

Morphology and Behavior of the Feeding Apparatus in *Cryptobranchus alleganiensis* (Amphibia: Caudata)

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ABSTRACT Cine and high-speed videographic analyses of feeding in *Cryptobranchus alleganiensis* demonstrate that prey are captured by either inertial suction or a strike combined with suction. Movements of cephalic elements during capture are generally similar to those of other suction-feeding vertebrates but more variable than those of most aquatic salamanders. Following capture, prey frequently are manipulated and transported into and out of the buccal cavity across the teeth.

Specific features of the skull, mandibles, hyoid apparatus, and cephalic musculature of *Cryptobranchus* correlate directly with behavior. Although the skull is massive, sutures of the anterior braincase permit limited torsion, the maxillae move on their attachments to the braincase, and left and right mandibles are separated by elastic connective tissues. These features provide flexibility and permit asynchronous and asymmetric movements of the mandibles. Equivalent asymmetry and asynchrony of hyobranchial movements are also correlated with specific structural arrangements that may be neither paedomorphic nor primitive.

Its feeding mechanics suggest that *Cryptobranchus* represents a unique and highly derived condition among salamanders. Its ability to modulate movements of the left and right sides of its head argues strongly for the existence of bilaterally asynchronous motor patterns, and patterns of force generation, similar to but much faster than those employed in mammalian mastication.

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Recent research on suction-feeding vertebrates has demonstrated similarities in basic patterns of cranial kinematics and muscle activity. The emerging consensus is that suction feeders conserve some patterns of skeletal movement and muscle activity across wide phylogenetic scales, but that many quantifiable features differ among taxa (Lauder, '85, '86; Wainright et al., '89; Reilly and Lauder, '92). Despite the hazards of extrapolating and generalizing from the data (Lauder, '86), two interpretations of these observations are (1) that differences are correlated with changes in peripheral morphology, and (2) that similarities derive from basic physical constraints associated with driving a rapid change in buccal volume.

Most past work has assumed that vertebrate suction feeders use bilaterally synchronous and symmetrical motor and movement patterns during prey capture. Here we describe aspects of the suction-feeding appara-

tus in *Cryptobranchus alleganiensis*, a salamander that uses bilaterally asynchronous and asymmetric movements (Cundall et al., '87).

Numerous recent studies explore the feeding apparatus in various species of aquatic salamanders (Erdman and Cundall, '84; Lauder and Reilly, '88; Lauder and Shaffer, '85, '86, '88; Shaffer and Lauder, '85a, b; Reilly and Lauder, '88, '89, '92). Much of this effort has been devoted to analyzing kinematic and muscle activity patterns in larval *Ambystoma*, animals with a stereotyped feeding mechanism that varies slightly among individuals but seems uninfluenced by differences in prey type (Reilly and Lauder, '89). Recent comparative studies among six species of aquatic salamanders (Reilly and

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Lauder, '92) showed that *Cryptobranchus* differed from the other species in having greater mandibular and hyoid excursions. Whereas all aquatic salamanders conform to basic kinematic patterns found in other suction feeders, multivariate kinematic and morphological comparisons placed *Cryptobranchus* well away from the other salamander taxa. The goals of this report are to consider (1) aspects of kinematic variation and potential movements of the feeding apparatus in *Cryptobranchus*, and (2) how the structure of the feeding apparatus makes possible the various kinematic patterns.

BACKGROUND

Cryptobranchus is a large salamander that inhabits moderate to fast-flowing streams and rivers of the Appalachian and Ozark regions of the eastern and central United States (Dun-dee, '71; Conant and Collins, '91). Although it is known to feed on a variety of invertebrates and small vertebrates, most prey items recovered from stomachs are crayfish (Nicker-son and Mays, '73). Reilly and Lauder ('92) suggested that the relatively greater mandibular and hyoid excursions of *Cryptobran-chus* may relate to its large size and flat head. However, neither Reilly and Lauder ('92) nor Shafland ('68) dealt with the bilateral asym-metry of jaw and hyoid kinematics described by Cundall et al. ('87).

Despite their extraordinary size, paedomor-phic nature, and periodic use in comparative anatomy teaching labs (Branch, '35), crypto-branchids have been the subjects of surpris-ingly few detailed anatomical treatments. Parker (1882) described the skull and vis-ceral arch skeleton of both the adult and selected developmental stages of *Cryptobran-chus*. Subsequent original works (Cope, 1889; Reese, '06) largely confirmed Parker's obser-vations. The only detailed account of skull development is that of Aoyama ('30) for *An-drias japonicus*. Cranial variation in Recent and fossil cryptobranchids was described by Meszoely ('66), Estes ('81), and Naylor ('81). All descriptions of the osseous parts of the skull and hyoid are in general agreement, but accounts of the cartilaginous regions contain numerous inconsistencies (e.g., Parker, 1882; Reese, '06; Branch, '35; Hilton, '50; Jollie, '62).

The cephalic muscles of *Cryptobranchus alleganiensis* and *Andrias japonicus* were described by Fischer (1864). His work was followed by less detailed studies by Mivart (1869, *C. alleganiensis*) and Humphry (1871,

A. japonicus). Drüner ('04) described the muscles of the hyoid, branchial arches, and larynx in both *C. alleganiensis* and *A. japoni-cus*, and Luther ('14) compared their trigemi-nal muscles. Schumacher ('58, '59) more re-cently added details of the cephalic muscles in *A. japonicus*. Collectively, the works of Fischer (1864), Drüner ('04), Luther ('14), and Schumacher ('58, '59) accurately de-scribe the suction apparatus, but several structural features critical to the function of the feeding apparatus were omitted. Our ana-tomical descriptions stress these features.

MATERIALS AND METHODS

Behavior of the feeding apparatus was de-termined from film and video recordings of six living *Cryptobranchus alleganiensis* (to-tal lengths of 20, 50, 51, 51, 56, and 56 cm) feeding on crickets, earthworms, and gold-fish. Feeding was recorded on Super-8 film at 18–36 fps using a Canon 1014 XLS movie camera, or filmed at 120 fps with an Instar video system; both systems used synchro-nized strobe illumination. Behavioral descrip-tions are based on frame-by-frame analysis of 38 strikes (24 Super-8 records; 14 video re-cords) and 410 manipulatory cycles (293 Su-per-8; 117 video).

Kinematic analyses were based on plots of the positions of discrete points on the head in successive frames of film or videotape. Actual points used for these analyses varied among sequences because the animals were not trained and rarely used the same postures in successive sequences. Further, animals were fed a variety of prey. Consequently, few se-quences were sufficiently comparable to ex-amine statistically. In these respects, this study differs from the approach of Reilly and Lauder ('92) in which all animals were treated the same way, fed the same prey, and filmed in a uniform manner to facilitate statistical analysis. Many of our sequences were ana-lyzed using movement notation, a series of symbols indicating direction and extent of movement. These symbols were applied to all independently movable parts of the feeding apparatus visible on film and provided a rapid means of recording and comparing the tim-ing of events. Anterior and oblique views gave the most useful data on the asymmetric behavior of the feeding apparatus.

To determine the potential mobility of cer-tain elements of the feeding apparatus, seven adult specimens (46.5–56.0 cm) of *Crypto-branchus* were anesthetized by immersion in 0.1% aqueous tricaine methanesulfonate. Ma-

nipulation of the mandible and hyoid apparatus provided information on their potential displacements. Stresses also were applied manually to different points on the skull to determine whether sites normally regarded as immobile sutures actually display some mobility. Angular displacements generally were measured using a goniometer or a protractor reticle in the ocular lens of a stereomicroscope. To determine where elements of the hyoid apparatus might be at peak hyoid depression, still radiographs were taken of the feeding apparatus in relaxed (compressed) and expanded (achieved by inflating latex balloons or 5 cc Foley catheters in the buccal cavity) positions.

Morphological descriptions of the feeding apparatus are based on dissections of eight preserved specimens (Carnegie Museum 58293, 58294, 58297, 58301; Lehigh Univ. 1345, 1349, 1404, 1410) and two dried skulls (prepared from specimens purchased from a commercial supplier). Dissections were performed with the aid of a stereo dissecting microscope and drawings were made by coor-

dinate transposition using an ocular grid micrometer.

Details of the structure of the mandibular symphysis were obtained both by microdissection and by removal and histological preparation of the symphyseal soft tissues from four specimens. These were serially sectioned (three transversely, one frontally) and mounted for staining with hematoxylin and eosin (Humason, '79), a trichrome stain (Hansen's hematoxylin, xylidine red, and light green), and iron gallein elastic tissue stain (Cherukian and Schenk, '76).

RESULTS

Form of the feeding apparatus

Skull

The skull is most easily considered in terms of regions that, although not anatomically distinct, appear to contribute in different ways to the mechanics of feeding. These regions are the upper jaws, the braincase, the orbital region, the postorbital region, and the suspensorium. Apart from these terms, and except

Abbreviations

A	articular	imp	intermandibularis posterior
Aa	articular cartilage of articular bone	laI	levator arcuum I
adm	anterior depressor mandibulae	laII, III	levators arcuum II, III
af	anterior fold of buccal muscoa	lme	levator mandibulae externus
AO	antorbital cartilage	lmp	levator mandibulae posterior
BB	basibranchial	msl	median symphyseal ligament
BH	basihyal	MX	maxilla
C	coronoid	NA	nasal
CBI-IV	ceratobranchials I-IV	OCC	occipital condyle
CH	ceratohyal	OS	orbitosphenoid
clig	capsular ligament	PA	parietal
csl	central symphyseal ligament	pdm	posterior depressor mandibulae
DE	dentary	PFR	prefrontal
dl	dorsal branchiohyoid ligament	PMX	premaxilla
dlmal	deep levator mandibulae anterior (superficial head)	pml	pterygomaxillary ligament
dlma II	deep levator mandibulae anterior (intermediate head)	PRO	prootic
dlmaIII	deep levator mandibulae anterior (deep head)	PS	parasphenoid
dly	dilator laryngeus	PT	pterygoid
dsc	dorsal symphyseal cartilage	PTa	pterygoid articular cartilage
dl	dorsal branchiohyoid ligament	PTP	pterygoid process
EBII	epibranchial II	Q	quadrate
em	epaxial musculature	Qa	quadrate articular cartilage
EO	exoccipital	rc	rectus cervicis
FR	frontal	S	stapes
gg	genioglossus	shc	superficial levator mandibulae anterior
gh	geniohyoideus	sl	suborbital ligament
HBII, III	hyobranchial II, III	slma	superficial levator mandibulae anterior
HHI-III	hypohyal I-III	so	subarcualis obliqui
hml	hyomandibular ligament	SQ	squamosal
ht	hyotrachealis	srI	subarcualis rectus I
ibl	interbranchial ligament	srII, III	subarcualis rectus II, III
ih	interhyoideus	ssl	superficial symphyseal ligament
ima	intermandibularis anterior	V	vomer
		vsc	ventral symphyseal cartilage
		V ₃	mandibular branch of trigeminal nerve

as noted, the terminology follows Francis ('34).

