Feeding

Basic Terms Used for Feeding Mechanisms of Vertebrates

In water (mostly)

1. Suspension-feeding (= filter-feeding) - filter small particles (alive or dead, depending on species) out of water column

2. Suction-feeding - open mouth, suck in food

3. Ram-feeding - open mouth, swim over food

   Ram-Suction Index - compares movement of food relative to movement of feeder

In air

4. Inertial-feeding - inertia of food is used to move it in oral cavity

5. Transport - movement of food within oral cavity (by water currents in aquatic vertebrates or tongue in tetrapods)

6. Mastication - physical reduction of food size by chewing

Evolution of Feeding Modes

Evolutionary trend: Highly kinetic skull, many elements eating food whole -> less kinetic skull, stronger jaw, chewing

Prey transported via water currents: It's a matter of filtering, ramming or suction

1. Intraoral prey transport by water currents
2. Gape constant prior to fast opening
3. Mouth opening caused by both lower jaw depression and head elevation
4. Recovery phase present
5. Hyoid retraction coincident with fast opening

On land: must bite, use tongue to move food

6. Tongue based intraoral transport

Faster movements - faster biting and inertial feeding

7. Short slow-open phase (SO) just prior to fast opening
8. Recovery phase absent
9. Inertial feeding present
11. Four-stage masticatory cycle for intraoral food processing
12. Gape increases mostly by lower jaw depression

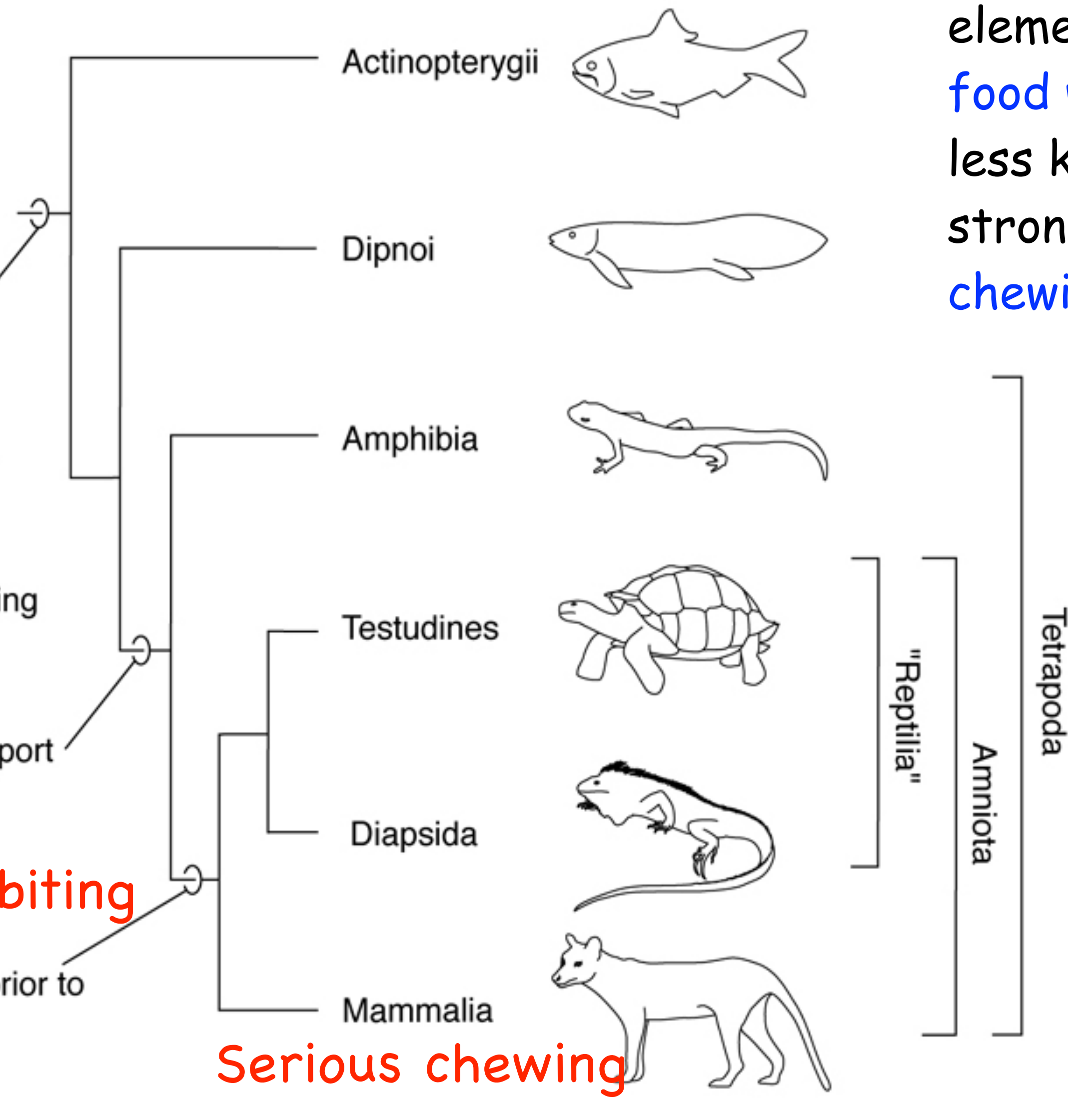
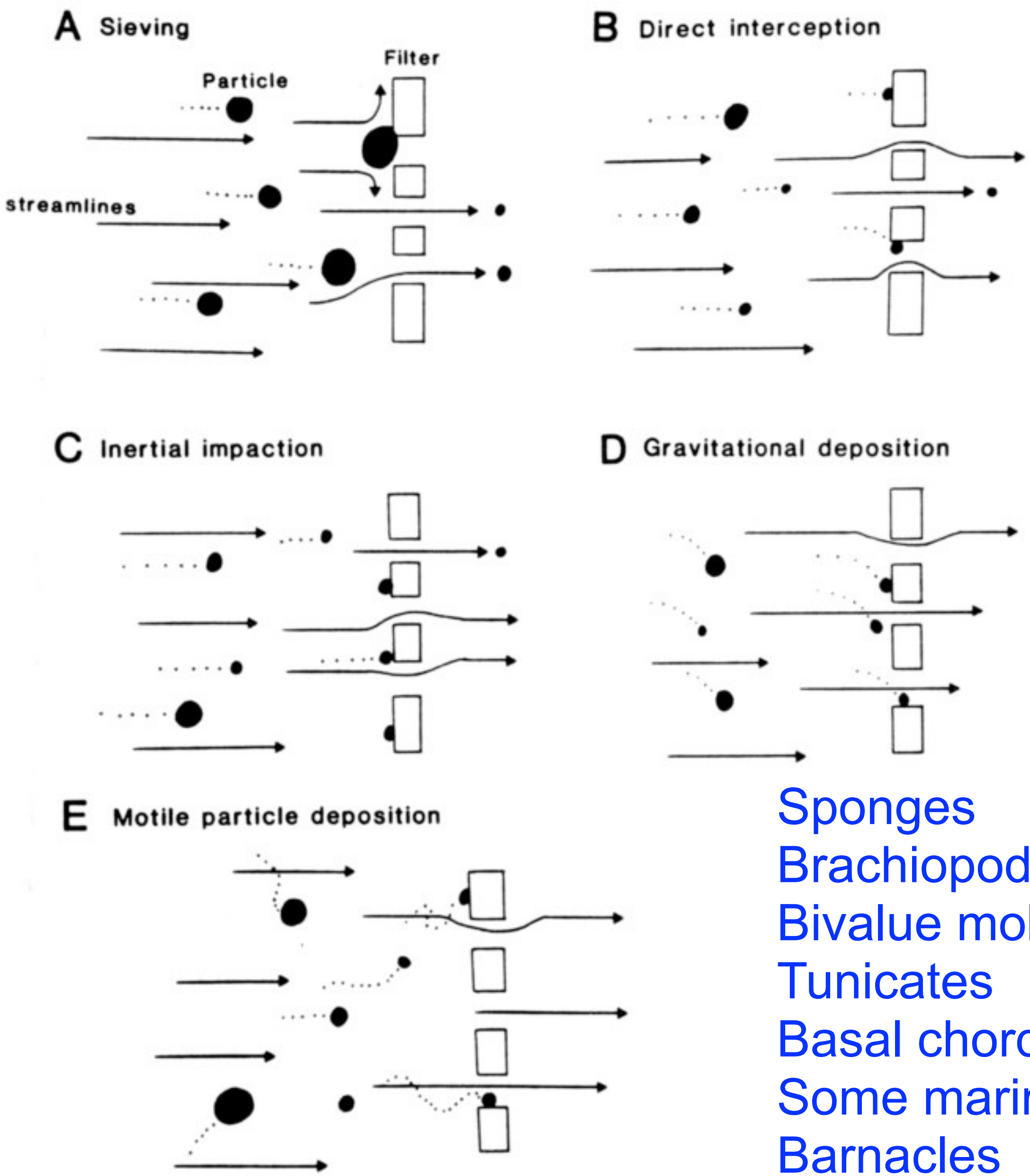
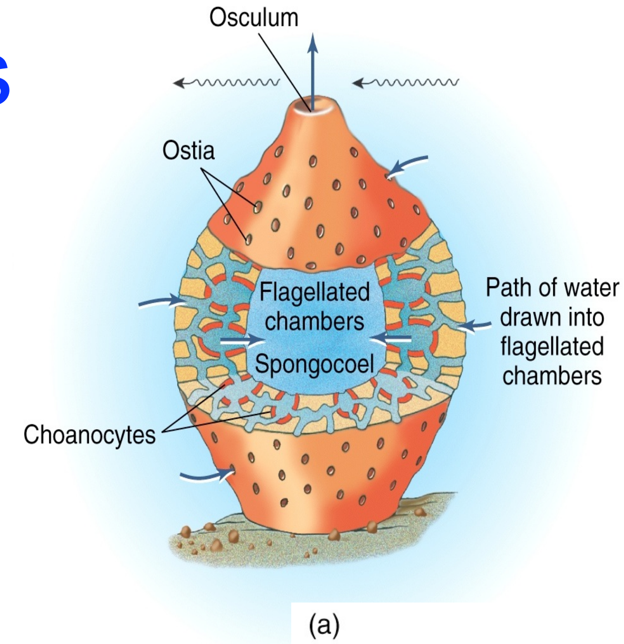


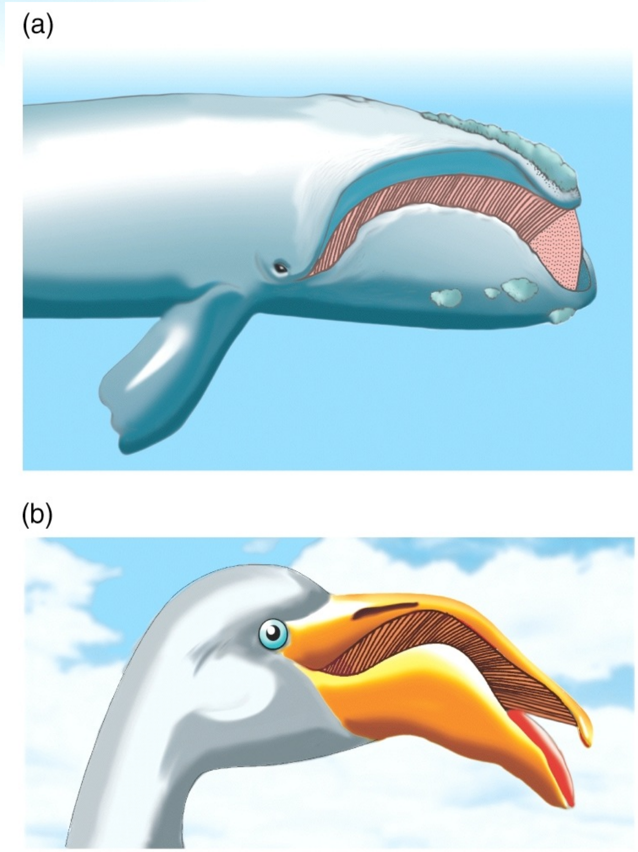
Fig. 16.21: Liem, Bemis, Walker, Grande

Filter feeding mechanisms





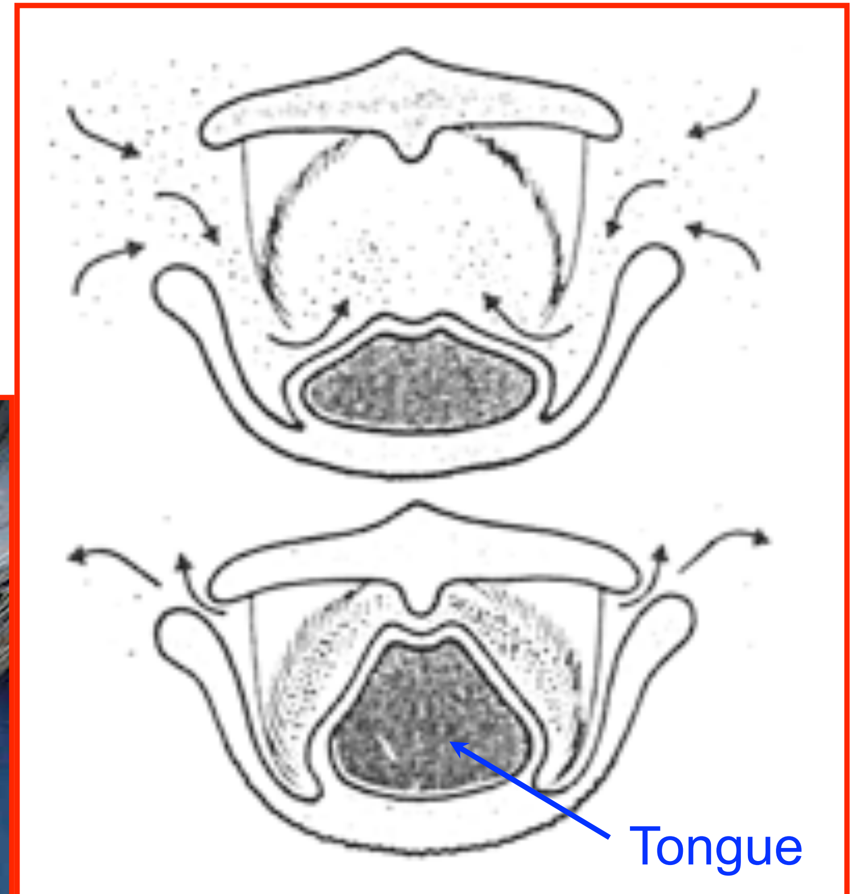
Sponges
Brachiopods
Bivalue mollusks
Tunicates
Basal chordates
Some marine worms
Barnacles
Sea fans
Baleen whales



