© 2018. Published by The Company of Biologists Ltd | Journal of Experimental Biology (2018) 221, jeb154427. doi:10.1242/jeb.154427

REVIEW

Aquatic–terrestrial transitions of feeding systems in vertebrates: a mechanical perspective

Egon Heiss[1,*], Peter Aerts[2,3] and Sam Van Wassenbergh[2,4]

ABSTRACT

Transitions to terrestrial environments confront ancestrally aquatic animals with several mechanical and physiological problems owing to the different physical properties of water and air. As aquatic feeders generally make use of flows of water relative to the head to capture, transport and swallow food, it follows that morphological and behavioral changes were inevitably needed for the aquatic animals to successfully perform these functions on land. Here, we summarize the mechanical requirements of successful aquatic-to-terrestrial transitions in food capture, transport and swallowing by vertebrates and review how different taxa managed to fulfill these requirements. Amphibious ray-finned fishes show a variety of strategies to stably lift the anterior trunk, as well as to grab ground-based food with their jaws. However, they still need to return to the water for the intra-oral transport and swallowing process. Using the same mechanical perspective, the potential capabilities of some of the earliest tetrapods to perform terrestrial feeding are evaluated. Within tetrapods, the appearance of a mobile neck and a muscular and movable tongue can safely be regarded as key factors in the colonization of land away from amphibious habitats. Comparative studies on taxa including salamanders, which change from aquatic feeders as larvae to terrestrial feeders as adults, illustrate remodeling patterns in the hyobranchial system that can be linked to its drastic change in function during feeding. Yet, the precise evolutionary history in form and function of the hyolingual system leading to the origin(s) of a muscular and adhesive tongue remains unknown.

KEY WORDS: Evolutionary transitions, Biomechanics, Foraging, Fish, Tetrapods

Introduction

It is generally appreciated that characteristics of the environment impose important selective pressure on an animal's build or 'habitus' (see Glossary) (Losos, 1990). From a mechanical point of view, interaction forces with, for instance, the substrate, food items and items used in a behavioral context, adaptively shape the movement apparatus (e.g. Drucker and Lauder, 2002). This holds true also for the interactions with the medium – aquatic or aerial – that animals live in. Mechanical properties (density and viscosity) differ considerably between both environments: water is approximately 800 times more dense and 50 times more viscous than air (e.g. Hughes and Brighton, 1967). To the benefit of most aquatic animals, this high density results in considerable hydrostatic lift forces contributing largely to the support of the body and food items against gravity (e.g. Losilevskii and Papastamatiou, 2016). However, when movement is involved, the flipside of the same coin shows up. Animals or objects moving through the water experience considerably higher drag forces, not only because of the higher viscosity, but (as soon as size and/or speed becomes significant) because of the high pressure differential over the body, the magnitude of which is largely determined by the fluid density (Fish, 2006).

These differences in density and viscosity also constrain aquatic and terrestrial feeding in different ways (Herrel et al., 2012). Whereas grasping and transporting food are mostly challenged by (but can also benefit from) gravitational and inertial effects on the food item in the terrestrial environment, it is largely the hydrodynamic forces that determine the feeding strategies and performance in the aquatic environment. Reaching or heading towards a food item on land normally does not affect the item's position and a food particle can 'easily' be grasped by hand, tongue or jaws, after which the particle's inertia may be exploited by the animal during further processing and intra-oral transport. An aquatic animal moving towards a food item will inevitably push water forward in front of it (creating a 'bow wave'), which will in turn exert a hydrodynamic force on the food item or prey (Van Wassenbergh et al., 2009b). The precise effect on the food particle depends on the interplay with all other forces (e.g. gravity, substrate friction, active escape forces, etc.), but the chances are rather high that, without remedy, food particles are simply carried with the flow induced by the approaching animal and might never be caught.

Therefore, ways to avoid this 'bow wave' effect are needed, and primary aquatic feeders, such as fishes, can do this by ensuring a backwards flow relative to the approaching body and, ultimately, relative to the buccal cavity. Options for this are essentially threefold. The first option is to enable free-flow through the gaping mouth and the buccal cavity while moving forwards. Food particles in this water volume remain unaffected and can thus be overtaken by the forward-moving buccal cavity (this is known as 'pure ram' feeding). The second option represents the other extreme: a backwards inertial flow is actively generated in front of the 'stationary' mouth aperture and through the buccal cavity. Particles in this flow, even if neutrally buoyant and passive (Van Wassenbergh and Aerts, 2009), will experience hydrodynamic forces that can transport them towards and through the buccal cavity (i.e. pure inertial suction). As for the 'bow wave', the precise effect depends on the interplay with all other forces acting on the food particles (Wainwright and Day, 2007). The third option is any active or passive combination of these first two options. However, regardless of which option is used, sufficiently wide gaping and expansion of the buccopharyngeal and opercular cavities (see Glossary) are required to capture and transport food. In the case of inertial suction, this expansion must be powerful and properly tuned

[1]Institute of Zoology and Evolutionary Research, Friedrich-Schiller-University Jena, Erbertstr. 1, 07743, Jena, Germany. [2]Department of Biology, University of Antwerp, Universiteitsplein 1, B-2610, Antwerp, Belgium. [3]Department of Movement and Sports Sciences, Ghent University, Watersportlaan 2, B-9000, Ghent, Belgium. [4]Département Adaptations du Vivant, Muséum National d' Histoire Naturelle, 57 rue Cuvier, Case postale 55, 75231, Paris Cedex 5, France.

*Author for correspondence (egon.heiss@uni-jena.de)

E.H., 0000-0002-5257-8889

Journal of Experimental Biology (2018) 221, jeb154427. doi:10.1242/jeb.154427

Glossary

Actinopterygian (ray-finned fish)
Member of a clade of bony fishes with paired fins consisting of webs of skin supported by bony rays. Actinopterygians are the sister group of sarcopterygians (lobe-finned fishes including tetrapods).
Amniotes
The group of tetrapod animals comprising reptiles, birds and mammals.
Analogues
Groups of organisms that have evolved similar traits independently from each other.
Buccopharyngeal cavity
Mouth–throat cavity (synonym: oropharyngeal cavity).
Ceratohyal
Part of the throat skeleton, ventral skeletal structure of the second visceral arch.
Dissorophoid
Member of Dissorophoidea, a clade of temnospondyl amphibians, putative ancestors of living amphibians.
Exaptation
A trait that evolved to serve one particular function but subsequently came to serve another is an exaptation for this new function.
Habitus
External appearance.
Hyobranchial
Refers to structures related to hyoid and gill-arch elements.
Hyoid
Part of the throat skeleton, comprising the skeletal structures of the second visceral arch.
Hypaxial muscle
Ventral trunk musculature.
Lateral line
System of water flow sense organs in aquatic vertebrates.
Lissamphibian
Member of the amphibian clade Lissamphibia comprising all living amphibians (salamanders, frogs, caecilians) and their extinct relatives.
Maxilla
Skeletal structure of the upper jaw.
Muscular hydrostat
Muscular system with no skeletal support (e.g. human tongue or elephant trunk) retaining constant volume because of the incompressibility of its content.
Neurocranium
Skull elements that form a protective case around the brain.
Opercular cavity
Gill chamber.
Opercular slit
Lateral opening of the gill chamber.
Papillae
Small, rounded protuberances on a part or organ of the body.
Pectoral girdle
Shoulder girdle.
Premaxilla
Skeletal structure of the upper jaw.
Sarcopterygian (lobe-finned fish)
Member of a clade of bony fishes with fleshy, lobed, paired fins that gave rise to tetrapods. Sarcopterygians are the sister group of actinopterygians.
Stem amniotes
Extinct tetrapod groups from the lineage leading to the last common ancestor of extant amniotes.
Stem amphibians
Extinct tetrapod groups from the lineage leading to the last common ancestor of lissamphibians.

(see Box 1) and the generation of the flow to capture and transport food will thus require considerable muscular effort. Clearly, such functional requirements represent a strong adaptive pressure and head morphology, muscle properties and motor control can be expected to be shaped accordingly (see Box 1).

Aquatic feeding is the ancestral feeding mode in vertebrate groups that gave rise to amphibious and terrestrial forms, but making use of aquatic feeding strategies out of water seems problematic. A ‘ram strategy’ might be useful to some extent to grasp prey (yet hampered by the fact that items are most often physically positioned on a solid substrate instead of ‘floating’ in the air), but intra-oral transport would be more problematic without an accompanying adjustment of the motor program and participation of functional units other than the head. Applying the ‘inertial suction strategy’ for food capture and transport on land seems virtually impossible for an aquatic-optimized feeder: because of the low viscosity and density of the air, fluid forces (friction and pressure differentials) are far too low to carry the prey with the flow, unless the generated flow rates could be increased massively. However, given a fixed capacity for volume expansion (determined by head morphology and dimensions), this would require much faster buccal expansion rates, and muscles adapted for aquatic feeding would need to function far away from their optima for power and efficiency (Hill, 1950).

Nevertheless, about 400 million years ago, some aquatic vertebrates transitioned to the land, and this raises the important question as to how the aquatic feeding morphology and motor strategies of the ‘colonists’ could be used successfully for their initial terrestrial feeding and how they were further modified and optimized to give the sophisticated feeding strategies used by later tetrapods. Mechanical analyses of terrestrial feeding in amphibious fishes (i.e. fishes that regularly leave water), salamanders and turtles may be very revealing in this respect. This Review focuses on aquatic–terrestrial transitions in vertebrates from a mechanical perspective in an evolutionary context. We first give an overview on suction feeding, the mode used by most aquatic vertebrates, and explain the challenges a primarily aquatic vertebrate is faced with when aiming for terrestrial feeding. We introduce fishes that do leave the water to feed on land as well as salamanders and turtles that can switch between aquatic and terrestrial feeding environments. We discuss how experimental approaches using extant organisms can help us understand how early tetrapods have left water, and conclude that the muscular tongue was one of the central evolutionary innovations for successful land invasion of tetrapods.

Suction feeders capturing prey on land

An animal with the generalized anatomy of a suction-feeding fish (Box 1, Fig. 1) will face several mechanical problems with capturing food on land, as illustrated schematically in Fig. 2. The first problem (problem 1 in Fig. 2) relates to posture and stability on land: because of their laterally flattened body shape, most fish will fall to their side when placed on land. The animal should therefore be able to stabilize at least its head against uncontrolled rolling. Second (problem 2 in Fig. 2), the orientation of the line between the upper and lower jaw tips of a suction feeder will generally be near-vertical. This gape orientation is unfavorable for grabbing small food items lying on the ground. Third (problem 3 in Fig. 2), strong depression of the hyoid (see Glossary), a typical movement by fish that assists in opening the mouth and generating suction (Box 1, Fig. 1), may result in contact between the hyoid and the ground surface. Such a hyoid–ground collision can push the head up, and move the mouth away from food on the ground. Fourth (problem 4 in Fig. 2), the retraction of the pectoral girdle (see Glossary) by the hypaxial muscles (see Glossary) during suction feeding (Box 1, Fig. 1) can interfere with support (and stability) of the body by the

Journal of Experimental Biology (2018) 221, jeb154427. doi:10.1242/jeb.154427

Box 1. Aquatic suction feeding in fishes

Generally, the buccopharyngeal cavity is expanded dorsoventrally as well as laterally to generate suction. Here, we consider the basis of both movements. The dorsoventral expansion involves sagittal-plane rotations of the lower jaw (yellow in Fig. 1), hyoid (pale blue in Fig. 1), pectoral girdle (red in Fig. 1) and neurocranium (see Glossary) (gray in Fig. 1). Shortly after the onset of lower jaw depression, the epaxial and hypaxial muscles contract (Fig. 1C), causing the neurocranium to be rotated dorsally (often referred to as 'neurocranial elevation') and the pectoral girdle to be retracted (Fig. 1A,B) (Muller, 1987; Thys, 1997; Camp and Brainerd, 2014). The increased angle between the neurocranium and the pectoral girdle causes the hyoid to be depressed (i.e. tip rotating ventrally) as it is pulled back by the sternohyoideus muscle (Muller, 1987; Van Wassenbergh et al., 2015). Contraction of the sternohyoideus, if present, will further increase the depression of the hyoid. The protractor hyoidei muscle, which connects the hyoid to the lower jaw, will cause depression of the lower jaw while being pulled posteriorly by the rotating hyoid. The effect of these movements is that the floor of the buccal cavity is pushed away from the roof of the buccal cavity (Fig. 1B).

Lateral expansion involves the abduction of the suspensoria (dark green in Fig. 1) and the opercular series of bones (orange in Fig. 1). Each suspensorium hinges with the neurocranium to allow lateral swinging (Gosline, 1971; de Visser and Barel, 1996). The forces responsible for pushing the suspensoria laterally come primarily from the retraction of the hyoid (by the sternohyoideus, and indirectly also resulting from hypaxial and epaxial activity) (Muller, 1989; Aerts, 1991; de Visser and Barel, 1996). During hyoid retraction, the inter-hyoid joint plays a central role in the transmission (and reorientation) of the forces from the sternohyoideus to the medial surface of the suspensoria (Aerts, 1991; Van Wassenbergh et al., 2013), causing both depression and lateral flaring of the hyoid while abducting the suspensoria.

Expanding the buccopharyngeal cavity, while the posterior slits are closed, causes water to be sucked into the mouth. Finally, aided by the action of muscles and other mechanical linkages, the momentum of this water helps the gill cover and branchiostegal membrane to be pushed open as these water masses move towards the branchiostegal and opercular slits (see Glossary). Together, these expanding elements form a wave of expansion of the buccal cavity that progresses from the mouth aperture to the opercular slits.

