Chapter 12
Feeding in Amphibians: Evolutionary Transformations and Phenotypic Diversity as Drivers of Feeding System Diversity

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Abstract Amphibians are different from most other tetrapods because they have a biphasic life cycle, with larval forms showing a dramatically different cranial anatomy and feeding strategy compared to adults. Amphibians with their exceptional diversity in habitats, lifestyles and reproductive modes are also excellent models for studying the evolutionary divergence in feeding systems. In the present chapter, we review the literature on amphibian feeding anatomy and function published since 2000. We also present some novel unpublished data on caecilian feeding biomechanics. This review shows that over the past two decades important new insights in our understanding of amphibian feeding anatomy and function have been made possible, thanks to a better understanding of the phylogenetic relationships between taxa, analyses of development and the use of biomechanical modelling. In terms of functional analyses, important advances involve the temperature-dependent nature of tongue projection mechanisms and the plasticity exhibited by animals when switch-

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ing environments (land to water) during their lifetime. Understanding the relationships between cranial and hyobranchial diversity and feeding function, and how these relationships are dependent on lifestyle, habitat use or reproductive mode are questions that remain to be answered. Given the availability of massive online databases with μCT data and robust comprehensive phylogenies, these analyses are becoming possible. Unfortunately, quantitative studies on muscular anatomy, essential to link variation in form to variation in function using modelling approaches, have lagged behind. Future studies quantifying feeding across a wide range of species will provide critical insights into the selective pressures underlying the evolution of the staggering diversity in feeding form and function of amphibians.

12.1 Introduction

Amphibians stand out from most other tetrapods as the majority of species have a biphasic life cycle with larval forms showing a dramatically different cranial anatomy and often different feeding behaviour compared to adults (O'Reilly et al. 2002). Excellent descriptions of the anatomy and function of the feeding system can be found in the Schwenk (2000) book and other work (Deban and Wake 2000; Nishikawa 2000; O'Reilly 2000; Wake and Deban 2000). In the present chapter, we review the literature on amphibian feeding anatomy and function published since then and introduce some novel unpublished data on caecilian feeding biomechanics.

Over the past two decades, important new insights in our understanding of the feeding anatomy and function in amphibians have been made possible by a better understanding of the phylogenetic relationships between taxa (e.g. Roelants and Bossuyt 2005; Roelants et al. 2007; Pyron and Wiens 2011; Wilkinson et al. 2011; Van Bocxlaer et al. 2006), analyses of development (e.g. Ericsson and Olsson 2004; Müller et al. 2005; Kleinteich et al. 2014; Schoch 2014; Fabrezi et al. 2016) and the use of biomechanical modelling (e.g. Kleinteich et al. 2008a, b; Heiss et al. 2013a, b; Van Wassenbergh and Heiss 2016; Konietzko-Meier et al. 2018). In terms of functional analyses, advances also involve investigations into the temperature-dependent nature of tongue projection mechanisms (e.g. Deban and Scales 2016; Scales et al. 2016; Deban and Bloom 2018) and the plasticity exhibited by animals switching environments (land to water) during their lifetime (e.g. Heiss et al. 2013a, b; Heiss and De Vylder 2016; Heiss et al. 2016).

The two decades since the publication of the Schwenk (2000) book have seen the controversy surrounding the relationships between the major lineages of amphibians largely resolved, thanks to analyses of complete mitochondrial genomes. These analyses group salamanders and frogs as sister taxa on the phylogeny with high bootstrap values and support the monophyly of the extant Amphibia (Zardoya and Meyer 2001; but see Carroll 2007 for an alternative view of amphibian relationships). This grouping is further supported by analyses of the anatomy of the inner ear (Maddin and Anderson 2012). Moreover, recent phylogenetic analyses have generated calibrated and well-resolved trees showing several episodes of accelerated amphibian evolution. For example, diversification accelerated after the Permian mass extinction and in the late Cretaceous (Roelants et al. 2007). The better understanding of the phylogenetic relationships among amphibian groups has subsequently allowed analyses of global patterns of amphibian phyletic diversity showing that islands often have poor phylogenetic diversity despite high species richness (e.g. Fritz and Rahbek 2012).

Advances in developmental biology show that extant and extinct amphibians share many features in the timing and spatial patterning of dermal skull bones (Schoch 2014). Whereas salamanders appear to have simplified skulls, skull bones of salamanders and frogs are likely derived from the cranial elements of temnospondyls, the ancestors of living amphibians, by truncation of the developmental trajectories (Schoch 2014). This was suggested to be the result of differences in the arrangement of the jaw adductors early on in development driving the resulting simplification in cranial elements in extant amphibians relative to their temnospondyl ancestors (Schoch 2014). Furthermore, detailed descriptions of the jaw adductors in larval anurans have demonstrated that the relative position of the mandibular ramus of the trigeminal nerve is more variable than previously thought, resulting in confusion surrounding the homology of the muscles in the three extant groups of amphibians (Haas 2001).

Despite earlier suggestions of stereotypy in feeding behaviour in amphibians, a comparative study on the evolution of motor control has elegantly demonstrated that stereotypy in amphibian feeding behaviour is the exception rather than the rule (Deban et al. 2001). By comparing feeding motor control across extant taxa, it has been suggested that the ancestral lissamphibian was likely capable of some modulation of feeding movements (Deban et al. 2001). This idea is supported by a recent biomechanical modelling study aiming to elucidate the feeding strategies of temnospondyl representatives like *Metoposaurus*. The study suggests that this animal was aquatic, yet exhibited a generalist feeding strategy using mostly, but not exclusively, bilateral biting behaviour (Konietzko-Meier et al. 2018). Feeding in extant amphibians is further characterised by an increased modulation of feeding movements using either feedforward or feedback mechanisms going hand in hand with a decrease in variation due to the need for precise coordination between different body parts (Deban et al. 2001).

In the following sections, we will review the major advances in our understanding of the anatomy and function of the feeding system in the three extant groups of amphibians.

12.2 Caecilians

The last two decades have been exciting times for researchers interested in caecilian biology. Caecilians are a relatively small group of amphibians with roughly 200 described species, most of which are head-first burrowers. This unusual lifestyle imposes severe constraints on the anatomy and function of the cranial system of these animals (Wake 1993; O'Reilly 2000). As maximal head diameter is related to the cost of burrowing, the laterally positioned jaw muscles are reduced and have

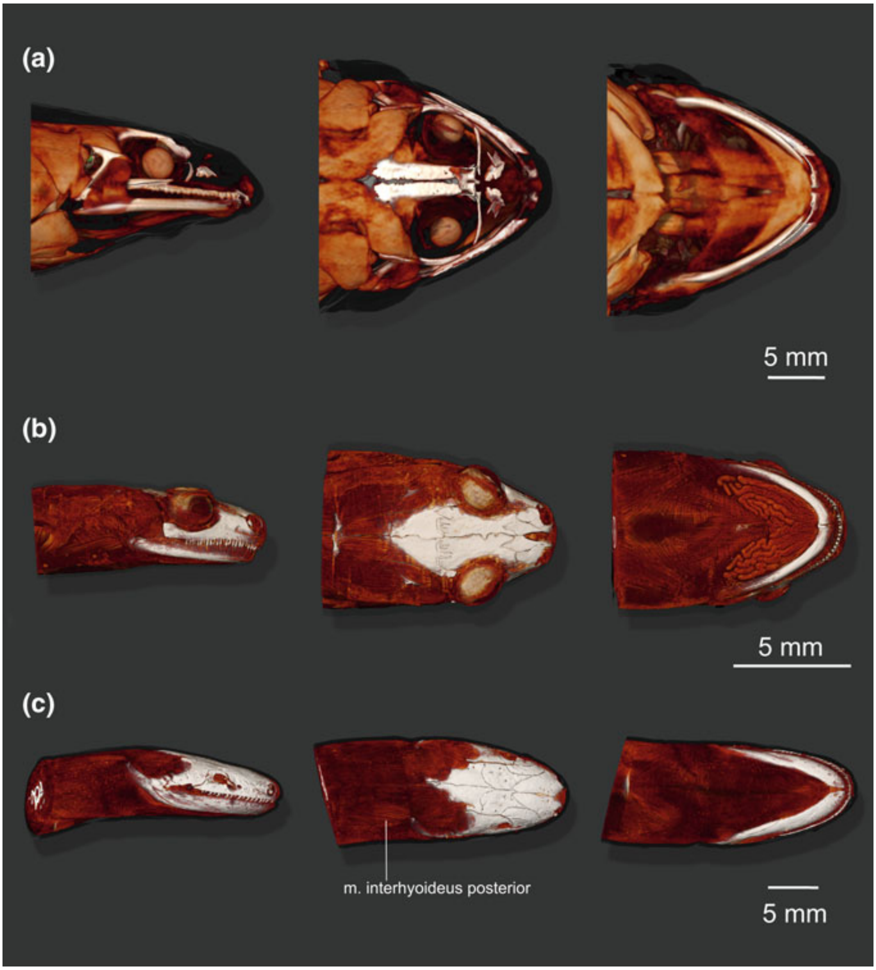


Fig. 12.1 Synchrotron imaging of the head muscles in **a** *Pelophylax esculenta*, **b** *Desmognathus fuscus*, **c** *Ichthyophis bannanicus* illustrating the radically different organisations of the jaw muscles in these clades. Indicated is the m. interhyoideus posterior in the caecilian

been supplemented by the interhyoideus posterior attaching to the ventral side of the retroarticular process to play an important role in jaw closing (Bemis et al. 1983; Nussbaum 1983; Fig. 12.1). The few data available on the diet of caecilians suggest that they are opportunistic foragers on soil invertebrates (Delêtre and Measey 2004; Gaborieau and Measey 2004; Measey et al. 2004; Kupfer et al. 2005) and occasionally eat larger scolecophidian snakes and lizards (Moll and Smith 1967; Presswell et al. 2002). The phylogenetic relationships of caecilians were revisited over the past two decades using both molecular (e.g. Roelants et al. 2007; San Mauro et al. 2014) and anatomical (Maddin 2011; Maddin et al. 2012a, b) approaches, resulting in a robust phylogenetic framework of caecilian evolution and a revised classification of the different families (Wilkinson et al. 2011). Additionally, an entirely new family of caecilians from Northeast India, closely related to the African Herpelidae, was discovered, enriching the diversity of this enigmatic group of amphibians (Kamei et al. 2012; Fig. 12.2). This robust phylogenetic framework has allowed researchers to demonstrate that free-living larvae re-evolved in the ancestral Seychelles caecilian (San Mauro et al. 2014). Descriptions of larval skin feeding in several taxa (Kupfer et al. 2006; Wilkinson et al. 2013) have further demonstrated that skin feeding is a likely precursor of viviparity that arose at the base of the Teresomata (San Mauro et al. 2014). The advent of microtomography in the past two decades (e.g. Kleinteich et al. 2008a, b) has further allowed detailed descriptions of the cranial anatomy (Sheratt et al. 2014), the braincase (Maddin 2011; Maddin et al. 2012a, b) and the inner ear (Maddin and Sherratt 2014) of caecilians. Although the fossil record of caecilians is scant, a re-description of the braincase of *Eocaecilia micropodia* confirmed its placement on the stem of caecilians, allowing for a better understanding of the evolution of this highly derived group of burrowing amphibians (Maddin et al. 2012a, b).