Feeding adaptations

Filter feeding mammal -
Baleen whales use ram feeding


baleen


Tongue


A classic ram feeder
You can tell a lot about an animal by it’s method of acquiring food

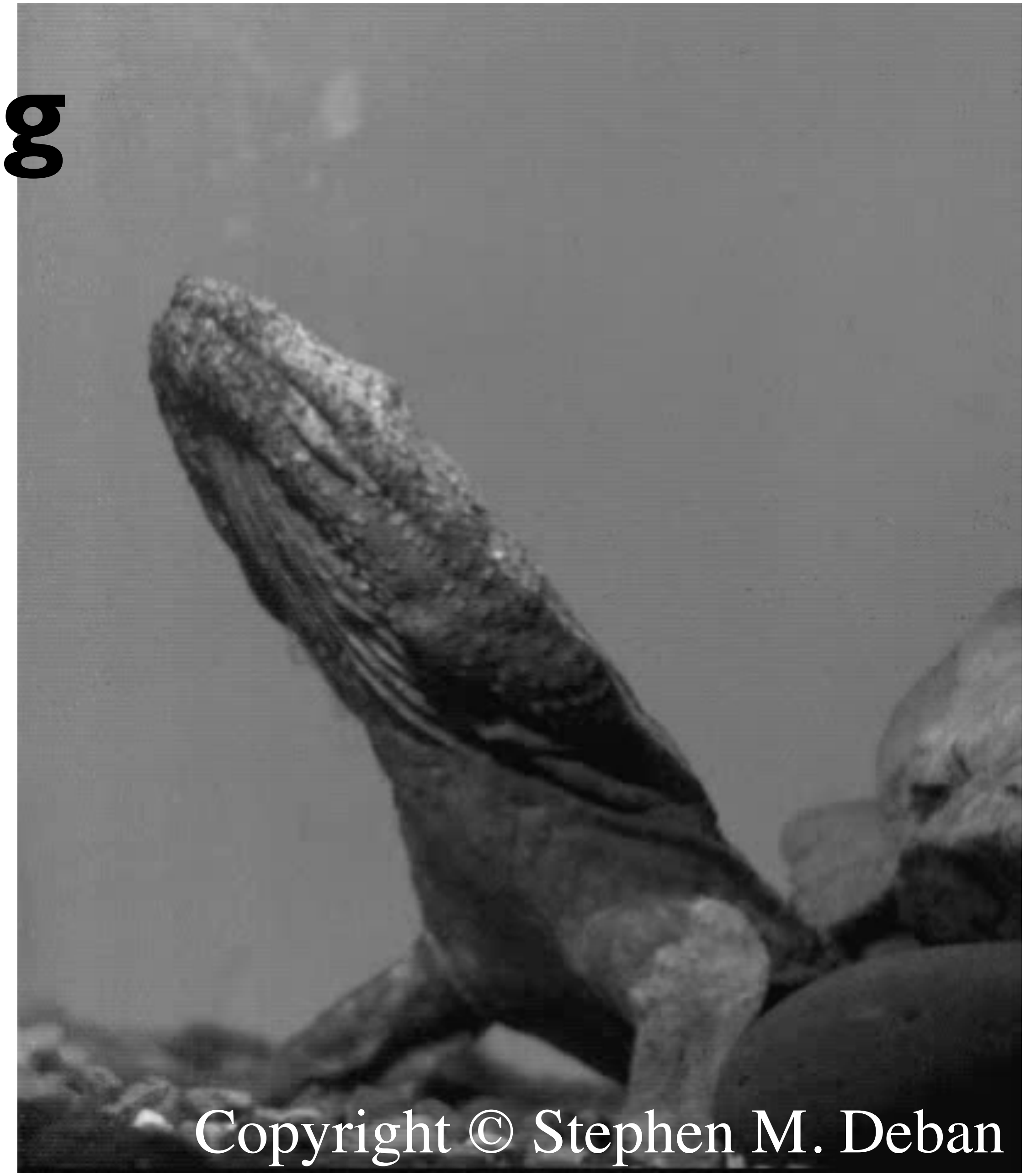
Suction -> Tongues

Suction Feeding

Cryptobranchus allgeganiensis
"hellbender"

A large salamander

Suction is produced by ventral movement of the throat.

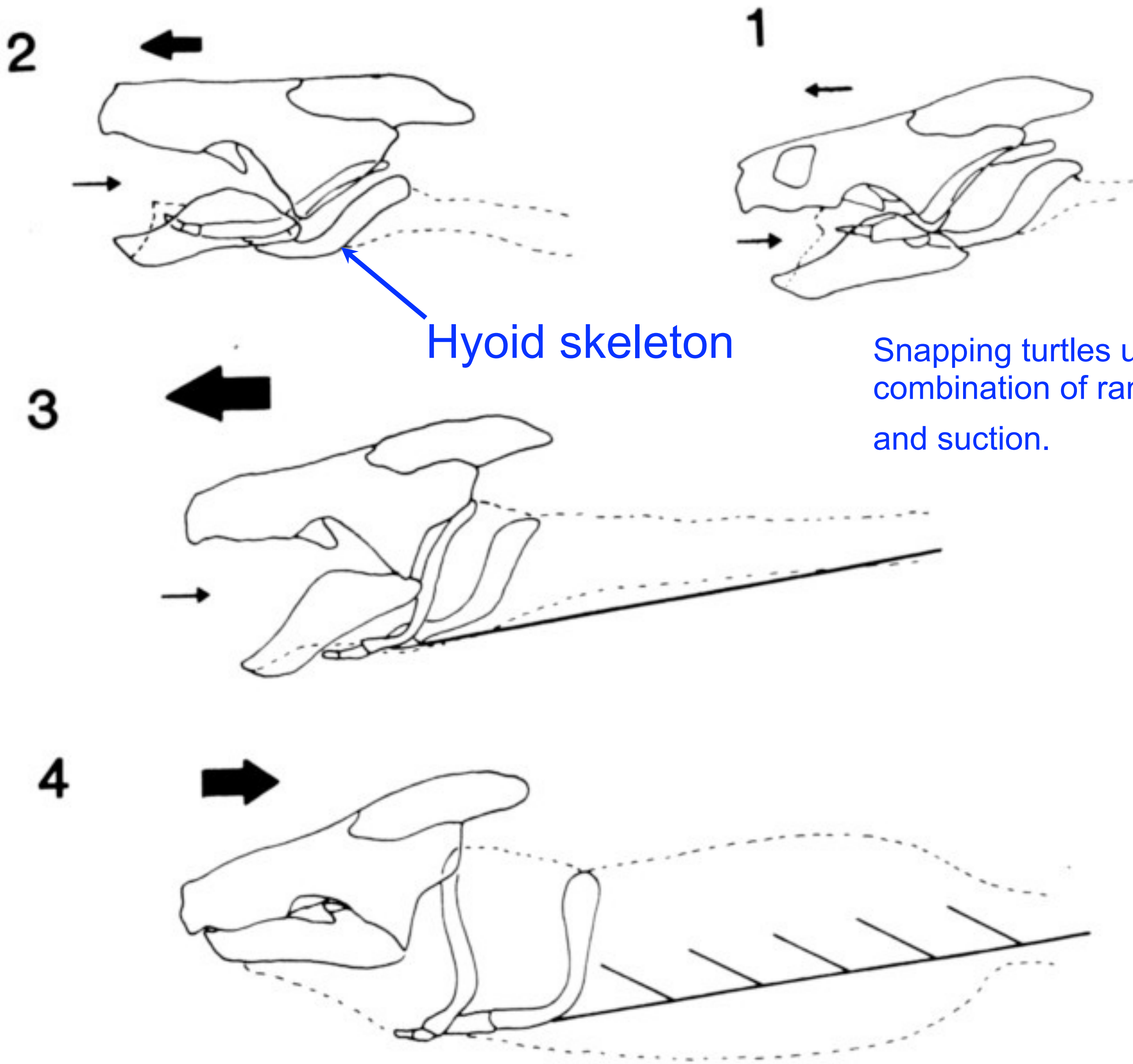


You can see the outlines of the hyobranchial apparatus quite well through the loose skin.

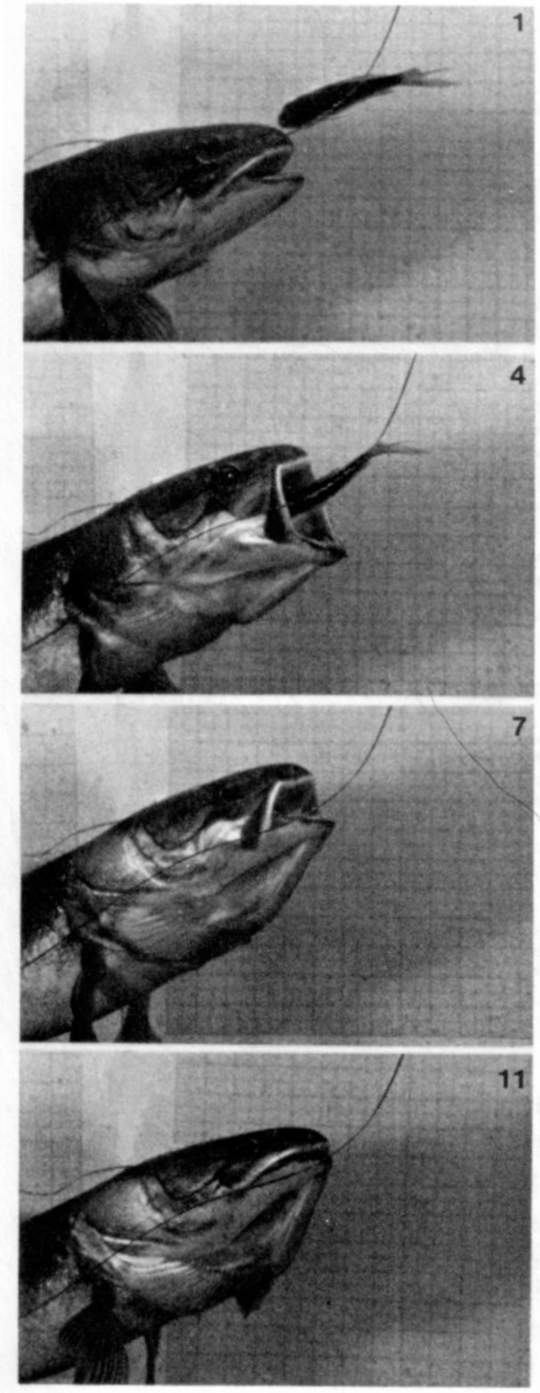
http://video.google.com/videoplay?docid=6884752966799287798&ei=4tblSM-HPJjUqAOqg-GZCw&q=hellbender&vt=lf&hl=en

Suction feeding

Mechanism of suction feeding

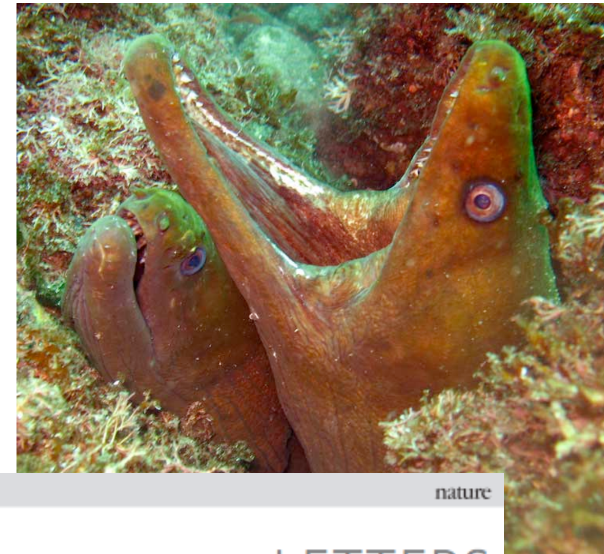


Snapping turtles use a combination of ram feeding and suction.