Note that, although not shown in Fig. 1, a protrusible upper jaw has independently evolved multiple times within ray-finned fishes (e.g. van Dobben, 1935; Alexander, 1967; Staab et al., 2012). Jaw protrusion involves forward movement of the premaxilla (dark blue in Fig. 1), coupled with rotation of the maxilla (pale green in Fig. 1) (Gosline, 1987), and is assumed to assist in closing the gap between the mouth and the prey in a dynamically efficient way (Osse, 1985; Holzman et al., 2008). Food that is not moved entirely into the buccal cavity will be grasped between the (often toothed) oral jaws, after which a second cycle of suction completes the capture.

pectoral fins or limbs. Sudden backward pulling of the pectoral girdle can cause a sudden, forward ground reaction force on the pectoral girdle. Fifth (problem 5 in Fig. 2), as mentioned above, sucking prey from a distance into the mouth using fluid-dynamic forces will no longer work in air. The animals will be forced to develop an alternative strategy for the initial capture of the food. Finally (problem 6 in Fig. 2), intra-oral fluid-dynamic transport will no longer work without water inside the buccopharyngeal cavity. To overcome each of these six problems, several species of amphibious fishes have developed solutions to enable them to exploit food on land.

Probably the most limited form of a transition from aquatic to terrestrial feeding by a fish is observed in the European catfish (*Silurus glanis*) (Table 1). These fishes have been reported to swim alongside the gravel beaches in shallow waters where pigeons gather together for drinking and cleaning. They manage to capture the pigeons by 'beaching' often more than half of their body outside of the water (Cucherousset et al., 2012). During successful attacks, pigeons that are grabbed between the upper and lower jaws are drawn backwards into the water. Similar beaching behavior is also known for aquatic mammals such as orca (*Orcinus orca*; Guinet and Bouvier, 1995) and bottlenose dolphins (*Tursiops* sp.; Sargeant et al., 2005). The head and anterior body of the European catfish is dorso-ventrally flattened, which appears to be sufficient to solve problem 1 (Fig. 2) and maintain a posture that is suitable for biting at birds, and quickly turn and crawl back into the water. However, because problems 2 and 3 (Fig. 2) persist, the catfish's mouth will be relatively high above the ground (hyoid bumping of the ground might occur, although there are no images showing this) with a horizontally pointing surface normal of the mouth opening. This will inevitably limit the range of potential terrestrial prey to those that are relatively large, presumably even to those taller than the height of the head of the beaching catfish.

Some amphibious fish that have a long, eel-like body exhibit a terrestrial feeding behavior in which the posture of the head is controlled in such a way that problems 2, 3 and 4 are also circumvented. They use the ground support and flexibility of their eel-like body to perform an elevation of the trunk and a dorso-ventral flexion of the anterior trunk region. This brings their head into a nose-down posture, which allows the mouth to grab relatively small food items from the ground (Fig. 3, Table 1). This behavior has been described for the eel-catfish *Channallabes apus* (Van Wassenbergh et al., 2006; Van Wassenbergh, 2013) and for the reedfish *Erpethoichthys calabaricus* (Van Wassenbergh et al., 2017). This feeding behavior is more versatile than that of the European catfish, as the ground surface can be scanned for smaller food by left and right yawing of the head (with help of the chemotactile barbels of *C. apus*) (Van Wassenbergh et al., 2006).

A re-orientation of the gape is also observed in another amphibious fish, the largescale foureyes (*Anableps anableps*). However, it uses a markedly different mechanism. Instead of lifting the trunk up and rotating the head down as in the catfish and reedfish (Fig. 4A–C, Table 1), the largescale foureyes entirely relies on the kinematics of its jaws to pick up food from the ground (Michel et al., 2015a). The tooth-bearing part of the upper jaw, the premaxilla (see Glossary), first performs mainly a forward translation while the lower jaw is depressed (resembling typical upper jaw protrusion) (Fig. 4A,B). Afterwards, the premaxilla can be rotated tip-down towards the food, driven by the retraction of the maxilla (see Glossary) by the A3-jaw adductor muscle division (Fig. 4C). The latter action can be performed seemingly independently from lower jaw adduction by the other jaw adductor muscle divisions, allowing more precise 'picking' of food from the bottom compared with other (i.e. non-cyprinodontiform) fishes (Hernandez et al., 2008, 2009; Michel et al., 2015a). Michel et al. (2015a) proposed that the increased amplitude of ventral protrusion (i.e. the continued downward movement of the premaxilla during lower jaw closing; Fig. 4B,C) shown by *A. anableps* compared with that of non-terrestrial feeding cyprinodontiform fishes could have been an important factor to allow terrestrial feeding in this species. Hyoid bumping (problem 3 in Fig. 2) is not observed as hyoid depression is limited (Fig. 4C) and the hyoid is located high enough above the ground owing to the pointed shape of the head. Whether pectoral girdle support interferes with the terrestrial feeding mechanism of *A. anableps* (problem 4, Fig. 2) is unknown owing to the lack of kinematic data regarding the pectoral girdle and/or fins. Problem 6

Journal of Experimental Biology (2018) 221, jeb154427. doi:10.1242/jeb.154427

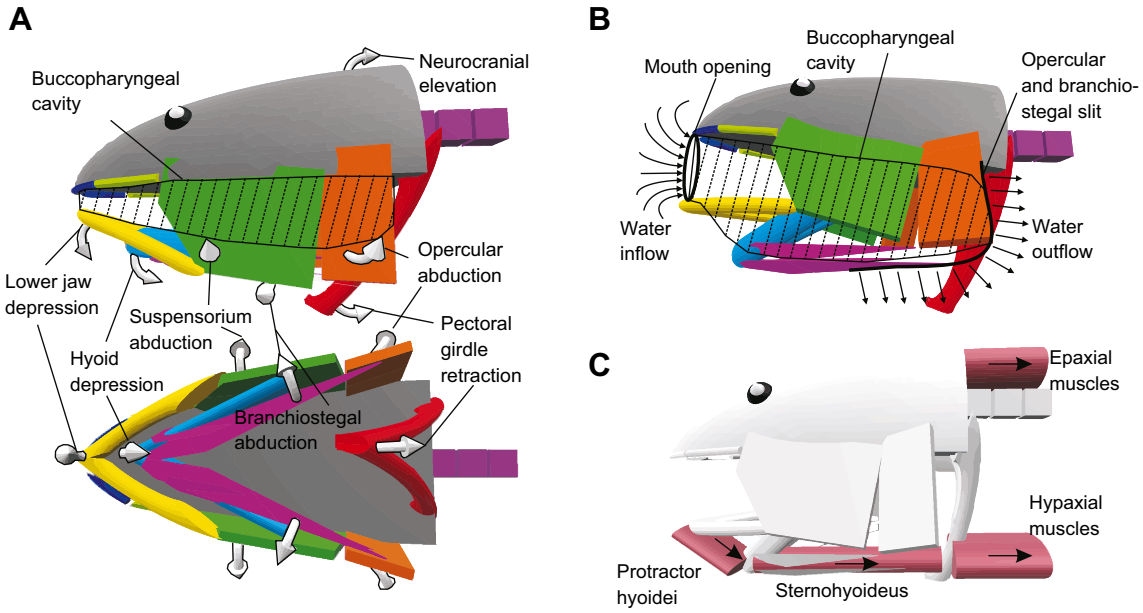

Fig. 1. Aquatic suction-feeding mechanism in a generalized ray-finned fish. (A) Initial configuration before suction force is generated. The white arrows indicate the direction of movement of the different skeletal elements that border the (unexpanded) buccopharyngeal cavity. (B) Expanded configuration of the buccopharyngeal cavity showing the resultant inflow of water into the mouth, and the subsequent outflow of water at the openings posterior to the opercular bones and branchiostegal membranes. (C) The most important muscles for suction feeding. Black arrows indicate the direction of movement during muscle contraction. See Box 1 for additional information.

persists as *A. anableps* must return into the water to swallow the food grabbed between the jaws on land.

Mudskippers (Oxudercinae), which feed on the muddy shores of mangroves (Stebbins and Kalk, 1961; Gordon et al., 1969), also make use of their protrusible upper jaw to capture prey on land. However, they do so in a way clearly different from that of the largescale foureyes (Table 1). Reorientation of the mouth opening (problem 2; Fig. 2) is much less the result of ventral protrusion of the premaxilla, but results from the nose-down rotation of the head (Fig. 4D,E). Although functionally similar to the downward-pointing head with elevated trunk region of the eel-catfish (Fig. 3), the pectoral fins are now used to lift the head and anterior trunk (Sponder and Lauder, 1981; Kawano and Blob, 2013; Michel et al., 2014) (Fig. 4, Table 1). X-ray video images have indicated not only that the lower jaw rotates over a relatively large angle but also that the shape of the lower jaw suggests that the anterior bony part (dentary) is rotated relative to the posterior bony part (angulo-articular) (Michel et al., 2014). This flexible lower jaw is placed against (or close to) the ground in front of the prey, while the maxilla is placed just behind the prey. Thereafter, a quick closing action of both the maxilla and lower jaw 'scoops' the food into the mouth (Michel et al., 2014) (Fig. 4E,F).

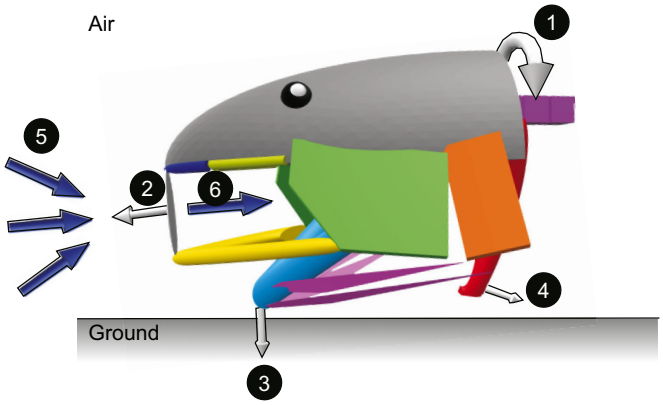

Fig. 2. Mechanical problems of a hypothetical transition to terrestrial feeding in a generalized suction-feeding fish. Morphological and/or behavioral adaptation that is related to six factors can be expected: (1) stabilization of the head, (2) orientation of the mouth opening, (3) ground-impact of the hyoid in its depressed position, (4) interference of pectoral girdle retraction with providing stable support to the pectoral fins or limbs, (5) fluid-dynamic transportation of food into the mouth (food capture) and (6) fluid-dynamic transportation of food inside the mouth towards the esophagus (swallowing). Skeletal elements are color-coded as in Fig. 1.

It was recently discovered that the mudskipper *Periophthalmus barbarus* use a 'hydrodynamic tongue' to capture and transport food on land (Michel et al., 2015b) (Table 1). From the moment the mouth opens, a convex meniscus of water becomes visible at the mouth aperture (Fig. 4D). This water further protrudes out of the mouth (Fig. 4E), and, just before the jaws are placed around the food, the water comes into contact with the food and spreads along the surface surrounding the food (Fig. 4F). While the jaws are closing and the food is engulfed, part of the expelled water is sucked back into the buccopharyngeal cavity. Essential in this process is the pronounced lifting of the hyoid while the mouth is opening – this compresses the mouth cavity and pushes the intra-oral water forward (Fig. 4D,E). Next, a depression of the hyoid (as typical for aquatic suction feeding; Fig. 1) expands the buccopharyngeal cavity and thereby causes water (plus food, and presumably some air) to be sucked back into the mouth and towards the back of the buccopharyngeal cavity. The term 'hydrodynamic tongue' has been used previously to describe the different, but more common, intra-oral, flow-driven transport of prey in aquatic fishes (Liem, 1991). In addition to this function, the hydrodynamic tongue of mudskippers also includes an extra-oral component during the initial capture of prey (Michel et al., 2015b).

The intra-oral water used as a hydrodynamic tongue enables the mudskipper to capture, transport and swallow food on land. X-ray

Journal of Experimental Biology (2018) 221, jeb154427. doi:10.1242/jeb.154427

Table 1. Summary of strategies used to solve the functional problems associated with terrestrial feeding in extant ray-finned fishes and tetrapods summarized in Fig. 2

