Morphological comparison of feeding apparatus in mudskippers

マッドスキッパー類の摂餌器官の形態比較

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1) General introduction

One of the major evolutionary events during land invasion by vertebrates is the transition of feeding mechanisms from suction in aquatic animals to prehension in terrestrial ones. Due to large differences in physicochemical characteristics of air and water, suction feeding is impractical on land, and thus, terrestrial vertebrates usually employ teeth on jaws for obtaining food. How feeding mechanisms were modified in the Devonian transitional vertebrates are little known. Recent investigations of fossils and extant amphibious fishes has partly revealed how early terrestrial vertebrates might have obtained food in terrestrial environment, and suggested all of them being carnivorous. However, these findings were based on hard structures (fossils) or macrophagous, carnivorous fishes, and little is know about herbivorous fishes grazing on land. There are a fraction number of amphibious fishes, i.e., oxudercine gobies, show a full spectrum of habitat transition from water to land and varying feeding habits; and surprisingly, their transition of feeding habit tentatively shows an inverse trend of the general acceptance. In this study, we used oxudercine gobies as model species to elucidate i) how feeding system of aquatic fish has transitioned as they invade land, and ii) is there any possibility of early emergence of terrestrial vertebrates being herbivorous or omnivorous?

2) Morphology of the feeding apparatus in the herbivorous mudskipper, *Boleopthalmus pectinirostris* (Linnaeus, 1758)

Among the mudskippers, *Boleophthalmus pectinirostris* is herbivorous and grazes on diatoms on exposed mudflats. In this study, we investigated the morphology of the feeding apparatus of this species to understand how feeding apparatus is modified for grazing on land. Dentition, and the skeletal and muscular systems of the branchial basket were examined through macroscopic and microscopic dissection, scanning electron microscopy, and micro-computed tomography scanning. The results show that the feeding apparatus of the fish has been modified presumably to transport diatom cells from the mudflats surface to the digestive tract with minimum admixture of mud particles. The modifications include horizontal orientation of the lower jaw teeth, horizontally aligned, high-density gill rakers on the third (only on the posterior row) and fourth (both rows) gill arches, large pharyngeal plates bearing numerous fine teeth, and the musculoskeletal system of the branchial basket.

3) Morphological comparison of the feeding apparatus in the mudskippers: *Boleophthalmus boddarti*, *Oxuderces nexipinnis*, *Scartelaos histophorus*, *Periophthalmus chrysospilos*, and *Periophthalmodon schlosseri*

In this study, we used five mudskippers, i.e., *Boleophthalmus boddarti* (moderately terrestrial, herbivorous), *Oxuderces nexipinnis* (nearly aquatic, herbivorous), *Scartelaos histophorus* (moderately terrestrial, omnivorous), *Periophthalmus chrysospilos* (highly terrestrial, carnivorous) and *Periophthalmodon schlosseri* (highly terrestrial, carnivorous), for anatomical comparison of the feeding apparatus. *B. boddarti* and *O. nexipinnis* are characterized by horizontal disposition of the dentary teeth, more densely spaced gill rakers on the posterior row of the third arch and both rows of the fourth arch, and large, ventrally curved pharyngeal plates bearing numerous fine teeth. *Ps. chrysospilos* and *Pn. schlosseri* have oral jaw bones with jaw-levers producing a greater biting force, rudimentary gill rakers, and pharyngeal plates studded with robust canine teeth. On the underside of the ventral pharyngeal plates, prominent ridge occurs, onto which much larger muscles attach. The jaw adductors are larger in these carnivorous mudskippers. *S. histophorus* shows an anatomical architecture which may be considered intermediate between those herbivorous and carnivorous species. On the basis of currently accepted relationships of oxudercine genera, their feeding habits, and the morphology of the feeding apparatus, we hypothesize that the oxudercine gobies had been adapted to feeding microalgae in shallow water before expanding

their niche onto land, and subsequently diverged to more specialized herbivorous (*Boleophthalmus*) and carnivorous groups (*Periophthalmus* and *Periophthalmodon*) feeding in higher intertidal habitats.