The upper jaw consists of the premaxilla, maxilla, and vomer (Figs. 1, 2). The prenasal described by Parker (1882) was absent in all specimens we examined but may represent one of a number of ectopic bones present in some specimens (Meszoely, '66). The medial ends of both the premaxilla and maxilla have short processes (nasal process of premaxilla; frontal process of maxilla) that project posteriorly to articulate with the anterior ends of the braincase. The external nares lie in the gap between the nasal and frontal processes (Fig. 2).

The premaxilla and maxilla bear a continuous, nearly hemispherical row of ~100 bicuspid teeth (Reese, '06; Kerr, '60). Cusps of anterior teeth are aligned with the transverse plane, and their distal tips curve posteriorly. In more posterior teeth, the tips point posteromedially and the cusps lie at ~45° to the transverse axis. In some posterior teeth, the apical and labial cusps are not aligned: the apical cusp lies more nearly in line with the transverse plane.

The anteroventral border of the vomer bears a second row of about 50 bicuspid teeth that lie concentric to but extend only half the length of the premaxillary-maxillary row (Fig.

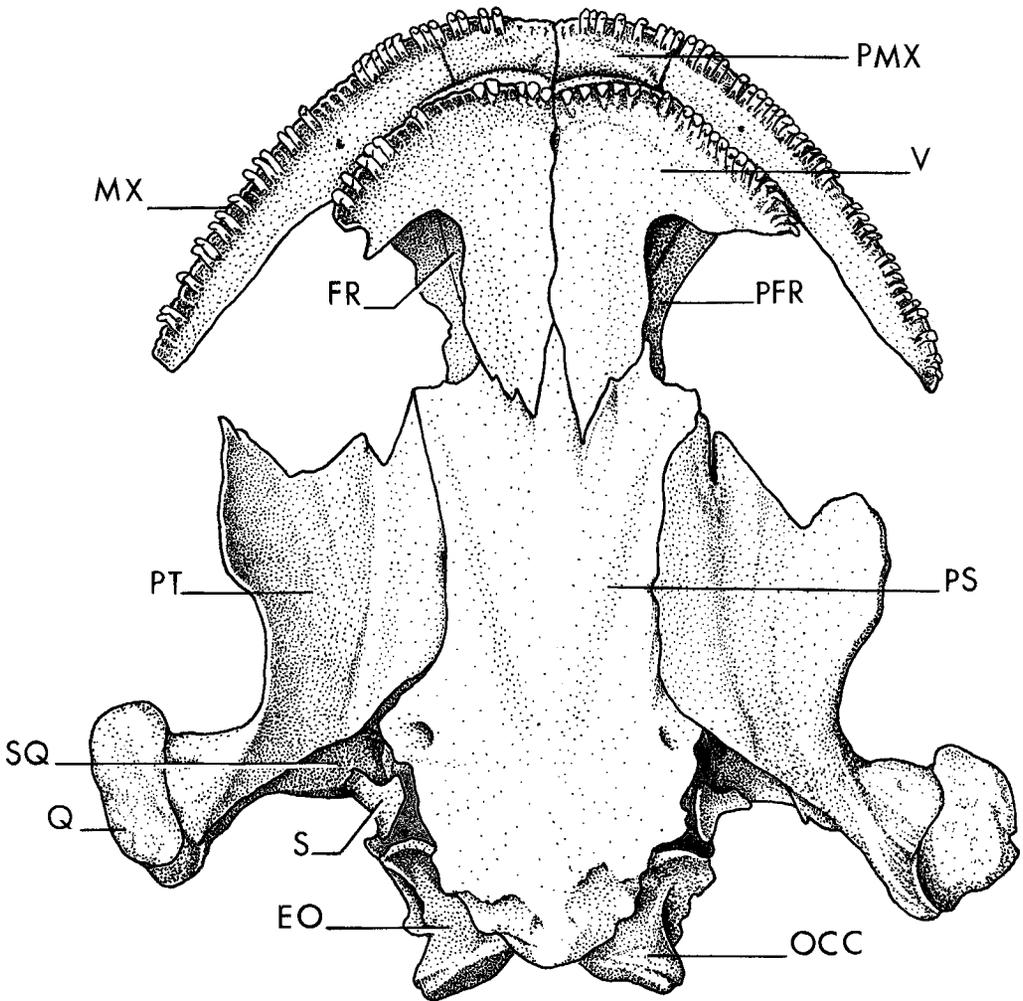


Fig. 1. *Cryptobranchus alleganiensis*. Ventral view of the skull. Cartilaginous regions indicated by solid gray tones.

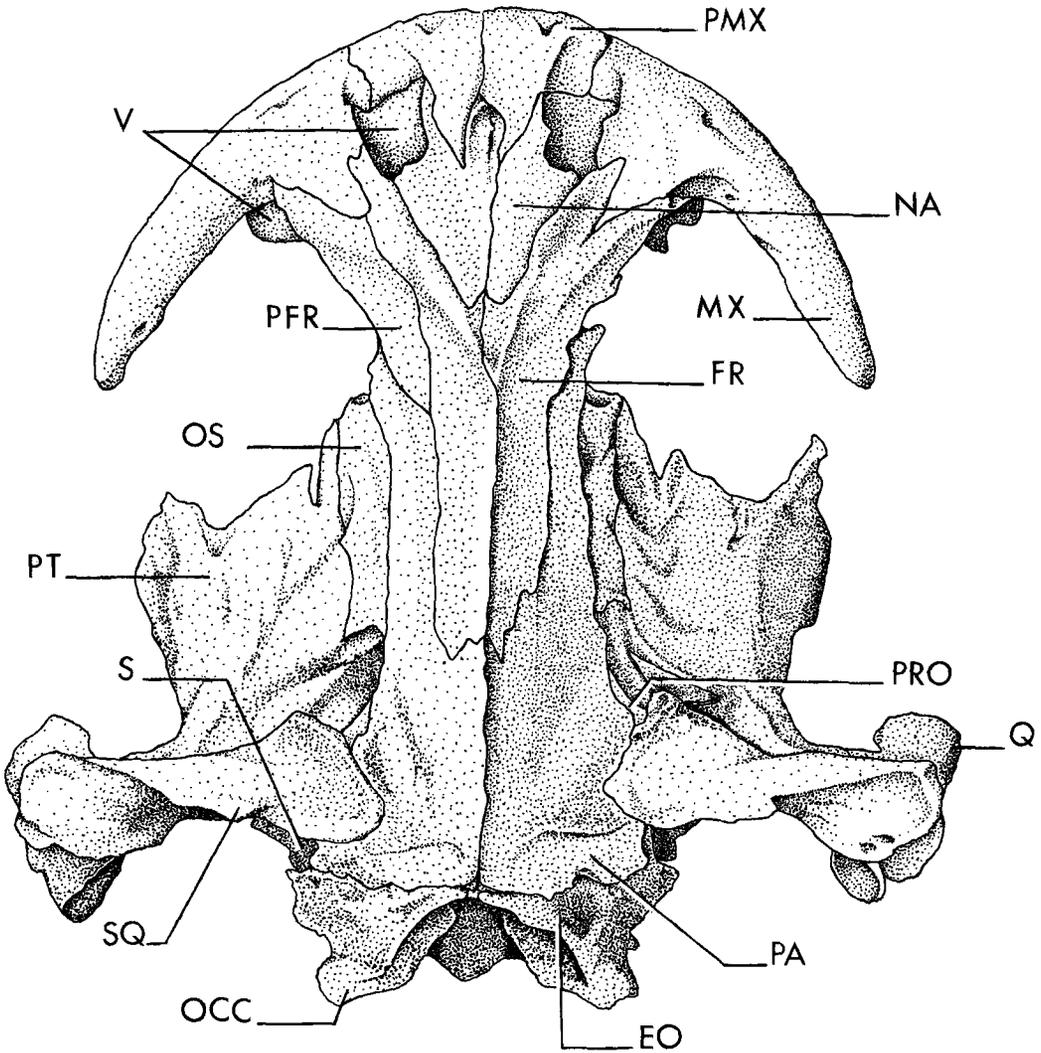


Fig. 2. *Cryptobranchus alleganiensis*. Dorsal view of skull. Note that this specimen lacks a discrete prefrontal on the right: the ventral surface of the frontal shows a groove at the point that the suture usually occupies. Cartilaginous prootic region left unshaded.

1). The lateral border of each vomer is emarginated at the point of entrance of the internal naris, and the remainder of the bone forms a posteriorly directed parasphenoid process that is flat and as wide as the premaxilla. An interdigitate and relatively tight suture connects the caudal edges of these processes to the parasphenoid, which forms the entire floor of the braincase.

The remainder of the bony braincase consists of the paired nasals, frontals, prefrontals, parietals, orbitosphenoids, prootics, and exoccipitals. Between the vomers and that

part of the roof of the braincase lying anterior to the orbitosphenoids is the complex nasoethmoid cartilage (Reese, '06). The ant-orbital process of this cartilage extends laterally (Fig. 3) to form the anterior floor of the orbital area. Although the bones of the braincase and the associated nasoethmoid cartilage appear to form a rigid housing for the brain and an immovable support for the upper jaw apparatus (Figs. 1-4), the anterior braincase does have limited flexibility.

Movements of the head of an anesthetized animal (and of skulls that had been soaked in

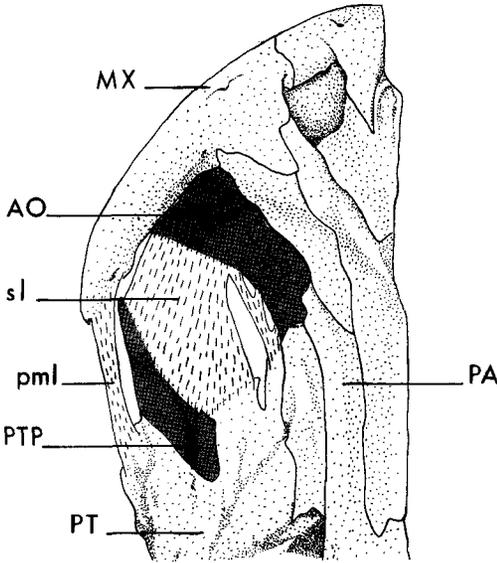


Fig. 3. *Cryptobranchus alleganiensis*. Anterodorsal view of the left half of the skull to show the orbital cartilages (gray) and ligaments.

water) indicate that the anterior tooth row of the upper jaw apparatus may rotate around the long axis of the braincase by as much as 3° to 4° to either side of its resting position. Further, each maxilla may flex about its joint with the premaxilla by 2° to 4° . These movements stem partly from the fact that attachments between the maxilla and the associated bones are syndesmotomic and partly from the flexibility of the thin bones in the roof of the anterior braincase. This flexibility ap-

pears to be enhanced by the orientation of sutures, both dorsally and ventrally, along radii of the circle formed by the premaxillary-maxillary complex (Fig. 5; see also vomero-parasphenoid sutures in Fig. 1). The geometric center of this circle lies very near the anterior end of the midsagittal crest of the frontals, which is also the narrowest region of the skull.