Organism	Problem 1 (posture and stability on land)	Problem 2 (orientation of gape)	Problem 3 (hyoid–ground collision)	Problem 4 (unstable body by retraction of pectoral girdle)	Problem 5 (initial capture without water)	Problem 6 (intra-oral and intrapharyngeal transport without water)
Ray-finned fishes						
Silurus glanis (European catfish)	Head and anterior body are dorsoventrally flattened	Not solved, probably only allows catching large prey (*S. glanis* preys on pigeons[1])	Probably not solved	Probably not solved	Use of bite to grasp pigeons[1]	Prey dragged back into the water; use of hydrodynamic intra-oral transport[1]
Channallabes apus (eel-catfish)	Use of eel-like body to gain ground support[2,3]	Lifting the trunk up and rotating the head down so that gape can be pointed downwards[2,3]	Hyoid region freely suspended by lifted trunk[2,3]	Pectoral region freely suspended by lifted trunk[2,3]	Use of bite[2,3]	Prey dragged back into the water; use of hydrodynamic intra-oral transport[2,3]
Erpethoichthys calabaricus (reedfish)	Use of eel-like body to gain ground support[4]	Lifting the trunk up and rotating the head down so that gape can be pointed downwards[4]	Hyoid region freely suspended by lifted trunk[4]	Pectoral region freely suspended by lifted trunk[4]	Use of bite[4]	Prey dragged back into the water; use of hydrodynamic intra-oral transport[4]
Anableps anableps (largescale foureyes)	Use of pectoral fins[5]	Highly movable jaw apparatus orients gape downwards[5]	No hyoid–ground collision observed[5]	Not known	Use of bite[5]	Prey dragged back into the water; use of hydrodynamic intra-oral transport[5]
Oxudercinae (mudskippers)	Use of pectoral fins[6–8]	Protrusible jaws and nose-down rotation of the head[8]	Hyoid region lifted by pectoral fins[6–8]	Pectoral girdle stabilized[8]	Prey scooped into the oral cavity by the closing jaws, assisted by 'hydrodynamic tongue'[6,8]	Use of 'hydrodynamic tongue'[8] and pharyngeal jaws[6]
Tetrapods						
Aquatic salamanders	Use of limbs[9–13]	Lifting of the trunk by the limbs and rotating head by movable neck[9,10,12,13]	Hyoid region lifted by forelimbs[9,10,12,13]	Pectoral girdle probably stabilized by trunk musculature	Use of bite[9–13]	Prey dragged back into the water; use of hydrodynamic intra-oral transport or use of lingual transport[9–13]
Terrestrial salamanders	Use of limbs[9]	Lifting of the trunk by the limbs and rotating head by movable neck or use of ballistic tongue[9,14,15]	Hyoid region lifted by forelimbs	Pectoral girdle probably stabilized by trunk musculature	Use of protractible tongue[9–15]	Use of lingual transport, supported by retraction of eyeballs into the oral cavity[16]
Anurans	Use of limbs	Lifting of the trunk by the limbs and rotating head by movable neck or use of ballistic tongue[17]	Hyoid region lifted by forelimbs[17] (in limbed forms) or elongated trunk (in limbless forms)	Pectoral girdle probably stabilized by trunk musculature	Use of protractible tongue[17–19]	Use of lingual transport, supported by retraction of eyeballs into the oral cavity[20]
Terrestrial gymnophions	Use of eel-like body to gain ground support	Lifting the trunk up and rotating the head down so that gape can be pointed downwards[21,22]	Hyoid region freely suspended by lifted trunk[21,22]	No pectoral girdle	Use of bite[21–23]	Lingual transport and inertial transport[21,22]
Aquatic turtles	Use of limbs[24–26]	Lifting of the trunk by the limbs and rotating head by movable neck[24–26]	Hyoid region lifted by forelimbs and elongated neck prevents hyoid–ground collision[24–26]	Position of pectoral girdle probably not affected by feeding muscles	Use of bite[24–26]	Prey dragged back into the water; use of hydrodynamic intra-oral transport or use of lingual transport[24–26]

Continued

Table 1. Continued

Organism	Problem 1 (posture and stability on land)	Problem 2 (orientation of gape)	Problem 3 (hyoid–ground collision)	Problem 4 (unstable body by retraction of pectoral girdle)	Problem 5 (initial capture without water)	Problem 6 (intra-oral and intrapharyngeal transport without water)
Terrestrial turtles	Use of limbs[27–29]	Lifting of the trunk by the limbs and rotating head by movable neck[27–30]	Hyoid region lifted by forelimbs and elongated neck prevents hyoid–ground collision[27–30]	Position of pectoral girdle probably not affected by feeding muscles	Use of bite or protractible tongue[27–30]	Use of lingual transport[30]
Lizards	Use of limbs[31] (in limbed forms), otherwise probably use of eel-like body to gain ground support	Lifting of the trunk by the limbs and rotating head by movable neck or use of protruding tongue[31–33]	Hyoid region lifted by forelimbs[31]	Position of pectoral girdle probably not affected by feeding muscles	Use of bite or protractible tongue[31–33]	Use of lingual transport and inertial transport (quick lateral or dorso-ventral head rotations)[32,33]
Snakes	Use of eel-like body to gain ground support[34]	Highly flexible body that allows high variety of movements[34–36]	Hyoid depression not relevant[34]	No pectoral girdle present	Use of bite[34–36]	Pterygoid walking and alternating compression–extension cycles by the anterior axial musculature[34–36]
Crocodiles	Use of limbs[37–39]	Lifting of the trunk by the limbs and rotating head by movable neck[37,38]	Hyoid depression plays minor role[38]	Position of pectoral girdle probably not affected by feeding muscles	Use of bite[37–39]	Inertial transport (quick lateral or dorso-ventral head rotations)[37,38]
Birds	Use of hindlimbs[40]	Upright posture; use of highly movable neck[41–43]	Hyoid depression plays minor role[41,42]	Pectoral girdle not relevant for feeding	Use of beak or protractible tongue[41–43]	Inertial transport (quick lateral or dorso-ventral head rotations) or lingual transport[41–43]
Terrestrial mammals	Use of limbs[40]	Lifting of the trunk by the limbs and rotating head by movable neck or use of protractible tongue or forelimbs[44–46]	Hyoid depression plays minor role[44]	Position of pectoral girdle probably not affected by feeding muscles	Use of bite, protractible tongue or forelimbs[44–46]	Use of lingual transport[44,45]

[1]Cucherousset et al. (2012); [2]Van Wassenbergh et al. (2006); [3]Van Wassenbergh (2013); [4]Van Wassenbergh et al. (2017); [5]Michel et al. (2015a); [6]Sponder and Lauder (1981); [7]Kawano and Blob (2013); [8]Michel et al. (2014); [9]Miller and Larsen (1989); [10]Miller and Larsen (1990); [11]Shaffer et al. (1991); [12]Heiss et al. (2013a); [13]Heiss et al. (2015); [14]Larsen and Guthrie (1975); [15]Deban (1997); [16]Regal and Gans (1976); [17]Nishikawa and Roth (1991); [18]Nishikawa and Gans (1996); [19]Nishikawa (2000); [20]Levine et al. (2004); [21]Bemis et al. (1983); [22]O'Reilly (2000); [23]Herrel and Measey (2012); [24]Natchev et al. (2009); [25]Heiss et al. (2010); [26]Stayton (2011); [27]Wochesländer et al. (1999); [28]Bels et al. (2008); [29]Natchev et al. (2015); [30]Wochesländer et al. (2000); [31]Montuelle et al. (2009); [32]Schwenk (2000b); [33]Smith (1984); [34]Cundall and Greene (2000); [35]Kardong (1977); [36]Moon (2000); [37]Cleuren and de Vree (1992); [38]Cleuren and de Vree (2000); [39]Erickson et al. (2003); [40]Taylor et al. (1982); [41]Homberger (1986); [42]Zweers et al. (1994); [43]Baussart et al. (2009); [44]Hiiemae (2000); [45]Schwenk (2000a); [46]McClearn (1992).

videos have revealed that food is transported towards the back of the mouth in a single gape opening–closing cycle, and that more than one food item can be captured, transported and swallowed on land before the fish needs to return to the water (Michel et al., 2015b). Mudskippers are currently the only amphibious fishes known to deal with the transport and swallowing problem on land (problem 6; Fig. 2). To avoid losing water on land, their gill slits are reduced, leaving only a small opening at the dorsolateral sides of the opercular bones (Michel et al., 2016). The typical rotation of the pectoral girdle relative to the rest of the skull during suction feeding (Fig. 1), which would cause the head to be rotated nose-up instead of nose-down if the pectoral girdle is anchored to the ground, is hardly noticeable during terrestrial feeding in the mudskipper (Michel et al., 2015b). Consequently, mudskippers show effective solutions for all of the mechanical problems (Fig. 2) associated with performing terrestrial feeding with an aquatic suction feeding apparatus. Their capacity to transport and swallow food on land implies that mudskippers reflect a higher level of terrestrialization compared with the other amphibious fishes mentioned above.

Solutions to the mechanical problems faced by fish when feeding on land can evolve before an amphibious lifestyle is adopted. Mechanical demands of certain modes of aquatic feeding can result in evolution of a trait that later proves beneficial for the terrestrial capture of prey. Such exaptations (see Glossary) for terrestrial feeding are likely to occur in groups that specialized in benthic feeding. Aquatic benthic feeders of the Gobiidae, the family to which also the mudskippers belong, have a sub-terminal mouth, and show a depression of the hyoid which does not hinder food

Journal of Experimental Biology (2018) 221, jeb154427. doi:10.1242/jeb.154427

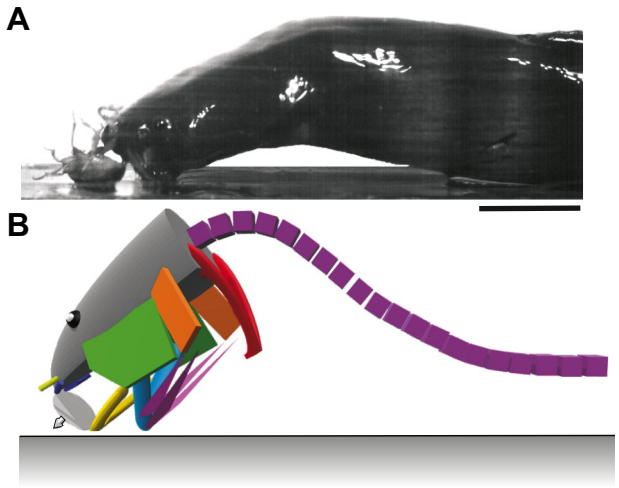

Fig. 3. Terrestrial capture of prey by the eel-catfish *Channallabes apus*. (A) Video frame just before the capture of a beetle (after Van Wassenbergh et al., 2006; scale bar, 1 cm). (B) Skeletal elements; color-coded as in Fig. 1. Lifting of the anterior trunk region allows the head to be tilted nose-down so that the jaws are suitably positioned to grab the prey.

capture even when the head and body remain close to the substrate (Maie et al., 2009). The problems of reorientation of the mouth opening (problem 2; Fig. 2) and ground-impact of the depressing hyoid (problem 3; Fig. 2) are thus similar for adopting an aquatic, benthic feeding lifestyle. However, most fish that feed on food lying on the substrate in the aquatic environment will tend to incline the entire body to steeper angles, e.g. cichlids (Rupp and Hulsey, 2014), eels (Mehta and Wainwright, 2007a,b), catfish (Van Wassenbergh et al., 2009a) and reedfish (Van Wassenbergh et al., 2017). As these postures are impossible outside water, not all aquatic solutions to benthic feeding facilitate the transition to terrestrial feeding.

In conclusion, amphibious fishes show a multitude of solutions to the mechanical problems they face when feeding out of water. Terrestrial food capture can be successful with or without support from the pectoral fins, and with or without a complex protrusible jaw system. Transport and swallowing, however, remain impossible without water, and only the mudskipper has evolved a solution to perform this action on land. Yet, the terrestrial feeding kinematics of several groups of amphibious fishes (overviewed in Wright and Turko, 2016) remains unstudied. For example, some blennies (Blennoidea) seldom submerge themselves under water, and are therefore described as terrestrial animals (Hsieh, 2010). Trichomycterid catfishes occupy a range of trophic niches, including small, eel-like fishes that live hidden among the leaf litter and mud (Glanapteryginae; de Pinna, 1998). Consequently, further studies will help us to clarify the morphological shifts that allow different fish to forage on land (Ashley-Ross et al., 2013). A better understanding how extant fish manage to feed on land with a feeding system primarily adapted for an aquatic environment will in turn shed light on the evolution of terrestrial feeding mechanisms in early tetrapods.

Transitions of early tetrapods

Today there is little doubt that tetrapods evolved in an aquatic environment (Coates and Clack, 1991; Clack, 2012; Schoch, 2014) and that the first tetrapods lived and foraged in water. For example, the well-known stem tetrapod *Acanthostega* from the Late Devonian (ca. 360 Mya; Fig. 5) was aquatic throughout its life (Coates and Clack, 1991; Clack and Coates, 1995; Schoch and Witzmann, 2011; Schoch, 2014). Similarly, the stem tetrapod *Ichthyostega* (Fig. 5), which lived approximately at the same time as *Acanthostega*, was basically an aquatic animal with internal gills, a lateral line system (see Glossary) and a typical fish-eater dentition (Schoch, 2014), but its axial and limb skeleton might have allowed short bouts of locomotion out of water (Pierce et al., 2012). However, *Ichthyostega* was not amongst the first tetrapods that stepped out of water. Trace fossils from the early Middle Devonian period of Poland (ca. 400 Mya) that pre-date any tetrapod body fossil by 18 Mya tell us that other as-yet-unknown four-legged vertebrates ventured for short excursions along the shore (Niedźwiedzki et al., 2010). In other words, the first tetrapods were still heavily bound to aquatic realms, and their limbs evolved as an alternative type of strong fins that were exapted for terrestrial locomotion (and solving the problem of stability shown in Fig. 2) in a second step (Clack, 2012; Pierce et al., 2012; Schoch, 2014).

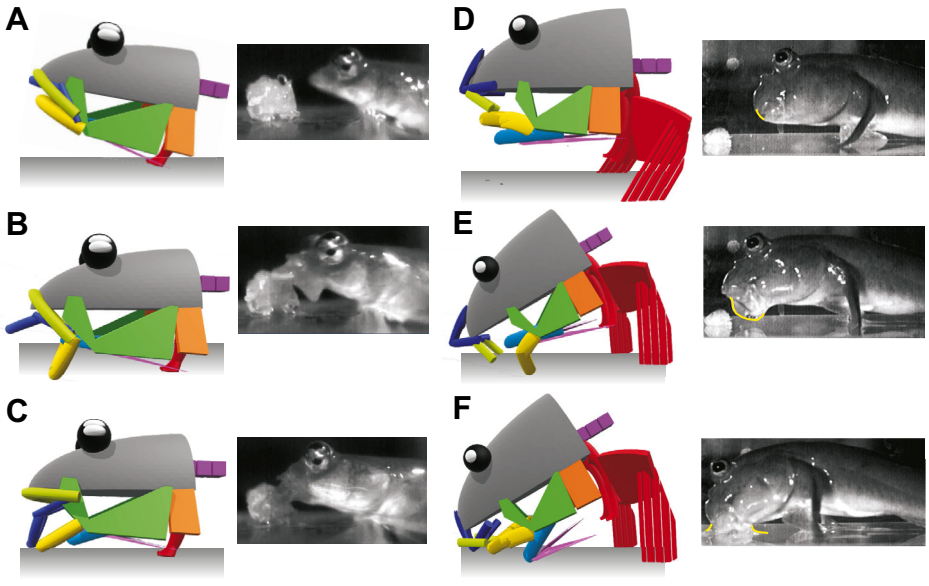

Fig. 4. Kinematics of terrestrial capture of food in fishes that do not have an elongate body. (A–C) *Anableps anableps*. (D–F) *Periophthalmus barbarus*. Schematic illustrations of the skeletal elements are shown left of the corresponding lateral-view images during successive stages [start (at top) to capture (bottom)] during food capture on land (based on Michel et al., 2015a,b). Skeletal elements are color-coded as in Fig. 1. The yellow lines on the images of *P. barbarus* illustrate the contours of the water protruding out of the mouth. This water subsequently aids in the transport of the food into and through the mouth cavity.