How do Moray Eels eat?

Predators living in crevices -- hard to expand thorax and buccal cavity to generate suction



495

The Journal of Experimental Biology 210, 495-504
Published by The Company of Biologists 2007
doi:10.1242/jeb.02663

Biting releases constraints on moray eel feeding kinematics

Rita S. Mehta* and Peter C. Wainwright
Section of Evolution and Ecology, University of California, One Shields Avenue, Davis, CA 95616, USA
*Author for correspondence (e-mail: rsmehta@ucdavis.edu)

Accepted 22 November 2006

Summary

We present an analysis of prey capture functional morphology in eels by comparing two species of moray eels, *Muraena retifera* and *Echidna nebulosa* (Family Muraenidae), to the American eel *Anguilla rostrata* (Family Anguillidae). The skulls of both moray species exhibited extreme reductions of several prominent components of the suction-feeding mechanism, including the hyoid bar, the sternohyoideus muscle and the pectoral girdle. Associated with these anatomical modifications, morays showed no evidence of using suction during prey capture. From 59 video sequences of morays feeding on pieces of cut squid we saw no hyoid depression and no movement of prey toward the mouth aperture during the strike, a widely used indicator of suction-induced water flow. This was in contrast to *A. rostrata*, which exhibited a robust hyoid, sternohyoideus muscle and pectoral girdle, and used suction to draw prey into its mouth. Average prey capture time in morays, about 500 ms, was roughly 10 times longer than in *A. rostrata*, and morays frequently reversed the direction of jaw and head rotation in the midst of the strike. We tested whether the absence of suction feeding reduces temporal constraints on feeding kinematics, permitting greater variance in traits that characterize timing and the extent of motion in the neurocranium, by comparing moray eel species with *A. rostrata*, two Centrarchids and a cichlid. Kinematic variance was roughly 5 times higher in morays than the suction-feeding species. Prey capture by suction demands a rapid, highly coordinated series of cranial movements and the loss of this mechanism appears to have permitted slower, more variable prey capture kinematics in morays. The alternative prey capture strategy in morays, biting, may be tied to their success as predators in the confined spaces of reef crevices where they hunt for cephalopods, crustaceans and fish.

Key words: moray eel, feeding, anatomical reduction, kinematic integration, *Muraena retifera*, *Echidna nebulosa*, *Amphilophus citrinellus*, *Lepomis macrochirus*, *Micropterus salmoides*.

Vol 449 | 6 September 2007 | doi:10.1038/nature06062 nature

LETTERS

Raptorial jaws in the throat help moray eels swallow large prey

Rita S. Mehta[1] & Peter C. Wainwright[1]

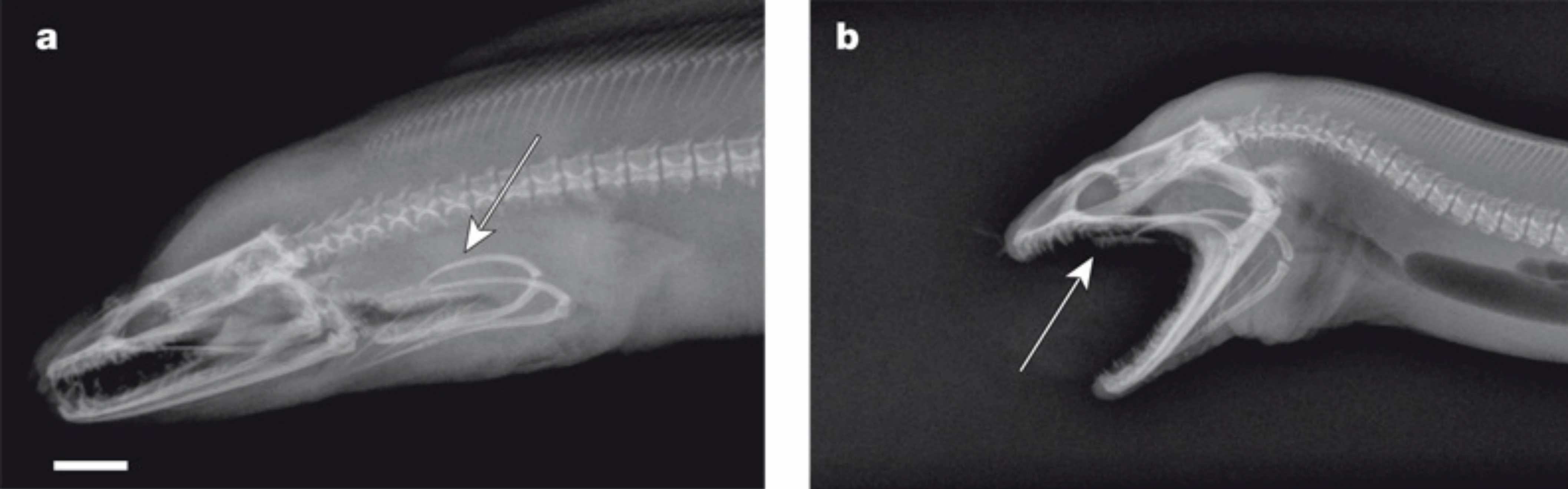
Most bony fishes rely on suction mechanisms to capture and transport prey[1]. Once captured, prey are carried by water movement inside the oral cavity to a second set of jaws in the throat, the pharyngeal jaws, which manipulate the prey and assist in swallowing[1,2]. Moray eels display much less effective suction-feeding abilities[3]. Given this reduction in a feeding mechanism that is widespread and highly conserved in aquatic vertebrates, it is not known how moray eels swallow large fish and cephalopods[4–7]. Here we show that the moray eel (*Muraena retifera*) overcomes reduced suction capacity by launching raptorial pharyngeal jaws out of its throat and into its oral cavity, where the jaws grasp the struggling prey animal and transport it back to the throat and into the oesophagus. This is the first described case of a vertebrate using a second set of jaws to both restrain and transport prey, and is the only alternative to the hydraulic prey transport reported in teleost fishes. The extreme mobility of the moray pharyngeal jaws is made possible by elongation of the muscles that control the jaws[8], coupled with reduction of adjacent gill-arch structures[9]. The discovery that pharyngeal jaws can reach up from behind the skull to grasp prey in the oral jaws reveals a major innovation that may have contributed to the success of moray eels as apex predators hunting within the complex matrix of coral reefs[10,11]. This alternative prey transport mode is mechanically similar to the ratcheting mechanisms used in snakes[12,13]—a group of terrestrial vertebrates that share striking morphological, behavioural[14] and ecological convergence with moray eels.

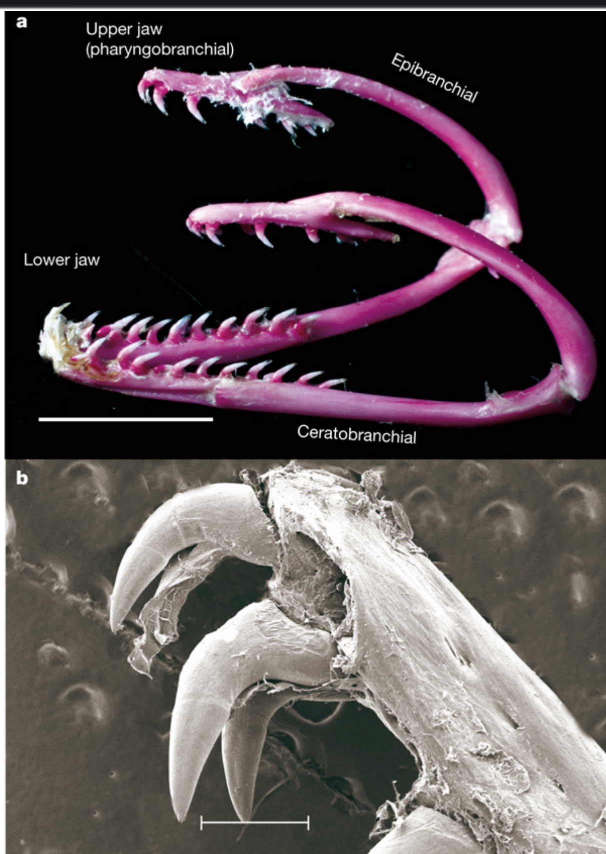
understanding the basis of their feeding performance may provide insight into their successful radiation on coral reefs.

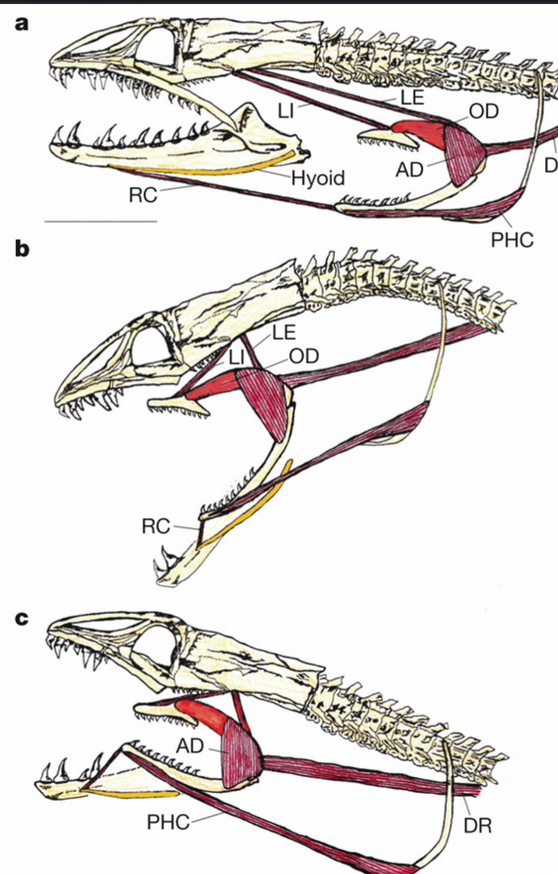
In a recent study, we described the feeding kinematics of two moray species with diverse dietary habits, calling attention to the marked reduction of important suction-producing cranial elements, particularly the hyoid skeleton and sternohyoideus muscle[3]. From kinematic analysis of feeding behaviour, we concluded that morays do not use suction to capture prey but, rather, apprehend prey by biting. Biting and suction are not mutually exclusive mechanisms[19]. Among ray-finned fishes, the use of a suction-induced flow of water is the only known mechanism for transporting prey from the oral jaws to the pharyngeal jaws and oesophagus[1,20].

Morays have a well-developed pharyngeal jaw apparatus that is positioned posterior to the skull—a more caudal position compared to the pharyngeal jaws of other teleosts[9,21] (Fig. 1a). In light of their reduced capacity to suction water with their jaws, we explored the possibility that morays have evolved an alternative to hydraulic-based prey transport to move large prey from the oral jaws to the pharyngeal jaws, a distance that is secondarily elongate in morays[9].