Between the occipital region and the orbit, the midsagittal crest and most sutures on the dorsal surface of the braincase run longitudinally. The crest and sutures are oriented approximately perpendicular to the direction of the fibers of the mandibular levators. At the caudal end of the parietals, crests associated with the attachment of the anterior epaxial muscles are oriented transversely, again perpendicular to the orientation of epaxial muscle fibers.

The floor of the braincase is formed by the parasphenoid. Posteriorly, low transverse crests mark the anterior attachment points of the subvertebral muscles. The vertical distance of these crests from the axis of rotation of the occipital condyles is one-third the distance between the occipital condyles and the transverse parietal crests. This difference in crest height (or distance from the axis of occipital condyle rotation), in combination with a difference in the cross-sectional area of epaxial and subvertebral muscles (epaxial cross-sectional area is approximately three times that of the subvertebral muscles), indicates that much greater force may be exerted in elevating the braincase than in depressing it.

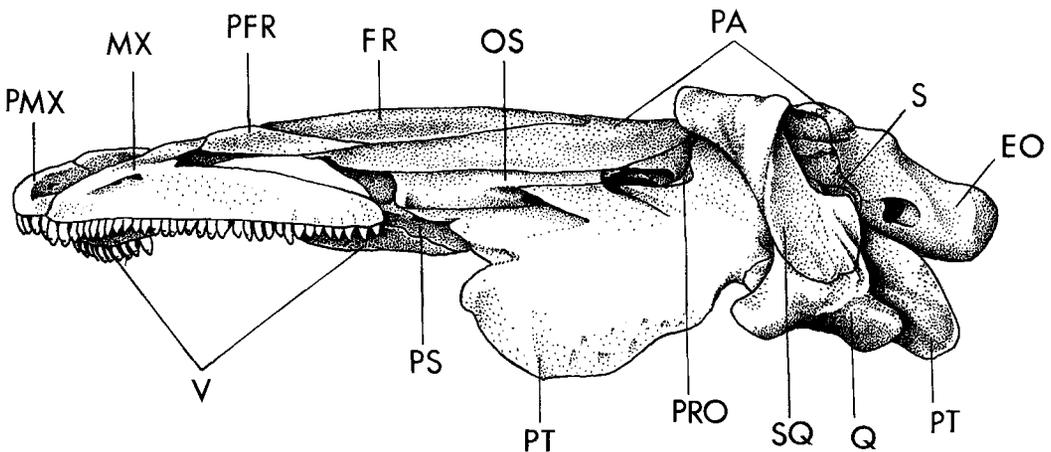


Fig. 4. *Cryptobranchus alleganiensis*. Lateral view of the skull.

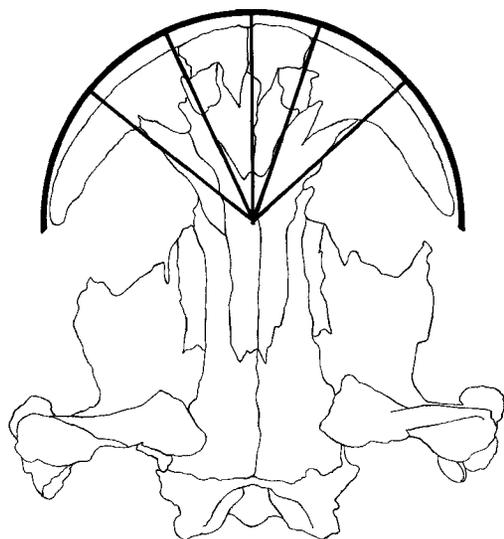


Fig. 5. *Cryptobranchus alleganiensis*. Dorsal view of braincase indicating sutural alignment along radii of a superimposed semicircle. Considerable lifting or depression of the free ends of the semicircle can occur with minimal movement at the distal ends of the sutures.

The orbital area of the skull is the large vacuity surrounded by the maxilla, prefrontal, orbitosphenoid, and pterygoid. The eye lies at its lateral edge, medial to the caudal end of the maxilla. Medial to the eye, a tough suborbital ligament (pterygo-maxillary membrane of Schumacher, '58) extends from the caudoventral edge of the antorbital cartilage to the medial edge of the pterygoid process (epipterygoid cartilage of Parker, 1882) and associated pterygoid (Fig. 3). Unlike the condition in *Andrias japonicus* (Schumacher, '58), this ligament does not attach to the medial edge of the maxilla.

The postorbital skull consists only of that part of the pterygoid lying anterior to the suspensorium. This part of the pterygoid is very broad and curves ventrally at its lateral border, which lies immediately medial to the mandible (Parker, 1882; Reese, '06). The mandibular levators cross over this bone to insert on the lower jaw. When the mandibles are abducted, the pterygoid acts as a simple pulley causing forces generated by contraction of the mandibular levators to be directed dorsally rather than medially. A thick pterygomaxillary ligament extends from the anterolateral corner of the pterygoid to the posterior tip of the maxilla (Fig. 3). Because this ligament attaches those regions of the

maxilla and pterygoid that have the greatest potential mobility, the function of the ligament remains unclear, although it undoubtedly prevents the anterior fibers of the mandibular levators from slipping between the pterygoid and maxilla.

Caudal to the postorbital skull, the pterygoid becomes a posterolaterally directed process that forms the ventral half of the suspensorium. The remainder of the suspensorium is formed by the squamosal and quadrate (Figs. 1, 2, 4). The structural relationships between the suspensorial elements and the braincase are complicated by the retention and incorporation of various regions of the chondrocranium between the squamosal and posterior pterygoid and between the pterygoid and the lateral wall of the braincase. Basically, the suspensorium is attached to the osseous braincase at two points. Dorsally, the spatulate proximal end of the squamosal is syndesmotically attached to the edge of the parietal (Fig. 2) and the extreme dorsal edge of the prootic. Ventrally, the medial edge of the pterygoid fits into a long groove formed primarily by the parasphenoid, the orbitosphenoid contributing to the dorsal edge of the groove. This joint is primarily syndesmototic but also contains some cartilage, presumably a remnant of the lamina orbitonasalis (de Beer, '37). The quadrate is tightly attached to the squamosal dorsally and to the pterygoid ventromedially.

Based on movements of dried skulls and dissected specimens, the entire suspensorium is capable of limited transverse rotation. Movement of the distal end of the suspensorium causes sliding and tension or compression at the squamosal-parietal joint (Figs. 2, 4). In dissected specimens, the pterygoid may be rotated around its long hinge joint with the parasphenoid $\sim 5^\circ$ to either side of the resting position. Rotation is greater in dried skulls.

The distal ends of the quadrate and pterygoid collectively form the joint between the braincase and the mandible, usually termed the quadrate-articular joint. Its arrangement in *Cryptobranchus* was briefly considered by Cundall et al. ('87). The articular cartilage is convex and broadest anteriorly (Fig. 6). Its anterior end fits into a depression formed by a cartilaginous surface on the anterolateral edge of the suspensorial process of the pterygoid. The posterior region of the articular fits against the medial edge of the quadrate and the cartilaginous surface of the posterior tip

of the suspensorial process of the pterygoid. The articular surface of the quadrate, also convex, fits into a membrane-bound sac lateral to the articular. Radiographs of an anesthetized specimen suggested that the articular slides laterally during abduction. At $\sim 30^\circ$ of abduction, the entire length of the articular is in contact with the convex surface of the quadrate. During extreme abduction, only the posterior articular is in contact with the suspensorium, and this contact appears to lie in the region formed by the most posterior tip of the pterygoid and adjacent quadrate.

The mandible is attached to the suspensorium by a robust ligament that extends from the periosteal surfaces surrounding the entire joint complex. The ligament is thickest laterally, containing an inverted Y-shape band of dense collagen that arises from the lateral crest of the squamosal and extends to the rostral and caudal ends of the joint. The remainder of the ligament is thinner and

composed of irregular bands of woven collagen. The arrangement of the ligament allows considerable freedom of rotation around the longitudinal and transverse axes.

Mandible

The mandible of *Cryptobranchus* is composed of dermal dentary and coronoid elements that form all of the mandible except the articular region, which is derived from Meckel's cartilage. The ventral region of the articular ossifies to form the articular bone and retroarticular process (Fig. 7). The shape of the lower jaw superficially but, incorrectly, appears hemispherical. The anterior half of the lower jaw is nearly hemispherical, whereas the posterior half is essentially straight.

Cundall et al. ('87) briefly described the asymmetric movement of the mandibles and the basic structure of the symphysis. The dentaries terminate anteriorly in plates of

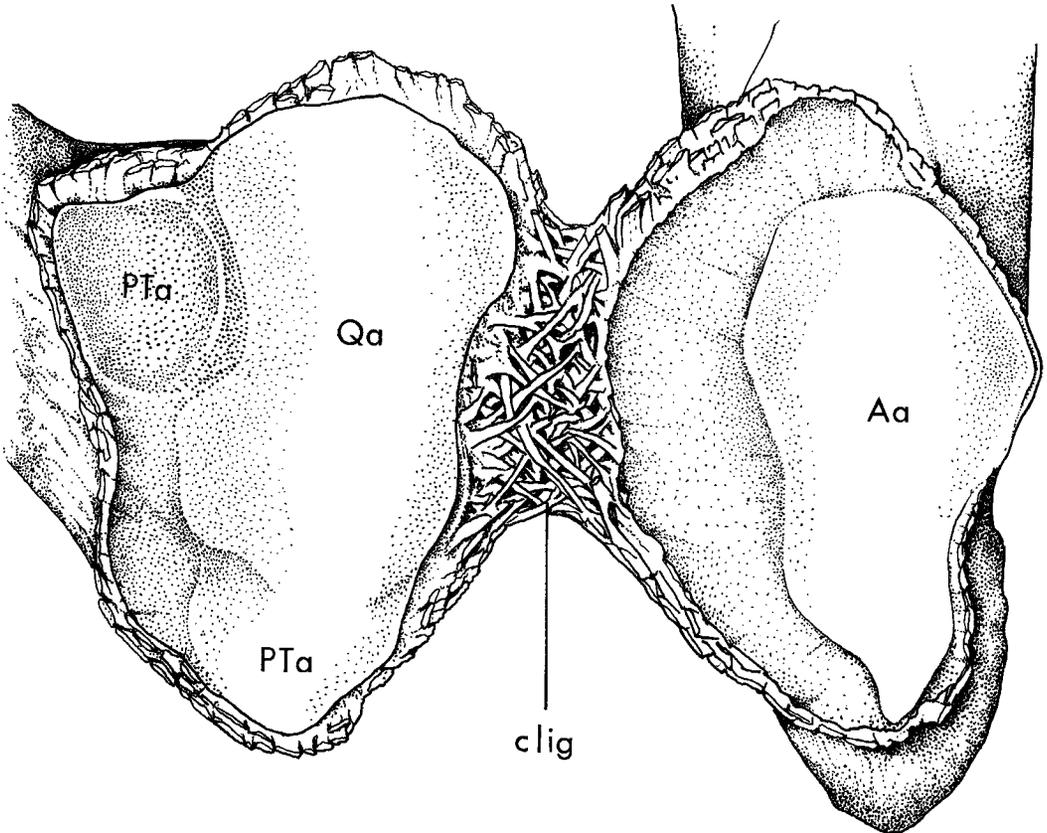


Fig. 6. *Cryptobranchus alleganiensis*. View of the opened quadrate-articular joint following severing of the medial capsular ligament.