Journal of Experimental Biology

Journal of Experimental Biology (2018) 221, jeb154427. doi:10.1242/jeb.154427

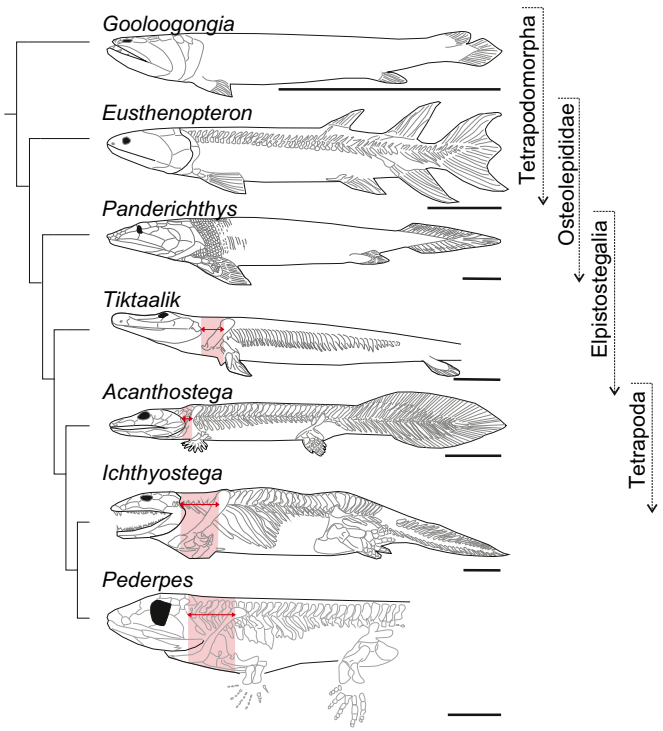

Fig. 5. Reconstructions of important taxa in the origin of terrestrial vertebrates (fossils from 385 to 348 Mya). The cladogram follows Clack (2009). The neck is highlighted in transparent red, with red arrows drawn from the posterior edge of the skull to the center of the pectoral girdle (cleithrum bone at the height of the vertebral axis). It illustrates the origin of the neck within Elpistostegalia, but its length relative to head length is still small in the earliest tetrapod fossils. Line drawings are based on Johanson and Ahlberg (1998) (*Gooloogongia*), Ahlberg and Milner (1994) (*Eusthenopteron*), Vorobyeva and Schultze (1991) (*Panderichthys*), Daeschler et al. (2006) (*Tiktaalik*), Ahlberg et al., 2005 (*Acanthostega* and *Ichthyostega*) and Clack (2002) (*Pederpes*). Scale bars, 0.1 m.

But why did stem tetrapods with a body primarily adapted for aquatic life leave water at all? Many theories were introduced in the last few decades trying to tackle that question (for an overview, see Romer, 1958; McNamara and Selden, 1993; Carroll, 2009; Niedźwiedzki et al., 2010; Clack, 2012; Schoch, 2014). Here, we will focus on the theory most appealing to us: that leaving water might have opened new possibilities to exploit food sources. As suggested by Niedźwiedzki et al. (2010) and Clack (2012), stem tetrapods might have exploited the niche of predating on stranded and trapped fish or invertebrates during low tide in intertidal zones. The trackways from Poland were found along intertidal and lagoonal zones and therefore can well support the hypothesis that the track-makers were heading along the shore in search for stranded and trapped marine animals (Niedźwiedzki et al., 2010; Clack, 2012).

How could prey be captured out of water with a feeding system primarily adapted for aquatic strikes (see mechanical problems shown in Fig. 2)? Similar to terrestrial actinopterygians (see Glossary) (Fig. 1), stem tetrapods still had a fish-like hyobranchial apparatus bearing internal gills (Clack, 2012) and lacked a movable tongue but were able to grasp prey out of water with their jaws. *Acanthostega* was probably capable of using suction feeding (Neenan et al., 2014; Porro et al., 2015), but, by making deductions from its dentition and skull structure, it also used direct bites, probably to capture larger prey (Markey and Marshall, 2007). Accordingly, it seems likely that, analogous to the fin-to-limb transition, the shift from a high-performance suction feeding mechanism to a firm biting mechanism (jaw prehension), as an exaptation for a terrestrial feeding mode, had already happened in water, and use of this mechanism on land to grasp prey was probably the next functional step. However, biting alone is useless if the gape cannot be directed to the food item. Although mudskippers are an example of how weight-bearing support from the pectoral fins can be used to bring their mouth towards terrestrial food, it is questionable whether the whole-body pivoting observed in mudskippers would have been possible in the considerably larger adult specimens of Late Devonian tetrapodomorphs. Mudskippers seldom surpass 0.2 kg (Khaironizam and Norma-Rashid, 2002), but fossils such as *Tiktaalik*, *Acanthostega* and *Ichthyostega* (all surpassing 0.5 m in length; Fig. 5) probably weighed 10 times more. However, around the time of the origin of the weight-supporting pectoral girdle and appendages, the first necks appeared in tetrapodomorphs (Fig. 5) – the pectoral girdle that previously attached directly to the back of the skull (e.g. red elements in Fig. 1) became disconnected from the skull to form a pectoral joint more posterior to the vertebral column (Daeschler et al., 2006; Shubin et al., 2015). This allowed the head to be moved while the pectoral girdle and appendage were statically supporting the head.

Upon the discovery of the first tetrapodomorph that had a neck, *Tiktaalik roseae* (Fig. 5), it was first proposed that the neck would allow dorsoventral flexion that could be used during feeding (Daeschler et al., 2006), perhaps in a way analogous to amphibious fishes (Van Wassenbergh et al., 2006). Later, it was proposed that *T. roseae* would use lateral instead of dorsoventral movements of the head to capture food on land and underwater (Hohn-Schulte et al., 2013). The investigators argued that (1) the head shape of *T. roseae* is somewhat reminiscent of crocodiles, which use lateral strikes of the head, and (2) the relatively long and narrow *T. roseae* jaws make it biomechanically more advantageous (less inertial cost and hydrodynamic resistance) to use side-snapping to capture prey in water (Hohn-Schulte et al., 2013). Additionally, it can be argued that a relatively long lower jaw, like those of the Late Devonian Osteolepididae (Fig. 5), might be too large to allow the mouth to be placed over the food, as observed in amphibious fishes (Figs 3 and 4). The smaller jaws of amphibious fishes require less height above the ground to be rotated over a large angle, allowing food to be grabbed from above. Rolling of the head and grabbing food on land with one side of the jaw could overcome this problem.

The ability to adjust the movement pattern of the head in order to effect the function of food prehension on land, such as sideways rolling of the head, could have made it unnecessary to evolve the morphology of the jaws during the transition(s) from water to land in Late Devonian tetrapodomorphs. This idea seems supported by analyses of the morphology and mechanics of the lower jaws in the transition from Devonian tetrapods to aquatic/semi-aquatic Carboniferous species – the changes are negligible (Neenan et al., 2014). The lower jaws of tetrapods only start showing considerable changes much later (Pennsylvanian age), when herbivory evolved within amniotes (see Glossary) (Anderson et al., 2011, 2013). These studies indicate that no different mechanical constraints are imposed on the lower jaw to function effectively during terrestrial feeding compared with aquatic feeding.

Once a food item is grasped by the jaws, it must be transported to the back of the oral cavity for swallowing. Though variable and overlapping, roughly three phases have been suggested both for aquatic and terrestrial gnathostomes (Lauder, 1983; Hiiemae and Crompton, 1985): food first needs to be transported from the front to the back of the oral cavity (oral phase) and to the back of the

pharyngeal cavity (pharyngeal phase) for the final transition into the esophagus (swallowing phase). The oral and pharyngeal transport phases are not strictly separated events but rather a continuum, and in the following we will use 'transport' or 'intraoral transport' when referring to food transport through the oropharyngeal cavity. In water, transport phases can be accomplished by the use of water currents, but how can transport be accomplished on land without the aid of water flow (see mechanical problem 6 in Fig. 2)? Stem tetrapods and actinopterygians feeding on land are faced with the same problem for transport, and, by making deductions from extant analogues (see Glossary), three plausible solutions have been proposed: (i) carrying a gulp of water out to land and using water in the mouth as a hydrodynamic tongue, (ii) dragging the prey back into the water to use suction for intraoral transport and (iii) inertial transport by quick lateral or dorso-ventral head rotations while temporarily releasing the tight grip on the prey.

Option i, carrying a gulp of water to be used as hydrodynamic tongue, is a mechanism found in mudskippers (Fig. 4D–F) (Michel et al., 2015b), and it might well be that some as-yet-unknown stem tetrapods used a convergent mechanism (Michel et al., 2016). Option ii, dragging prey back to the water, might be the easiest way to circumvent the problem of transport as well as swallowing prey captured on land, and is used in a variety of aquatic and amphibious vertebrates that occasionally strike prey on land (Lopez and Lopez, 1985; Miller and Larsen, 1990; Peddemors and Thompson, 1994; Bels et al., 1997; Summers et al., 1998; Werth, 2000; Stayton, 2011; Heiss et al., 2013a, 2015; Michel et al., 2015a; Natchev et al., 2015; Van Wassenbergh et al., 2017). Option iii is found in crocodilians (Cleuren and de Vree, 1992, 2000) and varanid lizards (Smith, 1982, 1986), where food is literally thrown through the mouth (Smith, 1982) by fast dorsal head rotation in concert with coordinated gape opening to accelerate prey backwards (Smith, 1982, 1986; Cleuren and de Vree, 1992, 2000). This form of inertial transport requires a movable neck that allows fast head movements relative to the trunk. In fact, as the shoulder girdle lost its tight connection to the skull during early tetrapod evolution (Fig. 5), the resulting movable neck can be considered one of the key innovations of tetrapods. Accordingly, aside from bringing a gulp of water on land, dragging captured prey back to the water for use in aquatic intra-oral transport mechanisms, it is likely that some stem tetrapods used a simple form of inertial oral transport on their occasional terrestrial excursions in search for food. Note that one group of ray-finned fishes, moray eels, has evolved the exceptional capacity to directly transport food from the jaws to the esophagus by extreme protrusion of the pharyngeal jaws (Mehta and Wainwright, 2007a,b). However, forward displacements of the pharyngeal jaws in fishes are generally confined to the posterior region of the pharynx (Liem and Greenwood, 1981; Sponder and Lauder, 1981; Wainwright, 1989). Yet, pharyngeal jaw transport has been shown to be involved in the mudskipper *Periophthalmus* when feeding on land (Sponder and Lauder, 1981). Given that denticles were also present on the gill arches in temnospondylians (e.g. Schoch, 2009), it cannot be entirely excluded that pharyngeal teeth movements played a role in the final phases of intra-oral transport in some tetrapods too. Nevertheless, permanent colonization of land was only possible after efficient feeding mechanisms independent of water had evolved.

Adopting terrestrial feeding without using water

A fish-like hyobranchial apparatus bearing gills might allow short excursions and occasional feeds on land but prevents any permanent adoption of terrestrial domains. Permanent 'terrestrialization' was only possible after reduction of the gills and development of a tool that allowed efficient food capture and intra-oral transport independent of water flow – the tongue. The tongue recruits a large part of the hyobranchial musculoskeletal system and therefore replaces, to a high degree, the suction-feeding apparatus otherwise used for food ingestion in water and the suspension of the gills. The functional consequences of this include a reduced capability to suction feed and the need for another respiratory system. Gill respiration was effectively replaced by lung and cutaneous respiration, and giving up high-performance suction feeding paved the way for further degrees of freedom to remodel the hyobranchial musculo-skeletal system into a lingual system (Heiss et al., 2013b).

However, owing to the poor preservation of soft tissue and cartilage in general and non-mineralized tissue of the hyobranchial system in early tetrapods in particular (Schoch, 2014), it is hard to define when and where the first tongue appeared in the evolution of tetrapods. Inferring from fossil records, we know that stem tetrapods were basically aquatic forms (Clack, 2012), but that stem amphibians and stem amniotes (see Glossary) evolved amphibious lifestyles and gradual transitions from an aquatic, gill-bearing larva to a more-or-less terrestrial adult with reduced gills (Schoch, 2014). While in the dissorophoid (see Glossary) zatracheids (stem amphibians) we have the first evidence for a remodeling of a larval, gill-bearing hyobranchial apparatus to an adult, tongue-supporting hyolingual skeleton, semouriamorphs (stem amniotes) evolved terrestrial forms along a separate line (Witzmann, 2013; Schoch, 2014). It is not clear whether stem amphibians and stem amniotes have evolved a tongue completely independently (Witzmann, 2013), but, if we consider lingual systems in extant tetrapods, it seems likely that the history of the tongue was subject of many parallelisms.

