

Asymmetric suction feeding in primitive salamanders

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Summary. During suction feeding, the primitive aquatic salamanders *Cryptobranchus alleganiensis* and *Andrias japonicus* frequently display asymmetric movements of the lower jaw and hyoid apparatus that have some similarity to working and balancing side kinematics of mammalian mastication.

Key words. Salamander; feeding; asymmetry.

Previous detailed studies of suction feeding in vertebrates have demonstrated, or assumed, that the right and left visceral arch elements of the head (jaws, hyoid and branchial arches) move symmetrically¹⁻⁶. Suction feeding usually entails very rapid movements of the feeding apparatus⁷, even in salamanders^{5,6}, and is characterized by marked overlap in the activity of antagonistic muscles^{1,5,8,9}. We were therefore surprised to discover asymmetries in jaw and hyoid movements during rapid suction feeding in the large, primitive aquatic salamanders *Cryptobranchus alleganiensis* and *Andrias japonicus*.

Cryptobranchus alleganiensis lives in unpolluted streams and rivers of the Appalachian and Ozark regions of the United States and feeds on a variety of aquatic invertebrates and small vertebrates^{10,11}. *Andrias japonicus* inhabits montane streams of the Japanese island of Hondo and exhibits food and habitat requirements similar to those of *Cryptobranchus*¹². We here report the nature of asymmetric movements of the feeding apparatus in these two species, the structural basis of these movements in *Cryptobranchus*, and the potential relevance of our findings to ideas concerning the evolution of vertebrate feeding mechanics.

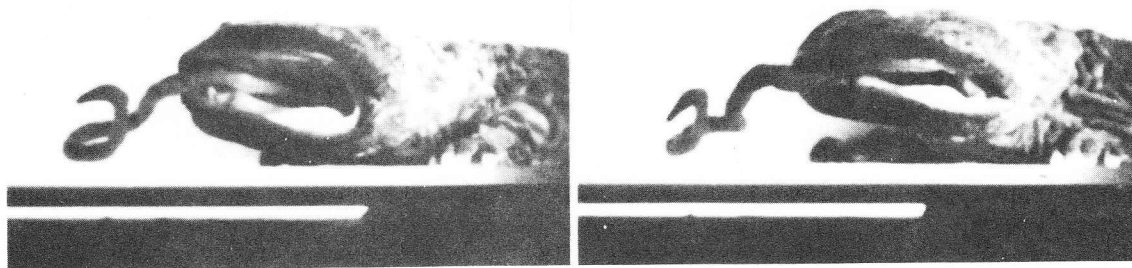


Figure 1. Anterolateral views of asymmetric jaw closure during a manipulatory cycle taken from two consecutive frames of Super-8 film shot at 24 fps.

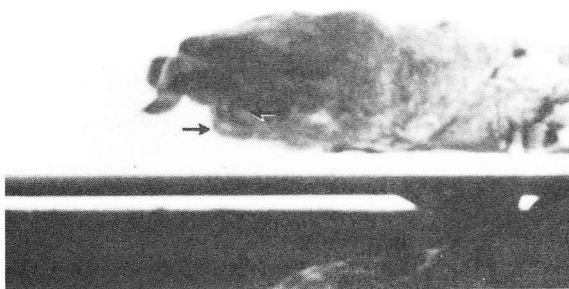


Figure 2. Lateral view of an asymmetric hyoid position achieved during a manipulatory cycle. Arrows point to positions of right and left hyopharyngals (see fig. 4).

Methods. Jaw and hyoid movements were analyzed from film records (strobe-synchronized Super-8 at 24 or 36 frames per second and high-speed video at 120 fps) of three *Cryptobranchus* (total lengths of 21, 51 and 56 cm, all caught at French Creek, Pennsylvania) feeding on crickets and earthworms, and two *Andrias* (total lengths 59 and 62 cm, captive reared) feeding on freshly killed small mice.