12.2.1 Anatomy

Advances in our understanding of the cranial anatomy of caecilians have been made through the use of μCT scans. A detailed description of the inner ear of caecilians, in comparison to salamanders and frogs, using 3D geometric morphometric approaches (Maddin and Sherratt 2014) demonstrates that caecilians share the presence of highly curved semicircular canals with frogs. However, these canals appear significantly shorter suggesting a reduced reliance on vestibulo-ocular reflexes in these burrowing animals. The elaboration of the sacculus is interpreted as an adaptation to enhance the detection of substrate-borne vibrations, undoubtedly important to fossorial animals like caecilians. Analyses of μCT data of the skull using geometric morphometrics show that cranial shape contains a strong phylogenetic signal (Sheratt et al. 2014), and that this signal varies in strength across the skull (Bardua et al. 2019). High-dimensional cranial shape data have also demonstrated that allometry (the influence of size on shape) varies in strength across the skull, at both the intraspecific (Marshall et al. 2019) and evolutionary (Bardua et al. 2019) level. However, some features of

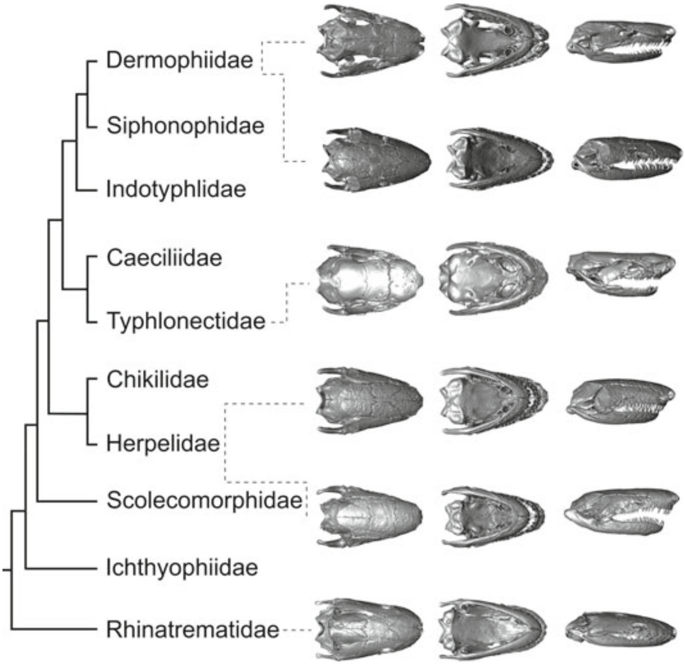


Fig. 12.2 Phylogenetic relationships among caecilian families. Modified after Kamei and coworkers (2012). Illustrated to the right of the phylogeny are the skulls of *G. seraphini*, *S. thomense* (Dermophiidae), *T. compressicauda* (Typhlonectidae), *H. squalostoma*, *B. taitanus* (Herpelidae) and *R. bivittatum* (Rhinatrematidae) in dorsal, ventral and lateral view

the skull show convergence and are likely adaptations to head-first digging. These include cranial fenestration, the covering of the eyes by bone, and the positioning of the mouth. Yet, surprisingly, these traits have evolved in a mosaic fashion rather than in concert. Unexpectedly, biomechanical analyses of skull performance during burrowing suggest no functional advantage of having a closed skull compared to the open zygokrotaphic skull type (Kleinteich et al. 2012), suggesting that the evolution of skull fenestration remains poorly understood.

In addition to studies focusing on the adult cranial morphology, several studies focus on the description of larval traits and the development of the skull and hyobranchial apparatus (Müller et al. 2005; Kleinteich and Haas 2007, 2011). In caecilians, oviparous species with biphasic life cycles possess free-living semiaquatic larvae that undergo metamorphosis. Interestingly, most cranial muscles in the larval *Ichthyophis kohtaoensis* are also present in the adult form, different from the marked changes that take place in anurans and some salamanders (Kleinteich and Haas 2007). Based on these developmental studies, the m. pterygoideus and the m. levator quadrati are unique to caecilians (Kleinteich and Haas 2007). Descriptions of the larval hyal and ventral branchial muscles in caecilians in comparison to salamanders further show that the 'bauplan' is similar in these taxa and likely corresponds closely to the one of the lissamphibian ancestor (Kleinteich and Haas 2011). Descriptions of cranial development in caecilians further demonstrate that among the first elements to ossify are the mentomeckelian, the dentary, the angular, the vomer and the premaxilla suggesting an early development of the caecilian jaw closing mechanism (Müller et al. 2005). However, the sequence of ossification in *Gegeneophis ramaswami* shows some differences with that described for *Dermophis mexicanus* (Wake and Hanken 1982), suggesting variability in developmental patterning across caecilians. The parasphenoid and the squamosal are the last elements to ossify. At least in *G. ramaswami* no ectopterygoid, basioccipital, supraoccipital, pleurosphenoid, postorbital, supratemporal or lacrimal are present (Müller et al. 2005). Unlike the double tooth row present in adults, larval caecilians that use skin feeding show teeth of variable morphology including unusual hooked morphologies, which are different from the typical monocuspid or bicuspid teeth in adults (Kupfer et al. 2006).

12.2.2 Function

Given the subterranean lifestyle of most caecilians, it is not surprising that only few studies have been devoted to the kinematics and function of their feeding mechanism. The few studies available have mostly focused on above-ground observations of feeding under laboratory conditions (Bemis et al. 1983; O’Reilly 2000). More recently, some effort has been devoted to describing the underground feeding behaviour of these animals in their tunnel systems using both external video and cineradiography (Measey and Herrel 2006; Herrel and Measey 2012). These studies demonstrate that lunges in caecilians can be quite fast. Moreover, although jaw opening is generally slow, jaw closing is as fast as observed in other vertebrates (Herrel and Measey 2012). Gape angles are often large, however, in contrast to what could have been expected given that these animals are feeding in underground tunnel systems that might constrain mouth opening. Moreover, gape profiles appear to be quite variable suggesting an important role for sensory feedback in adjusting the gape to instantaneous prey properties (O’Reilly 2000; Herrel and Measey 2012).

Additional observations of these animals feeding underground have demonstrated that they use rotational feeding to dismember or reduce oversized prey to within the limits of the jaws (Measey and Herrel 2006). Moreover, the forces exerted during spinning are quite large and are transferred from the body to the jaws, possibly explaining why relatively large bite forces and the dual jaw closing system involving both the jaw adductors and the interhyoideus posterior have evolved in these animals (Measey and Herrel 2006). Biomechanical modelling efforts have suggested that the efficacy of the dual jaw closing system is strongly dependent on the orientation of the quadrate and the retroarticular process. Moreover, mobility of the quadrate (streptostyly) is essential for the amplification of the force of the interhyoideus to the teeth (Summers and Wake 2005; Kleinteich et al. 2008a, b). The predicted functional advantage of this system is that relatively high bite forces can be generated over a wide range of gape angles (Kleinteich et al. 2008a, b), important for generalist feeders that use rotational feeding. The modelled bite forces of between 0.8 and 2 N (Kleinteich et al. 2008a, b) are within the range of the forces measured in vivo (0.62 N for *B. taitanus*; 1.09 N for *S. thomense*; Measey and Herrel 2006), providing experimental validation for the model. However, the model prediction that bite force should be relatively independent from gape has not been tested experimentally. Figure 12.3 presents previously unpublished data on the relationship between gape distance and bite force measured at the tip of the jaw in two species of caecilians (*D. mexicanus* and *I. cf kohtaensis*). The result suggests that both species are capable of producing relatively large forces at low gape. Whereas forces are maintained for the different gape distances tested in *Ichthyophis*, forces do appear to decline with gape in *Dermophis*. Further studies are needed to better understand how the unique jaw closing system in caecilians works, to better understand the diversity in jaw and muscle anatomy in this group, and to understand the precise function of the m. interhyoideus posterior. Preliminary results displayed in Fig. 12.4 show that the m. interhyoideus posterior is involved in many behaviours including buccal oscillation, ventilation, prey transport and burrowing. Interestingly, different parts of this large and complex muscle are recruited during different behaviours (Fig. 12.4). Moreover, whereas during buccal oscillation, ventilation, and feeding the left and right muscles are activated simultaneously, this is not the case during burrowing where a clear left––right asymmetry is present. These preliminary results illustrate the complexity of this muscle and its control and suggest that any hypotheses pertaining to the selective pressures that may have given rise to the recruitment of the interhyoideus posterior in the jaw system must incorporate the diversity of functions it fulfils.

Modelling studies focusing on larval stages from species with free-living suction feeding larvae (*I. c.f. kohtaoensis*) versus those that use skin feeding (*B. taitana*) or intrauterine feeding (*T. natans*) showed distinct differences between species. The species with suction feeding larvae showed strong differences in the mechanics of jaw closing between larval and adult stages (Kleinteich 2010), with the jaw system optimised to generate force at low gape angles. The other species show a muscular organisation and lever arms similar to adults (Kleinteich 2010), possibly due to the similar mechanical constraints associated with feeding at large gape angles in larval or neonate stages of these species.

12.3 Frogs

The nearly 7000 species of frogs make up the most species-rich group of amphibians, composing over 85% of the diversity of extant amphibians. Their origin dates back to at least the early Triassic, 55 million years before their first appearance in the fossil record, as estimated by relaxed molecular clock approaches (Roelants and Bossuyt 2005). Our understanding of the relationships between species of anurans has changed dramatically, thanks to new and comprehensive molecular phylogenies (e.g. San Mauro et al. 2005; Roelants and Bossuyt 2005; Frost et al. 2006; Van Bocxlaer et al. 2006; Roelants et al. 2007; Pyron and Wiens 2011; Fig. 12.5). This

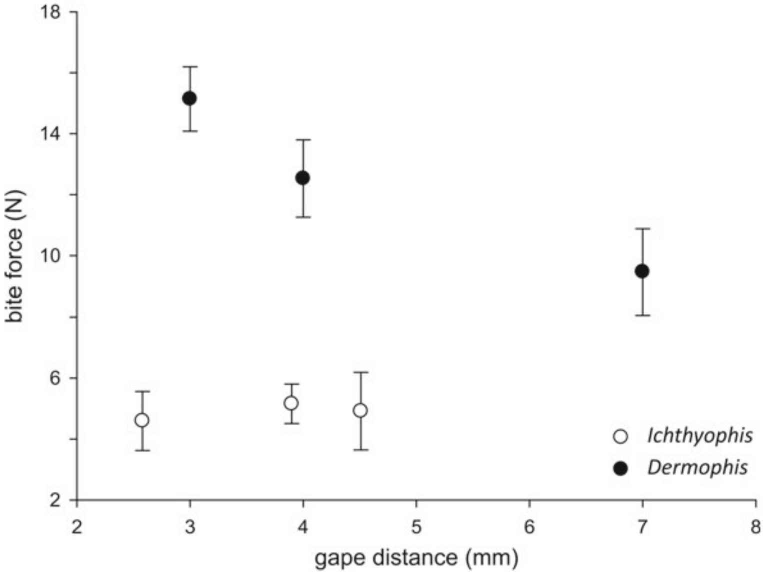
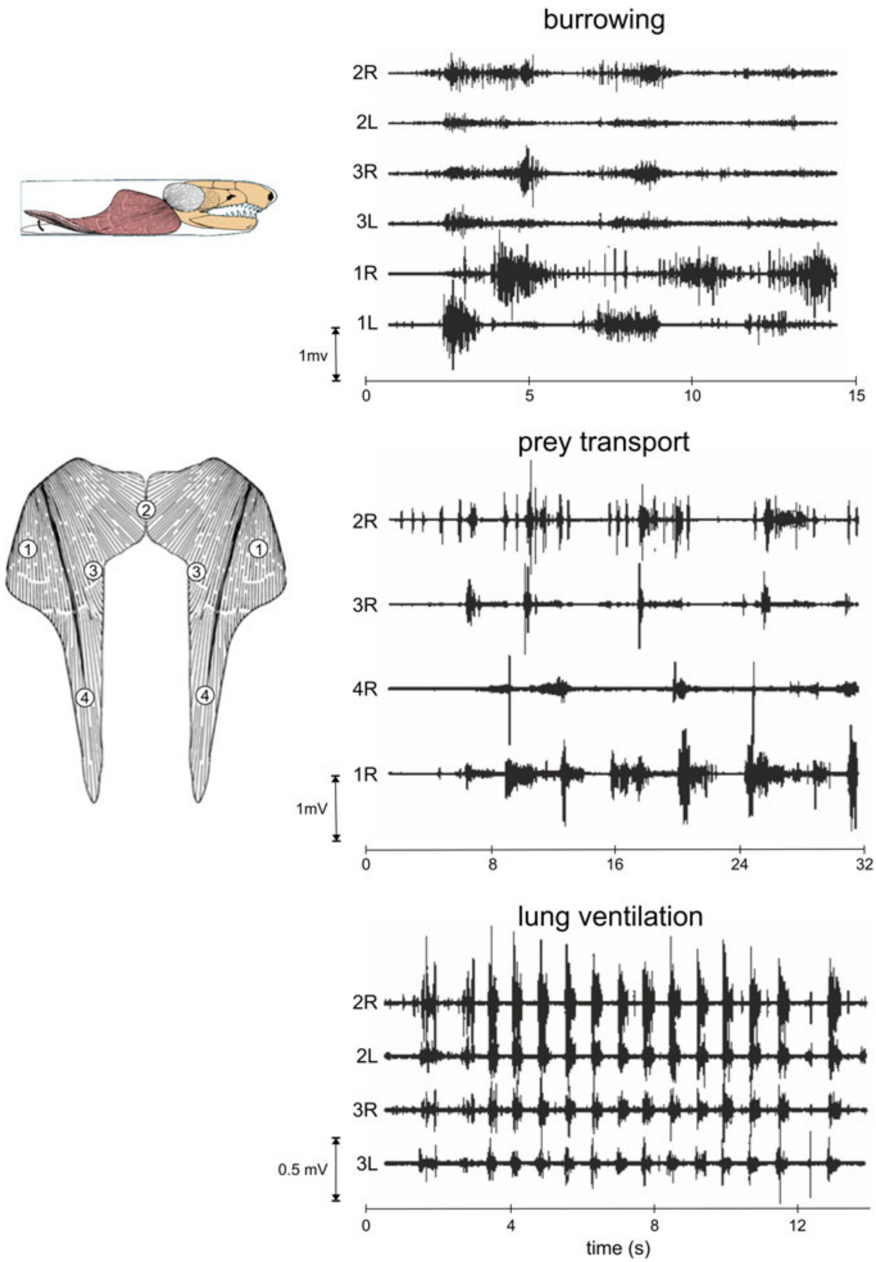