The tetrapod tongue is mainly used as a prehensile organ for the initial uptake of food and to manipulate or transport food within the mouth (Schwenk, 2000a). The tongue can be a highly movable organ moved out of the mouth to grasp food items that are then brought into the mouth by tongue retraction. Such initial food uptake by the tongue requires an adhesive potential of the tongue to overcome the inertia and gravitational forces acting on the food (Bramble and Wake, 1985). Specialized tongue surface microstructures such as papillae (see Glossary), in conjunction with mucus secretions, can enhance the adhesive potential (Bramble and Wake, 1985). The horned frog *Ceratophrys* has mastered tongue adhesion so comprehensively that, in theory, it is capable of lifting its own body weight by its tongue alone (Kleinteich and Gorb, 2014).

Once food is brought into the mouth, it is directly transported to the esophagus for swallowing, or to the posterior teeth for mechanical reduction, if chewing is applied beforehand (Schwenk, 2000a; Schwenk and Rubega, 2005; Herrel et al., 2012). Swallowing can be a complex affair and mechanisms differ substantially amongst tetrapods, but in most cases tightly coordinated contraction of pharyngeal and lingual muscles widen the esophageal sphincter and push the food bolus into the esophagus (e.g. Smith, 1984, 1992; Bramble and Wake, 1985; Schwenk, 2000a). However, next to the use of the tongue in concert with pharyngeal musculature, some tetrapods have evolved alternative mechanisms to carry food to the esophagus, as summarized in Table 1. Nonetheless, the tongue remains one of the central evolutionary innovations in tetrapods enabling all feeding stages independent of water, but tongue functions can be very different and tongue morphology can vary substantially amongst groups.

Journal of Experimental Biology (2018) 221, jeb154427. doi:10.1242/jeb.154427

In general, a tetrapod tongue is supported by skeletal elements – the hyolingual skeleton – and integrates mucosal, muscle and connective tissue elements. In lissamphibians (see Glossary), most birds and crocodilians, the tongue is a relatively simple mechanical system and consists of a mucosal sheath covering a simple (extrinsic) muscular system that rises from the supporting hyolingual skeleton, jaw or shoulder girdle (Özeti and Wake, 1969; Regal and Gans, 1976; Schwenk, 2000a; Tomlinson, 2000; Wake and Deban, 2000; Putterill and Soley, 2004; Erdoğan and Iwasaki, 2014). Other tetrapods, such as tortoises, squamates and mammals, have large bulged tongues and a muscular system with a complex arrangement of highly integrated internal (intrinsic) fibers oriented longitudinally, transversally, vertically, diagonally or circularly.

The muscular complexity mentioned above accounts for the unusual biomechanical properties of such tongues being able to function as muscular 'hydrostats' (see Glossary). In muscular hydrostats, the uncompressible volume of the muscle bodies has the effect that any decrease in one dimension causes a compensatory increase in at least one other dimension (Kier and Smith, 1985; Kier, 2012). For example, if we assume a cylindrical shape of such a system, elongation is achieved by diameter reduction caused by contraction of transverse, vertical or circular running fibers, whereas shortening is effected by an increase in diameter, caused by contraction of longitudinally oriented fibers. More-complex fiber constellation and activation patterns can cause coiling, bending or twisting movements. Accordingly, tongues exhibit a great range of movements that becomes especially evident in mammal and sauropsid tongues, which show motion ranges comparable with those of elephant trunks or squid tentacles (Kier and Smith, 1985; van Leeuwen et al., 2000; Kier, 2012). Muscular hydrostats are highly efficient lingual systems, but relatively simple tongues with marginal or no intrinsic musculature at all can be high-performing tools too, as exemplified by some frogs and salamanders that use elastic energy recoil mechanisms to catapult their sticky tongue pad towards distant prey that has virtually no chance to escape (Regal and Gans, 1976; Deban et al., 1997; Nishikawa, 2000; Wake and Deban, 2000; Deban and Richardson, 2011).

To understand the evolution of a functional tongue, salamanders are of special importance within extant tetrapods as they offer the unique opportunity to track the remodeling from a larval fish-like hyobranchial system bearing gills to a postmetamorphic tongue-bearing hyolingual system (see Fig. 6). Similar to bony fishes, larval salamanders are suction feeders with open gill slits (Lauder and Shaffer, 1985, 1988; Lauder and Reilly, 1988; Reilly and Lauder, 1992). As salamanders metamorphose, the head region undergoes massive changes, and the secondary tongue pad forms just anterior to the primary larval tongue (Opolka et al., 2001; Greven et al., 2013), while the hyobranchial musculoskeletal system gets reduced and rearranged in order to allow movements between what were previously fixed elements of hyoid and branchial arches (Reilly, 1987). In a simplified model, protraction and retraction of the tongue in the generalized postmetamorphic salamander is mainly achieved as the tongue-pad-bearing skeletal element – the basibranchial (in conjunction with hypo- and ceratobranchials) – is protracted and retracted relative to the ceratohyal (see Glossary) by action of the antagonistic subarcualis rectus and rectus cervicis muscles (Deban, 2003) (Fig. 6).

The cellular mechanisms controlling hyobranchial remodeling during metamorphosis in lissamphibians are still poorly understood. Most likely, thyroid-hormone-affected gene regulation accounts for the changes associated with hyobranchial remodeling during metamorphosis (Brown and Cai, 2007; Faunes et al., 2017; Laudet, 2011) and convergently triggered changes in gene regulation might also be the cause of evolutionary hyobranchial remodeling processes. So, similar to the fin-to-limb transition, regulatory changes in specific patterning genes (Shubin et al., 1997) might have led to the hyobranchial–hyolingual transition in tetrapod evolution. Currently, we do not have any knowledge on the form and function of the tongue in the first terrestrial tetrapods, but salamanders teach us that relatively small anatomical rearrangements in the hyobranchial system can lead to significant mechanical changes leading to a functional shift. Accordingly, it is plausible that similar modifications in the hyobranchial system in early crown tetrapods led to the evolutionary innovation of the tongue, which in turn paved the way for a successful invasion of land and the exploitation of terrestrial food sources.

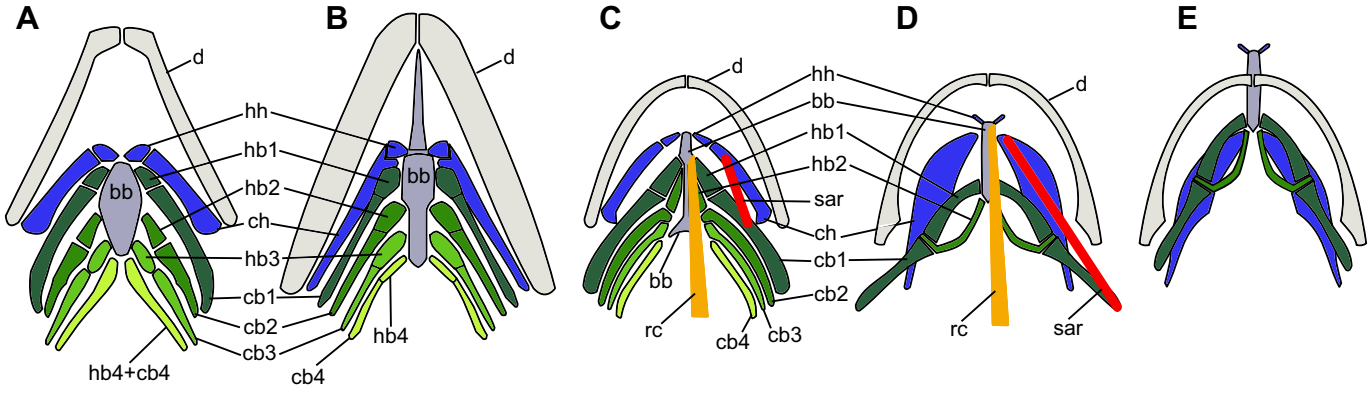

Fig. 6. Comparison of hyobranchial systems. (A) The basal actinopterygian *Polypterus*, (B) the extinct sarcopterygian (see Glossary) *Eusthepteron*, (C) a generalized salamander larva and (D,E) a generalized metamorphosed salamander with tongue either retracted (D) or protracted (E). All schemes are from ventral views and homologous structures have the same color code. Note the similarities among the hyobranchial architecture between the actinopterygian fish (*Polypterus*), the sarcopterygian fish (*Eusthenopteron*) and the salamander larva. During metamorphosis, salamanders reduce the posterior branchial arches and mechanically decouple the ceratohyal (ch, blue) from the basibranchial (bb, gray), a rearrangement specific for salamanders that allows protraction of the tongue-pad-bearing basibranchial by contraction of the subarcualis rectus (sar, red) muscle. Retraction is powered by the rectus cervicis muscle (rc). Note that, for clarity, only the left portions of the rc and sar are shown. Abbreviations: cb1–4, ceratobranchial 1–4; d, dentary; hb1–4, hypobranchial 1–4 (see Glossary); hh, hypohyal. Modified from Reilly and Lauder (1988) and Deban (2003).

Journal of Experimental Biology (2018) 221, jeb154427. doi:10.1242/jeb.154427

Switching between water and land

Demands between feeding in water and feeding on land are diverse and, to a large extent, conflicting (Bramble and Wake, 1985; Deban, 2003). Because of the different dynamic behavior of food particles when in water or air, substantially different morphological designs of the feeding apparatus are required (Bramble and Wake, 1985). For example, robust hyobranchial skeletons and associated muscles allow high-performance suction feeding in water, but such a design is useless on land, whereas a slender hyolingual skeleton supporting a muscular tongue is of great use on land but suboptimal for aquatic feeding (Bramble and Wake, 1985; Deban, 2003; Stinson and Deban, 2017). As shown in the previous sections, a feeding system primarily adapted for aquatic (suction) feeding can also be used to catch prey on land. Similarly, remodeling of a gill-bearing hyobranchial to a hyolingual tongue-bearing system might, in many cases, reduce suction feeding performance but does not prevent suction feeding per se. Indeed, we find many examples within salamanders, turtles and actinopterygian fishes that regularly switch between aquatic and terrestrial environments and have found different mechanical solutions to circumvent the trade-offs between efficient food uptake on land and in water.

Merely aquatic salamandrid newts use suction in water and a slightly modified suction strike on land and grasp prey using jaws (Miller and Larsen, 1989, 1990; Heiss et al., 2013a, 2015). A similar, but convergently evolved, strategy is used by semi-aquatic turtles, where suction feeding is performed in water, but their jaws seize prey on land (Fig. 7) (Natchev et al., 2009, 2015; Heiss et al., 2010; Stayton, 2011). Once food is held between the jaws, it is dragged back to the water, or in some cases swallowed on land by backward transport and transition into the esophagus by the tongue (Natchev et al., 2009, 2015). Some salamanders go further, and, while they still use suction feeding in water, they change to lingual prehension on land and catch prey by their protractible tongue (Fig. 7) (Reilly and Lauder, 1989; Lauder and Gillis, 1997; Deban and Wake, 2000; Wake and Deban, 2000; Heiss and De Vylder, 2016). In contrast, turtles are less flexible and only the fully terrestrial tortoises make use of their tongue for initial food uptake on land, but unlike their turtle relatives, extant tortoises have lost any capacity to feed under water (Natchev et al., 2015).

Flexible feeding systems allowing aquatic and terrestrial uptake of food demand a high degree of behavioral plasticity and flexibility, but structurally represent compromises and perform suboptimally in at least one medium (Bramble and Wake, 1985). The only solution to increase performance in both media would be to change the morphology of the feeding apparatus when changing from one to the other feeding medium. In fact, some salamandrid newts are such masters of change – they use suction feeding in water and catch prey by the tongue on land and reversibly change the anatomy of their feeding apparatus to meet the demands of the respective feeding circumstances (i.e. aquatic versus terrestrial feeding) (Heiss et al., 2013a, 2015, 2016, 2017; Van Wassenbergh and Heiss, 2016).

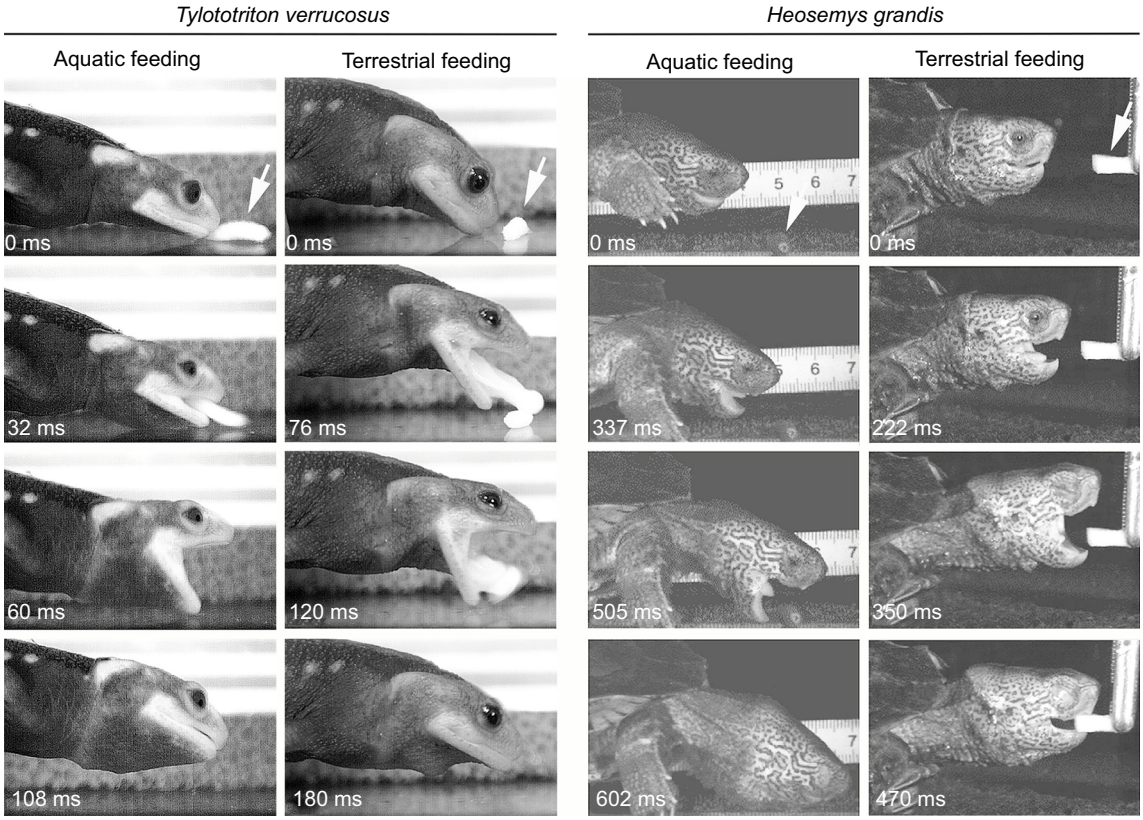

Fig. 7. Frame shots from high-speed recordings showing the semiaquatic salamandrid newt *Tylototriton verrucosus* and the semiaquatic turtle *Heosemys grandis* feeding in water and on land. For aquatic strikes, both use suction (note the inflated head–throat region caused by the engulfed water volume at the end of the strikes), but on land, the uptake mechanisms are different: whereas *H. grandis* retracts its small tongue and uses its jaws to grasp the offered food item, *T. verrucosus* uses its quickly protracted–retracted sticky tongue. Rule divisions: centimeters. White arrows indicate the test prey item. Images of *T. verrucosus* are modified from Heiss and De Vylder (2016), images of *H. grandis* feeding in water are modified from Lintner (2010) and images of *H. grandis* feeding on land are courtesy of P. Lemell, N. Natchev, C. Beisser and E. Heiss.