We used high-speed video to study intra-oral transport behaviour in reticulated morays, *M. retifera*. In each feeding sequence, once the prey was captured in the oral jaws, morays protracted their pharyngeal jaws forward to ensnare the prey, which was then pulled into the moray's throat (see Supplementary Movies 1 and 2). In 40 intra-oral transport sequences, morays protracted their pharyngeal jaws into the oral cavity 88% of the time. Pharyngeal jaw protraction extended


a
b


a
Upper jaw
(pharyngobranchial)
Epibranchial
Lower jaw
Ceratobranchial
b

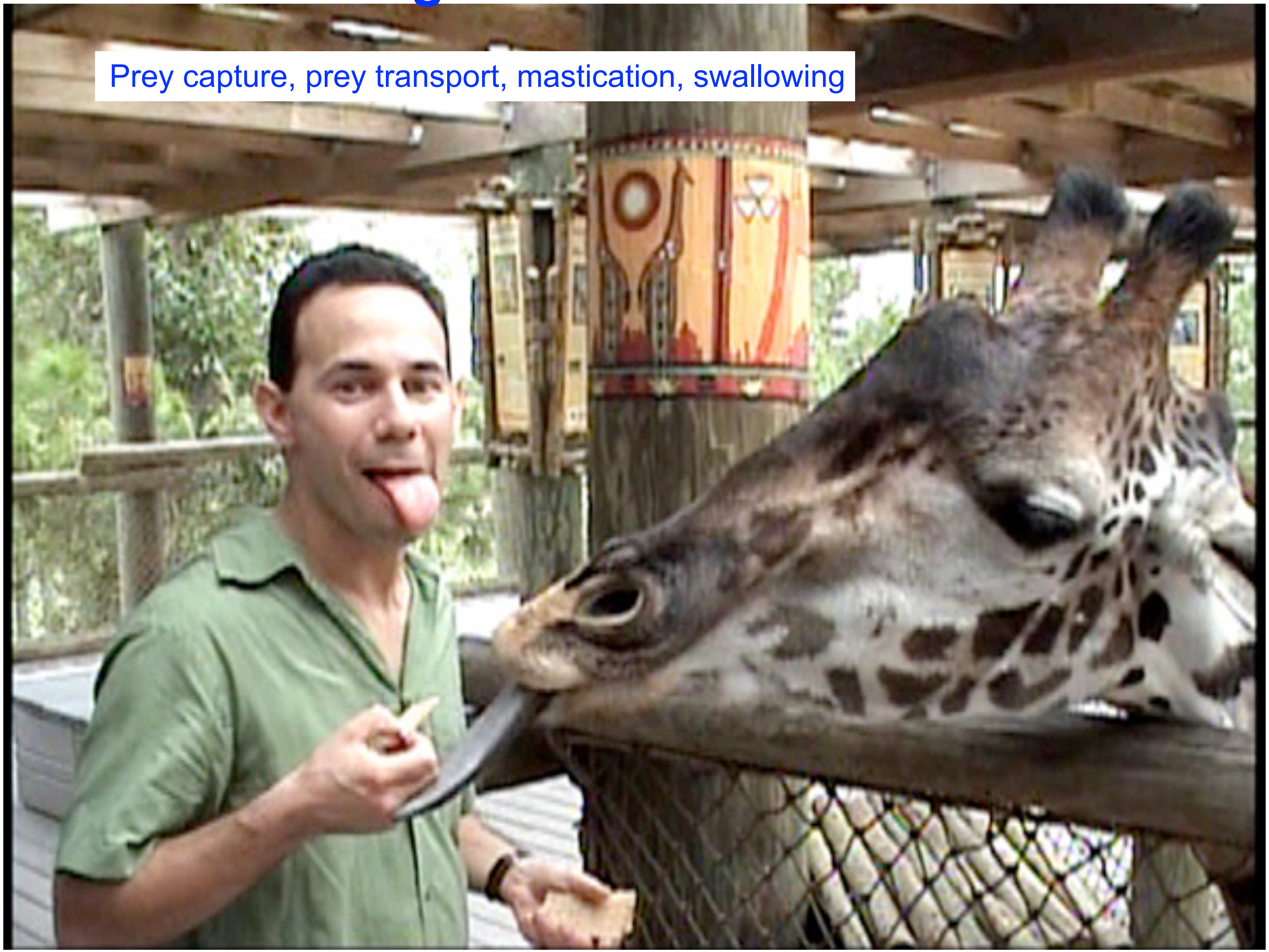

a
LI
LE
OD
AD
Hyoid
RC
DR
PHC
b
LE
LI
OD
RC
c
AD
PHC
DR

Intertial Feeding (intraoral transport)

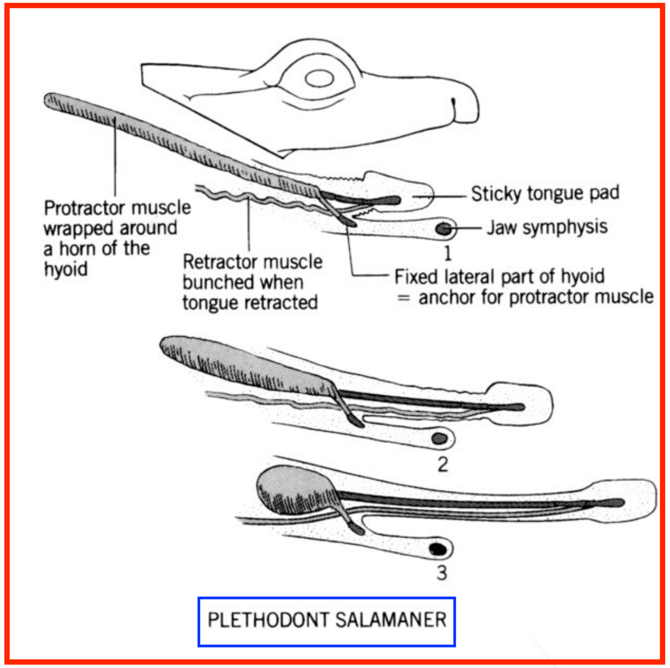
inertia of food is used to move it in oral cavity

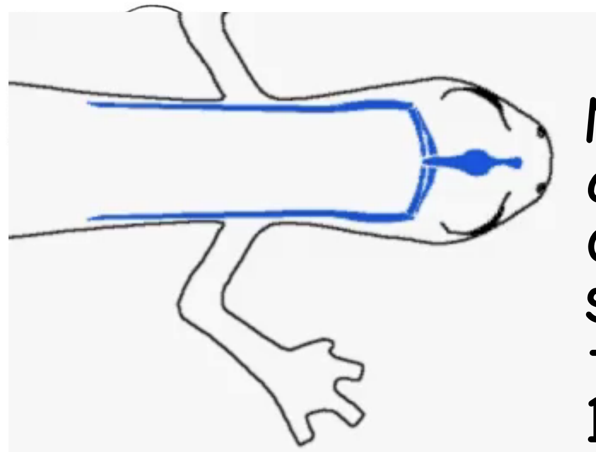
Usually involves rapid movement

Terrestrial feeding - evolution of the vertebrate tongue



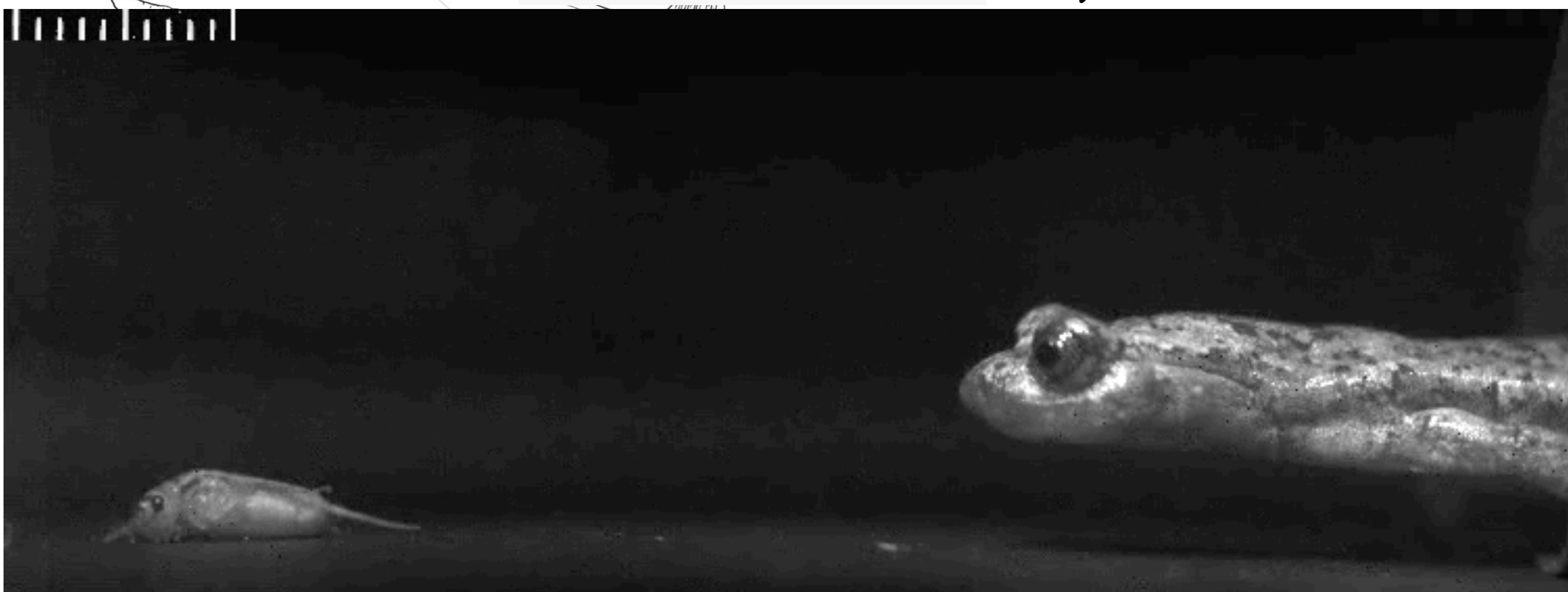
Ballistic tongues



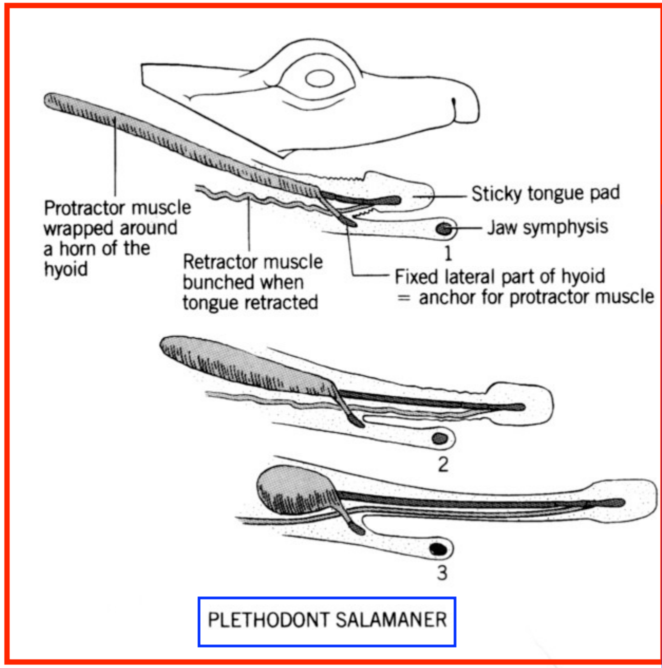


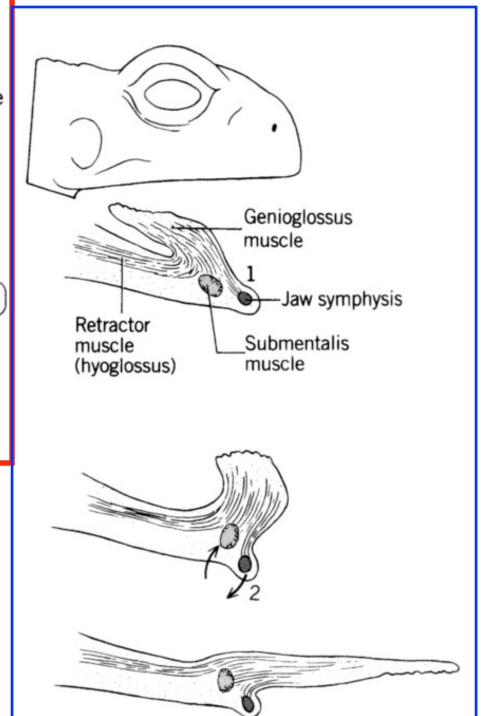
Plethodon salamanders: Shoot hyoid apparatus + tongue!