Fig. 12.3 Graph illustrating the relationships between gape distance and bite force in two species of caecilians. Note that whereas *Ichthypohis* (open circles) is capable of maintaining force over a range of gape angles, *Dermophis* (filled circles) shows a clear decrease in force with increasing gape. Symbols indicate means ± standard deviations

has resulted in a complete overturning of the traditional taxonomy and nomenclature of frogs over the past two decades (Frost et al. 2006). Importantly, these new phylogenies have allowed comprehensive analyses of convergence in morphology in some clades, such as ranid frogs (Bossuyt and Milinkovitch 2000), whilst demonstrating strong phylogenetic conservatism in skull shape in other clades, such as myobatrachids (Vidal-Garcia and Keogh 2017), and moderate phylogenetic signal across extant and extinct anurans (Bardua et al. 2018). Frogs are unique, even among amphibians, in that their larval stages are dramatically different from the adult stage. Thus, understanding the larval anatomy and function and how this impacts adult anatomy and function has been a major line of inquiry in this group (O'Reilly et al. 2002; Roelants et al. 2011; Ponssa and Vera Candioti 2012; Fabrezi et al. 2016).

12.3.1 Anatomy

Previous studies have provided excellent descriptions of the adult jaw musculature in anurans (see Nishikawa 2000 for a review). Recent important advances include the detailed description of the head anatomy of *Barbourula busuangensis* (Roček et al. 2016), a basal frog closely related to *Bombina* from which it diverged in the Paleogene (Blackburn et al. 2010). This frog possesses a basicranial articulation similar to that


burrowing
2R
2L
3R
3L
1R
1L
1mv
0
5
10
15
1
2
3
4
prey transport
2R
3R
4R
1R
1mV
0
8
16
24
32
lung ventilation
2R
2L
3R
3L
0.5 mV
0
4
8
12
time (s)

◀**Fig. 12.4** Figure illustrating the activation patterns of the different parts of the interhyoideus posterior muscle during different behaviours. Top left represents a schematic illustration on the position of the interhyoideus muscle in Caeciliidae (modified after Nussbaum 1983). Middle left indicates the positions along the muscle where patch electrodes were implanted. Top right shows the activation patterns of the different muscle parts during burrowing. Note the distinctly alternated activation patterns of especially the lateral part of the interhyoideus posterior. Just below are illustrated the activation patterns during intraoral transport. Note how different parts of the muscle are activated at different points in time. To the bottom right are illustrated the activation patterns of the muscle during lung ventilation. Note the distinctly synchronous activation of the different muscle parts

of temnospondyls and shows exceptionally strongly developed jaw adductors that cover the complete dorsal side of the skull (Roček et al. 2016), suggestive of strong bite forces. This has also been suggested for the recently re-discovered Hula painted frog, *Latonia nigriventer*, based on its reinforced skull and increased adductor muscle insertion surface (Biton et al. 2013, 2016). However, except for one study that has reported bite forces for the horned frog (*Ceratophrys cranwelli*; Lappin et al. 2017), little is known about the variation in bite force in frogs and its possible relation to anatomy and diet. Despite the attention that has been devoted to adult cranial anatomy, only relatively little has been published on the ontogenetic changes in cranial anatomy after metamorphosis. Yet, marked changes in skull shape take place postmetamorphosis, often coupled to changes in diet. Post-metamorphic changes in skull shape are described for five species of *Leptodactylus* (Ponssa and Vera Candioti 2012) using geometric morphometric approaches. The results of this study show that allometric changes are important, with changes in size driving most of the variation in shape (Ponssa and Vera Candioti 2012). Interestingly, the disparity analysis shows that the morphospace occupied by metamorphs was greater than that of adults (Ponssa and Vera Candioti 2012), suggesting ontogenetic canalisation of shape variance. Future studies investigating the diversity in skull morphology in adult frogs may show unexpected diversity in skull form (Fig. 12.5).

Many studies over the past two decades have focused on the cranial anatomy of tadpoles, in part due to the strong divergence in its morphology and function across groups (Haas et al. 2006, 2014; Alcalde et al. 2011; Fabrezi et al. 2016). Descriptions of the anatomy of the mandibular arch muscles in anuran tadpoles demonstrate major transformations in the anatomy of anuran larvae compared to other amphibian larvae (Haas 2001). These transformations include relocating the insertion site of the mandibular arch levators to power the movement of the larval upper jaw cartilages, splitting of ancestral muscles and the evolution of a muscle invading the lower lip of the oral disc (Haas 2001). Whereas most frogs show a rather similar arrangement of the larval muscles, filter-feeding microhylids show significant departures from this general organisation, especially the more anterior origin of the levator mandibulae muscles, a reduced size of the orbitohyoideus and an increased size of the interhyoideus (Haas 2001; Johnson et al. 2015). The changes in the orbitohyoideus and the interhyoideus have been suggested to be linked to the switch from substrate scraping using keratinized mouthparts to filter feeding on small suspended particles.

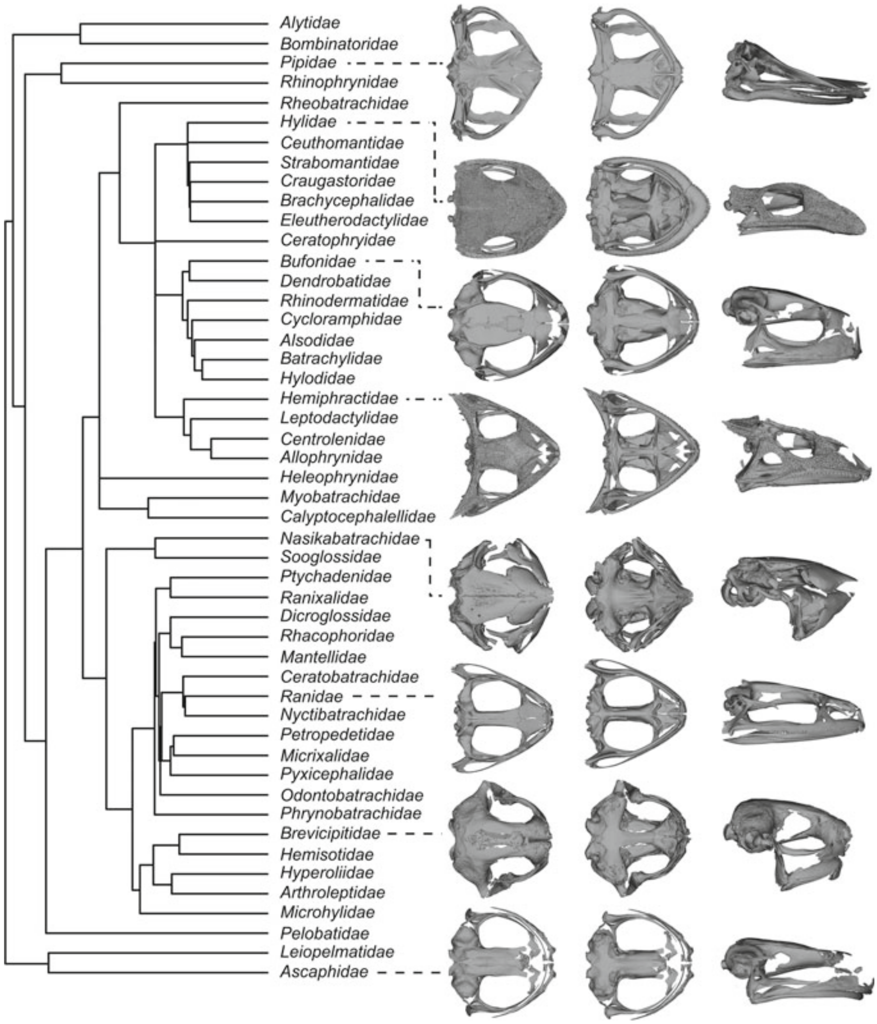


Fig. 12.5 Phylogeny of the families of frogs based on the timetree of life website (http://www.timetree.org/). Illustrated to the right are dorsal, ventral and lateral views of the skull and mandible in selected species showing the diversity in skull form across anurans. From top to bottom are illustrated the aquatic *Pipa pipa*, a hylid frog with skull ornamentation (*Tripirion petasatus*), a miniaturised bufonid (*Capensibufo sp.*), a hemiphractid frog (*Hemiphractus proboscideus*), the burrowing nasikabatrachid *Nasikabatrachus sahyadrensis*, a ranid (*Limnonectes macrocephalus*), the burrowing brevicepidid *Balebreviceps hillmani*, and the basal *Ascaphus truei*. Scans available at Morphosource (https://www.morphosource.org/)

Not only the musculature but also the anatomy of the mouthparts of tadpoles appears to be a good indicator of feeding guild as shown by a geometric morphometric study (Vera Candioti 2006). Whereas generalised tadpoles have a large ceratobranchial area, microphagous species have a well-developed and complex branchial basket and strongly reduced hypobranchial plates (Vera Candioti et al. 2004; Vera Candioti 2006). Macrophagous tadpoles, in contrast, have well-developed ceratohyals, a well-developed hypobranchial plate and a reduced branchial basket (Vera Candioti et al. 2004; Vera Candioti 2005, 2006; Haas et al. 2014). The latter feeding mode has evolved convergently several times in distantly related clades and shows morphological similarities associated with the unique functional demands imposed by the ingestion of large prey (Haas et al. 2014). Finally, megalophagous (i.e. those that eat very large prey) species like *Lepidobatrachus* are characterised by laterally expanded ceratobranchials (Vera Candioti 2006). Interestingly, these frogs also stand out because both larvae and adults capture large prey under water. The exaggerated adult traits including the posterior displaced jaw articulation are uniquely present in the tadpoles of this species (Fabrezi et al. 2016).