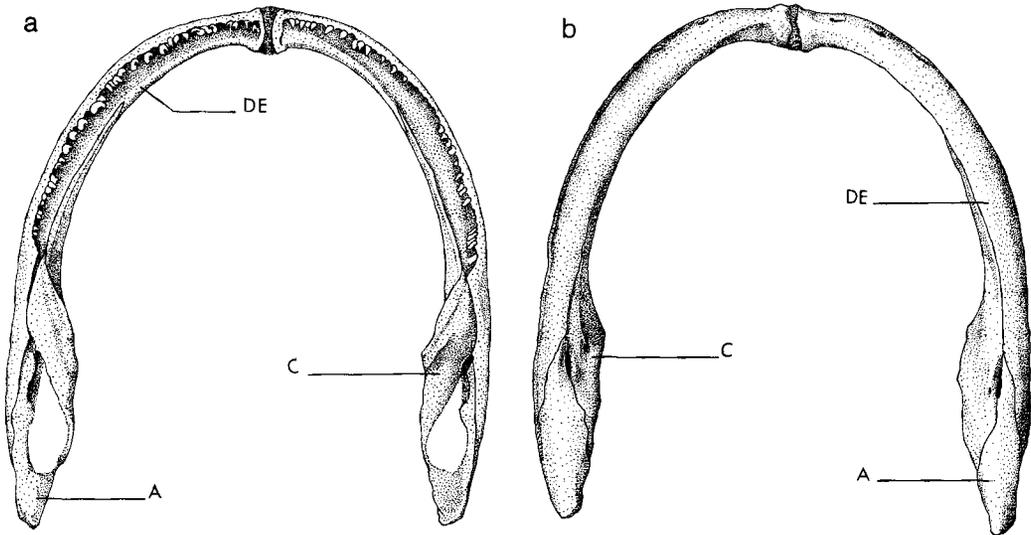


Fig. 7. *Cryptobranchus alleganiensis*. Dorsal (a) and ventral (b) views of the mandible. Articular cartilages left unshaded (details in Fig. 6), symphysis details shown in Fig. 8.

bone (symphyseal plates) that completely separate Meckelian cartilages of each side. Between the dentary tips lies a small dorsal pad of fibrocartilage and a much larger ventral pad of elastic cartilage (Fig. 8). The dorsal cartilage is directly surrounded by woven collagen, but the ventral cartilage is surrounded by a space containing only scattered collagen fibers. Between the pads is a band of dense collagen (median symphyseal ligament, Fig. 8) that is tightly attached to the symphyseal plates of the right and left dentaries. The labial surfaces of the dentary tips are connected by another thick ligament, which is densest and most regularly arranged in a narrow band (central symphyseal ligament) that overlies, and gives rise to, the median symphyseal ligament. The lingual side of the symphysis appears to be connected only by the dermal collagen underlying the buccal mucosa. The entire symphyseal complex is presumably the structure referred to by Reese ('06) as "a short ligament of cartilage."

Hyobranchial apparatus

Our dissections of the hyobranchial apparatus of adult *Cryptobranchus* (Figs. 9, 10) largely confirm the descriptions of Wiederheim (1877), Parker (1882), and Drüner ('04) but differ in a number of respects from later accounts (e.g., Reese, '06; Branch, '35; Jollie, '62; Meszoely, '66). Except for revi-

sions based on a reacceptance of early descriptions of hyobranchial anatomy, terminology follows Duellman and Trueb ('86) and Reilly and Lauder ('88b).

The hyobranchial apparatus contains elements of the hyoid and first four branchial arches. The apparatus has a number of structural features that bear directly on its function during feeding. The form and arrangement of the hypohyals and basihyal and their inclusion in a tough, ligamentous sheet create an extremely wide and pliable floor for the hyoid arch. The ceratohyals, which are extremely broad and flat, attach to the posterolateral edge of the second hypohyals, effectively flaring the anterior ends of the ceratohyals laterally. Although together the ceratohyals form about half the width of the floor of the mouth, their shape is probably related to support of the pharyngeal wall during hyoid depression (Fig. 10). The only ossified or calcified region of the hyoid arch is the small region of the ceratohyal that bends dorsolaterally.

The hyoid arch is attached to the mandible and braincase by a complex of ligaments and cartilages. A hyomandibular ligament extends from the posterior tip of the pterygoid and ventromedial edge of the articular to attach to much of the anterior face of the ceratohyal (Fig. 10). Dorsally, a hyoquadrate ligament (not illustrated) runs from the dorsal edge of the ceratohyal (stylohyal of Parker,

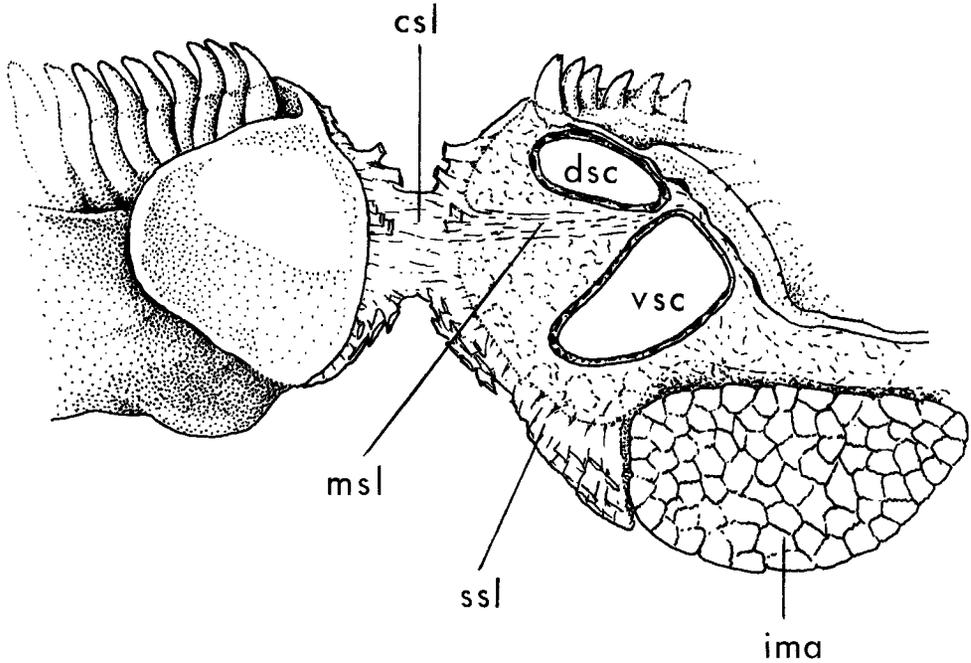


Fig. 8. *Cryptobranchus alleganiensis*. Sagittal view of the mandibular symphysis.

1882) to a region of the quadrate cartilage (presumably the hyoid process of Kingsbury and Reed, '09), which lies over the caudal edge of the squamosal. Within this ligament is a triangular cartilage (epihyal of Parker, 1882) that fills much of the space between the cranial border of the ceratohyal and the hyoid process. Collectively, these connections provide a stable and very strong axis of rotation for the ceratohyal, permitting the entire anteroventral hyoid arch to swing posteroventrally.

The basibranchial and branchial arches attach to, and support, the floor and lateral walls of the pharynx. The branchial arches are attached to an elevated cartilaginous knob (Parker, 1882) on the posteroventral surface of the basibranchial. This attachment allows limited rotation of the second hypobranchials and first ceratobranchials in all three planes. The first ceratobranchials are firmly attached to the second branchial arch by an interbranchial ligament. In dissected specimens, retraction of the basibranchial produces stress lines in the region of the interbranchial ligament connecting the first ceratobranchial to the elbow joint of the second branchial arch. This evidence, in combination with the shape and

cartilaginous nature (radiographs indicate no calcium deposits, contrary to Parker, 1882; Jollie, '62) of the first ceratobranchial, suggest that it serves to direct the movement of the second branchial arch during hyobranchial depression. The posterodorsal tips of the branchial arches, including the cartilaginous third (which is calcified, not ossified, in contrast to Parker, 1882; Reese, '06; and Jollie, '62) and fourth ceratobranchials, are attached to the dorsal edge of the ceratohyal by the dorsal branchiohyoid ligament. This ligament is long enough to permit considerable dorsoventral and lateral movement but generally constrains the branchial arches to posteroventral rotation during retraction of the basibranchial.

The hyoid and branchial arches have numerous muscular connections but no major ligamentous attachments apart from the dorsal branchiohyoid ligament. Although the hypohyals and basibranchial are tightly attached to the dermis of the tongue pad, they can separate to a distance approximately equal to the length of the first hypohyals. When separated, the basihyal remains associated with the hypohyals and is completely free of the basibranchial. Stretching of the

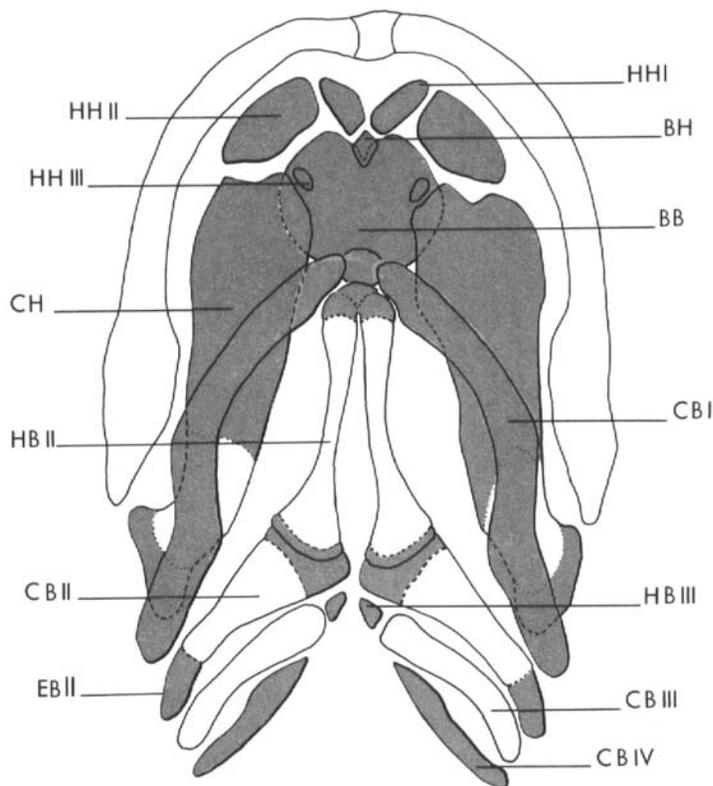


Fig. 9. *Cryptobranchus alleganiensis*. Ventral view of resting hyobranchial apparatus. Ossi-fied/calci-fied regions remain unshaded.

tongue pad and its contained cartilage may occur in the lateral as well as longitudinal directions.