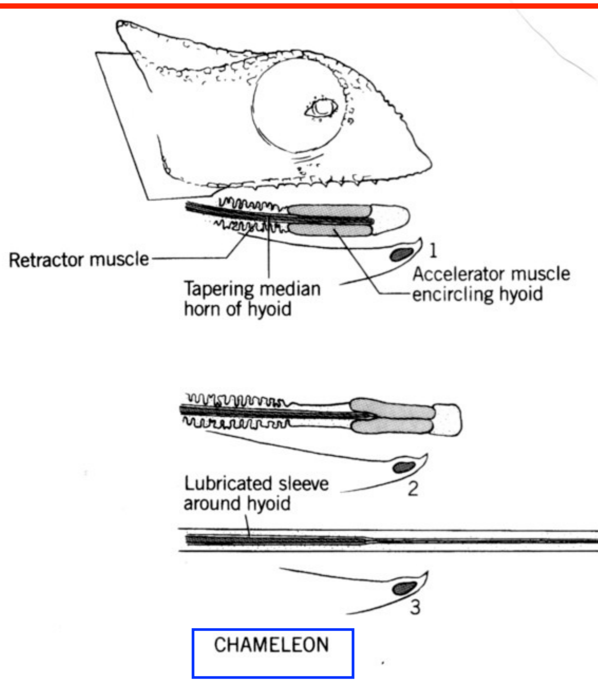
Muscles squeeze the hyoid apparatus, which is cartilaginous. It acts like a spring, ballistically shooting the tongue (Deban et al., 1997)



Ballistic tongues





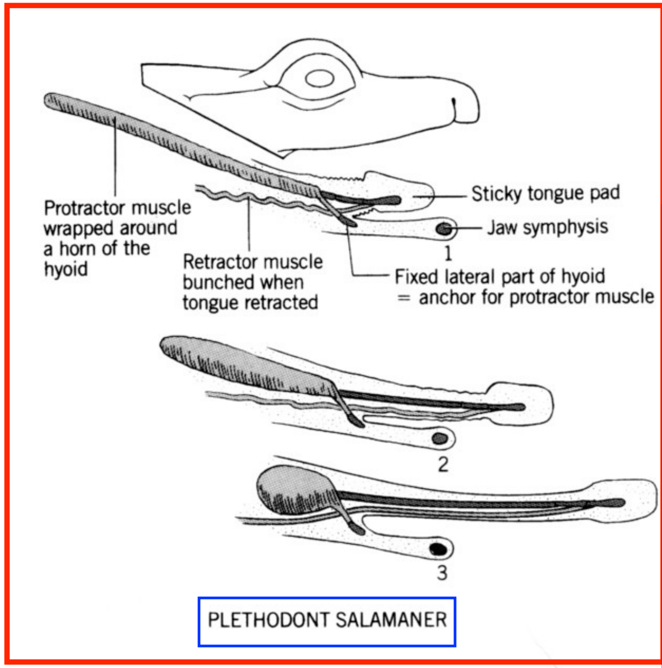


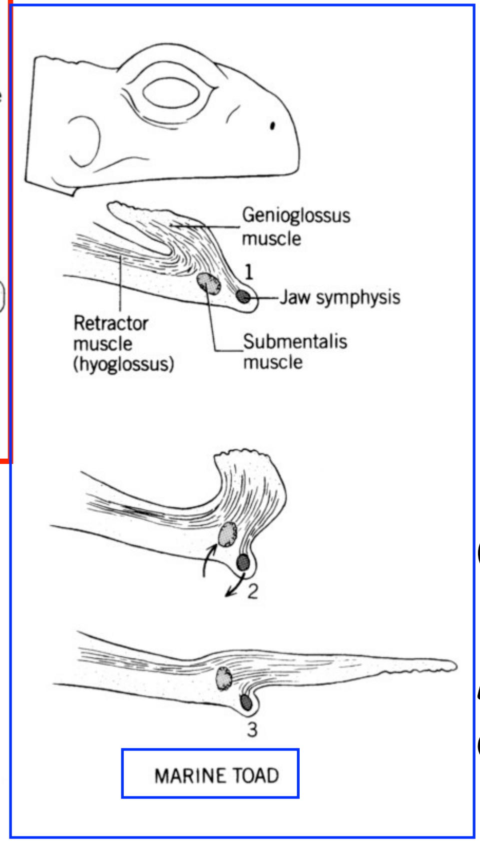
Bufo: fleshy tongue (no skeletal elements)

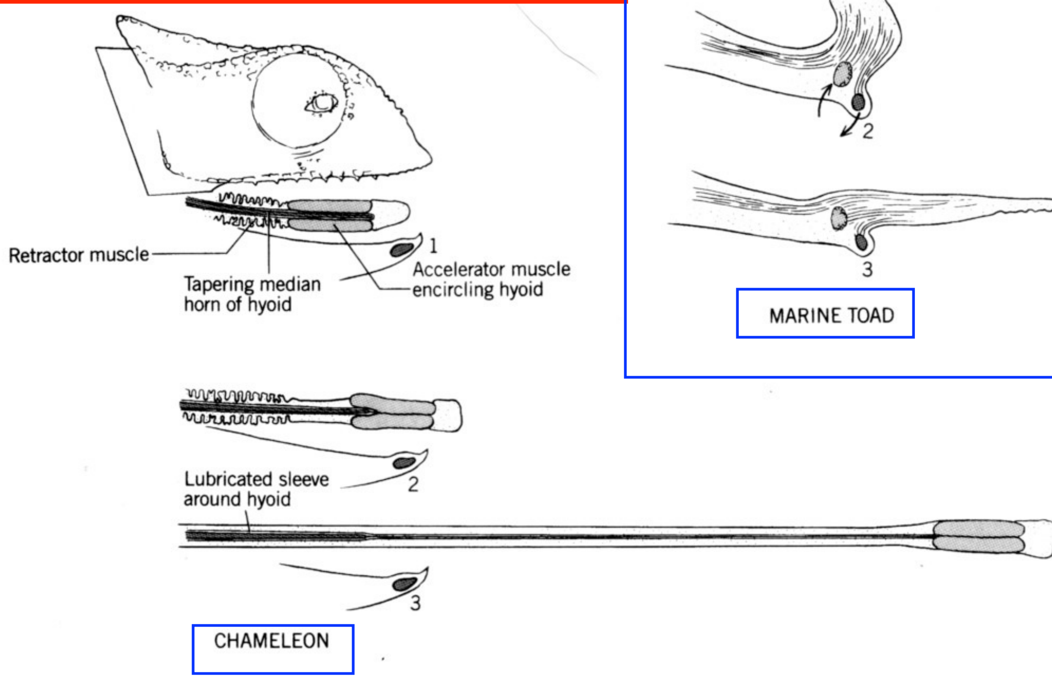
Mouth opening muscles lower the jaw extremely rapidly.

The tongue is attached to the tip of the lower jaw and is literally whipped out of the mouth and stretched to a length of over two jaw lengths. (Lappin et al., 2006)

Ballistic tongues



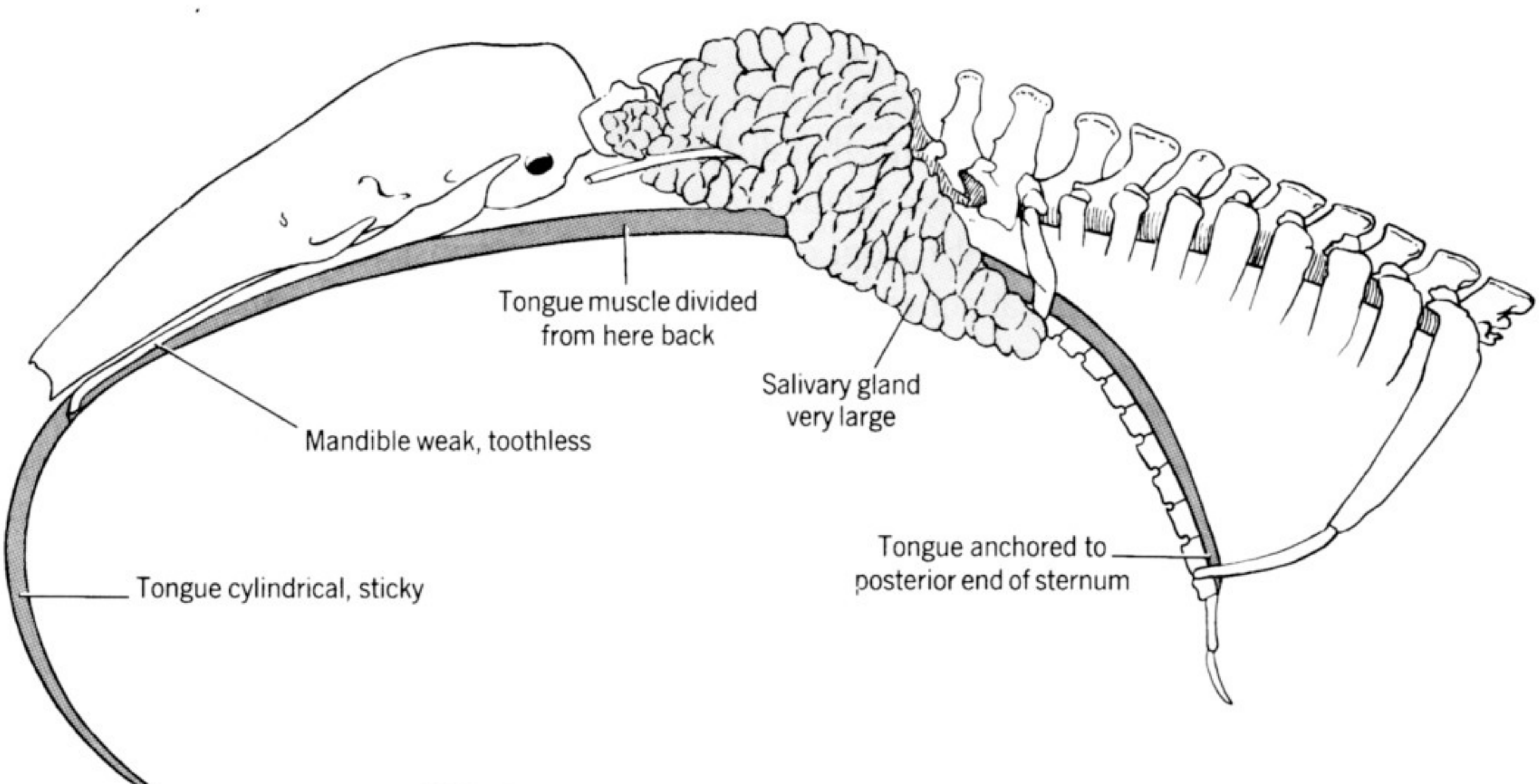




Chameleon:

Accelerator muscle "squeezes" on the tapered hyoid, which projects the fleshy tongue tip.

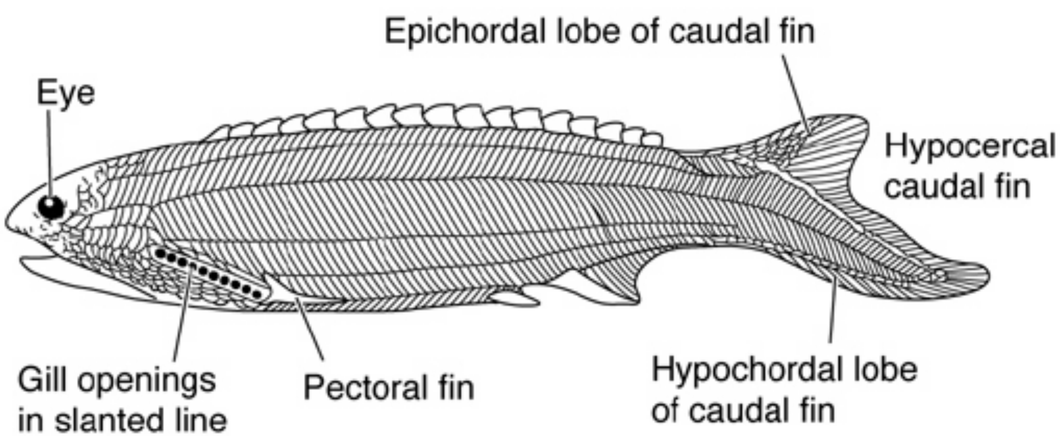
Retraction, via muscle contraction, is much slower.



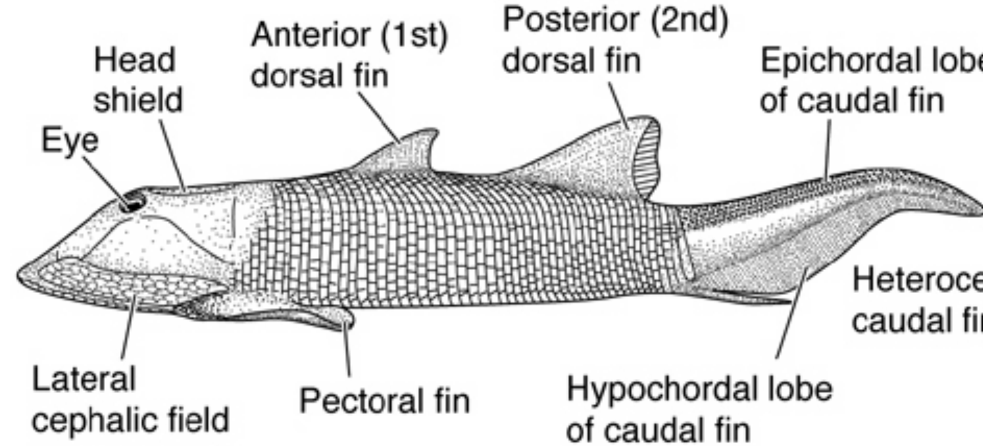
COLLARED ANTEATER, *Tamandua*

Teeth!