12.3.2 Function

Despite the many recent studies on tadpole anatomy, experimental observation of feeding in tadpoles remains scant. Suction feeding has been described in the tadpole of the pipid *Hymenochirus boettgeri* showing that they use visual cues to target and follow prey and then capture it using an explosive buccal expansion powered by hyobranchial movements including a depression of the ceratohyal and a retraction of the basibranchial, coupled to cranial elevation and lower jaw depression (Deban and Olson 2002). Interestingly, the depression of the lower jaw unfurls the soft tissues surrounding the mouth creating a tubular mouth with a circular opening, maximising the flow in front of the mouth (Deban and Olson 2002). Most tadpoles do not use suction to capture elusive prey, but passively filter particles from the water column or scrape the substrate for a food item with the keratinized beak (Larson and Reilly 2003). A study using electromyography demonstrated that in addition to the three muscles used during gill irrigation (the m. hyoangularis, m. orbitohyoideus, and the anterior m. interhyoideus), the m. intermandibularis, the m. suspensorioangularis and the levator mandibulae longus are also recruited during feeding (Larson and Reilly 2003). The transition from gill irrigation to feeding involved an overall shortening of the gape cycle and a shift in the relative length of the opening relative to the closing phases (Larson and Reilly 2003). Tadpoles of the species *Xenopus laevis* are obligate suspension feeders that use buccal pumping for both gill irrigation and suspension feeding. Interestingly, during growth they switch from a flow regime dominated by viscous forces to an intermediate regime. This goes hand in hand with a reduction in the velocity of jaw and hyoid movements (Ryerson and Deban 2010). To test the role of fluid viscosity on the kinematics of feeding, the authors manipulated fluid viscosity to show that there is an increase in absolute velocities and excursions at higher viscosity without impacting the duration of movements (Ryerson and Deban 2010).

Feeding in adult frogs has been investigated in detail and is summarised by Nishikawa (2000). Although frogs can use their jaws or tongues to capture prey, the tongue is nearly always protruded from the mouth and thus plays a critical feeding role. Three main types of tongue protraction mechanisms have been identified: mechanical pulling, inertial elongation and hydrostatic elongation (Nishikawa 2000). Whereas mechanical pulling relies on the contraction of the tongue protractors to shorten the tongue, inertial elongation is made possible by transferring momentum from the lower jaw to the tongue during rapid jaw opening to elongate the tongue upon projection (Mallett et al. 2001; Im et al. 2015; see Figs. 12.6 and 12.7). Hydrostatic elongators use intrinsic tongue muscles to change the shape of the tongue, resulting in an elongation of the tongue up to 200% of its resting length (Nishikawa 2000; Meyers et al. 2004). Each strategy has advantages and drawbacks. The rapid protraction of the tongue observed during inertial elongation results in high velocities but low accuracy. In contrast, the use of a much slower hydrostatic elongation goes hand in hand with a much higher degree of precision (Nishikawa 2000; Monroy and Nishikawa 2009, 2011). Yet, some frogs are capable of switching between different capture strategies, using jaw prehension to capture large prey and tongue projection for smaller more mobile prey. The choice among these alternative strategies depends on a hierarchical decision-making process (Monroy and Nishikawa 2011) that weighs visual and motor feedback during prey capture (Corbacho et al. 2005; Monroy and Nishikawa 2011).

Recent studies have focused on the role of elastic energy storage in driving the rapid jaw opening that powers ballistic prey capture in toads and other inertial elongators (Lappin et al. 2006; Deban and Lappin 2011; Sandusky and Deban 2012). In toads, this rapid jaw opening is largely powered by a well-developed jaw opener muscle (m. depressor mandibulae), which is active up to 250 ms prior to mouth opening (Lappin et al. 2006). The peak instantaneous power during mouth opening can reach 9600 Wkg^{-1}, suggesting that elastic recoil of the muscle and the series elastic elements drive the rapid mouth opening and subsequent tongue protrusion (Lappin et al. 2006). To test this idea, Deban and Lappin (2011) recorded tongue projection at different temperatures. The results showed that the mouth opening and tongue projection velocity and acceleration were not affected by temperature, in contrast to that of other movements (tongue retraction, prey transport). However, the jaw opener muscle was activated for a significantly longer time before jaw opening at colder temperatures suggesting a slowing of its contractile rate (Deban and Lappin 2011). This study demonstrates the role of elastic energy storage in driving jaw opening and tongue projection in toads. Interestingly, whereas jaw opening was equally thermally independent in *Rana pipiens*, another inertial elongator, tongue projection velocity and acceleration did show thermal dependence, suggesting that active muscle contraction contributes to tongue projection in this species (Sandusky and Deban 2012).

The very fast coupled jaw and tongue system in toads is critically dependent on the coordination of tongue and jaw movements (Nishikawa 2000). Yet, frogs are capable of accurate tongue projection even during body displacement, suggesting that the jaw system is coupled to the vestibular system. A recent study on the neuroanatomy of

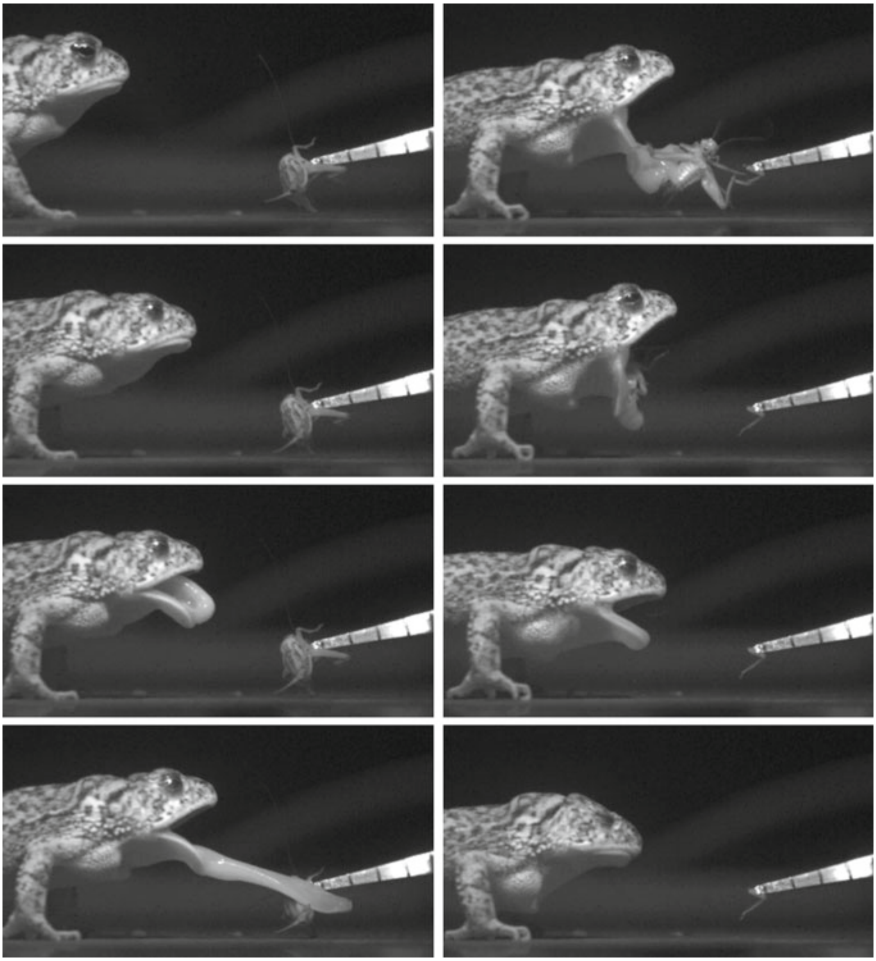


Fig. 12.6 Series of images illustrating a prey capture cycle in a *Bufo* recorded at 10 kHz. Note how the animal closes its eyes before opening its mouth. Jaw opening is extremely rapid and provides the required inertia for tongue projection and elongation. The rapid jaw opening is powered by the release of elastic energy stored in the jaw opener muscle and consequently jaw opening is temperature independent. After prey contact, the tongue is retracted and the jaw opened maximally allowing unhindered passage of the prey into the mouth. Mouth closure is much slower than mouth opening and purely muscle-powered and thus temperature-dependent

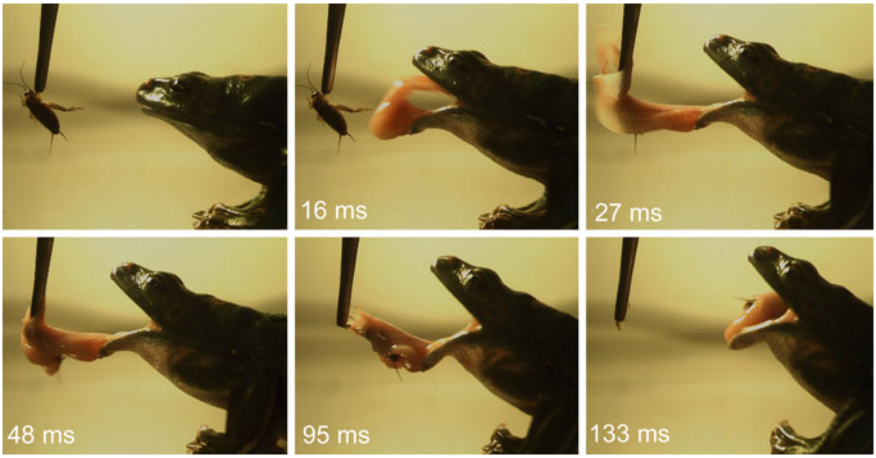


Fig. 12.7 Single frames of high-speed videosequence of predatory strike of Chinese Gliding Frog (*Rhacophorus dennysi*)

the ranid frog, *Pelophylax esculentus*, shows that in the rhombencephalon, an area of overlap is present between the incoming vestibular afferents and the trigeminal motor neurons (Birinyi et al. 2018). The identified contacts between vestibular axon terminals and trigeminal motoneurons may be the morphological substrate that allows a rapid response in the trigeminal system to affect prey capture during head movement (Birinyi et al. 2018).

One exception on the use of the tongue during prey capture in frogs is associated with the evolution of an aquatic lifestyle. Interestingly, an aquatic lifestyle and prey capture mode originated independently in several families of frogs, providing an excellent test case for understanding how the physical constraints of underwater prey capture have impacted the evolution of feeding form and function. Most aquatic animals use suction feeding to capture prey although some aquatic salamanders still use their tongues to capture prey under water (Deban and Wake 2000). Most studies have focused on pipid frogs, at least partly because of their availability in laboratories and the pet trade. Pipids are a group of highly derived aquatic frogs that all use suction feeding to capture prey under water (Dean 2003; Carreño and Nishikawa 2010; Fernandez et al. 2017). In all species of pipids examined, the internal buccopharyngeal pressure was found to drop below ambient at the onset of mouth opening (Carreño and Nishikawa 2010), suggesting that these animals effectively use suction. However, whereas some species (*H. boettgeri* and *P. merlini*; Dean 2003; Carreño and Nishikawa 2010) rely solely on inertial suction to transport prey into and through the buccal cavity, others like *P. pipa* and *X. laevis* also use their forelimbs for prey capture (Carreño and Nishikawa 2010; Anzeraey et al. 2017). Moreover, the use of the forelimbs and hands is dependent on the size and mobility of the prey and so different grasping strategies are used depending on the type and size of prey offered (Anzeraey et al. 2017). Interestingly, in *Pipa pipa* the use of suction feeding and its associated kinematics depend not only on movements of the jaw and hyoid but also on the depression of the pectoral girdle (Fernandez et al. 2017). Moreover, in this species, aquatic suction feeding is modulated to a great extent and capture success depends on the size of the prey and its distance from the frog at the onset of a lunge (Fernandez et al. 2017). Despite the many independent radiations of an aquatic lifestyle in frogs, little is known about aquatic prey capture in species other than pipids. A recent study reports prey capture behaviour in the strictly aquatic Nyctibatrachid frog *Lankanectes* (Pethiyagoda et al. 2014). These animals detect prey with tactile stimuli and scoop prey into the mouth with their hands. Although the authors suggested that no suction is used during underwater prey capture, the visible depression of the mouth floor in the images provided in the paper suggests otherwise (Pethiyagoda et al. 2014). On land, these frogs lunge at prey and also use their hands to move prey into the mouth (Pethiyagoda et al. 2014), as is documented for other frogs (Gray et al. 1997).