Musculature

Much of the cephalic musculature in *Cryptobranchus* can be divided into four main functional groups: mandibular levators, mandibular depressors, hyobranchial depressors, and hyobranchial elevators (or buccal constrictors).

Mandibular levators. The massive musculature responsible for elevation of the mandible occupies most of the anterior portion of the skull (Fig. 11). It consists of the deep levator mandibulae anterior, superficial levator mandibulae anterior, levator mandibulae externus, and the levator mandibulae posterior. The deep levator mandibulae anterior (Fig. 12) consists of three sheets of fascicles. The deepest sheet arises from the orbitosphe-

noid and lateral edges of the frontal and prefrontal. An intermediate sheet arises from the prefrontal and frontal, and a superficial sheet arises from the frontal and anterior portions of the parietal. The tendinous sheets of all three fascicles converge to form a single tendon, which attaches to the medial ridge of the coronoid. The long and thin superficial levator mandibulae anterior (Figs. 11, 12) originates from aponeuroses attached to the first and second vertebrae. Its fibers run anteriorly and laterally, terminating in a long tendon that curves around the medial end of the squamosal to insert on the medial ridge of the coronoid.

The large levator mandibulae externus (Figs. 11, 13) occupies the space between the squamosal and the end of the maxilla. Fibers forming the medial two-thirds of the muscle diverge from the medial end of the dorsal ridge of the squamosal and run anterolaterally to insert on the dorsal surfaces of the

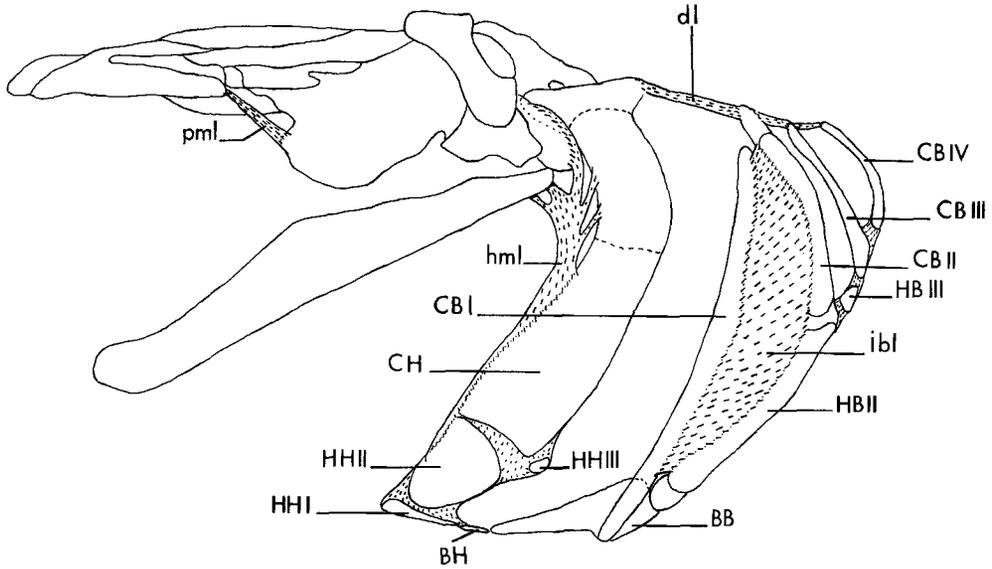


Fig. 10. *Cryptobranchus alleganiensis*. Lateral view of the skull and hyobranchial apparatus. Buccal cavity is expanded to indicate relative positions of hyoid elements during feeding.

dentary and coronoid behind the tooth row. The lateral third of the levator mandibulae externus arises from the remainder of the dorsal ridge of the squamosal and inserts on the lateral surface of the dentary.

The small levator mandibulae posterior (Fig. 11) lies ventral to the levator mandibulae externus and the mandibular branch of the trigeminal nerve. Its fibers originate on a ridge on the anterolateral surface of the squamosal just ventral to the origin of the levator mandibulae externus. Fibers of the two muscles are closely associated and difficult to separate near their origins. Superficial fibers of the levator mandibulae posterior extend anterolaterally to insert on the dorsal surface of the dentary caudal to the insertion of the externus muscle. The deeper fibers are relatively short and attach to the posteromedial portion of the dentary, the lateral edge of the coronoid, and the adjacent surface of Meckel's cartilage.

Mandibular depressors. In comparison to the levators, the mandibular depressors occupy a small region of the skull. This group includes only the anterior depressor mandibulae and the posterior depressor mandibulae (Figs. 11, 13). In its resting condition, the robust anterior depressor mandibulae covers the posterior surface of the squamosal, the dorsal end of the ceratohyal and most of the quadrate-articular joint. The anterior depres-

sor originates on the most medial tip of the squamosal by a tendon which also attaches loosely to the caudal border of the levator mandibulae externus. Ventrally, the fibers of the anterior depressor converge on a short, thick tendon which attaches to the posterodorsal tip of the articular. Caudal to the anterior depressor mandibulae, a narrower posterior depressor arises from the dorsal fascia and extends anteriorly and ventrally to insert on the articular immediately posterior to the insertion of the anterior depressor.

Hyobranchial depressors. The two muscles that depress the hyobranchial apparatus (rectus cervicis and subarcualis rectus I) are located on the ventral surface of the head deep to several superficial hyobranchial levators. The large, triangular rectus cervicis (Figs. 14, 15) occupies the space between the second ceratobranchials. Posteriorly, it becomes continuous with the rectus abdominis, the entire complex passing dorsal to the procoracoid of the pectoral girdle. Anteriorly, the fibers converge on a large tendon which attaches to the ventral knob and posteromedial surface of the basibranchial. On each side, a small bundle of fibers diverges from the main muscle mass. This bundle travels ventral to the anterior end of the second hypobranchial to insert on the posterolateral border of the basibranchial dorsal to the ceratohyal.

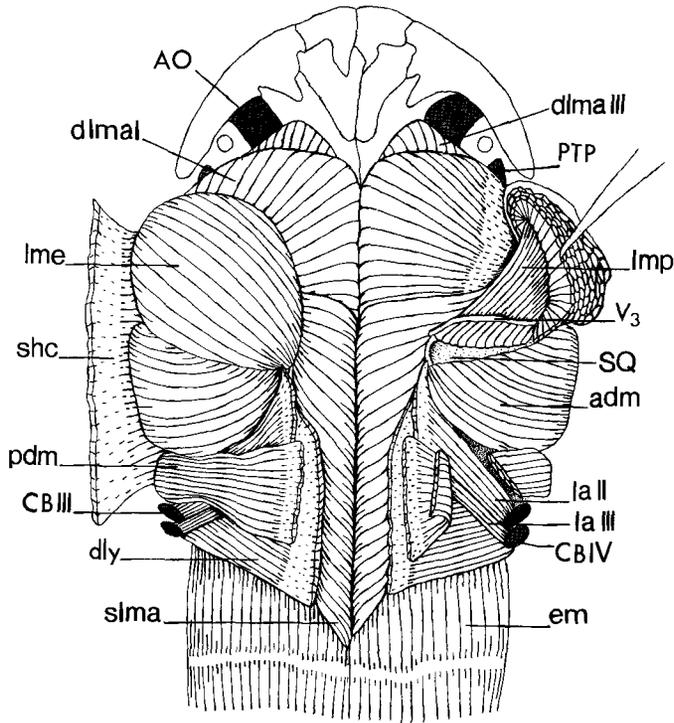


Fig. 11. *Cryptobranchus alleganiensis*. Dorsal view superficial cephalic musculature. Cartilaginous skeletal elements in gray. The origin of the levator mandibulae

externus on right medial side has been removed and the distal part of the muscle pulled laterally to show the underlying levator mandibulae posterior.

The subarcualis rectus I (Figs. 13–15) arises from a thick tendon attached to the anterior edge of the ceratohyal. Deep fibers run posteriorly to attach to the cranial surface of the distal third of the first ceratobranchial. Superficial fibers run parallel to deeper fibers but attach to the caudal surface of the first ceratobranchial. A small bundle of fibers arises from the medial edge of the ceratohyal, diverges from the main muscle mass, and inserts on the lateral surface of the elbow joint of the second branchial arch.

Hyobranchial levators. Based on their anatomical positions, the intermandibularis posterior, interhyoideus, superficial hyoid constrictor, geniohyoideus, genioglossus, and levatores arcuum all elevate the hyobranchial apparatus. The first three muscles constrict the outer buccopharyngeal wall. The geniohyoideus and genioglossus pull the hyobranchial apparatus anteriorly, opposing the action of the rectus cervicis. The levatores arcuum are included in this group because of their potential action in elevating and protracting the distal ends of the branchial

arches. However, as noted below, these small muscles could both depress and elevate the hyobranchium.

The intermandibularis posterior (Fig. 13) is a thin transverse sheet of fibers posterior to the anterior intermandibularis and ventral to the anterior hyobranchial elements. It arises from the dorsomedial surface of the dentary by a tendinous sheet and inserts on the midventral raphe.

The interhyoideus (Fig. 13) arises from the posteromedial tip of the ceratohyal and lateral surface of the quadrate, fans out over the ventrum, and inserts on the midventral raphe, the anterior half of the insertion extending deep to the intermandibularis posterior. The thin superficial hyoid constrictor (Figs. 11, 13) lies caudal to the interhyoideus, covering the depressor musculature and much of the posterior hyobranchial apparatus. It arises from the dorsal fascia, wraps around the lateral surface of the head, and inserts on the midventral raphe.

The paired geniohyoid muscles extend deep to the intermandibularis posterior and inter-

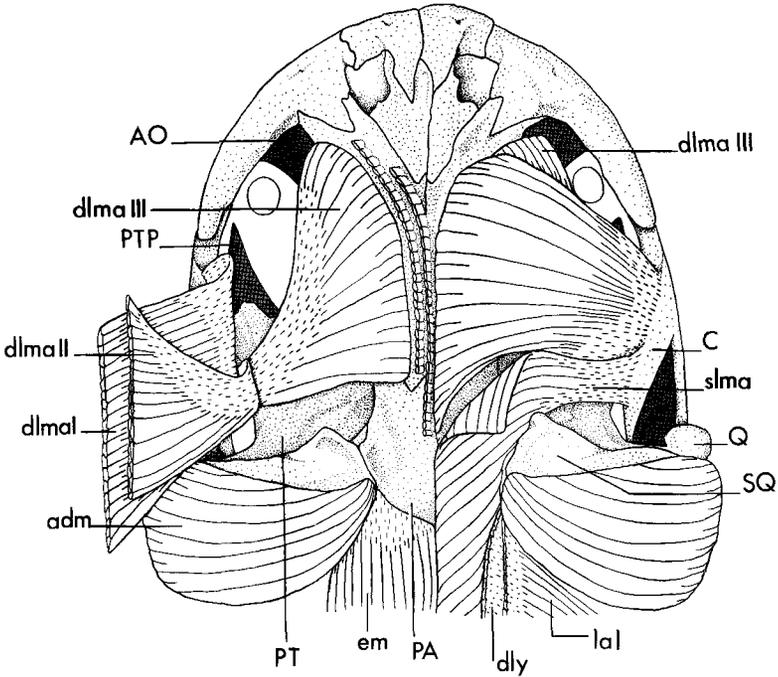


Fig. 12. *Cryptobranchus alleganiensis*. Dorsal view deep musculature. Levator mandibulae externus removed to show the different regions of the deep levator mandibulae anterior (left) and the superficial levator mandibulae anterior (right).

hyoideus. Their superficial fibers arise from the dentary, lateral to the mandibular symphysis, by a tendon that is associated medially with the attachment of the intermandibularis anterior. The superficial fibers then extend caudally to insert on the ventral epimysium of the rectus cervicis (Fig. 13), deeper fibers terminating in a tendon attached to the posterolateral surface of the second hypobranchial (Fig. 14). The anterodorsal surface of each geniohyoideus is closely associated with the anterior fold of the buccal lining.