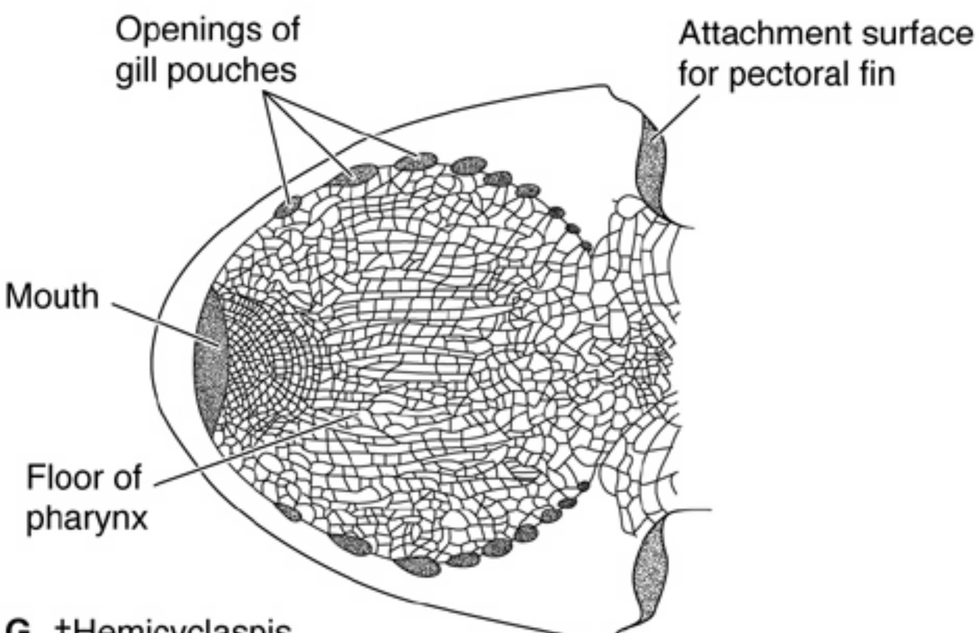
Early Fish: Heavy creatures with armored plates



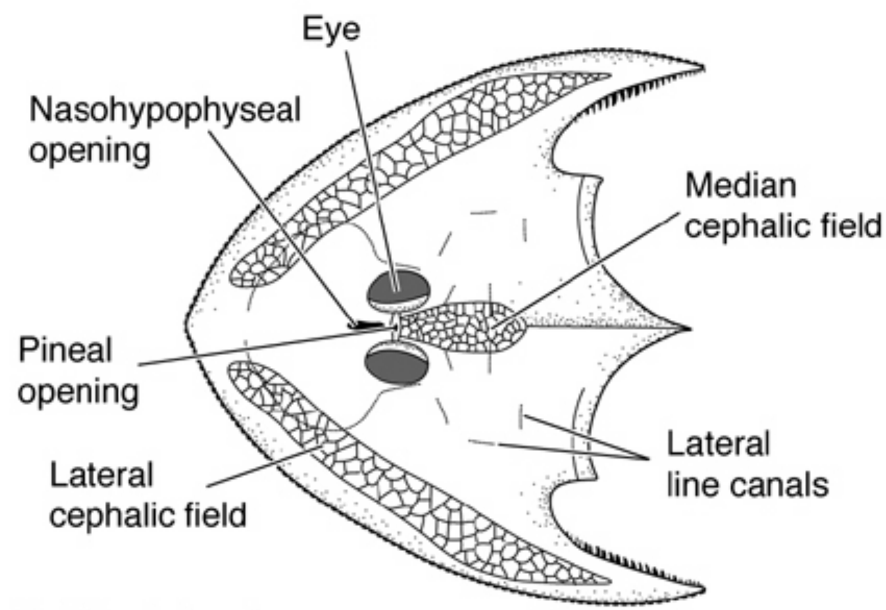
E. †Pterolepis



F. †Ateleaspis



G. †Hemicyclaspis

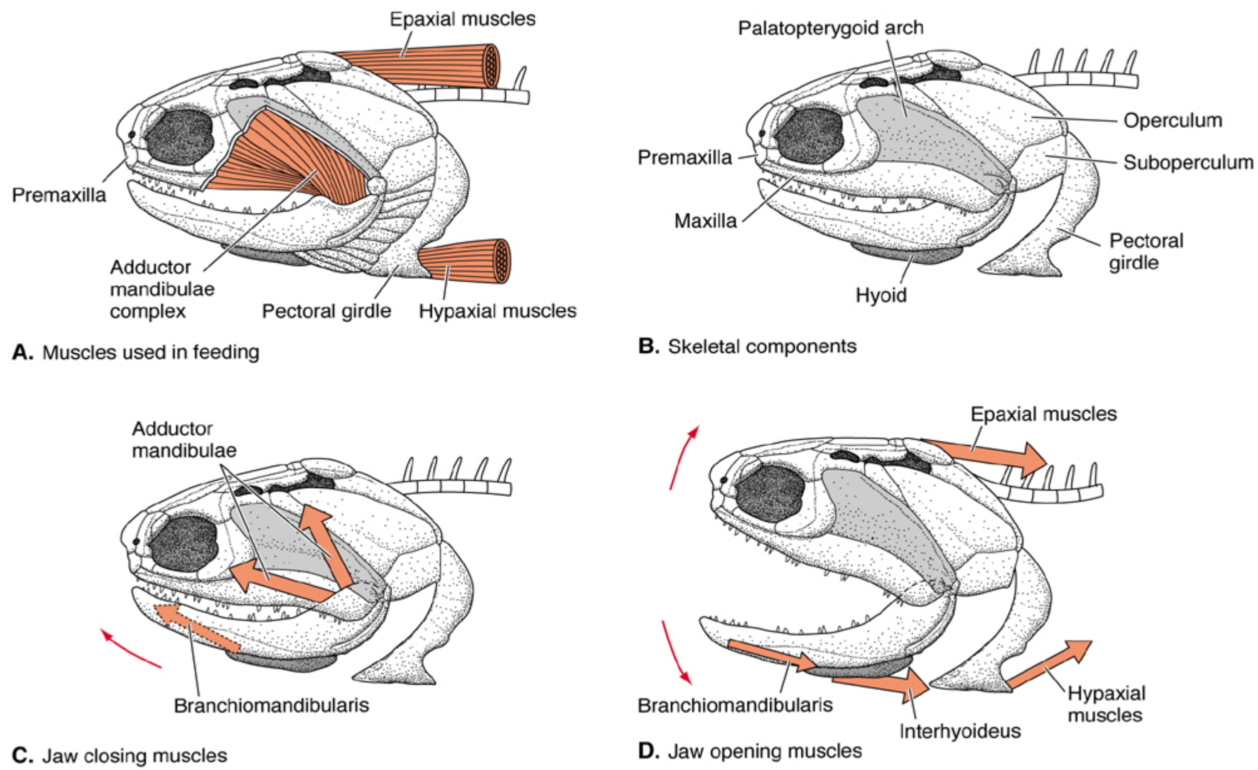


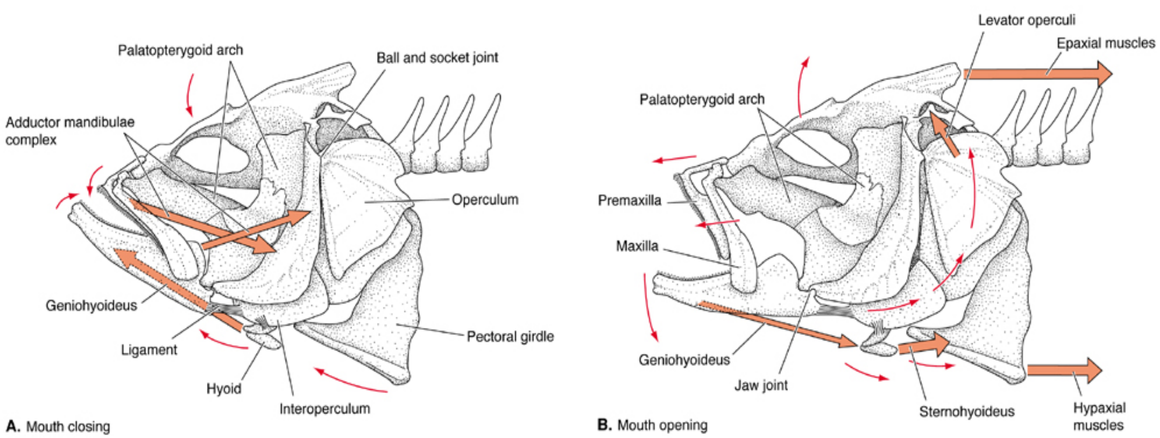
H. †Cephalaspis

Fig. 3.3

Jaws: Fishes

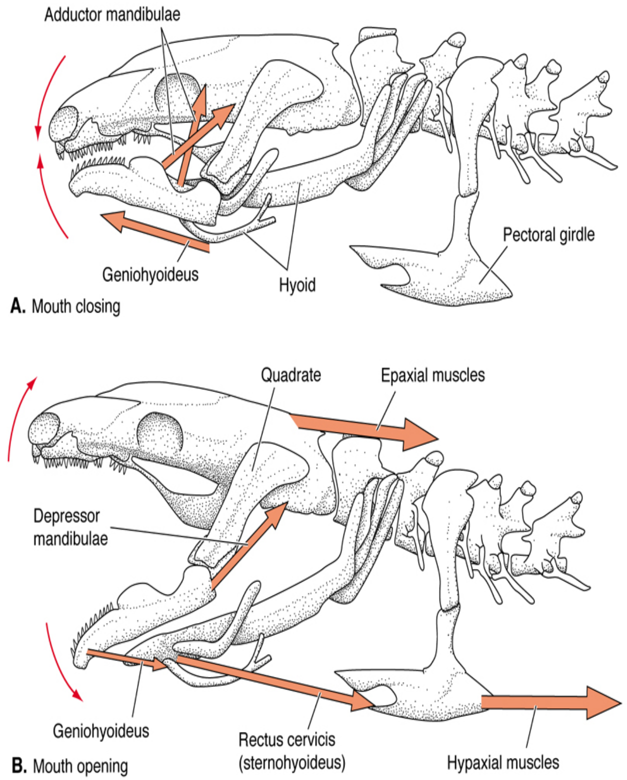
Primitive fish
(Heavy skull for a fish)



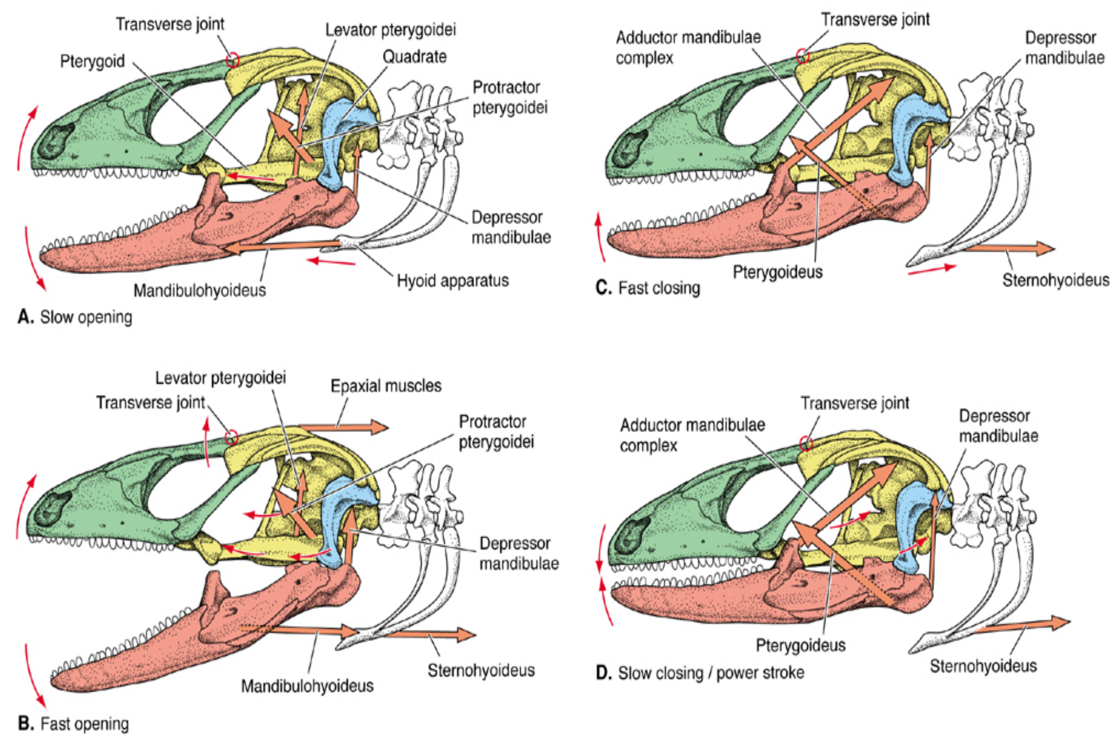


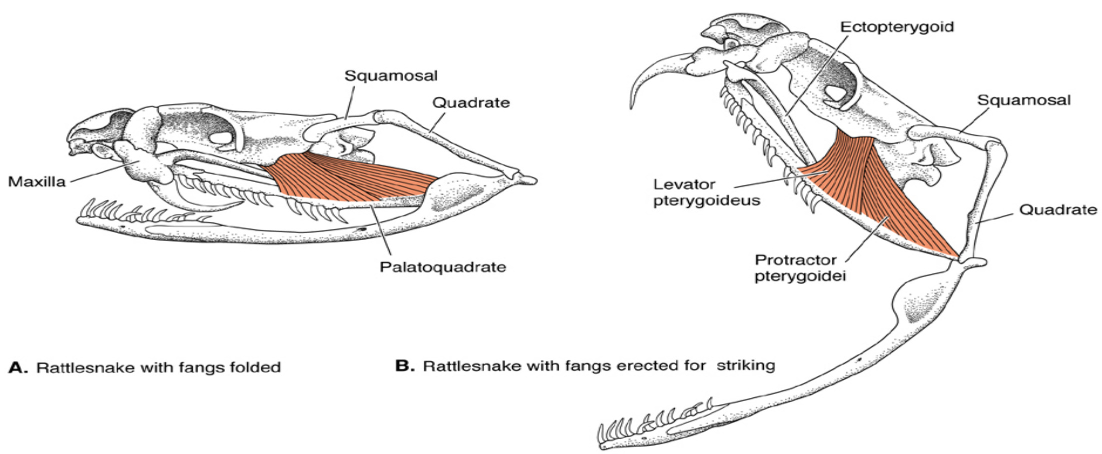
Modern fish
(Light skull, many elements)