Specifically, some salamandrid newts change seasonally between an aquatic and a terrestrial life and as they switch habitat, they also undergo modifications of their feeding apparatus. In the aquatic phase, they grow labial lobes (Matthes, 1934), which are skin folds that restrict the gape opening anteriorly and increase suction feeding performance measured by a suction flow velocity that is increased by up to 30% (Van Wassenbergh and Heiss, 2016). Labial lobes then disappear when the newts leave the water and change to the terrestrial lifestyle. At this point, the formerly smooth tongue grows microscopic slender papillae and the mucus-producing goblet cells increase in number to supply the tongue with more mucus (Heiss et al., 2017). The integration of microscopic slender papillae and mucus has been shown to increase adhesive potential of the amphibian tongue (Kleinteich and Gorb, 2015) and accordingly, the newts increase their potential prey capture success by gaining a sticky tongue pad as they change to their terrestrial lifestyle. As newts seek their home-waters again in the spring, the lingual papillae disappear and the goblet cell number decreases, whereas labial lobes recommence growing again (Matthes, 1934; Heiss et al., 2017).

Even if a feeding apparatus undergoes some changes to account for different demands, it will always represent some kind of compromise, and amphibious species that switch between aquatic and terrestrial feeding usually perform at a lower efficiency than those specialized for one medium. By contrast, salamanders, turtles and actinopterygians have convergently found ways to exploit food sources from two very different environments where prey abundance can vary in time. Considering such analogues in conjunction with fossil records (fossil tracks) it makes it more plausible that the first tetrapods that left the water some 400 Mya were indeed driven by the search for new food sources in intertidal zones.

Concluding remarks

Transitions from aquatic to terrestrial habitats are well known as pivotal events in vertebrate evolution, and this article synthesizes the mechanical demands of capturing, transport and swallowing of food on land for ancestrally aquatic as well as amphibious species. We have illustrated how several amphibious fishes and tetrapods deal with these different mechanical challenges to feed on land. Such experimental studies on extant organisms allow useful insights and deductions regarding how the first terrestrial tetrapods managed the physical challenge to feed on land on their way towards land invasion. In fact, biomechanical studies on fishes, amphibians and other vertebrates that feed in both environments (e.g. Fig. 7) will remain of central importance to improving our understanding of the functional–morphological trade-offs involved in aquatic–terrestrial transitions. Promising approaches for future work include, amongst others, studying the effect of phenotypic plasticity and flexibility on aquatic–terrestrial feeding transitions. For example, it was shown that the basal extant actinopterygian *Polypterus* can be raised out of water and that such individuals adopt terrestrial-style kinematics and anatomy of their locomotor system (Standen et al., 2014). Analogous to this, behavior and anatomy of its feeding apparatus might change accordingly when raised out of water. Similarly, representatives of the tetrapod sister group, i.e. extant lungfishes, might be raised on land or at least trained to feed on land, and it will be interesting to know how they change their feeding system to capture, transport and swallow food out of water. Furthermore, paedomorphic or larval salamanders are a promising model to study how a basically aquatic tetrapod with limbs and a hyobranchial system bearing gills manages to feed out of water: a very similar condition first tetrapods were faced with. Using such model organisms in integrative experimental, analytical and computational approaches such as biplanar X-ray recordings, XROMM (X-ray reconstruction of moving morphology), finite element analysis (FEA) or computational fluid dynamics (CFD) offers the opportunity to obtain deeper insights into the mechanics of feeding transitions in extant vertebrates, which in turn helps to explain one of the most crucial steps in our own history: the evolution of terrestriality and successful invasion of land.

Acknowledgements

We thank A. Herrel, D. Adriaens, K. Michel, B. Vervust, J. Brecko for their help in our research on the biomechanics of feeding in amphibious fishes, N. Natchev, P. Lemell, C. Beisser and J. Weisgram for their contributions on turtle feeding research and David Hattan along with two anonymous reviewers for their valuable comments on the manuscript.

Competing interests

The authors declare no competing or financial interests.

Funding

This work was supported by a New Research Initiative grant from the Special Research Fund (Bijzonder Onderzoeksfonds) (NOI-BOF) of the University of Antwerp, a grant from the Agence Nationale de la Recherche (ANR-16-ACHN-0006-01) to S.V.W. and a research grant of the German Research Foundation (Deutsche Forschungsgemeinschaft) to E.H. (EH 7788/1-1)

References

Aerts, P. (1991). Hyoid morphology and movements relative to abducting forces during feeding in *Astatotilapia elegans* (Teleostei: Cichlidae). *J. Morph.* **208**, 323-346.

Ahlberg, P. E. and Milner, A. R. (1994). The origin and early diversification of tetrapods. *Nature* **368**, 507-514.

Ahlberg, P. E., Clack, J. A. and Blom, H. (2005). The axial skeleton of the Devonian tetrapod *Ichthyostega*. *Nature* **437**, 137-140.

Alexander, R. McN. (1967). The functions and mechanisms of the protrusible upper jaws of some acanthopterygian fish. *J. Zool., Lond.* **151**, 43-64.

Anderson, P. S. L., Friedman, M., Brazeau, M. D. and Rayfield, E. J. (2011). Initial radiation of jaws demonstrated stability despite faunal and environmental change. *Nature* **476**, 206-209.

Anderson, P. S. L., Friedman, M. and Ruta, M. (2013). Late to the table: diversification of tetrapod mandibular biomechanics lagged behind the evolution of terrestriality. *Integr. Comp. Biol.* **53**, 197-208

Ashley-Ross, M. A., Hsieh, S. T., Gibb, A. C. and Blob, R. W. (2013). Vertebrate land invasions-past, present, and future: an introduction to the symposium. *Integr. Comp. Biol.* **53**, 192-196.

Baussart, S., Korsoun, L., Libourel, P.-A. and Bels, V. (2009). Ballistic food transport in toucans. *J. Exp. Zool.* **311A**, 465-474.

Bels, V. L., Davenport, J. and Delheusy, V. (1997). Kinematic analysis of the feeding behavior in the box turtle *Terrapene carolina* (L.), (Reptilia: Emydidae). *J. Exp. Zool.* **277**, 198-212.

Bels, V. L., Baussart, S., Davenport, J., Shorten, M., O'Riordan, R. M., Renous, S. and Davenport, J. (2008). Functional evolution of feeding behaviour in turtles. In *Biology of Turtles* (ed. J. Wyneken, M. H. Godfrey and V. Bels), pp. 189-212. Boca Raton, FL: CRC Press Taylor & Francis Group.

Bemis, W. E., Schwenk, K. and Wake, M. H. (1983). Morphology and function of the feeding apparatus in *Dermophis mexicanus* (Amphibia: Gymnophiona). *Zool. J. Linn. Soc.* **77**, 75-96.

Bramble, D. M. and Wake, D. (1985). Feeding mechanisms of lower tetrapods. In *Functional Vertebrate Morphology* (ed. M. Hildebrand, D. Bramble, K. Liem and D. Wake), pp. 230-261. London: Belknap Press of Harvard University Press.

Brown, D. D. and Cai, L. (2007). Amphibian metamorphosis. *Dev. Biol.* **306**, 20-33.

Camp, A. L. and Brainerd, E. L. (2014). Role of axial muscles in powering mouth expansion during suction feeding in largemouth bass (*Micropterus salmoides*). *J. Exp. Biol.* **217**, 1333-1345.

Carroll, R. L. (2009). *The Rise of Amphibians: 365 Million Years of Evolution*. Baltimore, MD: Johns Hopkins University Press.

Clack, J. A. (2002). An early tetrapod from 'Romer's Gap'. *Nature* **418**, 72-76.

Clack, J. A. (2009). The fish-tetrapod transition: new fossils and interpretations. *Evo. Edu. Outreach* **2**, 213-223.

Clack, J. A. (2012). *Gaining Ground: The Origin and Evolution of Tetrapods*. Bloomington, IN: Indiana University Press.

Clack, J. and Coates, M. I. (1995). *Acanthostega gunnari*, a primitive, aquatic tetrapod? *Bull. Mus. Natl. Hist. Nat. Paris* **17**, 359-372.

Cleuren, J. and de Vree, F. (1992). Kinematics of the jaw and hyolingual apparatus during feeding in *Caiman crocodilus*. *J. Morphol.* **212**, 141-154.