Dorsal to each geniohyoideus is a tiny, strap-shape genioglossus (Figs. 14, 15). This muscle arises from the lingual surface of the dentary, wraps around the anterior fold of the buccal lining, and inserts on the anterior edge of the first hypohyal. Its fibers are closely associated with the connective tissue of the buccal lining, which, coupled with its small size, makes this muscle difficult to discern.

The levatores arcuum arise from the dorsal fascia and insert on the dorsal tips of the second and third branchial arches and the posterolateral surface of the fourth branchial arch (Figs. 11, 15).

There are a number of additional cephalic muscles whose structural relationships and potential actions do not fit any of the above groupings. All of these muscles have been described previously (Fischer, 1864; Drüner, '04; Francis, '34; Schumacher, '59) and are illustrated here. They include the tiny intermandibularis anterior (Fig. 13), which connects the ventromedial surfaces of the dentaries immediately lateral to the mandibular symphysis; several small branchial muscles (subarcuales obliqui, subarcuales recti II and III) that move the branchial arches relative to each other; and two extrinsic laryngeal muscles (dilator laryngeus, hyotrachealis).

Spinal musculature. The anterior trunk muscles are also important during feeding because they either move or stabilize the braincase relative to the vertebral column. These muscles are divided into epaxial (cranial levator) and subvertebral (cranial depressor) groups. In *Cryptobranchus*, these major groups are subdivided in a manner similar to that described by Auffenberg ('59) for *Siren*, *Necturus*, and *Amphiuma* (see also Erdman

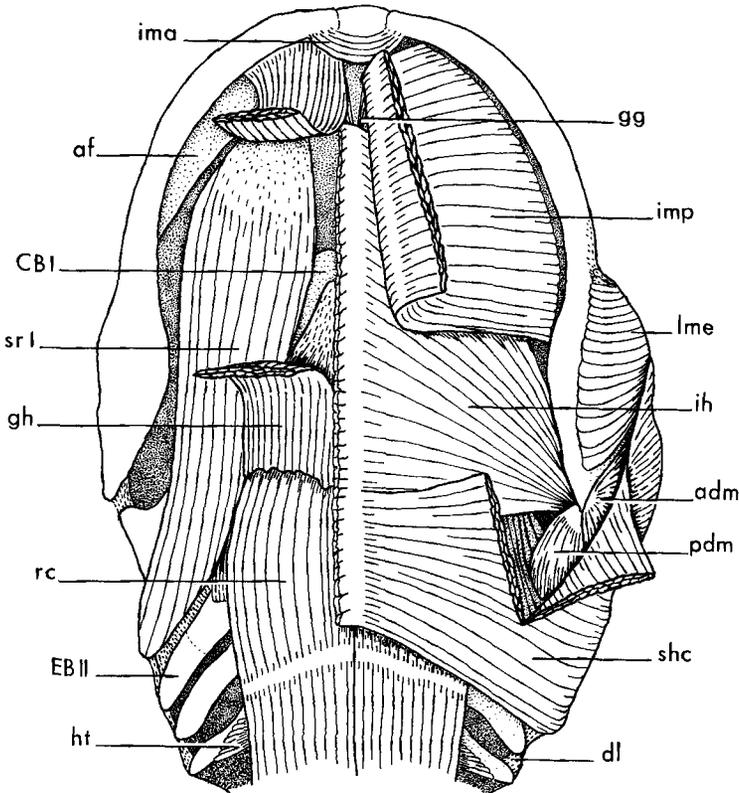


Fig. 13. *Cryptobranchus alleganiensis*. Ventral view of the superficial musculature on the right. Intermandibular posterior, interhyoideus, and superficial hyoid constrictor removed on left to show deeper musculature underneath.

and Cundall, '84). As noted in the description of the braincase, the cranial levators are thicker and attach farther from the axis of rotation of the occipital condyles than do the cranial depressors.

Features of the integument and buccopharyngeal lining

Unlike *Amphiuma*, *Cryptobranchus* lacks labial folds, although the integument in the upper labial region is tightly attached only to the premaxillae (Cope, 1889). As a result, the caudal half of this integument is mobile and may be pulled ventrally during mandibular adduction or pushed dorsally by prey caught in the angle of the mouth. The integument covering the hyobranchial apparatus has numerous longitudinal folds similar to those in *Andrias* (Liu, '50). As noted in most descriptions of *Cryptobranchus*, a single gill opening (spiracle) lies between the third and fourth

ceratobranchials (epibranchials of most previous workers), although this is covered by integument in some individuals (CM 58294 of this study; Nickerson and Mays, '73). Within the mouth, the buccopharyngeal lining forms a large recess (anterior fold) ventral to the anterior end of the hyoid arch. Consequently, the tongue pad is free anteriorly when the hypobranchium is at rest. During hyoid depression, the anterior fold is stretched to maximum length and forms the cranial wall of the buccal cavity. In preserved specimens, the buccopharyngeal lining has numerous narrow longitudinal folds everywhere except the surface of the tongue pad and that region encompassed by the parasphenoid and upper jaw.

Behavior

Movements of the head of *Cryptobranchus* during prey capture resemble those described for other suction-feeding vertebrates (Lauder,

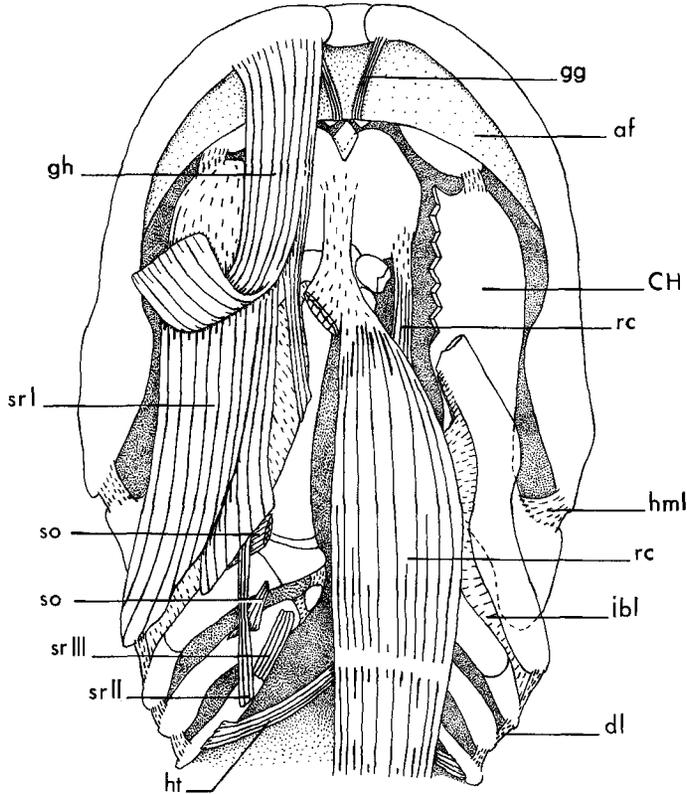


Fig. 14. *Cryptobranchus alleganiensis*. Ventral view of the deep hyobranchial musculature. Interhyoideus, superficial hyoid constrictor, and intermandibularis posterior removed from both sides. The left geniohyoideus, and subarcualis rectus I, as well as the medial edge of the

ceratohyal have been removed to show the lateral insertion of the rectus cervicis muscle. The right rectus cervicis muscle has been removed to show deep interbranchial musculature.

'85). *Cryptobranchus* catches prey by either inertial suction, or a strike combined with suction. The use of at least two kinematically different programs for prey capture in *Cryptobranchus* approximates the pattern reported for *Amphiuma* by Erdman and Cundall ('84) but is more diverse than patterns reported by Reilly and Lauder ('89, '92). Following capture, prey are manipulated using repeated suction movements that are more variable kinematically than those used for capture. Swallowing is achieved by compressive movements of the head that involve a radical change in the timing of events used for capture and manipulation. The following account emphasizes the kinematic events of capture and manipulation of prey. Swallowing is not considered because there were too few records of this behavior.

Prior to prey capture, *Cryptobranchus* frequently exhibits a variable number of small

excursions of the hyoid apparatus. These movements may be associated with olfaction or may represent a behavior similar to the preparatory phase of percomorph teleosts (Lauder, '85) in which the volume of the buccopharyngeal cavity is reduced to a minimum before the onset of capture.

Inertial suction

Suction is widely described in terms of the pressure changes within the suction apparatus, e.g., expansive phase. In the absence of pressure recordings, we use kinematic events to describe the process. These events are mouth opening, mouth closing, hyobranchial depression, and hyobranchial elevation. These phases all vary among capture sequences in both extent and timing. Due to this variability, the following is a generalized description of the various skeletal movements and timing of events in *Cryptobranchus*.

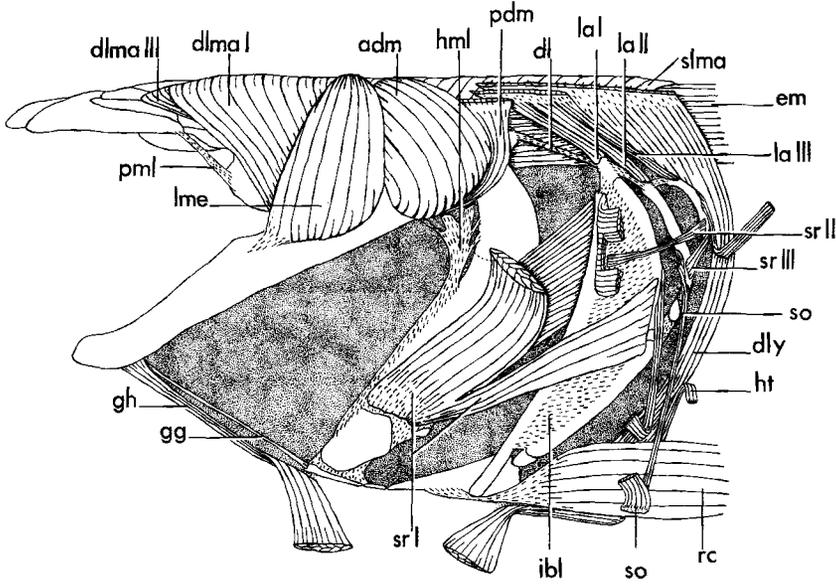


Fig. 15. *Cryptobranchus alleganiensis*. Lateral view of musculature. Buccal cavity expanded and interhyoideus, superficial hyoid constrictor, and intermandibularis posterior removed.