Salamander (Amphibian)



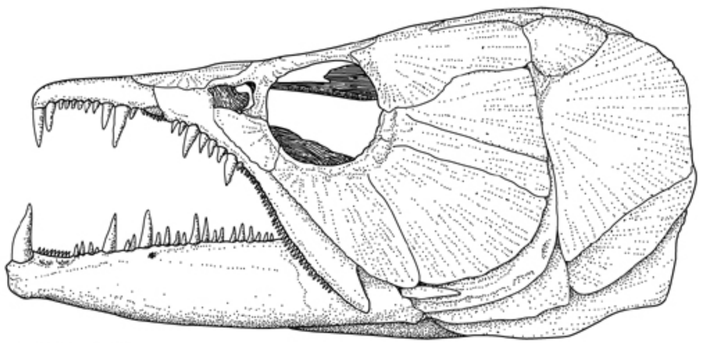
Lizard



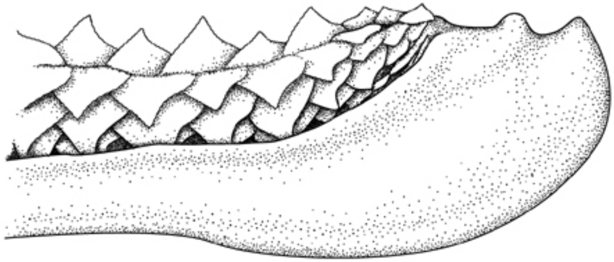


Snake - highly kinetic skull

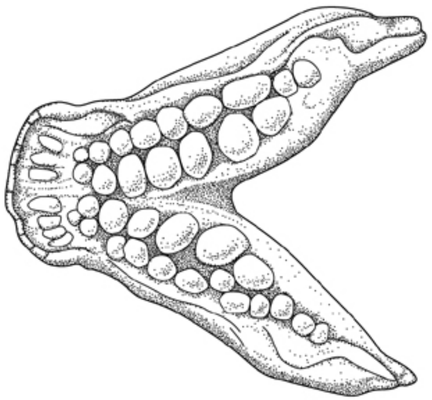
Teeth of "lower vertebrates" are not so strongly attached



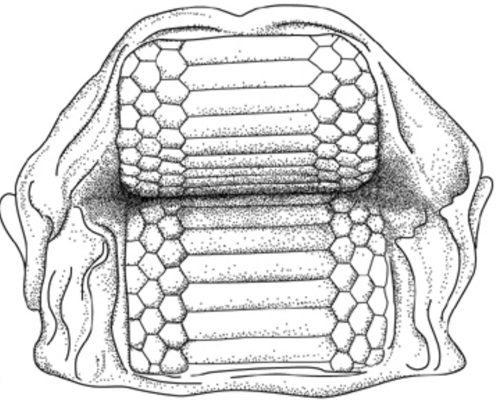
A. Characin



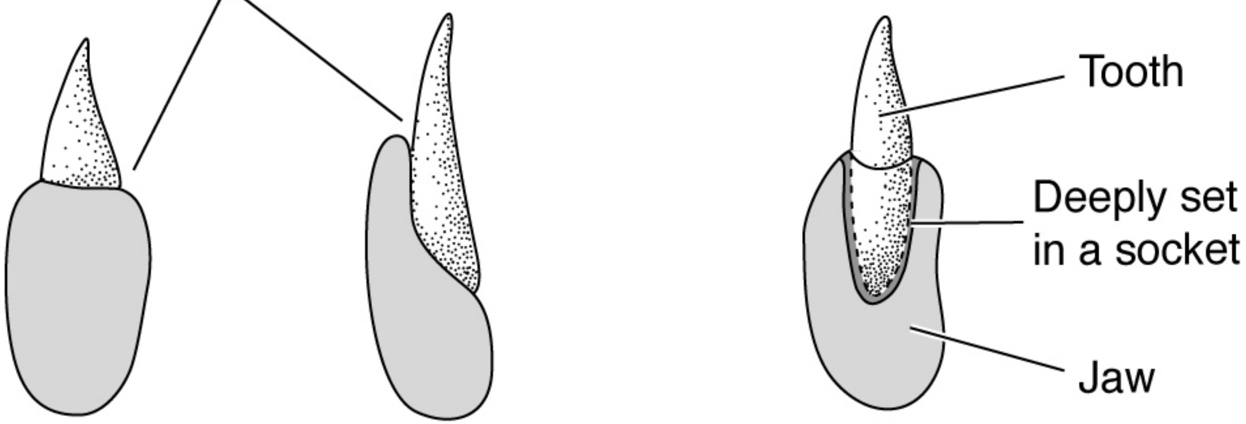
B. Shark



C. Porgy



D. Ray



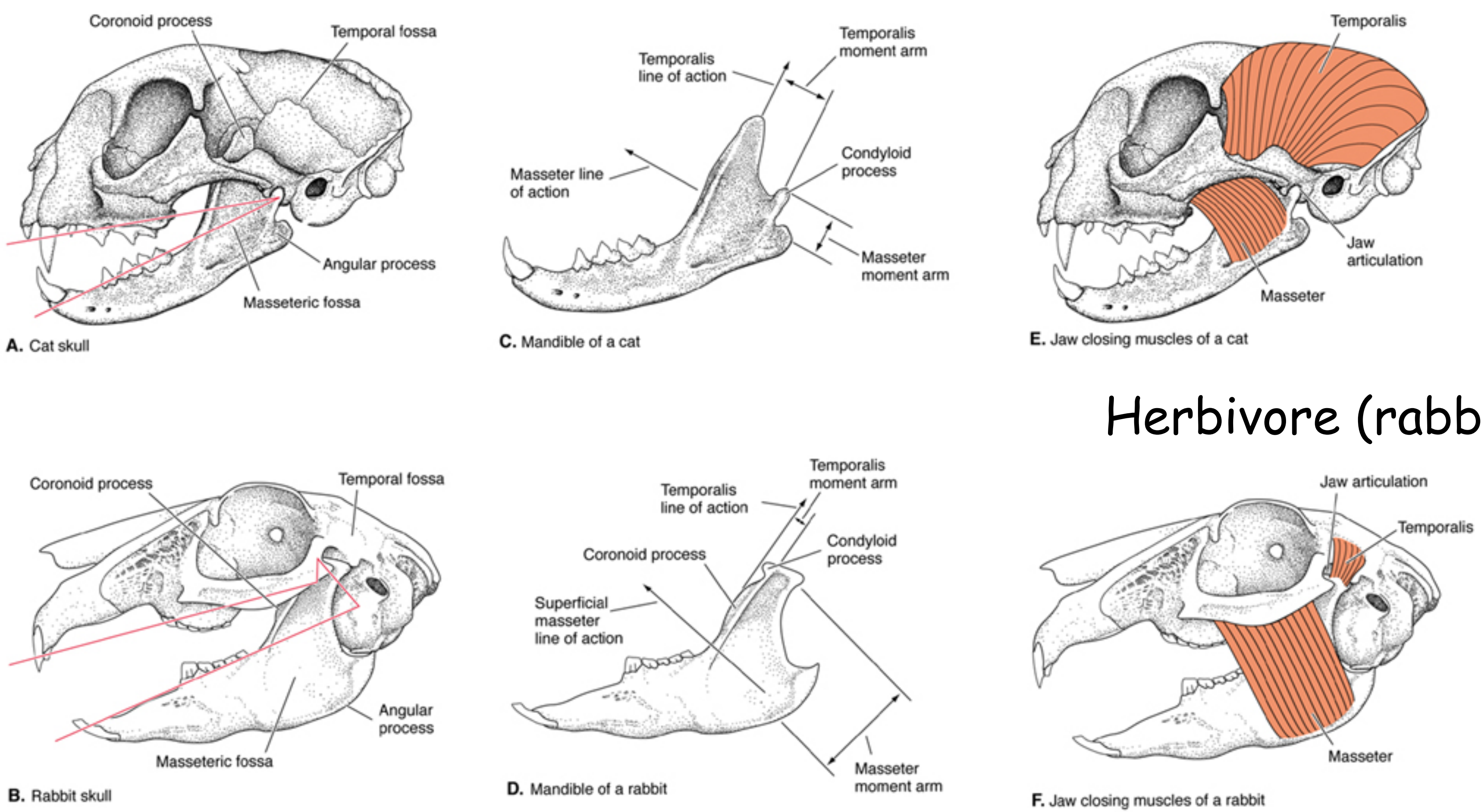
A. Acrodont **B.** Pleurodont **C.** Thecodont

Mammals

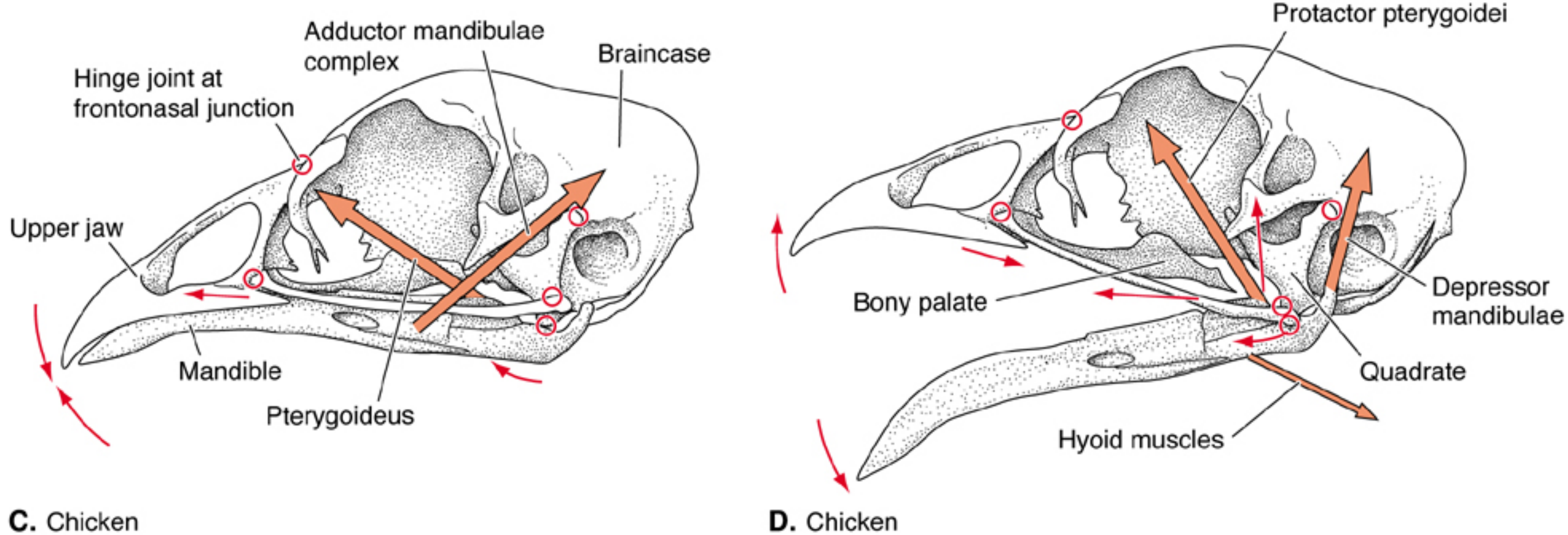
Size and arrangement of muscles determines bite force/speed

Canivore (cat)