12.3.3 Adhesive Mechanisms

The evolution of a tongue for prey capture is considered an important innovation in terrestrial vertebrates (Iwasaki 2002). Several lineages of tetrapod have evolved sticky tongues that use adhesion to catch and pull prey into the mouth. In chameleons (Sauropsida: Squamata: Chamaeleonidae), many frogs (Lissamphibia: Anura) and some plethodontid salamanders (Lissamphibia: Caudata: Plethodontidae), the adhesive tongue can be fired ballistically at prey (Nishikawa et al. 1992; Wainwright and Bennett 1992a, b; Nishikawa and Gans 1996; Deban et al. 1997; Nishikawa 2000; de Groot and van Leeuwen 2004; Schwenk and Rubega 2005; Deban et al. 2007; Anderson and Deban 2010; Anderson et al. 2012; Fig. 12.7). While the morphology, kinematics and neuromuscular control of these highly eversible tongues have been studied in detail (Regal and Gans 1976; Gans and Gorniak 1982a, b; Nishikawa 2000; Herrel et al. 2001, 2002, 2009; Deban 2003), the actual adhesive mechanism was described only recently.

The ability to catch a diverse array of prey puts special demands on the adhesive performance of frog tongues. The attachment to the prey must be strong enough to prevent the prey from escaping before it is grasped by the jaws. The duration of the tongue in contact with the prey is short, usually in the range of 10–60 ms (Nishikawa and Roth 1991; Deban and Nishikawa 1992; Nishikawa and Gans 1996; Nishikawa 2000; Deban and Lappin 2011) (Figs. 12.6 and 12.7). Frog tongue surfaces are covered by mucus and so form a wet adhesive system (Zylberberg 1977; Iwasaki et al. 1998). Recently, adhesive forces were measured and tongue contact areas were visualised in the horned frog (*Ceratophrys sp.*; Kleinteich and Gorb 2014). These frogs are sit-and-wait predators that feed on a wide variety of different prey, including lizards, snakes, rodents, frogs, annelids, crabs, spiders and insects (Duellman and Lizana 1994). In the experiments, animals were motivated to project their tongues towards microscope glass slides that were connected to a force transducer (Fig. 12.8a–f) that

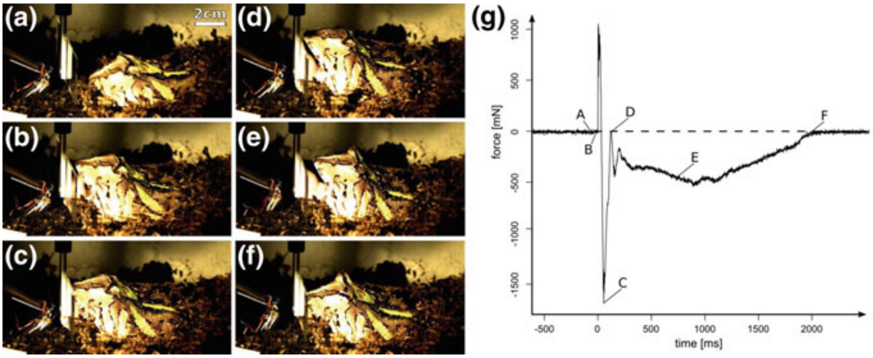


Fig. 12.8 Representative experimental trial with a horned frog (*Ceratophrys* sp.). (**a**–**f**): still frames from a high-speed video sequence (500 fps) showing how the frog adheres to and detaches its tongue from the glass slide; **g** force over time curve, highlighting the specific force values in time that refer to the still frames in (**a**–**f**). Positive force values relate to pushing forces (i.e. tongue impact); negative force values relate to pulling forces (i.e. adhesion). **a** before the impact onto the glass slide, the frog lunges towards the cricket. **b** contact initiation. The mouth of the frog is widely open and the dorsal surface of the tongue gets in contact with the glass slide. **c** the moment at which the measured adhesive force is maximal. By lunging towards the target, the frog is in close proximity to the glass slide with the tongue attached to it. **d** depending on the movements of the frog and its tongue, we observed some variation in the force after the initial peak of adhesive force. Here, the pulling force drops to almost zero, indicating that the frog is not pulling its tongue at this special moment. However, the video sequence shows that the tongue still is in full contact with the glass slide. **e** pulling phase. The frog is moving backwards and we measured pulling forces again. However, during this phase, pulling is notably weaker than at the initial peak of the adhesion curve. **f** tongue contact release. The tongue is not in contact with the glass slide anymore. From Kleinteich and Gorb (2014)

measured striking and adhesive forces (Fig. 12.8g). Additionally, the tongue prints that were left on the glass slides could be measured directly (Fig. 12.9). The experiments showed that *Ceratophrys* frogs generate adhesive forces well beyond their own body weight (Kleinteich and Gorb 2014). Previously published data on salamanders (*Bolitoglossa occidentalis*) with a body weight of 1.1–1.6 g have shown that these animals generated maximum impact forces only equivalent to 0.04 g (Thexton et al. 1977). Both the impact and adhesive force measured for *Ceratophrys* frogs were consistently in the range of the body weight of the frogs (impact up to 6.5 times the body weight; adhesion up to 3.4 times the body weight). This might be why in salamanders, tongue projection relies strongly on the tongue skeleton, which is fired out of the mouth (Lombard and Wake 1976; Deban et al. 1997), whereas in frogs that use tongue projection, the purely muscular tongue is projected out of the mouth by a rapid depression of the lower jaw (Nishikawa and Gans 1996; Nishikawa 2000).

In addition to being useful for catching elusive prey, fast tongue projection mechanisms may also have evolved in amphibians to generate a high contact pressure during the capture of heavy prey objects. A positive correlation between contact pressure and adhesive strength is found (Fig. 12.10) (Kleinteich and Gorb 2014).

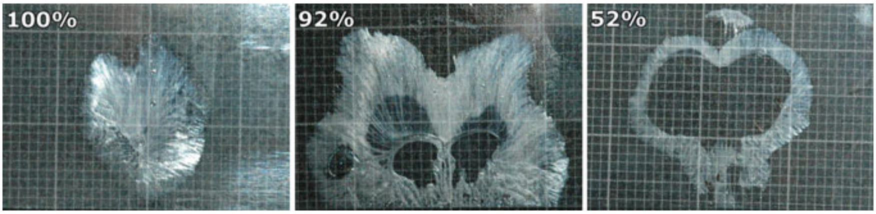


Fig. 12.9 Tongue prints of a horned frog (*Ceratophrys* sp.) on microscope glass slides; the scale paper in the background is 1 mm. The values in the upper left corner depict the relative mucus coverage of the overall contact area. A high degree of variation in the shape of frog tongue prints and relative mucus coverage was observed (ranging from 1 to 100%). From Kleintech and Gorb (2014)

This leads to the suggestion that the frog tongue can be considered as a biological pressure-sensitive adhesive system. Surprisingly, a lower mucus coverage of the contact area was related to stronger adhesion. This shows that beyond the presence of mucus, other mechanisms may add to the adhesive properties of the tongue. The mucus-covered area was correlated with the duration of the contact, and the adhesive force increased with a decreased impact duration. This relationship between adhesion and impact duration can be explained by the dominant effect of viscous forces at thinner layers of mucus.

Although mucus coverage is variable, frog tongues are certainly not dry. Wet adhesion occurs due to the effects of capillarity and viscosity or Stefan adhesion (Emerson and Diehl 1980). Also van der Waals interactions, suction and glue effects may contribute to adhesion in a biological wet adhesive system. Because the force over the duration of a pulling event is positively correlated with the contact area, it is likely that a larger contact area allows for higher energy dissipation during contact breakage. This means that the adhesive bond can be maintained for prolonged periods of time. This is also the case in technical pressure-sensitive adhesives (PSAs) (Creton 2003). During prey capture in frogs, this effect could be even more important than the strength of the adhesive bond, because it helps to secure mobile prey while it is pulled into the mouth. Pressure-sensitive adhesives (PSAs) are of common technical use, e.g. in the form of adhesive tapes or labels (Creton 2003). The force over time relationship during detachment of the tongue (Fig. 12.8g) is very similar to those of PSAs (Zosel 1989; Lakrout et al. 1999; Creton 2003). In both, a high first adhesive peak is followed by a plateau where the adhesive force remains more or less constant over a longer period of time before the contact breaks. For PSAs, cavities arise during the peak force phase (Lakrout et al. 1999). At some point, these cavities will coalescence and thus cause the contact to break. However, depending on the properties of the PSA and the opposing surface, before coalescence, cavity formation may result in fibrillation (Zosel 1989). PSA contacts with a high degree of fibrillation are characterised by longer adhesion duration, but also by the remains of PSA material (fibrils) on the contact material (Creton 2003). Fibrillation events

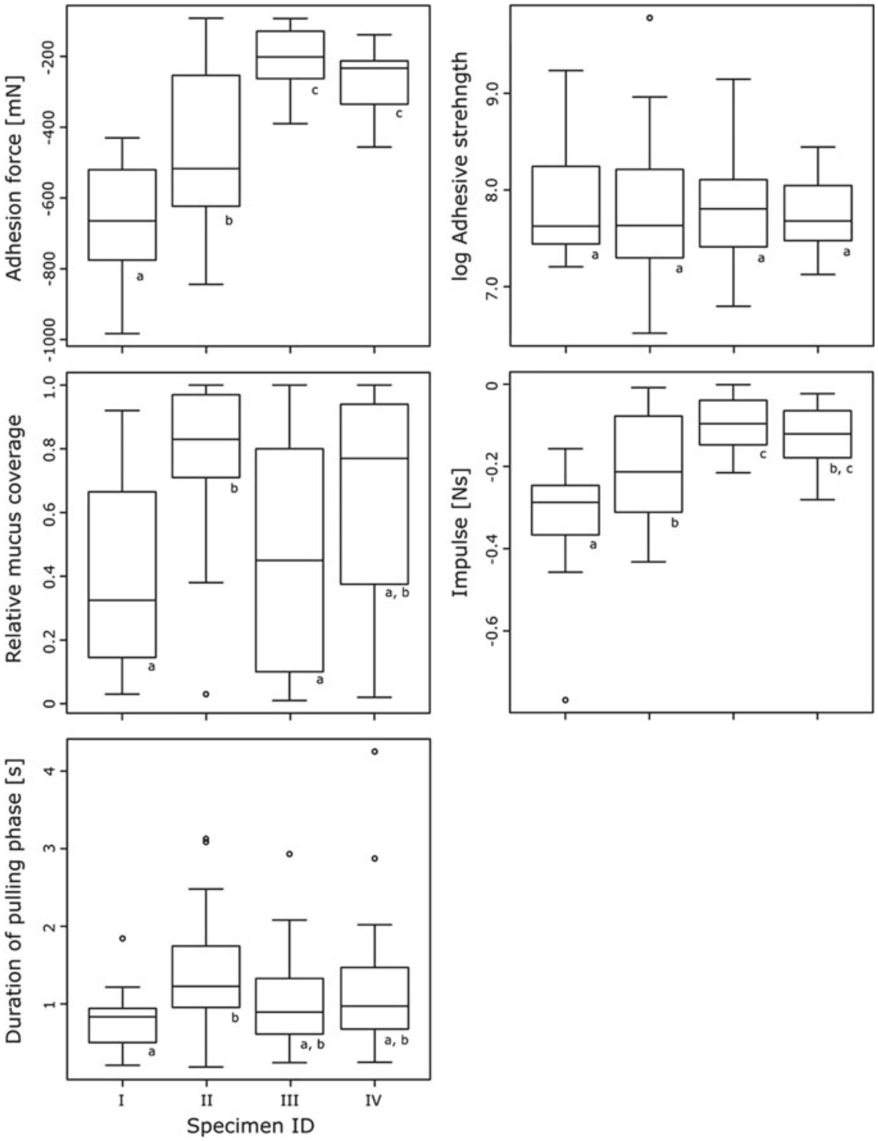


Fig. 12.10 Box-and-Whisker plots illustrating the mean, the lower and upper quartiles and the lower and upper extremes and outliers of an adhesive performance of different specimens of the *Ceratophrys* sp. frogs. Different letters show statistical significance ($p < 0.05$). From Kleintech and Gorb (2014)

were observed in contact between the tongue of the frog and the glass slides during high-speed video recordings (Kleintech and Gorb 2014).