Mouth opening usually begins with slight depression of the mandible (asymmetric in 42% of capture sequences, Cundall et al., '87) followed almost immediately (0–16 ms) by elevation of the braincase and caudal ends of the branchial arches. Continued opening entails a rapid elevation of the entire braincase, whereas the tip of the mandible retains its initial position. At the same time, the anterior, median elements of the hyoid apparatus are retracted and slightly depressed and the branchial arches move laterally. At the end of opening (peak gape), the mandible has reached its maximum abduction primarily as a result of the upward movement of the entire braincase (Fig. 16). The median hyoid elements are retracted but still lie directly in line with the ventral surface of the body anterior to the pectoral girdle. Typically, at this point in the cycle the midpoints of the branchial arches have moved farther laterally and the dorsal tips of these arches remain elevated. The duration of mouth opening ranges from ~30 to >80 ms.

The beginning of mouth closing phase is marked by adduction of the mandible and continued retraction of the median hyoid elements. As the mandible is elevated, the distance between its tip and the anterior edge of the hyoid apparatus increases while the branchial arches continue their lateral move-

ment. Two external features suggest that the pressure in the buccal cavity remains negative well into mouth-closing phase. First, the floor of the buccal cavity appears straight or concave. Positive intrabuccal pressures, in contrast, cause the floor of the buccal cavity to appear convex. Second, the skin between the hyoid apparatus and the mandible curves inward. Because there are no muscles positioned to generate this deformation of the skin, it must be produced by negative intrabuccal pressure. Finally, the various lateral elements of the hyoid apparatus are readily visible in the right lighting because the skin between them curves markedly inward.

The remainder of the closing phase is marked by movements suggesting an increase in intrabuccal pressure. As the jaws close, the caudal end of the hyoid apparatus drops ventrally (Fig. 16) as do the caudal tips of the branchial arches. The integument between the lateral elements of the hyoid apparatus loses its dimpled appearance and becomes smooth, making it impossible to see the positions of these arches. The skin anterior to the basihyal bows outward. Peak hyoid depression occurs somewhere in the shift from apparent negative to positive intrabuccal pressure, although its definition invariably depends on which end of the median hyoid elements is being plotted. In most se-

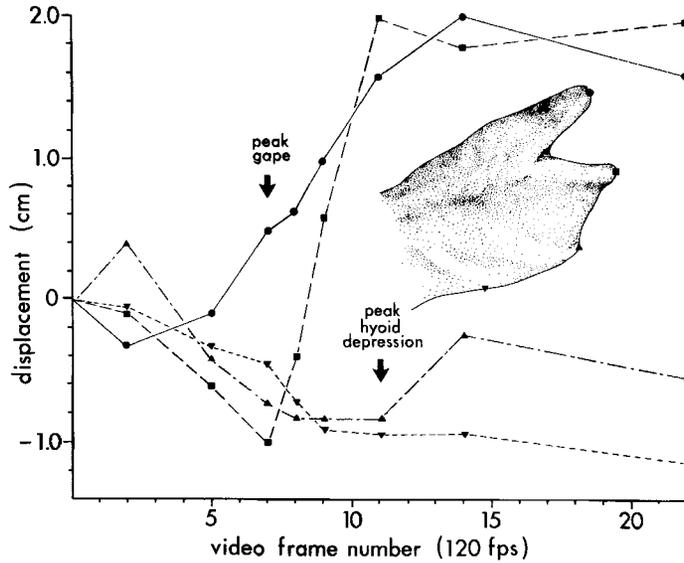


Fig. 16. *Cryptobranchus alleganiensis*. Plot of movements of the tip of the snout, tip of the mandible, and the anterior and posterior hyoid during inertial suction. The inset figure (traced from video frame 8) shows the positions of the points plotted.

quences, the anterior end of the hyobranchial apparatus achieves maximum depression about 8–24 ms before the caudal end.

Whenever inertial suction is employed for relatively small prey, there is a distinct recovery phase. During this phase, the hyobranchial apparatus returns to a resting position by gradual compression of the buccopharyngeal cavity from the caudal end forward. The exact pattern of water flow was not determined, but displacements of small particles in the water surrounding the head suggest that much of the water leaves the buccopharyngeal cavity through the mouth. In the few instances in which the smallest specimen used inertial suction to capture crickets, the prey prevented the hyoid apparatus from returning to a resting position although attempted compression of the buccopharyngeal cavity still began caudally.

Behavior of the gill opening during inertial suction is difficult to see because the opening is partially concealed by a large skin fold. Caudolateral views of the head during inertial suction show that the outer edge of the gill opening is flared open at the end of the expansive phase but appears to close as the distal ends of the branchial arches move ventrally in the later part of the compressive phase. Movement of water through the gill opening has not been determined and there-

fore its function during feeding remains obscure.

Inertial suction results in little forward or lateral movement of the head. Suction is generated by elevation of the braincase and retraction of the hyobranchial apparatus. When catching small prey, *Cryptobranchus* frequently uses very small excursions of both the braincase and hyobranchial elements. As the magnitude of skeletal excursions increases, inertial suction grades into the kinematic pattern characteristic of the strike.

The strike

During a strike, both the gape and the extent of hyobranchial depression approach maximum potential values (Table 1). Despite the fact that all movements of a strike occur very rapidly (strike duration, excluding recovery phase, ranging from 40–80 ms), they are surprisingly variable. The major differences between the strike and inertial suction are described below.

During mouth opening for the strike, elevation of the braincase was combined with lateral or forward movement of the snout, the rear of the braincase following the trajectory of the rapidly rising caudal ends of the mandible. During asymmetric strikes, the strike is always directed toward the side showing initial mandibular depression. At peak gape,

TABLE 1. Kinematic values for strikes of four *Cryptobranchus* as a function of head depth compared to equivalent values from Reilly and Lauder ('92)¹

#	HL	HD	%PG	n	SD	GR	%PH	n	SD	HR	Prey
1	29	8	96	6		81-114	89	9		35-128	crickets
2	85	36	—	0		—	45	5		29-50	worms
3	79	34	46	3		39-52	36	4		29-39	worms
4	72	28	74	4		65-84	85	6		47-125	goldfish
all			78		(23)	39-114	70		(33)	29-128	
*			86		(4.5)		69		(5.5)		

¹Abbreviations: #, animal number; HL, head length (in mm); HD, head depth (in mm); PG, peak gape; n, number of measurements; SD, standard deviation; GR, range of gape values; PH, peak hyoid depression; HR, range of values for hyoid depression; *, values from Reilly and Lauder ('92), taking their absolute values and dividing by the mean they gave for head depth and then correcting standard error values.

the anterior edge of the hyoid apparatus is depressed, retracted, and stretched laterally to form a flat plate that is wider than at the resting condition. Duration of the opening phase averages 25 ms for the smallest specimen. Mouth closing differs only slightly from that of inertial suction in that there is greater lateral and ventral displacement of the branchial arches. Finally, the recovery phase is shorter than that of inertial suction.

Prey manipulation

Manipulation frequently follows the recovery phase both in the strike and in inertial suction. During manipulation, the prey item is transported in and out of the buccal cavity across the teeth. This mechanism is very similar to the one used by the lungfish *Lepidosiren paradoxa* (Bemis and Lauder, '86). Manipulations are usually accompanied by violent wagging of the head in either dorsoventral or mediolateral planes. During manipulation, a number of different mechanical processes are utilized. *Cryptobranchus* can depress the mandible prior to snout elevation, depress the mandible and hyoid apparatus simultaneously, exhibit mandibular depression and elevation without depressing the hyoid apparatus (23% of manipulations), or depress the hyoid prior to depression of the mandible. In addition, it is not uncommon for hyoid and mandibular movements during prey manipulation to be asymmetrical (10% of hyoid and 42% of mandibular manipulations recorded); one side of the hyoid or mandible then exhibits greater depression or retraction than the other (Cundall et al., '87).

Potential displacements of the mandible and hyoid

From our observations on anesthetized specimens, some *Cryptobranchus* can depress the mandible up to 90°, although half

the larger specimens examined had maximum gape angles of ~75°. Movements around the mandibular symphysis (Fig. 17) are highly variable: maximum dorsal flexion (with mandibles depressed 20°-30°) ranged from 12° to 55°; maximum ventral flexion ranges from 10° to 40°. Total flexion at the symphysis ranges from 35° to 70°; smaller values occur in larger adults. Maximum hyoid movements, determined from 35 mm film records of displacements, approximate those seen during strikes and by the use of a Foley catheter to inflate the buccal cavity (Fig. 18). In lateral view, the ceratohyal appears to rotate ventrally ~70°-80°. There is additional rotation of the major part of this arch around its own long axis (the medial edge of the arch swings laterally producing an angular rotation of ~45°-60°) to maximize the curvature of the arch in enlarging the buccal cavity. More posterior elements of the hyoid apparatus are pulled caudally at their ventral ends to the point where the arches are approximately vertical to the floor of the skull although distinctly curved in lateral view (Fig. 18). The displacement of the caudal (or dorsal) ends of the arches seen in Figure 3 shows that the caudal, anchored ends of the hyoid apparatus can shift dorsoventrally a distance at least 1.5 times the maximum height of the vertebrae.

DISCUSSION

The motions of the head of *Cryptobranchus alleganiensis* during suction feeding appear more complex than those of other aquatic salamanders described to date. Here, we briefly review relationships between the structure and behavior of the head of *Cryptobranchus* and consider some of the more obvious implications of these findings for control mechanisms.

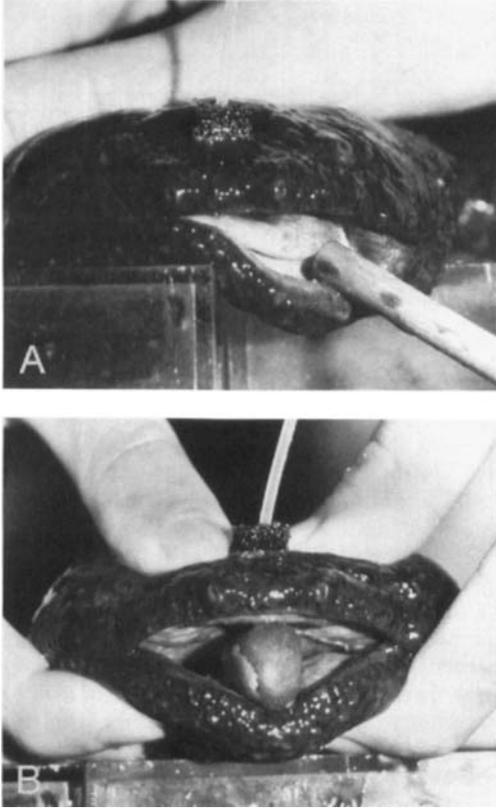


Fig. 17. *Cryptobranchus alleganiensis*. Anterior views of the head of an anesthetized specimen to show (a) the left mandible pulled ventrally, showing ventral flexion at the mandibular symphysis, and (b) forced dorsal displacement of the mandibles around the mandibular symphysis.