4) Morphological comparison of the feeding apparatus in the mudskippers: *Parapocryptes serperaster*, *Pseudapocryptes elongatus*, *Periophthalmus modestus*, and *Periophthalmodon septemradiatus*

We expanded our study to mudskipper species showing extremes of terrestriality including *Parapocryptes serperaster* (no/low terrestriality, herbivorous), *Pseudapocryptes elongatus* (low terrestriality, omnivorous), *Periophthalmus modestus* (high terrestriality, carnivorous), and *Periophthalmodon septemradiatus* (high terrestriality, carnivorous) in order to consolidate the hypothesis. Feeding apparatus of *Pa. serperaster* resembles the configurations of those in the herbivorous mudskippers (*B. boddarti* and *B. pectinirostris*) with horizontal disposition of the dentary teeth, numerous teeth on the oral jaws, densely spaced gill rakers on the last three rows, strong curvature of the pharyngeal plates bearing with numerous papilliform teeth, and musculoskeletal system of the branchial basket. *Pd. elongatus* shares the feeding morphology of the omnivorous mudskipper (*S. histophorus*) with horizontal orientation of dentary teeth, lesser number of the oral jaw teeth, and the morphology of the pharyngeal plates, except the morphology of gill rakers comparable with those of the herbivorous mudskippers. The anatomical features of *Ps. modestus* and *Pn. septemradiatus* are identical to those of the carnivorous mudskippers (*Ps. chrysospilos* and *Pn. schlosseri*) with larger jaw-lever closing ratio, less developed gill rakers, and the musculoskeletal system related to the branchial basket. The findings in the present study strengthen our hypothesis of feeding habit transition in the oxudercine gobies. Further investigation on the remaining genera could elucidate the hypothesis.

5) General discussion and future direction

Evolution of feeding apparatus during land invasion of vertebrates: The suction-to-biting transition coincides with flexible-to-firm alteration of the feeding system, which is thought to have happened in the late Devonian when vertebrates invaded land. The prominent changes include loss of the operculogular series, reduction and modification of the branchial system forming a tongue, and rigidity of the lower jaws and skull roof. These morphological changes facilitate biting which presumably occurred when vertebrates were still in aquatic environment, and all of early vertebrates are carnivorous. Herbivores emerged later evidenced by diversity of the oral jaw closing mechanisms and tooth morphology allowing processing plant materials. Our findings suggest that there are possible cases of early emerge species being semi-terrestrial herbivorous or omnivorous grazers, and as expansion their niche onto land, they diverged into specialized carnivores and herbivores. Feeding system of oxudercine gobies share major morphological features with typical fish but they employ various feeding strategies to exploit food on land.

Adaptions for terrestrial grazing in herbivorous and omnivorous mudskippers: Typical herbivorous fishes retain food particles suspended in water column or adhesive surfaces. In the ingestion stage, they employ ram feeding or suction feeding to obtain food, or using comb-like teeth on the oral jaws to encrust algae off surfaces in some species. In order to retain food particles, they use dead-end sieving or cross-flow mechanisms with or without using mucus. In case of the herbivorous and omnivorous mudskippers, their food mixed with mud particles and most density on the top layer of mud surface. Therefore, they employ horizontal distribution of dentary teeth to obtain top layer of mud surface with different behaviors. How they sieve food particles is unknown but our data suggest dead-end mechanism employed. Further investigation using endoscopy or electromyography methods together with feeding behavior could clarify the issue.

Adaptations for terrestrial feeding in carnivorous mudskippers: As vertebrates feeding on land, they usually employ elongate body, the pectoral fins, the capability of jaw rotation, or limbs to place the gape on prey. In the intraoral transport, most amphibious fishes return to water for swallowing, whereas tetrapods employ the tongue to transport food into the esophagus. Possession of the tongue allows terrestrial vertebrates feeding far from water's edge. In the case of carnivorous mudskippers, they employ pectoral fins and the rotation of the oral jaw to orientate the gape on prey. Some species use hydrodynamic tongue for capture. The intraoral transport in the carnivorous mudskippers is little known. There are only two studies on this issue with some limitations of experimental design. We found that *Pn. septemradiatus* feeds far from water's edge and rarely ventures into water. They do not have the tongue. There must be a feeding mechanism allowing them freely feed on land without using water, which could be a model species to gain insight into the feeding transition of early terrestrial vertebrates.