The adhesive strength measured for the frog tongues is notably lower than, e.g. in gecko feet that are reported to adhere with approximately 60 kPa (Irschick et al. 2006). In another wet adhesive system, the suctorial disc of the northern clingfish *Gobiesox maeandricus*, adhesive strengths of approximately 40 kPa are reported (Wainwright et al. 2013). The toe pads of some tree frogs, however, show lower adhesives strength (approximately 1 kPa; Barnes et al. 2006) than the frog tongue measures. Each of these systems is tuned to very different demands on performance. Tree frog and gecko toes are used for arboreal locomotion; the clingfish suctorial disc makes a strong quasi-static adhesion on rough surfaces submerged in seawater. Frog tongues, on the other hand, are a very dynamic system in which high velocities and accelerations play a key role.

As mentioned above, adhesive force per unit area, or adhesive strength, is significantly higher in trials with lower mucus coverage. This demonstrates that mucus itself is not just simply some sort of liquid adhesive or glue. Very likely, the microstructure and surface energy of the tongue surface has an important contribution to the frog tongue adhesion. However, little is known about the surface structure of frog tongues. Previous studies focused almost exclusively on species within the Ranidae and Bufonidae, neglecting the wide diversity of frogs. Recently, Kleinteich and Gorb (2016) examine the tongue surface in nine different frog species, comprising eight different taxa, i.e. the Alytidae, Bombinatoridae, Megophryidae, Hylidae, Ceratophryidae, Ranidae, Bufonidae and Dendrobatidae (Fig. 12.11). In all species examined, there were fungiform and filiform papillae on the tongue surface. Further, a high degree of variation of the tongues in different frogs was observed. These differences can be seen in the size and shape of the papillae, in the fine structures on the papillae, as well as in the three-dimensional organisation of subsurface tissues. Notably, the fine structures on the filiform papillae in frogs comprise hair-like protrusions (Megophryidae and Ranidae), microridges (Bufonidae and Dendrobatidae) or can be irregularly shaped, or absent. Some of this variation might be related to different degrees of adhesive performance and may point to differences in prey of different frog taxa (Kleinteich and Gorb 2016).

As mentioned above, the frog tongue stickiness is the result of different features working in concert: the muscle arrangement properly catapulting the tongue, the tongue microstructure and the presence of saliva loaded on the tongue. In spite of the fact that the role of saliva is in principle clear (to wet the prey and provide strong connection with the tongue surface), the mechanisms of these interactions have only been described recently. Noel et al. (2017) performed material tests on the tongue, and rheological tests of the saliva of the common leopard frog *Rana pipiens*, a species that is able to capture a prey in under 0.07 s. Touching the frog tongue with a finger (Fig. 12.12) indicates that the tongue together with its saliva coverage has a stickiness similar to chewing gum. The trial of the finger removal resulted in the tongue stretching rather than in breakage of the bond. The authors used a floating spring–mass–damper system to model prey capture (Fig. 12.12) (Noel et al. 2017), which led to the conclusion that the tongue's unique stickiness results from

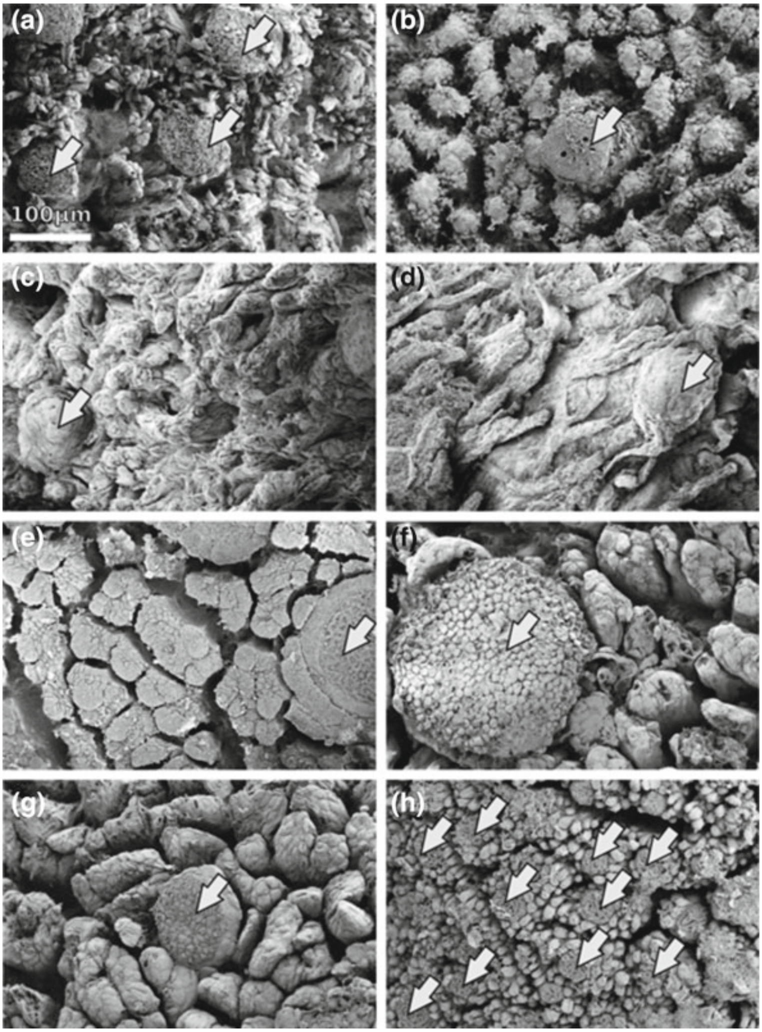


Fig. 12.11 Scanning electron microscopy of frog tongue surfaces (after fixation, dehydration and critical point drying). All images are at the same scale. **a** *Bombina variegata*, **b** *Discoglossus pictus*, **c** *Ceratophrys ornata*, **d** *Litoria infrafrenata*, **e** *Megophrys nasuta*, **f** *Rana* (*Lithobates*) *pipiens*, **g** *Bufo bufo*, **h** *Oophaga histrionica*. Frog tongue surfaces are covered by fungiform papillae (arrows), which are embedded in a matrix of smaller filiform papillae. The examined species differ notably in the size and the shape of the papillary surface structures. From Kleinteich and Gorb (2016)

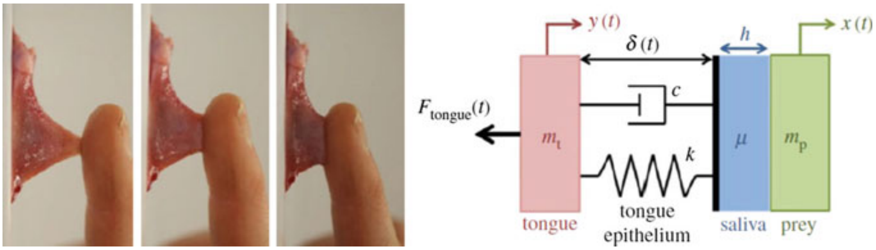


Fig. 12.12 Finger retracted from tongue surface showing its strong adhesion and the model of tongue using mass–spring–damper system. From Noel et al. (2017)

a combination of a soft, viscoelastic tongue material coupled with non-Newtonian saliva. The viscoelastic tongue acts like a car's shock absorber during the capture, absorbing energy to prevent separation from the insect (Noel et al. 2017). The shear-thinning saliva spreads over the prey during the tongue's impact, grips it firmly during tongue retraction and slides off during swallowing. These properties give the tongue 50 times greater work of adhesion than is known for synthetic polymer materials (Noel et al. 2017).

Previous studies of mucus from other animals suggest that mucus from a frog's tongue consists of mucins—serine-, threonine- and proline-rich glycoproteins (Harding et al.1983; Perez-Vilar and Hill 1999; Celli et al. 2005; Bansil and Turner 2006). Therefore, it can be expected that the interface between the mucus and the target surface should contain chemical bonds associated with glycoproteins. Moreover, fibrils are likely formed at the mucus–tongue interface. To test this hypothesis, Fowler et al. (2018) examined the chemical structure of the surface of mucus after a tongue strike by collecting both near-edge X-ray absorption fine structure (NEXAFS) microscopy images and sum frequency generation (SFG) vibrational spectra from layers of mucus left after frog tongue strikes on cleaned glass slides. A uniform distribution of amide, hydroxyl, and carbon–carbon bonds across the mucus surface was found. Difference spectra of individual spectra extracted from these images reveal structures consistent with fibril formation as well as a disorder of oligosaccharide groups near the mucus surface. SFG spectra revealed surface-active modes which likely originated from serine and threonine within the mucin protein. In combination, the results suggest that glycoproteins are well ordered at the mucus–tongue interface (Fig. 12.13). This supports the idea that the frog sticky-tongue mechanism is a pressure-sensitive adhesive. Accordingly, fibrils form as the tongue is retracted, increasing the ability of mucus to withstand large strains applied by the retracting tongue. Without fibril formation, mucus would be highly susceptible to delamination from the tongue (Fowler et al. 2018). In conclusion, the combination of a highly dynamic tongue projection, high adhesive strength and the versatility in attaching to structurally and chemically variable surfaces (e.g. fur, feathers, cuticle) makes the frog tongue a unique example for biological wet adhesion. These principles may inspire the design of reversible adhesives for high-speed applications.