Anatomy

Several structural features of *Cryptobranchus* have attracted little previous attention but are functionally significant during suction feeding. These include flexibility of anterior skeletal elements and the mandibular symphysis, and the shape of the quadrate-articular joint. Also, ossification patterns in the hyoid apparatus have been considered from developmental and phylogenetic perspectives but not from a functional one.

The skull of *Cryptobranchus alleganiensis* contains syndesmotomic connections between the upper jaws and the braincase that permit limited rotation of the maxillae. In addition, the orientation of sutures of the anterior braincase permits slight twisting or flexion that may absorb forces applied asymmetrically to the skull during prey capture or ma-



Fig. 18. *Cryptobranchus alleganiensis*. Radiographs of lateral view with the buccal cavity (a) at rest (view slightly oblique), and (b) inflated with a Foley catheter.

nipulation. Considering that *Cryptobranchus* eat crayfish (Netting, '29; Nickerson and Mays, '73), the capacity of its skull to absorb mechanical shocks might reduce the probability of injury during prey capture.

Maxillary movement in some suction feeders may serve to decrease the size of the oral opening (Lauder and Liem, '81; Bemis and Lauder, '86; Erdman and Cundall, '84). In *Cryptobranchus*, however, the greatest excursions of the caudal end of the maxilla are directed dorsally, lending further support to the notion that the skull is designed to absorb shocks encountered while catching prey with firm exoskeletons.

The structure of the mandibular symphysis and the quadrate-articular joint, both briefly considered by Cundall et al. ('87), allow the mandibles to rotate about their long axes. The flexibility afforded by both joints accounts for the asymmetry of mandibular motion during prey capture and manipulation. Given the same volumetric change per unit time, reducing gape size increases water velocity (Lauder, '85). In an animal with a wide, hemispherical mouth, such as

Cryptobranchus, the ability to depress the mandibles asymmetrically or asynchronously may be advantageous for two reasons: it limits gape size during initial suction, and it allows the entrainment of a water volume with enclosed prey from areas lateral to as well as directly anterior to the mouth. Asymmetric mandibular depression produces the lateral strike noted by Green ('33). The ability of *Cryptobranchus* to tailor its kinematic response to immediate conditions may be particularly useful in an environment where mobility is often limited, such as the rock-strewn stream bottoms on which these salamanders are typically found.

Cryptobranchids traditionally have been considered primitive (Estes, '81), a conclusion supported by more recent analyses (Duellman and Trueb, '86; Hillis, '91). A number of features (absence of septomaxillae and lacrimals, which typically are among the last skull bones to ossify in other salamanders; presence of two medial elements and parts of the third and fourth branchial arches, larval elements typically lost in adult salamanders; Duellman and Trueb, '86) suggest that *Cryptobranchus* is also paedomorphic. However, many of the unique morphological features of the head and hyobranchial apparatus appear to facilitate asymmetric suction feeding. For example, multiple hypohyal elements and the extraordinary width of the basibranchial make the buccal floor stiff yet flexible. Given the width of the buccal floor, the size of typical prey (crayfish), and the speed of the gape cycle during suction feeding, flexibility may distribute forces that might otherwise damage the system. Given the size of adult *Cryptobranchus*, the limited calcification or ossification of the hyoid and first branchial arches might also represent a structural response to a need for flexibility in a bilateral system the two sides of which may work asymmetrically or asynchronously.

Kinematic profiles

The feeding apparatus of *Cryptobranchus* moves like that of other suction-feeding vertebrates (Lauder, '85). Prey is captured by the suction generated from a rapid expansion of the buccal cavity. As in teleostome fishes (Lauder, '85), dipnoans (Bemis and Lauder, '86) and aquatic salamanders (Erdman and Cundall, '84; Lauder and Shaffer, '85; Reilly and Lauder, '92), the expansion results from rapid elevation of the braincase and depression of the mandible and hyobranchial apparatus. Peak hyoid depression is achieved as

the mandible elevates during the compressive phase. Like Reilly and Lauder ('92), we also found that rapid hyoid depression occurred at, or following, peak gape. Closing of the mouth at the end of the gape cycle was followed by slow compression of the buccal cavity, often with the mouth slightly open. Despite these similarities, some aspects of the feeding mechanism in *C. alleganiensis* differ from those described for other suction-feeding salamanders.

Cryptobranchus utilizes a range of movements, the ends of the range being referred to by us as inertial suction and the strike. The kinematic flexibility of *Cryptobranchus* appears similar in many respects to that described for cichlids as modulatory multiplicity (Liem, '78, '79). As reported by Erdman and Cundall ('84) for *Amphiura*, the selection of one mode over the other appears to depend on the size and activity of the prey. Presentation of relatively small and inactive prey generally elicits inertial suction. Whereas the extent and timing of skeletal excursions varies considerably among inertial suction capture sequences, none approached the maximal values seen during strikes. Hence, inertial suction is best characterized as a minimal functional response to capturing a relatively small and sluggish prey item.

The kinematic profile described by Reilly and Lauder ('92) for *Cryptobranchus* is kinematically intermediate to inertial suction and the strike as described here. Their mean values for peak gape and peak hyoid depression are, respectively, three-quarters and one-half the maximum values obtained by us for strikes. The very small standard errors of their means ($n = 20$) for gape and hyoid depression suggest very limited ranges. We deduce that Reilly and Lauder ('92) observed a restricted range of movements.

With the exception of *Amphiura* (Erdman and Cundall, '84), all other suction feeding salamanders studied to date (Shaffer and Lauder, '85a; Reilly and Lauder, '92) have been described as using a single mode of feeding to capture prey. The marked differences between the kinematic accounts of Reilly and Lauder ('92), on the one hand, and Erdman and Cundall ('84) and this report on the other, suggest two questions. First, what are the possible reasons for the differences in descriptions? Second, if *Amphiura* and *Cryptobranchus* use two or more modes of feeding, what potential benefits accrue to the salamanders?

The differences between descriptions may reflect different methods of analyzing behavioral records. They may also reflect real differences in the recorded behaviors. Our data incorporate differences in the types of prey presented, the angle of filming, and the size of *Cryptobranchus*. However, the use of worm chunks by Reilly and Lauder ('92) as prey for all species of aquatic salamanders, despite natural history data suggesting that worms represent very minor components of a natural diet for either *Amphiuma* or *Cryptobranchus*, suggests that the relatively uniform kinematic profiles they obtained simply reflect the uniformity of prey presented.

With regard to the second question, the salamanders may benefit in several ways. When catching small, relatively immobile prey, the smaller excursions of inertial suction may allow the salamanders to expend less energy than is required for the dramatic excursions of the strike. Erdman and Cundall ('84) proposed that use of inertial suction for small prey also may reduce the probability of detection by predators or injury due to misdirected strikes. Conversely, the large excursions of the strike may increase the probability of catching elusive or larger prey. Meaningful tests of these hypotheses will require considerably more data from field and laboratory studies.

As Greene ('86, '93) eloquently pointed out, if functional morphology hopes to realize any understanding of the relationships between structure and the behavioral potentials of an animal, it must first ensure that it is gaining a real measure of behavior through comparisons with behavioral or natural history data acquired in the field. Our data on *Cryptobranchus*, and natural history data (Nickerson and Mays, '73), suggest that Reilly and Lauder ('92) examined only part of the behavioral repertoire of *Cryptobranchus*. If this is true, then the limited kinematic dissimilarities among aquatic salamanders found by Reilly and Lauder ('92) understate the functional differences among these species. It is possible that Reilly and Lauder examined a basal kinematic pattern common to all suction-feeding salamanders—in essence, a plesiomorphic behavioral pattern. Whereas the goal of their study was to examine how morphology, kinematics, and motor pattern interact, it seems likely that if the last two are artificially limited, what they can tell us about morphology will be equally limited.

Bidirectional flow

Lauder and Shaffer ('86) and Lauder and Reilly ('88) showed that ontogenetic or surgical closure of gill slits, and enforced bidirectionality of water flow, reduced aquatic prey capture performance in ambystomatid salamanders. Adults of other aquatic salamander families characterized by small or closed gill slits (amphiumids and cryptobranchids) are expected to suffer the same reduced performance. Although *Amphiuma* and *Cryptobranchus* share some peculiar kinematic features (delay of rapid hyoid depression and sharp depression of the snout following the gape cycle) that differentiate them from unidirectional suction-feeding salamanders, kinematic performance of *Amphiuma* and *Cryptobranchus* during the gape cycle did not differ markedly from that in unidirectional suction-feeding salamanders (Reilly and Lauder, '92). Whether bidirectional suction-feeders differ in capture performance remains untested. Reilly and Lauder noted that *Cryptobranchus* may accommodate the limitations of bidirectional flow by increasing the capacity of the buccal cavity. Our behavioral and anatomical data support this contention.

In *Cryptobranchus*, reduction of gill aperture area is offset by features of the buccopharyngeal wall that allow the volume of the buccal cavity to keep increasing as pressure rises at the end of hyobranchial retraction. Specifically, the branchiohyoid ligament attaching the caudal tips of the ceratohyal and ceratobranchials to the rear of the mandible and its suspensorium allow the entire hyoid apparatus to move dorsally or ventrally relative to the vertebral column. The timing of events suggests that at the end of muscle-generated suction (peak gape), the volume of water entering the buccal cavity has sufficient inertia to cause continued flow into the buccal cavity, creating rapidly rising positive pressure in the cavity. As a result, the buccal walls expand outward and the hyoid apparatus is pushed ventrally. This may reduce backwash from the buccal cavity as the mouth is closing.

Implications for control mechanisms

Asynchronous and asymmetric patterns of force generation among the right and left members of muscle pairs controlling jaw movements are characteristic of mammalian mastication (Hiimae and Crompton, '85). Presumably such patterns characterize prey transport in snakes (Cundall, '83), although

force patterns have yet to be measured. For *Cryptobranchus*, the evidence for asymmetric or asynchronous patterns comes entirely from kinematic data. However, the system has the capacity for producing asynchronous or asymmetric jaw and hyoid movements at speeds that imply motor programming (Marsden et al., '84) but with a diversity of responses requiring considerable flexibility in the program, or possibly use of different fractions of the program (Grillner, '85). What is particularly fascinating is the possibility that the complex motor patterns of mammalian mastication may represent refinements of phylogenetically primitive motor patterns. The existence of this motor potential is kinematically detectable only in species with morphological specializations for independent movements of the left and right sides of the head, such as *Cryptobranchus* or snakes. The essential features of working- and balancing-side kinematics would be mechanically advantageous to any bilaterally symmetrical predator using its jaws to capture, manipulate or reduce prey (Cundall et al., '87). After all, prey would rarely encounter the predator's jaws in a bilaterally symmetrical manner. Closing phases would therefore have to accommodate widely different resistances to closing on each side of the head. The capacity to modulate forces generated by the jaw muscles of the left and right sides might have been selected originally because it reduced the probabilities of damage to the feeding apparatus.

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