Amphiuma does not burrow in dense soils. Tapering of the snout and elongation of the jaws may facilitate burrowing in loose substrates and passage through narrow crayfish burrows. Additionally, these features, in association with the form of the tooth rows, may allow Amphiuma to utilize larger and more active prey than other aquatic salamanders with smaller mouth openings.

Some major differences in cephalic architecture between Amphiuma and smaller aquatic salamanders or salamander larvae may scale force generation to an increase in size. The elaborate otic region and numerous well defined fossae and crests increase the surface area for attachment of the massive levator musculature. The unipinnate arrangement of the anterior levator and the bipinnate arrangement of the mandibular depressor increase force generation with minimal additional bulk (Gans and Bock, '65; Alexander, '68). Further arrangement of the posterior depressor, which connects the mandible and the branchial arm, may simplify the problem of applying simultaneous force to both elements during expansion. A similar arrangement has arisen independently in the Sirenidae, another suction feeding group with large species (Martof, '74).

Cope (1886) originally described the presence of an atlas-mandibular ligament in Amphiuma, and numerous subsequent authors (see Salthe, '73) have referred to the structure. Hinderstein ('71) has provided a description of the ligament in desmognathines that differs in a number of important respects from the structure in Amphiuma. First, in Amphiuma, a collagenous band is formed by the coalescence of tendon fibers extending from the insertional ends of the levator mandibulae muscle fibers arising from the anterior vertebrae. Thus, this band has no direct attachment to any of the trunk vertebrae and is more appropriately called a tendon. Secondly, the tendon does not lie within the levator mandibulae, but instead along the ventrolateral edge of the muscle. Levator mandibulae fibers arise from the dorsolateral aspect of the neural arches of the anterior vertebrae, and insert into a tendinous sheet extending from the dorsal edge of the tendon to form the unipinnate arrangement described above.

Amphiuma is also superfically similar to desmognathines in possesing stalked occipital condyles (Cope, 1886). In desmognathines these processes are presumed to be associated with increased mobility at the craniovertebral joint that permits the occipital condyles to slide ventrally on the atlas as the snout is raised (Hinderstein, '71). This displacement is presumed to be necessitated by the arrangement of the atlas-mandibular ligment. In Amphiuma, there is extraordinary craniovertebral flexibility, but this mobility of the braincase is not associated with structural limitations to mandibular rotation because there is no atlas-mandibular ligament.

The structural arrangement of the hyoid combined with behavioral analysis suggest that the apparatus is designed to generate maximum instantaneous buccal inflow. Similar caudal ossification is seen in other aquatic salamanders (Weidershiem, 1877; Ozeti and Wake, '69) but only Amphiuma possesses a fused branchial arm. Fusion of certobranchial I and epibranchial I would increase the rigidity of the branchial arm during rapid expansions against large pressure gradients generated during the strike. The anterior connective tissues surrounding the basi- and hyophyal cartilages appear to provide a semi-elastic rigidity to the anterior buccal floor, and may play an integral role in buccal floor depression during the strike and in shock absorption during the crushing of prey with hard, irregular external surfaces, such as crayfish.

## Mechanism

The only previous detailed description of aquatic salamander feeding (Matthes, '34) reported a single mode of capture but was limited to observations of salamanders feeding on worms. Amphiuma also exhibits only stationary capture when feeding on worms. Unlike Amphiuma which feeds on relatively elusive prey such as crayfish, fish, frogs, snakes, and other Amphiuma (Bromley, '20, '39; Baker, '37), larval salamanders typically feed on worms and insect larvae (Cochran, '52), and elusive prey do not appear to comprise a large portion of the regular diet. However, it appears possible that other aquatic salamanders may also strike at agile prey. Although Amphiuma also feeds on smaller, less active prey, such as worms, the elongate jaws of Amphiuma have the potential for a relatively large gape. Effective use of the larger gape without significant reduction in inflow velocity may have been the driving force that lead to the strike mechanism.

The behavior of the spiracle is clearly crucial to the efficiency of the buccal pump mechanism in Amphiuma. Outflow of ink through the spiracle during closure in stationary capture supports Regal's ('66) contention that the spiracle in Amphiuma promotes unidirectional water flow. The timing of the spiracle during the strike may not promote unidirectional flow, but seems to be timed to prevent development of excessive intrabuccal pressure, and the excessive anterior efflux of water during the critical stages of mouth closure.

Two distinct capture patterns in Amphiuma appear to be correlated with mobility of prey items, similar to a pattern seen in some teleosts (Liem, '78, '79, '80). In Amphiuma, asynchronous mandibular and hyoid excursions are seen during capture of sluggish prey whereas simultaneous expansion and depression accompany capture of agile elusive prey. EMG recordings in cichlids (Liem, '78) show that two distinct neuromuscular patterns are utilized during capture and that these patterns are determined prior to feeding through an evaluation of prey activity by the predator. Synchronous contraction of cephalic muscles results in a high velocity suction which is used in the capture of agile prey, and asynchronous contraction is used during capture of sluggish prey. Simultaneous depression of the hyoid and mandible, and thus possibly synchronous activity of the jaw depressors and rectus cervicis, may similarly result in a higher velocity suction in Amphiuma. Although there is no

EMG data to verify muscle activity patterns in Amphiuma, it is possible that a pattern similar to that observed in some teleosts is seen here.

Lauder ('83) describes suction feeding in several species of Lepomis (sunfish) which feed on a variety of prey. EMG data reveal that these teleosts exhibit considerable variability in muscle activity patterns that vary with the type of prey. Lauder ('83) attributes the two stereotyped suction mechanisms seen in Cichlids (Leim, '78) to limitations imposed by cranial structure. Variability similar to that seen in Lepomis is seen during stationary capture in Amphiuma. Such variability within a feeding pattern would allow the predator to match displacements to relative prey size. The consistency observed between sequences in the strike may be due to the fact that the strike results from maximum activation of the system. The retention of a highly variable stationary mechanism after the appearance of the strike (assuming that stationary capture is primitive) may be based on any of the following considerations. First, the stationary mode of capture may be more efficient energetically. Second, stationary capture involves small displacements that would create less disturbance in the water column that may attract predators. Third, stationary capture reduces the likelihood of damage to Amphiuma that may result from a misdirected strike. Although additional investigation is necessary to discover the range of responses to different types of prey, the elongate jaws and variability of feeding mechanisms allows Amphiuma to utilize prey of diverse sizes, shapes and behavior.

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