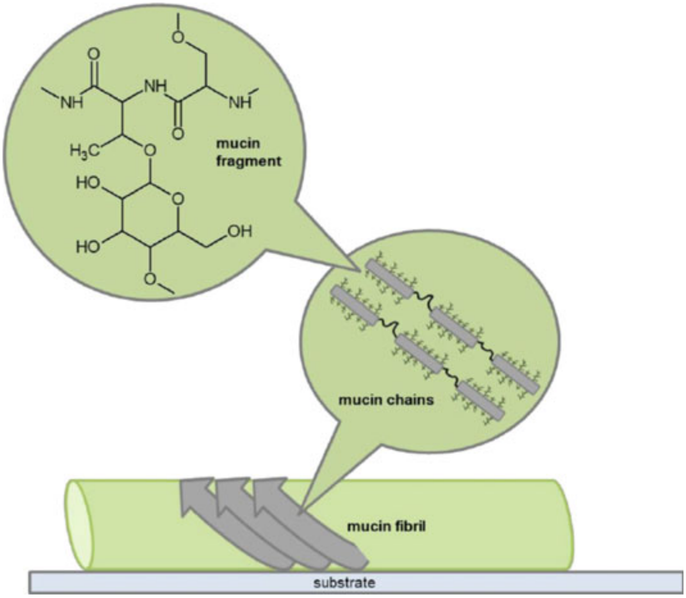


Fig. 12.13 Proposed mucin tertiary, secondary and primary structure at the mucus surface after tongue detachment, based upon NEXAFS and SFG spectroscopic analysis. The surface of mucus was found to be dominated by protein structures which agree with fibrillar mucin glycoproteins along with hydrophobic alkyl chains. From Fowler et al. (2018)

12.4 Salamanders

Salamanders are a fascinating group of amphibians with diverse lifestyles, developmental modes and the unique specialisations for ballistic tongue projection as observed in plethodontid salamanders (Deban and Wake 2000; Wake and Deban 2000; Wake 2013). One of the most interesting features of salamanders is the diversity of habitats they feed in (Deban and Wake 2000; Wake and Deban 2000). Not only are many species aquatic, many others feed in an aquatic environment during their larval phase (Deban and Marks 2002). However, in contrast to most frogs, many salamander larvae use similar mechanisms of prey capture as do adults (Deban and Wake 2000). The seasonal return of many species to an aquatic habitat further puts specific constraints on feeding as animals have to switch between two dramatically different physical environments as adults (e.g. Heiss et al. 2015, 2016; Van Wassenbergh and Heiss 2016). Interestingly, many species of salamanders show cannibalistic forms (Park et al. 2005; Jefferson et al. 2014; Nishimura 2018) and develop large differences in head size and shape allowing them to eat large prey (Nishimura 2018). These cannibalistic forms consequently show differences in diet, yet do not exclusively prey on conspecifics (Denoël et al. 2006; Jefferson et al. 2014).

12.4.1 Anatomy

Although the anatomy of the cranium, hyobranchial system and the associated musculature has been well described in salamanders (see Deban and Wake 2000; Wake and Deban 2000 for an overview), several recent papers have provided insights into the diversity of the anatomy of the feeding system. Although some of these papers have focused on skull anatomy to better understand the phylogenetic relationships among some groups (Ehmcke and Clemen 2003; Buckley et al. 2010; Wu et al. 2012; Darda and Wake 2015), others have focused on the evolutionary patterns in skull shape using geometric morphometric approaches (Ivanović and Arntzen 2014, 2018; see also Fig. 12.14 for an overview of the diversity of skull morphologies in salamanders). These studies show, for example, strong patterns of allometry in skull shape in *Triturus* newts with little modularity (Ivanović and Kalezić 2010; Ivanović and Arntzen 2014). Moreover, shape changes are associated with changes in habitat use with the most divergent morphologies being observed in the most aquatic of the species examined (Ivanović and Arntzen 2014). Skull shape variation in salamandrid salamanders is accentuated in the frontosquamosal arch, a unique feature of Salamandridae (Ivanović and Arntzen 2018). Interestingly, a reduction of this arch occurred independently at least three times in the group, likely due to changes in the ossification rate (Ivanović and Arntzen 2018). External head shape has also been studied extensively in plethodontid salamanders and has been shown to be heritable (Adams 2011) and driven by competitive interactions between species (Adams 2010).

Developmental studies have documented the cranial muscle differentiation and development in the Mexican axolotl (Ericsson and Olsson 2004). By using desmin antibodies, Ericsson and Olsson (2004) reconstructed the cranial musculature in three dimensions to show a clear division between the interhyoideus and the interhyoideus posterior muscles, thus illustrating their distinct origins. Studies documenting the ossification sequence of the skull in plethodontid salamanders have further demonstrated a caudal to rostral ossification sequence (Ehmcke and Clemen 2000). Experimentally induced arrested development in *Salamandra salamandra* larvae had long-term effects on their tooth-bearing bones providing insights into the origin of the vomeropterygopalatinum known from some newts (Clemen and Greven 2018). Tongue development was described in both a metamorphosing hynobiid salamander and the paedomorphic *Ambystoma mexicanum*. In this study, the authors focused on the development of the secondary tongue and the lingual glands and showed strong similarities between the metamorphosing species and the paedomorphic species when induced to metamorphose (Greven et al. 2013). The anatomy, function and evolution of jaw and hyobranchial muscles in larval forms of hynobiid and cryptobranchid salamanders was also described. Unexpectedly, great similarity between the two groups was observed despite the paedomorphic nature of the latter (Kleinteich et al. 2014). The authors further demonstrated using a biomechanical model that the flattened shape of the hyobranchial apparatus in resting position

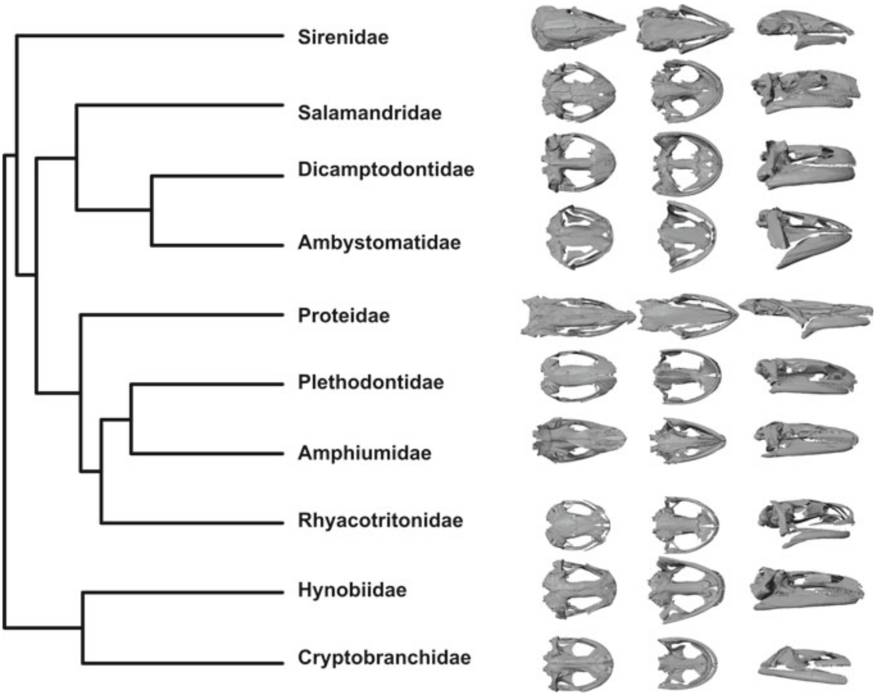


Fig. 12.14 Phylogeny of salamander families illustrating the diversity in skull form. The phylogeny was derived from the timetree of life website (http://www.timetree.org/). Illustrated next to the phylogeny are a dorsal, ventral and lateral view of the skull of representatives of each family. Proteidae: *Proteus anguinus*, Plethodontidae: *Plethodon fourchensis*, Rhyacotritonidae: *Rhyacotriton olympicus*, Cryptobranchidae: *Andrias davidianus*, Dicamptodontidae: *Dicamptodon ensatus*, Sirenidae: *Pseudobranchus striatus*, Salamandridae: *Neurergus kaiseri*, Hynobiidae: *Liua shihi*, Ambystomatidae: *Ambystoma dumerelii*, Amphiumidae: *Amphiuma tridactylum*

in these aquatic species is likely beneficial for fast and successful suction feeding (Kleinteich et al. 2014).

12.4.2 Function

Most of the studies on feeding in salamanders are focused on the highly specialised high-power tongue projection mechanism in plethodontid salamanders (e.g. Deban and Dicke 2004; Deban et al. 2007; Herrel et al. 2009). By comparing muscle anatomy with the instantaneous power requirements during tongue projection, Deban and colleagues (2007) demonstrate that required power output exceeds the magnitude of power output that can be generated by vertebrate muscle by an order of magnitude. This suggests the use of elastic energy storage and recovery during tongue projection in these animals. Studies investigating the activity of the tongue projector muscle further show that the muscle becomes active over 100 ms before actual tongue projection, leaving enough time for energy to be stored in collagenous elements (Deban et al. 2007). Moreover, the activation of the tongue projector muscle (the subarcualis rectus) is modulated in response to prey distance. Its activation changes from a posterior to anterior wave of activation at short distances that do not require ballistic projection, to an all-at-once activation at longer distances (Deban and Dicke 2004). However, no effect of prey capture success on activation patterns is observed suggesting a feedforward control of muscle activation as observed in other ballistic systems (Deban and Dicke 2004).

To test the idea that ballistic tongue projection is indeed powered by elastic energy storage, prey capture events were recorded at a range of temperatures. If indeed tongue projection is powered by elastic energy storage, then the kinematics of projection should be independent of temperature. This was observed in several species (Deban and Richardson 2011) and ballistic tongue projection showed Q_{10} values (change in performance over 10 °C) close to one. Muscle-powered tongue retraction, on the other hand, was strongly temperature-dependent with Q_{10} values ranging between 1.63 and 4.97. However, with decreases in temperature, increases in the duration of activation and an earlier onset of the tongue projector muscle were observed (Anderson et al. 2014). This mechanism using elastic energy storage resulting in a temperature independence of its performance appears to be universally present in plethodontids using ballistic tongue projection, including even the smallest miniaturised forms like *Thorius* (Deban and Bloom 2018). In comparison, non-ballistic plethodontid salamanders like *Desmognathus* or *Plethodon* power tongue projection with their muscles and show lower power outputs and a thermal dependence of the kinematics and performance of tongue movements (Deban and Scales 2016; Scales et al. 2016). A comparison of the anatomy of the tongue projector muscles further demonstrates that ballistically projecting plethodontids show elaborated and elongated collagen aponeuroses and the absence of myofibers inserting on the tongue skeleton. Whereas the elongated collagen fibres likely allow for greater elastic energy storage, the absence of a direct connection of the muscle with the tongue skeleton permits ballistic tongue projection (Deban and Scales 2016; Scales et al. 2016). This suggests that the switch from a muscle-powered to an elastically powered tongue projection involves only relatively minor changes in anatomy. This may, in turn, explain the multiple independent origins of elastic energy storage in plethodontids that provides them with a robust high-performance prey capture system featuring greater tongue projection distances at higher velocity that are independent of variation in ambient temperature (Deban and Scales 2016; Scales et al. 2016).

Despite their reduced tongue projection performance, some plethodontids of the genus *Desmognathus* show another unique feeding adaptation. Indeed, *Desmognathus* salamanders are unusual even among plethodontids in that they eat large prey including other salamanders, and they also use biting in courtship and defence (Deban and Richardson 2017). During biting, these salamanders use ventral head flexion, which contributes to bite force through the unique atlanto-mandibular ligaments (Dalrymple et al. 1985; Deban and Richardson 2017). As salamanders of the genus *Desmognathus* often hide in cracks or under stones, they have relatively flat heads. Despite this, they have large jaw adductor muscles and an unusually well-developed quadratopectoralis muscle. By using head flexion during biting, these animals can generate bite forces that are ten times greater than those of similarly sized plethodontid salamanders, e.g. *Pseudotriton*, and on par with those observed in lizards (Deban and Richardson 2017). The use of head flexion couples the action of the quadratopectoralis muscle to jaw adduction by means of the atlanto-mandibular ligament allowing these species to generate five times more bite force than they would be able to do without head flexion (Deban and Richardson 2017).