Cleuren, J. and de Vree, F. (2000). Feeding in crocodilians. In *Feeding: Form, Function, and Evolution in Tetrapod Vertebrates* (ed. K. Schwenk), pp. 337-358. San Diego, CA: Academic Press.
Coates, M. I. and Clack, J. A. (1991). Fish-like gills and breathing in the earliest known tetrapod. *Nature* **352**, 234-236.
Cucherousset, J., Boulêtreau, S., Azémar, F., Compin, A., Guillaume, M. and Santoul, F. (2012). 'Freshwater killer whales': beaching behavior of an alien fish to hunt land birds. *PloS ONE* **7**, e50840.
Cundall, D. and Greene, H. W. (2000). Feeding in snakes. In *Feeding: Form, Function and Evolution in Tetrapod Vertebrates* (ed. K. Schwenk), pp. 293-333. San Diego, CA: Academic Press.
Daeschler, E. B., Shubin, N. H. and Jenkins, F. A. Jr. (2006). A Devonian tetrapod-like fish and the evolution of the tetrapod body plan. *Nature* **440**, 757-763.
de Pinna, M. C. C. (1998). Phylogenetic relationships of Neotropical Siluriformes (Teleostei: Ostariophysi): historical overview and synthesis of hypotheses. In *Phylogeny and Classification of Neotropical Fishes* (ed. L. R. Malabarba, R. E. Reis, R. P. Vari, Z. M. Lucena and C. A. S. Lucena), pp. 279-330. Porto Alegre: Edipucrs.
de Visser, J. and Barel, C. D. N. (1996). Architectonic constraints on the hyoid's optimal starting position for suction feeding of fish. *J. Morphol.* **228**, 1-18.
Deban, S. M. (1997). Modulation of prey-capture behavior in the plethodontid salamander *Ensatina eschscholzii*. *J. Exp. Biol.* **200**, 1951-1964.
Deban, S. M. (2003). Constraint and convergence in the evolution of salamander feeding. In *Vertebrate Biomechanics and Evolution* (ed. J. Gasc, A. Casinos and V. Bels), pp. 163-180. Oxford: BIOS Scientific Publishers.
Deban, S. M. and Richardson, J. C. (2011). Cold-blooded snipers: thermal independence of ballistic tongue projection in the salamander *Hydromantes platycephalus*. *J. Exp. Zool. A* **315**, 618-630.
Deban, S. M. and Wake, D. B. (2000). Aquatic feeding in salamanders. In *Feeding: Form, Function and Evolution in Tetrapod Vertebrates* (ed. K. Schwenk), pp. 65-94. San Diego, CA: Academic Press.
Deban, S. M., Wake, D. B. and Roth, G. (1997). Salamander with a ballistic tongue. *Nature* **389**, 27.
Drucker, E. G. and Lauder, G. V. (2002). Wake dynamics and locomotor function in fishes: interpreting evolutionary patterns in pectoral fin design. *Integr. Comp. Biol.* **42**, 997-1008.
Erdoğan, S. and Iwasaki, S.-I. (2014). Function-related morphological characteristics and specialized structures of the avian tongue. *Anat. Anz.* **196**, 75-87.
Erickson, G. M., Lappin, A. K. and Vliet, K. A. (2003). The ontogeny of bite-force performance in American alligator (*Alligator mississippiensis*). *J. Zool. Lond.* **260**, 317-327.
Faunes, F., Gundermann, D. G., Muñoz, R., Bruno, R. and Larraín, J. (2017). The heterochronic gene Lin28 regulates amphibian metamorphosis through disturbance of thyroid hormone function. *Dev. Biol.* **425**, 142-151.
Fish, F. E. (2006). The myth and reality of Gray's paradox: implication of dolphin drag reduction for technology. *Bioinsp. Biomim.* **1**, R17-R25.
Gordon, M. S., Boëtius, I., Evans, D. H., McCarthy, R. and Oglesby, L. C. (1969). Aspects of the physiology of terrestrial life in amphibious fishes I. The mudskipper, *Periophthalmus sobrinus*. *J. Exp. Biol.* **50**, 141-149.
Gosline, W. A. (1971). *Functional Morphology and Classification of Teleostean Fishes*. Honolulu, HI: The University Press of Hawaii.
Gosline, W. A. (1987). Jaw structures and movements in higher Teleostean fishes. *Jpn. J. Ichthyol.* **34**, 21-32.
Greven, H., Richter, H. and Clemen, G. (2013). Formation of the secondary tongue in *Hynobius leechi* and *Ambystoma mexicanum* (Amphibia: Urodela). *Vertebr. Zool.* **63**, 217-232.
Guinet, C. and Bouvier, J. (1995). Development of intentional stranding hunting techniques in killer whale (*Orcinus orca*) calves at Crozet Archipelago. *Can. J. Zool.* **73**, 27-33.
Heiss, E. and De Vylder, M. (2016). Dining dichotomy: aquatic and terrestrial prey capture behavior in the Himalayan newt *Tylototriton verrucosus*. *Biol. Open* **5**, 1500-1507.
Heiss, E., Natchev, N., Beisser, C., Lemell, P. and Weisgram, J. (2010). The fish in the turtle: on the functionality of the oropharynx in the common musk turtle *Sternotherus odoratus* (Chelonia, Kinosternidae) concerning feeding and underwater respiration. *Anat. Rec.* **293**, 1416-1424.
Heiss, E., Aerts, P. and Van Wassenbergh, S. (2013a). Masters of change: seasonal plasticity in the prey-capture behavior of the Alpine newt *Ichthyosaura alpestris* (Salamandridae). *J. Exp. Biol.* **216**, 4426-4434.
Heiss, E., Natchev, N., Gumpenberger, M., Weissenbacher, A. and Van Wassenbergh, S. (2013b). Biomechanics and hydrodynamics of prey capture in the Chinese giant salamander reveal a high-performance jaw-powered suction feeding mechanism. *J. R. Soc. Interface* **10**, 20121028.
Heiss, E., Aerts, P. and Van Wassenbergh, S. (2015). Flexibility is everything: prey capture throughout the seasonal habitat switches in the smooth newt *Lissotriton vulgaris*. *Org. Divers. Evol.* **15**, 127-142.
Heiss, E., Handschuh, S., Aerts, P. and Van Wassenbergh, S. (2016). Musculoskeletal architecture of the prey capture apparatus in salamandrid newts with multiphasic lifestyle: does anatomy change during the seasonal habitat switches? *J. Anat.* **228**, 757-770.
Heiss, E., Handschuh, S., Aerts, P. and Van Wassenbergh, S. (2017). A tongue for all seasons: extreme phenotypic flexibility in salamandrid newts. *Sci. Rep.* **7**, 1006.
Hernandez, L. P., Ferry-Graham, L. A. and Gibb, A. C. (2008). Morphology of a picky eater: a novel mechanism underlies premaxillary protrusion and retraction within cyprinodontiforms. *Zoology* **111**, 442-454.
Hernandez, L. P., Gibb, A. C. and Ferry-Graham, L. (2009). Trophic apparatus in cyprinodontiform fishes: functional specializations for picking and scraping behaviors. *J. Morphol.* **270**, 645-661.
Herrel, A. and Measey, G. J. (2012). Feeding underground: kinematics of feeding in caecilians. *J. Exp. Zool.* **317A**, 533-539.
Herrel, A., Van Wassenbergh, S. and Aerts, P. (2012). Biomechanical studies of food and diet selection. In *eLS*, pp. 1-9. Chichester: Wiley.
Hiiemae, K. M. (2000). Feeding in mammals. In *Feeding: Form, Function and Evolution in Tetrapod Vertebrates* (ed. K. Schwenk), pp. 411-448. London: Academic Press.
Hiiemae, K. M. and Crompton, A. W. (1985). Mastication, food transport and swallowing. In *Functional Vertebrate Morphology* (ed. M. Hildebrand, D. Bramble, K. Liem and D. Wake), pp. 262-290. London: Belknap Press of Harvard University Press.
Hill, A. V. (1950). The dimensions of animals and their muscular dynamics. *Sci. Prog., Lond.* **38**, 209-230.
Hohn-Schulte, B., Preuschoft, H., Witzel, U. and Distler-Hoffmann, C. (2013). Biomechanics and functional preconditions for terrestrial lifestyle in basal tetrapods, with special consideration of *Tiktaalik roseae*. *Hist. Biol.* **25**, 167-181.
Holzman, R., Day, S. W., Mehta, R. S. and Wainwright, P. C. (2008). Jaw protrusion enhances forces exerted on prey by suction feeding fishes. *J. R. Soc. Interface.* **5**, 1445-1457.
Homberger, D. G. (1986). *The Lingual Apparatus of the African Grey Parrot Psittacus erithacus Linne (Aves: Psittacidae): Description and Theoretical Mechanical Analysis. Ornithological Monograph No. 39*. Washington, DC: American Ornithologists' Union.
Hsieh, S.-T. T. (2010). A locomotor innovation enables water-land transition in a marine fish. *PLoS ONE* **5**, e11197.
Hughes, W. F. and Brighton, J. A. (1967). *Schaum's Outline of Theory and Problems of Fluid Dynamics*. New York: McGraw-Hill, Inc.
Johanson, Z. and Ahlberg, P. E. (1998). A complete primitive rhizodont from Australia. *Nature* **394**, 569-573.
Kardong, K. V. (1977). Kinesis of the jaw apparatus during swallowing in the cottonmouth snake, *Agkistrodon piscivorus*. *Copeia* **1977**, 338-348.
Kawano, S. M. and Blob, R. W. (2013). Propulsive forces of mudskipper fins and salamander limbs during terrestrial locomotion: implications for the invasion of land. *Integr. Comp. Biol.* **53**, 283-294.
Khaironizam, M. Z. and Norma-Rashid, Y. (2002). Length-weight relationship of mudskippers (Godiidae: Oxudercinae) in the coastal areas of Selangor, Malaysia. *Naga WorldFish Center Quart.* **25**, 20-22.
Kier, W. M. (2012). The diversity of hydrostatic skeletons. *J. Exp. Biol.* **215**, 1247-1257.
Kier, W. M. and Smith, K. K. (1985). Tongues, tentacles and trunks: the biomechanics of movement in muscular-hydrostats. *Zool. J. Linn. Soc.* **83**, 307-324.
Kleinteich, T. and Gorb, S. N. (2014). Tongue adhesion in the horned frog *Ceratophrys* sp. *Sci. Rep.* **4**, 5225.
Kleinteich, T. and Gorb, S. N. (2015). Frog tongue acts as muscle-powered adhesive tape. *R. Soc. Open Sci.* **2**, 150333.
Larsen, J. H. and Guthrie, D. J. (1975). The feeding system of terrestrial tiger salamanders (*Ambystoma tigrinum melanostictum* Baird). *J. Morph.* **147**, 137-154.
Lauder, G. V. (1983). Food capture. In *Fish Biomechanics* (ed. P. W. Webb and D. Weihs), pp. 2080-2311. New York: Praeger Publishers.
Lauder, G. V. and Gillis, G. (1997). Origin of the amniote feeing mechanism: experimental analyses of outgroup clade. In *Amniote Origins: Completing the Transition to Land* (ed. S. S. Sumida and K. L. M. Martin), pp. 169-206. San Diego, CA: Academic Press.
Lauder, G. V. and Reilly, S. M. (1988). Functional design of the feeding mechanism in salamanders: causal bases of ontogenetic changes in function. *J. Exp. Biol.* **134**, 219-233.
Lauder, G. V. and Shaffer, H. B. (1985). Functional morphology of the feeding mechanism in aquatic ambystomatid salamanders. *J. Morphol.* **185**, 297-326.
Lauder, G. V. and Shaffer, H. B. (1988). Ontogeny of functional design in tiger salamanders (*Ambystoma tigrinum*): are motor patterns conserved during major morphological transformations? *J. Morphol.* **197**, 249-268.
Laudet, V. (2011). The origins and evolution of vertebrate metamorphosis. *Curr. Biol.* **21**, R726-R737.
Levine, R. P., Monroy, J. A. and Brainerd, E. L. (2004). Contribution of eye retraction to swallowing performance in the northern leopard frog, *Rana pipiens*. *J. Exp. Biol.* **207**, 1361-1368.