To determine the structural basis of asymmetric jaw and hyoid movements, we dissected eight *Cryptobranchus alleganiensis*. In addition, the symphyseal soft tissues of two specimens were removed, sectioned and stained for elastin¹³ or collagenous connective tissue¹⁴. Potential movements of the different parts of the cephalic skeleton were determined by manual manipulation of seven live *Cryptobranchus* anesthetized with tricaine methanesulfonate. Photographic and radiographic records of these manipulations were compared with measurements made directly on the animal.

Results. The basic patterns of suction feeding in *Cryptobranchus* and *Andrias* were similar to those in other suction feeding salamanders^{5,6}. Duration of complete gape cycles during prey capture varied from 32 to 96 ms. After capture, prey were manipulated using movements of the jaws and hyoid apparatus which were similar to movements used in capture but varied considerably in timing and extent.

During both prey capture and manipulation, the mandibles of *Cryptobranchus* sometimes flexed around the mandibular symphysis by as much as 40°. The result of this flexion was quite spectacular, the animal appearing to open or close one side of its mouth almost independently of the other side (fig. 1). This behavior was exhibited often enough (14 (42%) of 33 analyzable prey capture sequences, 170 (42%) of 410

analyzable manipulation sequences) to indicate that it is a normal function of the feeding apparatus in this species. Further, in 24% of manipulation sequences showing asymmetric jaw movements, hyoid movements were also asymmetric (fig. 2).

Andrias displayed asymmetric movements similar in frequency and timing to those of *Cryptobranchus*. However, flexion around the mandibular symphysis rarely exceeded 20°.

Asymmetric mandibular depression during prey capture was directly correlated with prey position relative to the head. In those sequences showing asymmetric movement, the mandible on the side of the head closest to the prey opened earlier and further than the opposite mandible. Asymmetric mandibular or hyoid movements were less clearly correlated with the position of prey in the jaws or buccal cavity. Marked asymmetric movements were exhibited by both larger *Cryptobranchus* during feeding on earthworms which had a mass insufficient to cause any direct mechanical effect on the hyoid or mandible. Worms were occasionally held by the teeth of the maxilla and dentary of one side while the opposite side exhibited gaping (chewing?) motions. Like the lungfish *Lepidosiren*⁹, these salamanders invariably spent

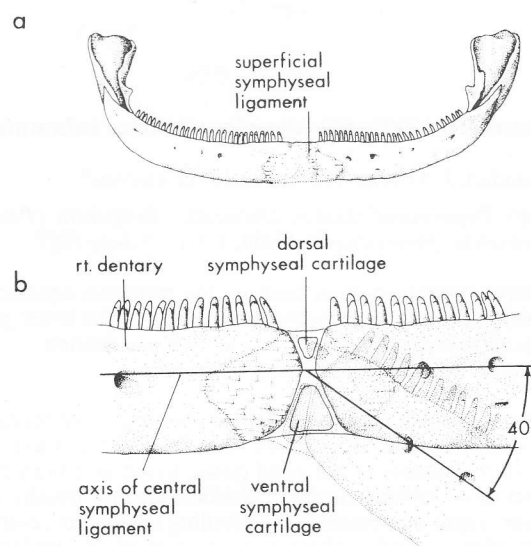


Figure 3. a Anterior view of the lower jaw of *C. alleganiensis*. b Enlargement of the symphyseal region of (a) to show positions of cartilaginous symphyseal pads and their probable deformations during ventral flexion of the symphysis. The joint also permits 5–15° of dorsal flexion in most specimens.