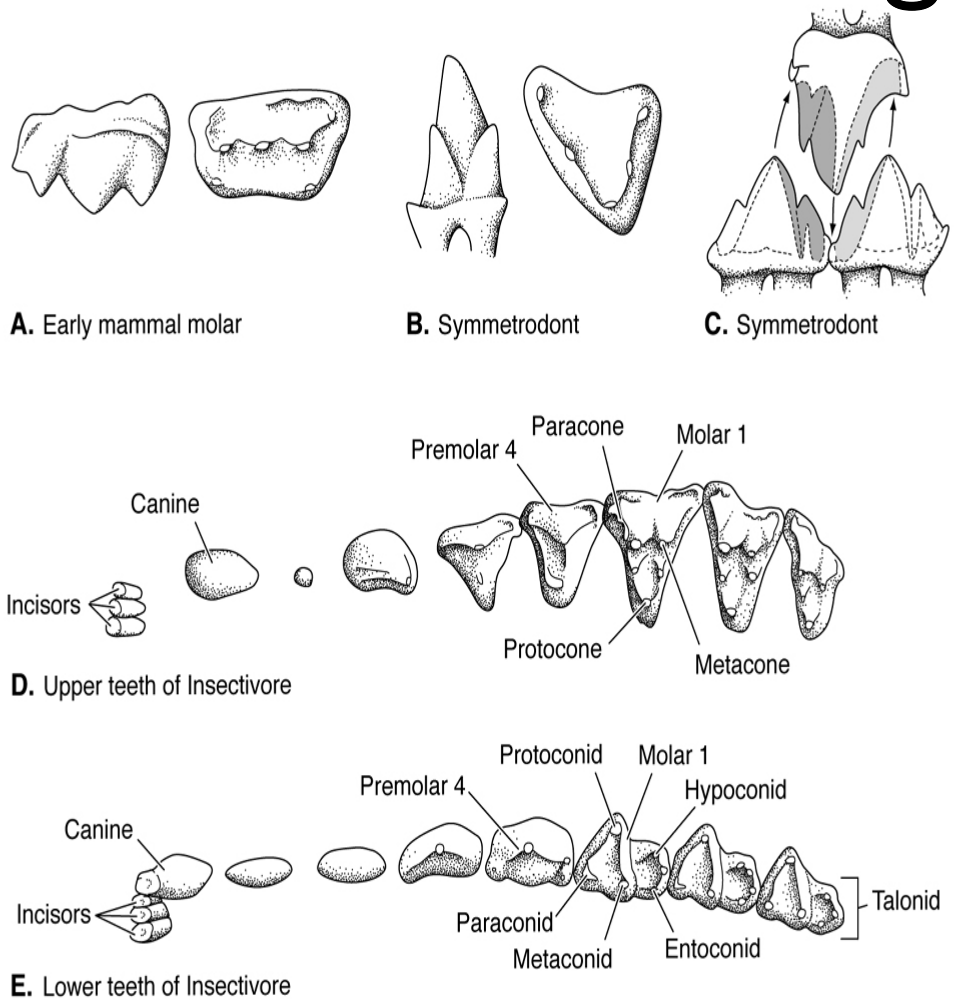
Herbivore (rabbit)

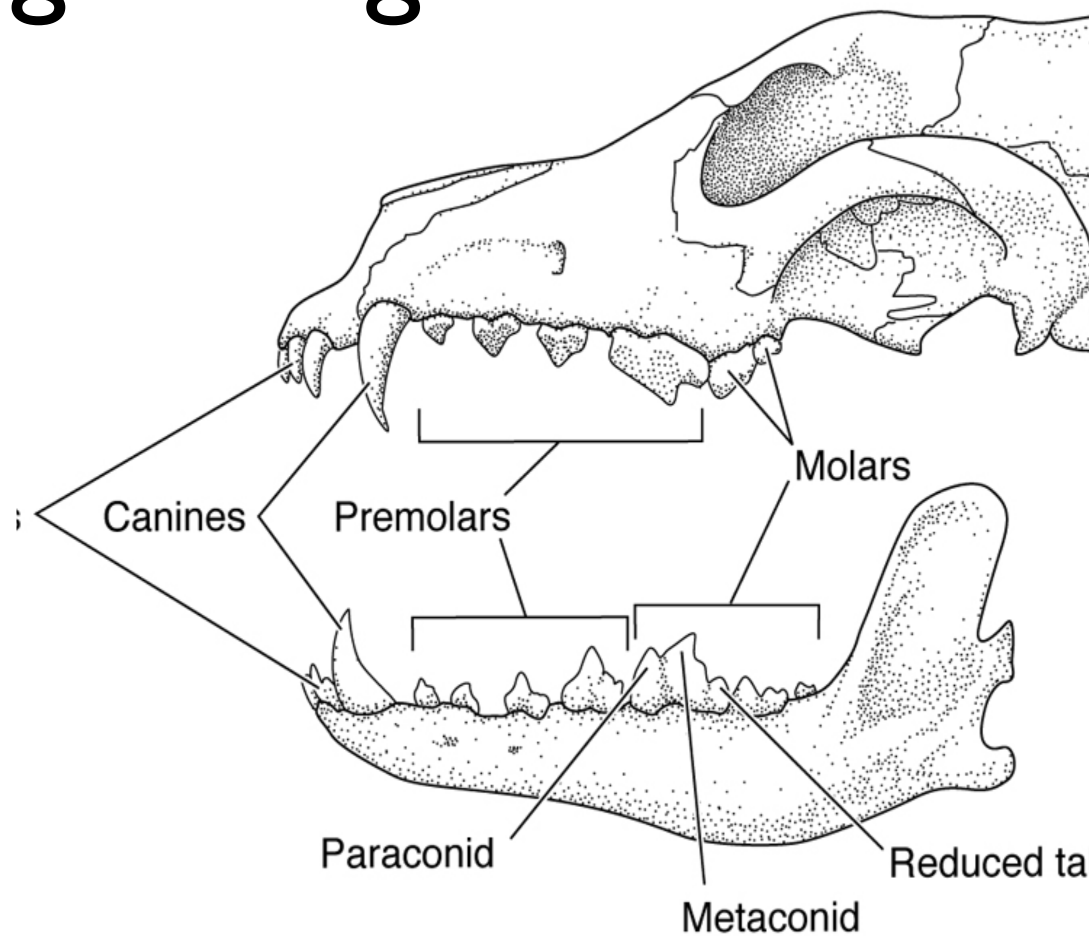


Birds

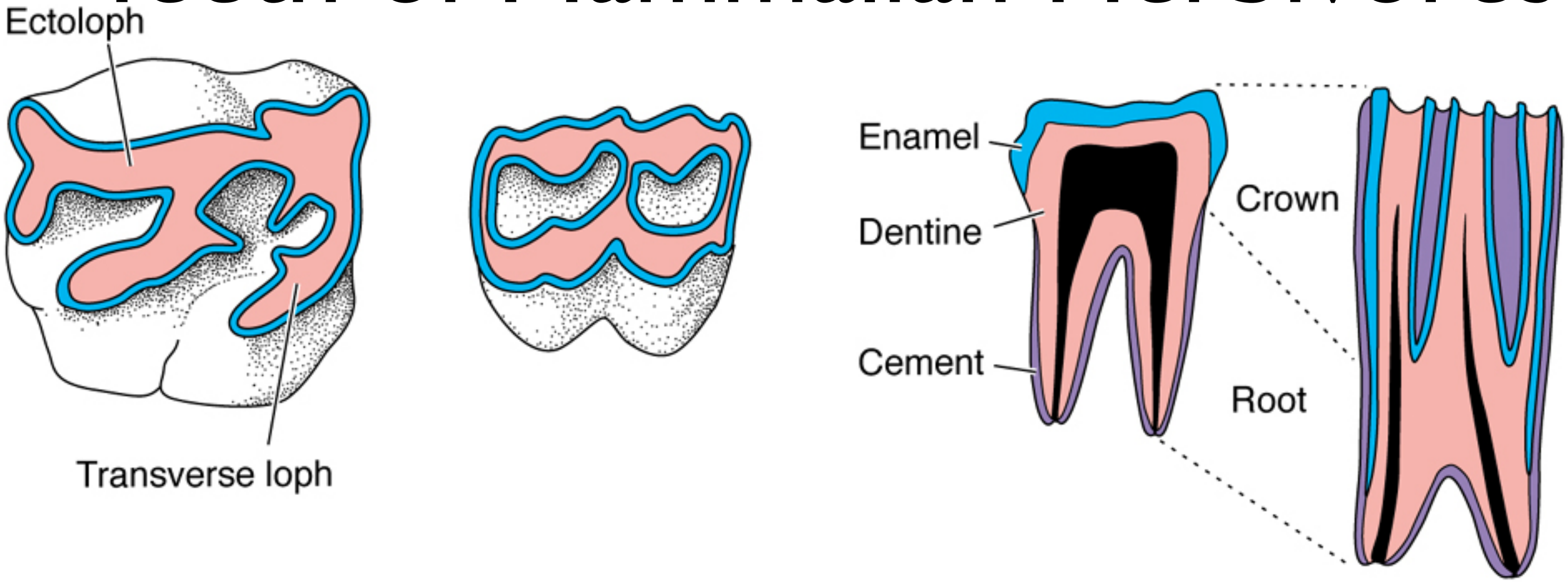

Adductor mandibulae complex
Braincase
Hinge joint at frontonasal junction
Upper jaw
Mandible
Pterygoideus
C. Chicken
Protactor pterygoidei
Bony palate
Depressor mandibulae
Quadrate
Hyoid muscles
D. Chicken

Mammals have strongly attached teeth, molars -- match upper w/ lower for cutting/grinding





Teeth of Mammalian Herbivores



A. Rhinoceros molar **B.** Deer molar **C.** Low and high crowned molars

Teeth adapted for processing three principal kinds of foods.

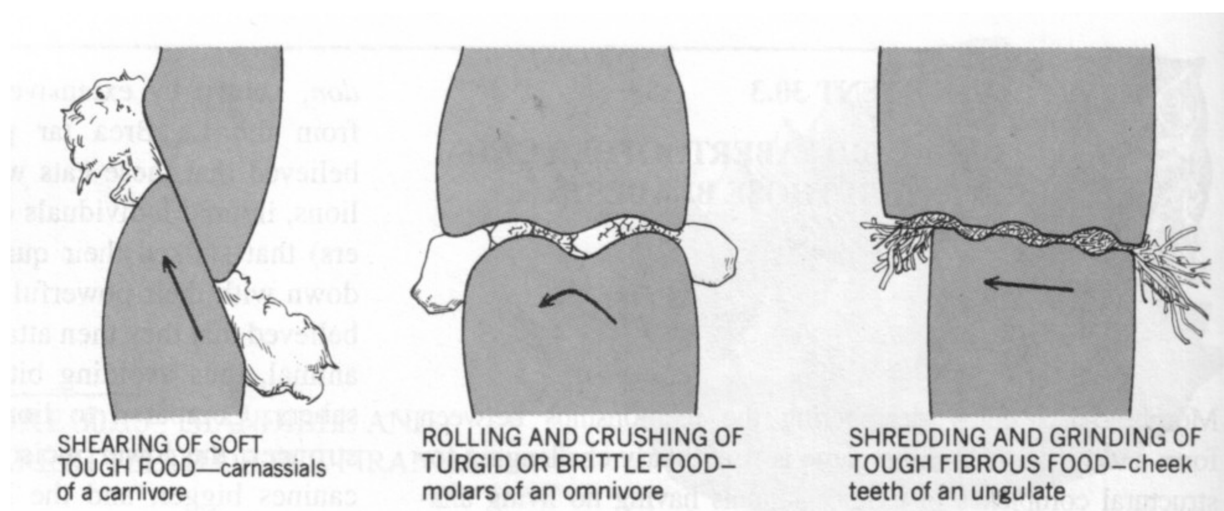


Fig. 16.9

There's more than one way to chew a meal....

The Journal of Experimental Biology 210, 2811-2818
Published by The Company of Biologists 2007
doi:10.1242/jeb.004267

Death roll of the alligator: mechanics of twist feeding in water

Frank E. Fish[1,*], Sandra A. Bostic[1], Anthony J. Nicastro[2] and John T. Beneski[1]
[1]*Department of Biology and* [2]*Department of Physics, West Chester University, West Chester, PA 19383, USA*
*Author for correspondence (e-mail: ffish@wcupa.edu)

Accepted 14 May 2007

Summary

Crocodilians, including the alligator (*Alligator mississippiensis*), perform a spinning maneuver to subdue and dismember prey. The spinning maneuver, which is referred to as the 'death roll', involves rapid rotation about the longitudinal axis of the body. High-speed videos were taken of juvenile alligators (mean length=0.29 m) performing death rolls in water after biting onto a pliable target. Spinning was initiated after the fore- and hindlimbs were appressed against the body and the head and tail were canted with respect to the longitudinal body axis. With respect to the body axis, the head and tail bending averaged 49.2° and 103.3°, respectively. The head, body and tail rotated smoothly and freely around their individual axes of symmetry at 1.6 Hz. To understand the dynamics of the death roll, we mathematically modeled the system. The maneuver results purely from conservation of angular momentum and is explained as a zero angular momentum turn. The model permits the calculation of relevant dynamical parameters. From the model, the shear force, which was generated at the snout by the juvenile alligators, was 0.015 N. Shear force was calculated to scale with body length to the 4.24 power and with mass to the 1.31 power. When scaled up to a 3 m alligator, shear force was calculated at 138 N. The death roll appears to help circumvent the feeding morphology of the alligator. Shear forces generated by the spinning maneuver are predicted to increase disproportionately with alligator size, allowing dismemberment of large prey.

Key words: death roll, alligator, *Alligator mississippiensis*, feeding, maneuverability.

https://www.youtube.com/watch?v=I9KXRHk3AkU

Death Roll

https://www.youtube.com/watch?v=I9KXRHk3AkU