Another salient feature of salamanders is the presence of many paedomorphic species that remain fully aquatic as adults. Given the dramatic differences in density and viscosity between water and air, aquatic species of salamanders typically feed using suction rather than using tongue prehension (Deban and O'Reilly 2005; Heiss et al. 2013a, b; Kucera et al. 2018). One interesting exception to this general rule is primitive plethodontid salamanders (Desmognathini and Hemidactyliini) that are biphasic, and thus still undergo metamorphosis with a change of environment from the larval stage to the adult one (biphasic developmental cycles have been lost in more derived forms showing instead a direct development with animals hatching as miniaturized version of the adult) (Deban and Marks 2002). Aquatic adults, however, do not use suction feeding but rather lunge towards prey and use either tongue and jaw prehension to capture prey under water (Deban and Marks 2002). This suggests that the evolution of tongue projection has compromised the use of suction feeding in these animals. Suction feeding in adult paedomorphic forms is different than that observed in other aquatic animals, being powered largely by rapid jaw separation rather than by hyobranchial depression, as suggested for the Chinese giant salamanders based on computational fluid dynamics models (Heiss et al. 2013a, b). Indeed, hyoid depression occurs relatively late in comparison to the rapid jaw opening in aquatic salamanders (Deban and Wake 2000; Deban and O'Reilly 2005; Heiss et al. 2013a, b) and allows an expansion of the pharyngeal cavity needed to accommodate the water that has been sucked in by rapid jaw opening. However, in contrast to these paedomorphic forms, several species of salamandrids are semiaquatic or even fully aquatic as adults. A study comparing the suction feeding kinematics and performance in fully aquatic forms like *Paramesotriton labiatus* to semiaquatic salamandrids like *Pleurodeles*, *Notophthalmus*, *Triturus* or *Cynops* showed that the greater mineralization of the hyobranchial apparatus in the fully aquatic form allowed for higher suction feeding performance as quantified using particle image velocimetry (Stinson and Deban 2017a, b). Irrespective of the mechanism, however, all aquatic forms studied appear to use inertial suction feeding to move prey into the mouth (Deban and O'Reilly 2005; Heiss et al. 2013a, b; Stinson and Deban 2017a, b; Kucera et al. 2018).

In contrast to the large paedomorphic forms that are permanently aquatic, many salamanders seasonally switch lifestyles becoming aquatic during the reproductive season (Heiss et al. 2013a, b, 2015, 2016). Some can even be facultatively paedomorphic (Denoël 2002; Heiss 2017), with paedomorphic forms being better suction feeders than non-paedomorphic ones (Denoël 2004). Whereas newts use lingual prehension on land when in the terrestrial phase as do most salamandrids (Wake and Deban 2000), they switch to using suction feeding in their aquatic phase when capturing prey under water (Heiss et al. 2013a, b). This remains so even if the aquatic phase is relatively short (Heiss and De Vylder 2016). Interestingly, when capturing prey on land, but when they are in their aquatic life phase, *Ichthyosaurus alpestris* individuals switch to a jaw-based prey capture with a kinematic profile similar to that observed during suction feeding (Heiss et al. 2013a, b). Unlike plethodontids, these newts can also use suction when feeding under water in the terrestrial life phase (Heiss et al. 2013a, b), however, in a less coordinated fashion (Heiss et al. 2015). Interestingly, the kinematics of feeding on land and under water are rather similar in these semiaquatic species suggesting that only small modification of the motor programme can suffice to successfully feed in environments with dramatically divergent physical properties (Heiss et al. 2015). However, distinct morphological changes do occur between the two life phases and have been shown to impact feeding performance in different environments (Van Wassenbergh and Heiss 2016; Heiss et al. 2016). In addition to species-specific changes in the hyolingual musculature (Heiss et al. 2016), some species like *Lissotriton vulgaris* develop labial lobes when in the aquatic phase (Van Wassenbergh and Heiss 2016). Using computational fluid dynamics, the researchers demonstrate that the labial lobes increase suction distance and suction force by approximately 15% (Van Wassenbergh and Heiss 2016). The dynamic growth and resorption of the labial lobes provides these animals with a low-cost modular system that significantly improves feeding performance under water without requiring major modifications of the musculoskeletal system.

12.5 Future Directions

Amphibians are excellent model systems to study the evolutionary divergence in feeding systems given their exceptional diversity in habitats, lifestyles and reproductive modes. Understanding the relationships between cranial and hyobranchial diversity and feeding function and how these relationships are dependent on lifestyle, habitat use or reproductive mode are questions that can be answered given the availability of massive online databases with μCT data and robust comprehensive phylogenies. Unfortunately, quantitative analyses on muscular anatomy essential to link variation in form to variation in function using modelling approaches have lagged. Future studies quantifying feeding performance across a wide range of species will provide insights into the selective pressures underlying the evolution of the staggering diversity in feeding form and function of amphibians.

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Feeding in Vertebrates

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Foreword

This volume, assembled and edited by Bels and Whishaw, is a significant, scholarly, assessment of the current research on the evolution of vertebrate feeding systems in the context of the “form–function complex”. It constitutes a major contribution that: (1) illustrates the continuing integration across biological subfields to analyze complex systems, (2) celebrates technical advances, ranging from CT scanning and PIV to sophisticated analytical and statistical methodologies, (3) incorporates phylogenetic perspectives that are essential for evolutionary research, and (4) shows how diversity of methods and organisms is essential for advancing the field of evolutionary morphology.

Anatomy/morphology reigned as the king of the biological sciences in the mid—to the late nineteenth century, where its dominance was evident in Germany in particular. But newer fields, especially physiology and development, gradually superseded the older approaches, which slowly declined in influence. By the 1960s and 1970s, the change was evident. Functional morphology—exploration of the form–function interaction—developed rapidly and the first glimmerings of biomechanics could be seen. Phylogenetics became a necessary component of comparative investigations, including a renewed focus on the relation of ontogeny to phylogeny. Hypotheses and tests were increasingly emphasized. Development, behavior, and ecology became major components of functional studies. A renaissance of morphology was evident by the early 1980s. Key to the rebirth was a new sharp focus on problems and solutions, rather than description for its own sake. Studies of trophic systems began to consider the links among perception, integration, and action. Integrative approaches, frequently including either/both ontogenetic and paleontological time dimensions, were increasingly utilized. Central to the new movements were the rebirth of venerable organizations, for example, the American Society of Zoologists, which became the Society of Integrative and Comparative Biology (SICB) near the end of the twentieth century, and the appearance of new international organizations, such as the International Congress of Vertebrate Morphology (ICVM), which reliably meets every third year at diverse sites around the world. The programs of these organizations offer amazingly rich and diverse arrays of speakers and workshops and attract large audiences of lively young people, as well as more seasoned researchers. We live in an age of excitement and opportunity for research in the field relevant to the present volume.

We are delighted to see that this entire volume presents the advances in our science using cases to represent the diversity of research perspectives on major chordate and vertebrate lineages. By presenting these in such a broadly comparative framework, many new ideas and extensive new research into the functional biology, *sensu lato*, of feeding will be stimulated.

This volume is a thoughtful, erudite, compendium of research formulation and ideas. The authors and editors have given researchers a forward-thinking overview. We predict that it will prove to be a resource for researchers in many subfields of biology, serving to integrate and synthesize new conceptions of the evolution and function of trophic systems.

Marvalee H. Wake
David B. Wake

Acknowledgements

The genesis of this book is based on the invitation of Lars Koerner from Springer to provide a new insight of our understanding of the evolution of the feeding behaviors and mechanisms in vertebrates. We would express our gratitude for his support and understanding through the approval process at Springer and the conceptual construction of the book. This book concerns our understanding of feeding in chordates and vertebrates and its role in the ecological and evolutionary processes.

The book was conceptualized by Vincent Bels (Museum national d'Histoire naturelle, Paris, France), who then asked Ian Q. Whishaw (University of Lethbridge, Lethbridge, Canada) to join him as co-editor, providing them with an excellent opportunity to work together on this project devoted to the understanding of the evolution of feeding behavior.

This volume would never have been possible without the contributions of experts, who covered a series of field of researches from anatomy, biomechanics, to neurobiology, and behavioral ecology to attempt to provide hopefully an integrative approach of feeding behavior of chordates and vertebrates. We are highly indebted to all of them, and acknowledge their wonderful work, patience, understanding, and comprehension to build this book that tries to integrate a variety of approaches for future researches. Such book would not be possible without the help of a lot of colleagues who reviewed one or more of the chapters, providing absolutely excellent insights substantially improve of all of the contributions: Peter Aerts, *University of Antwerp, Antwerpen, Belgium*; Elizabeth Brainerd, *Brown University, Providence, USA*; Chris Broeckhoven, *University of Antwerp, Antwerpen, Belgium*; Matthew McCurry, *The Australian Museum, Sydney, Australia*; Ariel Camp, *University of Liverpool, Liverpool, UK*; Andrew Clark, *College of Charleston, Charleston, USA*; Gregory M. Erickson, *Florida State University, Tallahassee, USA*; Lara Ferry, *Arizona State University, Glendale, USA*; Serkan Erdogan, *Namik Kemal University, Terkirdag, Turkey*; Egon Heiss, *Friedrich-Schiller-University of Jena, Jena, Germany*; Juan Pablo Gailer, *Universität Hamburg—Zoologisches Museum, Hamburg, Germany*; Paul M. Gignac, *Oklahoma State University, Tulsa, USA*; Anthony Herrel, *Museum national d'Histoire naturelle, Paris, France*;

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Finally, we are pleased to thank Arumugam Deivasigamani and Anette Lindqvist for their invaluable help in the editorial and production processes of the book.

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Editors and Contributors

About the Editors

Vincent Bels was born in Verviers, Belgium. His Ph.D., Ethology and Functional Morphology, at the University of Liège (Liège, Belgium), integrated theoretical concepts to morphology and behavior in feeding animals. He has used lizards as a model to clarify the process of behavioral ritualization in evolution. He was Research Fellow and then Assistant at the University of Liège (Belgium). Then taught Biology, Zoology, and Ecology and developed applied research methods for studying feeding behavior in domestic animals at Hautes Ecoles (Hainaut, Belgium) and the Associated Agronomic Centre (Belgium). He is now a Professor at the Muséum national d'Histoire naturelle (Paris, France), where he has served as joint director of one Research Mixed Unit (CNRS/MNHN, France). He has taught Functional Morphology at the University of Mons (Belgium). He belongs to the Scientific Committee of Muséum National d'Histoire Naturelle (Paris, France), and serves at Scientific Sections of the Centre National de Recherche Scientifique (CNRS, France). He has authored over 80 peer-reviewed articles, 10 chapters, and 6 books on feeding and locomotion in Vertebrates. In 1994, he edited "Biomechanics of Feeding in Vertebrates" in the series *Advances in Comparative and Environmental Physiology* (Volume 18) published by Springer. This volume provides a comprehensive description of the evolution of feeding behavior in vertebrates by integrating feeding in aquatic and terrestrial animals. Professor Bels' research is dedicated to feeding, drinking, and displays in lizards, turtles, and birds but he has also studied feeding and the relation between feeding and locomotion in vertebrates. His research goal is to integrate behavioral, physiological, and morphological science into a comprehensive understanding of the "Form–Function" relationship of the trophic system in vertebrates.

Ian Q. Whishaw received his Ph.D. from Western University and is a Professor of Neuroscience at the University of Lethbridge. He has held visiting appointments at the University of Texas, University of Michigan, Cambridge University, and the University of Strasbourg. He is a fellow of Clair Hall, Cambridge, the Canadian Psychological Association, the American Psychological Association, and the Royal Society of Canada. He is a recipient of the Canadian Humane Society Bronze medal for bravery, the Ingrid Speaker Gold medal for research, the distinguished teaching medal from the University of Lethbridge and the Donald O Hebb Prize. He has received the Key to the City of Lethbridge and has honorary doctorates from Thompson Rivers University and the University of Lethbridge. He is a coauthor of a major introductory textbook in Behavioural Neuroscience and a major senior textbook in Neuropsychology. His research addresses the neural basis of skilled movement and the neural basis of brain disease. The Institute for Scientific Information includes him in its list of most cited neuroscientists. His hobby is training horses for western performance events.

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