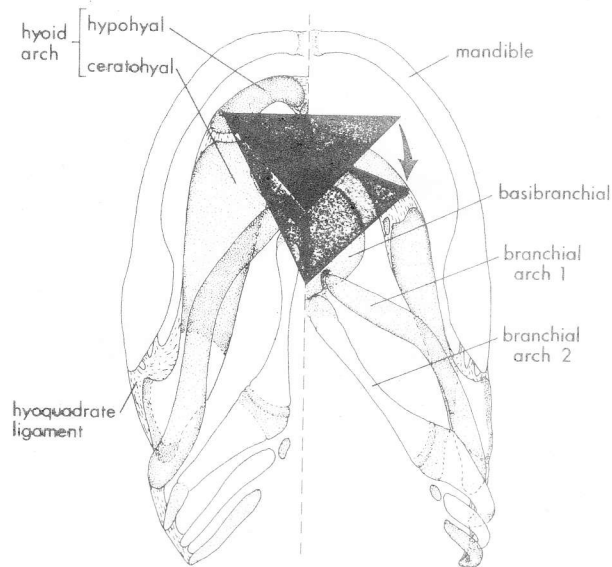


Figure 4. Ventral view of the mandibles and hyoid apparatus of *C. alleganiensis* to show the triangular arrangement of hyoid and branchial arch attachments. Relaxed condition is shown at left, asymmetrically abducted condition is shown at right. Abduction results in elongation of the triangle because the basibranchial is loosely attached to the ventral hyoid arch elements, whose forms and attachments, in turn, also allow some spreading of the base of the triangle.

minutes manipulating prey prior to swallowing. All animals switched to a different pattern of jaw and hyoid movements during swallowing.

The mandibular symphysis in *Cryptobranchus* is highly mobile (max. angular displacement = 45–70°). Unlike many species of salamanders, the dentaries of *Cryptobranchus* are separated by two pads of elastic cartilage (fig. 3). The larger ventral pad fills a triangular space between the dentaries and is compressible, even in preserved specimens. In combination with the mobility of the quadrate-articular joint between the mandibles and the skull, the arrangement of these cartilages and the surrounding symphyseal ligaments permits about 40° of ventral flexion but limits dorsal flexion to 5–15° in most specimens. In one specimen, the symphysis flexed 55° dorsally but only 15° ventrally.

In *Cryptobranchus*, asymmetric movements of the hyoid, if viewed as rotation around the longitudinal axis, approach 80° (approximately 40° to either side of the horizontal plane). The triangular arrangement of movable attachments between the median and paired elements (fig. 4) permits considerable independent motion of the distal ends of the left and right ceratohyals. Despite slight structural differences¹⁵, the hyoid of *Andrias* also occasionally displays asymmetry in its movements.

Discussion. The structure and behavior of the feeding apparatus in *Cryptobranchus* and *Andrias* are unique among previously studied suction-feeding vertebrates. However, during reduction or transport of prey, the heads of various fishes^{16,17}, reptiles^{18–20}, and mammals^{21,22} display bilaterally asymmetric or asynchronous patterns of bone movement that are generated by similarly asymmetric or asynchronous patterns of muscle activity. *Cryptobranchus* and *Andrias* are the first amphibians in which asymmetric jaw movements have been demonstrated. Whether the structural attributes

of *Cryptobranchus* and *Andrias* which permit these movements are primitive or derived features for salamanders remains unclear although, on the basis of other characters, cryptobranchids are generally regarded as primitive salamanders²³. On the other hand, the potential for bilateral asymmetry is probably a primitive feature of the control system of the vertebrate feeding apparatus because: 1) it appears in some representatives of virtually all major vertebrate clades, and 2) it seems functionally related to a simple property of feeding, which is that prey (or food) can rarely be expected to be symmetrical or to occupy positions that are bilaterally symmetrical with respect to the oral cavity. We suggest that in many vertebrate taxa, the nature of attachments between right and left skeletal elements severely limits kinematic asymmetry although the behavior of neural and muscular systems may display considerable asymmetry. As cautioned by Lauder and Norton²⁴, future electrophysiological studies of feeding in lower vertebrates should not assume bilateral symmetry in nervous or muscular activity.

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