Liem, K. F. (1991). Functional morphology — hydrodynamic tongue. In *Cichlid Fishes: Behaviour Ecology and Evolution* (ed. M. H. A. Keenleyside), pp. 143-144. New York, NY: Chapman & Hall.
Liem, K. F. and Greenwood, P. H. (1981). A functional approach to the phylogeny of the pharyngognath teleosts. *Amer. Zool.* **21**, 83-101.
Lintner, M. (2010). Funktionsmorphologische Untersuchungen der Nahrungsaufnahme von *Heosemys grandis*, Gray 1860 (Chelonia, Geoemydidae) mit Berücksichtigung der Ontogenie. *Master's thesis*, University of Vienna, Vienna, Austria.
Lopez, J. C. and Lopez, D. (1985). Killer whales (*Orcinus orca*) of Patagonia, and their behavior of intentional stranding while hunting nearshore. *J. Mammal.* **66**, 181-183.
Losilevskii, G. and Papastamatiou, Y. P. (2016). Relations between morphology, buoyancy and energetics of requiem sharks. *R. Soc. Open Sci.* **3**, 160406.
Losos, J. B. (1990). Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards: an evolutionary analysis. *Ecol. Monogr.* **60**, 369-388.
Maie, T., Wilson, M. P., Schoenfuss, H. L. and Blob, R. W. (2009). Feeding kinematics and performance of Hawaiian stream gobies, *Awaous guamensis* and *Lentipes concolor*: linkage of functional morphology and ecology. *J. Morphol.* **270**, 344-356.
Markey, M. J. and Marshall, C. R. (2007). Terrestrial-style feeding in a very early aquatic tetrapod is supported by evidence from experimental analysis of suture morphology. *Proc. Natl. Acad. Sci. USA* **104**, 7134-7138.
Matthes, E. (1934). Bau und Funktion der Lippensäume wasserlebender Urodelen. *Z. Morphol. Oekol. Tiere* **28**, 155-169.
McClearn, D. (1992). Locomotion, posture and feeding behavior of kinkajous, coatis, and raccoons. *J. Mammal.* **73**, 245-261.
McNamara, K. and Selden, P. (1993). Strangers on the shore. *New Sci.* **139**, 23-27.
Mehta, R. S. and Wainwright, P. C. (2007a). Biting releases constraints on moray eel feeding kinematics. *J. Exp. Biol.* **210**, 495-504.
Mehta, R. S. and Wainwright, P. C. (2007b). Raptorial jaws in the throat help moray eels swallow large prey. *Nature* **449**, 79-82.
Michel, K. B., Adriaens, D., Aerts, P., Dierick, M. and Van Wassenbergh, S. (2014). Functional anatomy and kinematics of the oral jaw system during terrestrial feeding in *Periophthalmus barbarus*. *J. Morphol.* **275**, 1145-1160.
Michel, K. B., Aerts, P., Gibb, A. C. and Van Wassenbergh, S. (2015a). Functional morphology and kinematics of terrestrial feeding in the largescale foureyes (*Anableps anableps*). *J. Exp. Biol.* **218**, 2951-2960.
Michel, K. B., Heiss, E., Aerts, P. and Van Wassenbergh, S. (2015b). A fish that uses its hydrodynamic tongue to feed on land. *Proc. R. Soc. B.* **282**, 20150057.
Michel, K. B., Aerts, P. and Van Wassenbergh, S. (2016). Environment-dependent prey capture in the Atlantic mudskipper (*Periophthalmus barbarus*). *Biol. Open* **5**, 1735-1742.
Miller, B. T. and Larsen, J. H. Jr. (1989). Feeding performance in aquatic postmetamorphic newts (Urodela: Salamandridae): are bidirectional flow systems necessarily inefficient? *Can. J. Zool.* **67**, 2414-2421.
Miller, B. T. and Larsen, J. H. (1990). Comparative kinematics of terrestrial prey capture in salamanders and newts (Amphibia:Urodela:Salamandridae). *J. Exp. Zool.* **256**, 135-153.
Montuelle, S. J., Herrel, A., Libourel, P.-A., Reveret, L. and Bels, V. L. (2009). Locomotor–feeding coupling during prey capture in a lizard (*Gerrhosaurus major*): effects of prehension mode. *J. Exp. Biol.* **212**, 768-777.
Moon, B. R. (2000). The mechanics of swallowing and the muscular control of diverse behaviours in gopher snakes. *J. Exp. Biol.* **203**, 2589-2601.
Muller, M. (1987). Optimization principles applied to the mechanism of neurocranium levation and mouth bottom depression in bony fishes (Halecostomi). *J. Theor. Biol.* **126**, 343-368.
Muller, M. (1989). A quantitative theory of expected volume changes of the mouth during feeding in teleost fishes. *J. Zool. Lond.* **217**, 639-662.
Natchev, N., Heiss, E., Lemell, P., Stratev, D. and Weisgram, J. (2009). Analysis of prey capture and food transport kinematics in two Asian box turtles, *Cuora amboinensis* and *Cuora flavomarginata* (Chelonia, Geoemydidae), with emphasis on terrestrial feeding patterns. *Zoology* **112**, 113-127.
Natchev, N., Tzankov, N., Werneburg, I. and Heiss, E. (2015). Feeding behaviour in a 'basal' tortoise provides insights on the transitional feeding mode at the dawn of modern land turtle evolution. *PeerJ* **3**, e1172.
Neenan, J. M., Ruta, M., Clack, J. A. and Rayfield, E. J. (2014). Feeding biomechanics in *Acanthostega* and across the fish–tetrapod transition. *Proc. R. Soc. B.* **281**, 20132689.
Niedźwiedzki, G., Szrek, P., Narkiewicz, K., Narkiewicz, M. and Ahlberg, P. E. (2010). Tetrapod trackways from the early Middle Devonian period of Poland. *Nature* **463**, 43-48.
Nishikawa, K. (2000). Feeding in frogs. In *Feeding: Form, Function and Evolution in Tetrapod Vertebrates* (ed. K. Schwenk), pp. 117-147. San Diego, CA: Academic Press.
Nishikawa, K. C. and Gans, C. (1996). Mechanisms of tongue protraction and narial closure in the marine toad *Bufo marinus*. *J. Exp. Biol.* **199**, 2511-2529.
Nishikawa, K. C. and Roth, G. (1991). The mechanism of tongue protraction during prey capture in the frog *Discoglossus pictus*. *J. Exp. Biol.* **159**, 217-234.
O'Reilly, J. C. (2000). Feeding in caecilians. In *Feeding: Form, Function and Evolution in Tetrapod Vertebrates* (ed. K. Schwenk), pp. 149-166. San Diego, CA: Academic Press.
Opolka, A., Wistuba, J. and Clemen, G. (2001). The secondary tongue of *Salamandra salamandra*: histochemical and ultrastructural aspects of the developing lingual epithelium. *Ann. Anat.* **183**, 25-36.
Osse, J. W. M. (1985). Jaw protrusion, an optimization of the feeding apparatus of teleosts? *Acta Biotheor.* **34**, 219-232.
Özeti, N. and Wake, D. B. (1969). The morphology and evolution of the tongue and associated structures in salamanders and newts (family Salamandridae). *Copeia* **1969**, 91-123.
Peddemors, V. and Thompson, G. (1994). Beaching behaviour during shallow water feeding by humpback. *Aquat. Mamm.* **20**, 65-67.
Pierce, S. E., Clack, J. A. and Hutchinson, J. R. (2012). Three-dimensional limb joint mobility in the early tetrapod *Ichthyostega*. *Nature* **486**, 523.
Porro, L. B., Rayfield, E. J. and Clack, J. A. (2015). Descriptive anatomy and three-dimensional reconstruction of the skull of the early tetrapod *Acanthostega gunnari* Jarvik, 1952. *PloS ONE* **10**, e0118882.
Putterill, J. and Soley, J. (2004). General morphology of the oral cavity of the Nile crocodile, *Crocodylus niloticus* (Laurenti, 1768). II. The tongue. *Onderstepoort J. Vet. Res.* **71**, 263-277.
Regal, P. J. and Gans, C. (1976). Functional aspects of the evolution of frog tongues. *Evolution* **30**, 718-734.
Reilly, S. M. (1987). Ontogeny of the hyobranchial apparatus in the salamanders *Ambystoma talpoideum* (Ambystomatidae) and *Notophthalmus viridescens* (salamandridae): the ecological morphology of two neotenic strategies. *J. Morphol.* **191**, 205-214.
Reilly, S. M. and Lauder, G. V. (1988). Atavisms and the homology of hyobranchial elements in lower vertebrates. *J. Morphol.* **195**, 237-245.
Reilly, S. M. and Lauder, G. V. (1989). Kinetics of tongue projection in *Ambystoma tigrinum*: quantitative kinematics, muscle function, and evolutionary hypotheses. *J. Morphol.* **199**, 223-243.
Reilly, S. M. and Lauder, G. V. (1992). Morphology, behavior, and evolution: comparative kinematics of aquatic feeding in salamanders. *Brain Behav. Evolut.* **40**, 182-196.
Romer, A. S. (1958). Tetrapod limbs and early tetrapod life. *Evolution* **12**, 365-369.
Rupp, M. F. and Hulsey, C. D. (2014). Influence of substrate orientation on feeding kinematics and performance of algae-grazing Lake Malawi cichlid fishes. *J. Exp. Biol.* **2017**, 3057-3066.
Sargeant, B. L., Mann, J., Berggren, P. and Krützen, M. (2005). Specialization and development of beach hunting, a rare foraging behavior, by wild bottlenose dolphins (*Tursiops* sp.). *Can. J. Zool.* **83**, 1400-1410.
Schoch, R. R. (2009). Evolution of life cycles in early amphibians. *Annu. Rev. Earth Planet. Sci.* **37**, 135-162.
Schoch, R. R. (2014). *Amphibian Evolution: The Life of Early Land Vertebrates*. John Wiley & Sons.
Schoch, R. R. and Witzmann, F. (2011). Bystrow's Paradox–gills, fossils, and the fish-to-tetrapod transition. *Acta Zool.* **92**, 251-265.
Schwenk, K. (2000a). An introduction to tetrapod feeding. In *Feeding: Form, Function and Evolution in Tetrapod Vertebrates* (ed. K. Schwenk), pp. 21-61. London: Academic Press.
Schwenk, K. (2000b). Feeding in lepidosaurs. In *Feeding: Form, Function and Evolution in Tetrapod Vertebrates* (ed. K. Schwenk), pp. 175-291. London: Academic.
Schwenk, K. and Rubega, M. (2005). Diversity of vertebrate feeding systems. In *Physiological and Ecological Adaptations to Feeding in Vertebrates* (ed. J. M. Starck and T. Wang), pp. 1-41. Enfield, NH: Science Publishers.
Shaffer, H. B., Austin, C. C. and Huey, R. B. (1991). The consequences of metamorphosis on salamander (*Ambystoma*) locomotor performance. *Physiol. Zool.* **64**, 212-231.
Shubin, N., Tabin, C. and Carroll, S. (1997). Fossils, genes and the evolution of animal limbs. *Nature* **388**, 639-648.
Shubin, N., Daeschler, E. B. and Jenkins, F. A. Jr (2015). Origin of the tetrapod neck and shoulder. In *Great Transformations in Vertebrate Evolution* (ed. K. P. Dial, N. Shubin and E. L. Brainerd), pp. 63-76. Chicago, IL: The University of Chicago Press.
Smith, K. K. (1982). An electromyographic study of the function of the jaw adducting muscles in *Varanus exanthematicus* (Varanidae). *J. Morphol.* **173**, 137-158.
Smith, K. K. (1984). The use of the tongue and hyoid apparatus during feeding in lizards (*Ctenosaura similis* and *Tupinambis nigropunctatus*). *J. Zool. Lond.* **202**, 115-143.
Smith, K. K. (1986). Morphology and function of the tongue and hyoid apparatus in *Varanus* (Varanidae, Lacertilia). *J. Morphol.* **187**, 261-287.
Smith, K. K. (1992). The evolution of the mammalian pharynx. *Zool. J. Linn. Soc.* **104**, 313-349.
Sponder, D. L. and Lauder, G. V. (1981). Terrestrial feeding in the mudskipper *Periophthalmus* (Pisces: Teleostei): a cineradiographic analysis. *J. Zool.* **193**, 517-530.

Staab, K. L., Holzman, R., Hernandez, L. P. and Wainwright, P. (2012). Independently evolved upper jaw protrusion mechanisms show convergent hydrodynamic function in teleost fishes. *J. Exp. Biol.* **215**, 1456-1463.
Standen, E. M., Du, T. Y. and Larsson, H. C. E. (2014). Developmental plasticity and the origin of tetrapods. *Nature* **513**, 54-58.
Stayton, C. T. (2011). Terrestrial feeding in aquatic turtles: environment-dependent feeding behavior modulation and the evolution of terrestrial feeding in Emydidae. *J. Exp. Biol.* **214**, 4083-4091.
Stebbins, R. C. and Kalk, M. (1961). Observations on the natural history of the mudskipper *Periphthalmus sobrinus*. *Copeia* **1961**, 18-27.
Stinson, C. M. and Deban, S. M. (2017). Functional trade-offs in the aquatic feeding performance of salamanders. *Zoology* **125**, 69-78.
Summers, A. P., Darouian, K. F., Richmond, A. M. and Brainerd, E. L. (1998). Kinematics of aquatic and terrestrial prey capture in *Terrapene carolina*, with implications for the evolution of feeding in cryptodire turtles. *J. Exp. Zool.* **281**, 280-287.
Taylor, C. R., Heglund, N. C. and Maloiy, G. M. (1982). Energetics and mechanics of terrestrial locomotion. 1. Metabolic energy consumption as a function of speed and body size in birds and mammals. *J. Exp. Biol.* **97**, 1-21.
Thys, T. (1997). Spatial variation in epaxial muscle activity during prey strike in largemouth bass (*Micropterus salmoides*). *J. Exp. Biol.* **200**, 3021-3031.
Tomlinson, C. (2000). Feeding in paleognathous birds. In *Feeding: Form, Function, and Evolution in Tetrapod Vertebrates* (ed. K. Schwenk), pp. 359-394. San Diego, CA: Academic Press.
van Dobben, W. H. (1935). Über den Kiefermechanismus der Knochenfische. *Arch. Neerl. Zool.* **2**, 1-72.
van Leeuwen, J. L., De Groot, J. H. and Kier, W. M. (2000). Evolutionary mechanisms of protrusible tentacles and tongues. *Neth. J. Zool.* **50**, 113-139.
Van Wassenbergh, S. (2013). Kinematics of terrestrial capture of prey by the eel-catfish *Channallabes apus*. *Integr. Comp. Biol.* **53**, 258-268.
Van Wassenbergh, S. and Aerts, P. (2009). Aquatic suction feeding dynamics: insights from computational modelling. *J. R. Soc. Interface.* **6**, 149-158.
Van Wassenbergh, S. and Heiss, E. (2016). Phenotypic flexibility of gape anatomy fine-tunes the aquatic prey-capture system of newts. *Sci. Rep.* **6**, 29277.
Van Wassenbergh, S., Herrel, A., Adriaens, D., Huysentruyt, F., Devaere, S. and Aerts, P. (2006). Evolution: a catfish that can strike its prey on land. *Nature* **440**, 881.
Van Wassenbergh, S., Lieben, T., Herrel, A., Huysentruyt, F., Geerinckx, T., Adriaens, D. and Aerts, P. (2009a). Kinematics of benthic suction feeding in Callichthyidae and Mochokidae, with functional implications for the evolution of food scraping in catfishes. *J. Exp. Biol.* **212**, 116-125.
Van Wassenbergh, S., Brecko, J., Aerts, P., Stouten, I., Vanheusden, G., Camps, A., Van Damme, R. and Herrel, A. (2009b). Hydrodynamic constraints on prey-capture performance in forward-striking snakes. *J. R. Soc. Interface* **7**, 773-785.
Van Wassenbergh, S., Leysen, H., Adriaens, D. and Aerts, P. (2013). Mechanics of snout expansion in suction-feeding seahorses: musculoskeletal force transmission. *J. Exp. Biol.* **216**, 407-417.
Van Wassenbergh, S., Day, S. W., Hernández, L. P., Higham, T. E. and Skorczewski, T. (2015). Suction power output and the inertial cost of rotating the neurocranium to generate suction in fish. *J. Theor. Biol.* **372**, 159-167.
Van Wassenbergh, S., Bonte, C. and Michel, K. B. (2017). Terrestrial capture of prey by the reedfish, a model species for stem tetrapods. *Ecol. Evol.* **7**, 3856-3860.
Vorobyeva, E. and Schultze, H.-P. (1991). Description and systematics of panderichthyid fishes with comments on their relationship to tetrapods. In *Origins of the Higher Groups of Tetrapods* (ed. H.-P. Schultze and L. Trueb), pp. 68-109. Ithaca, NY: Comstock.
Wainwright, P. C. (1989). Functional morphology of the pharyngeal jaw apparatus in perciform fishes: an experimental analysis of the Haemulidae. *J. Morphol.* **200**, 231-245.
Wainwright, P. C. and Day, S. W. (2007). The forces exerted by aquatic suction feeders on their prey. *J. R. Soc. Interface* **4**, 553-560.
Wake, D. B. and Deban, S. M. (2000). Terrestrial feeding in salamanders. In *Feeding: Form, Function and Evolution in Tetrapod Vertebrates* (ed. K. Schwenk), pp. 95-116. San Diego, CA: Academic Press.
Werth, A. (2000). Feeding in marine mammals. In *Feeding: Form, Function and Evolution in Tetrapod Vertebrates* (ed. K. Schwenk), pp. 475-514. San Diego, CA: Academic Press.
Witzmann, F. (2013). Phylogenetic patterns of character evolution in the hyobranchial apparatus of early tetrapods. *Earth. Env. Sci. Trans. R. Soc. Edinb.* **104**, 145-167.
Wochesländer, R., Helge, H. and Weisgram, J. (1999). Feeding mechanism of *Testudo hermanni boettgeri* (Chelonia, Cryptodira). *Neth. J. Zool.* **49**, 1-13.
Wochesländer, R., Gumpenberger, M. and Weisgram, J. (2000). Intraoral food transport in *Testudo hermanni* (Chelonia, Cryptodira) – a radiographic video analysis. *Neth. J. Zool.* **50**, 445-454.
Wright, P. A. and Turko, A. J. (2016). Amphibious fishes: evolution and phenotypic plasticity. *J. Exp. Biol.* **219**, 2245-2259.
Zweers, G. A., Berkhoudt, H. and Van den Berge, J. C. (1994). Behavioral mechanisms of avian feeding. In *Advances in Comparative and Environmental Physiology* (ed. V. L. Bels, M. Chardon and P. Vandewalle), pp. 241-279. Berlin: Springer-Verlag.