Chapter 13
Feeding in Lizards: Form–Function and Complex Multifunctional System

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Abstract Living lizards exploit almost all terrestrial ecosystems where they play the roles of both predator and prey in complex food webs. Bels et al. (Biomechanics of feeding in Vertebrates, 197–240, 1994) and Schwenk (Feeding: form, function and evolution in Tetrapod Vertebrates, 459–485, 2000) provided first detailed overviews about the anatomical and functional traits of the feeding stages and phases of the feeding cycle in these tetrapods. Here, we synthesize recent literature in order to provide discussion of the evolution of their feeding behavior from capture to swallowing.

13.1 Introduction

Lizards, involved at various levels of many trophic chains, exploit a large diversity of food/prey (see, for example, Pianka 1973, 2017; Pough 1973; Auffenberg 1981, 1988; Whitaker 1987; Dubas and Bull 1991; King 1996; Traveset and Sáez 1997; Corlett 1998; Fialho et al. 2000; Vitt 2000; Valido et al. 2003; Vitt et al. 2003; Olesen and Valido 2004; Sazima et al. 2005; Luiselli 2008; Losos 2009, 2011; Siqueira et al. 2013; Gomes et al. 2014; Vitt and Pianka 2014; Balakrishna et al. 2016; Zhang et al. 2018). As soon as they leave the egg, lizards need to feed while at the same time avoid predators (Pianka 2017; Sazima 2017; Webber et al. 2016; La May et al. 2016; Shine

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V. Bels and I. Q. Whishaw (eds.), *Feeding in Vertebrates*,
Fascinating Life Sciences, https://doi.org/10.1007/978-3-030-13739-7_13

and Tamayo 2016; Fukudome and Yamawaki 2016; Bellini et al. 2015; Karameta et al. 2015; Sandoval-Comte et al. 2014). In its most general sense, feeding is defined as "*…The behaviour by means of which an animal of one species, the predator, kills and eats a member of another species, the prey…*" (McFarland 2014).

In lizards, feeding behavior is divided into successive stages: ingestion or capture, processing, intraoral transport, and swallowing including pharyngeal packing and compression (Schwenk 2000). Over the last 30 years, a large number of studies show the links between the diet of lizards, the morphology of their trophic system, and their feeding behavior (Bels et al. 1994; Schwenk 2000; Bels 2003; see below). Each feeding stage is under the control of complex neuronal mechanisms variably influenced by a series of factors including environmental constraints (e.g., prey availability), physiological status (e.g., satiation), phylogenetic and ontogenetic trajectories, as well as individual characteristics (e.g., cognition, parasitism). Each stage involves a series of opening–closing gape cycles, and each cycle is controlled by a "motor pattern" (DeVree and Gans 1994; Bels et al. 1994; Schwenk 2000; Herrel et al. 2001a; Schwenk and Rubega 2005; Ross et al. 2010). The gape cycle is *per definition* a "fixed action pattern" (FAP, Tinbergen 1952), or more precisely a "modal action pattern" (MAP, Barlow 1968) under the control of a central pattern generator (CPG) as defined by Barrows (2017) "*…a behavior that is recognizable, describable at least in statistical terms, indivisible into smaller units, and "widely distributed in similar form throughout an interbreeding population* (Barlow… in Hinde 1982, 47)." These MAPs are initiated by information received from various sensory inputs (i.e., visual, olfactive, and vomerolfactive), but the CPG corresponding to the network of neurons generating the specific motor outputs driving jaw and hyo-lingual movements in each feeding cycle remains to be clearly determined.

The activated muscles belong to a variety of anatomical systems, i.e., the axial, appendicular, and trophic systems. Indeed, recently, postcranial movements have been shown to be associated with the movements of the trophic elements in the MAP of food capture in lizards (Montuelle et al. 2009a, 2012a, b; Montuelle and Kane, this volume). Apart from these observations, the majority of studies of lizard feeding focus only on cranial movements (e.g., head and lingual skeletal and muscular systems). The FAP of the feeding cycle in each phase exhibits the three kinds of stereotypy suggested by Schleidt (1974) (i) the degree of completeness, (ii) the degree of coupling, and (iii) the degree of variability.

One issue of interest during the last 20 years is that, because the trophic system is used in many behaviors, the behavioral and functional responses of the trophic elements during feeding must be considered with respect to trade-offs among various constraints (Schwenk 2000; Huyghe et al. 2008; Urošević et al. 2014; Wittorski et al. 2016; Bels et al. 2019). Such trade-offs do not necessarily modify the FAP, but rather modulate it (see below). This chapter focusses on a comparative approach to discuss some aspects of the evolution of the trophic system and the feeding behavior per se from food/prey capture to swallowing.

In this chapter, we examine the evolution of the behavioral (kinematic) properties of the feeding behavior of lizards. Feeding behavior of lizards has been studied from various perspectives attempting to link experimental research (e.g., kinematics, bite force) with observed ecological data (i.e., diet, habitat) and conceptual approaches (natural selection). Over the last three decades, a large number of studies have attempted to reveal the relationships among morphological, functional, and behavioral traits of the trophic system in these tetrapods. In general, the morphological and associated functional and behavioral approaches are used to understand the selective pressures that ultimately determine the characteristics of the trophic system as a whole. Indeed, each food/prey selected by each lizard influences the intercorrelation between traits related to morphology, performance, behavior, and fitness as suggested by Arnold (1983) and reviewed by Garland and Losos (1994), and more recently by Irschick and Higham (2016). For clarity, we follow the definition proposed by Schwenk (2000, see, p. 50) for determining the phases that constitute feeding behavior as a whole: capture (ingestion), reduction (chewing), intraoral transport, and swallowing (pharyngeal compression and pharyngeal packing).

The majority of studies linking feeding morphology and behavior from a functional perspective are carried on under experimental conditions to collect valuable data. Field studies are unfortunately very scarce (Fig. 13.1). Therefore, since the beginning of this experimental approach within the last three decades, the major source of functional data is high-speed videography, which can be implemented in two or three dimensions, and/or with cinefluoroscopy (i.e., Bels et al. 1994; Herrel et al. 1996; 1997a, b, 1998a, b; Schwenk 2000; Montuelle 2012b). Typically, the animals are filmed either in outdoor enclosure where unrestrained prey capture events can be performed, or in experimental devices allowing control of particular conditions, including various physiological measures. The range of food/prey usually tested in the literature is relatively narrow. For insectivorous species, for example, only a few varieties of insects are used, usually crickets, mealworms, grasshoppers, and ants. In other cases, rodents are used for omnivorous and carnivorous species. Some very particular food items are presented in specialized lizards, such as fruits and vegetables with highly different textures (e.g., bananas, apples, leaves) for herbivorous species.

Fig. 13.1 Typical posture of *Iguana delicatissima* (La Désirade, Guadeloupe, France) feeding on plant material. In nature, this iguanian lizard uses lingual prehension for all kinds of food

13.2 Food Diversity

Functionally, lizards have access to a wide diversity of food (i.e., Pianka 1973; Dalrymple 1979; Estes and Williams 1984; Mou and Barbault 1986; James 1991; Pérez-Mellado and Casas 1997; Traveset and Sáez 1997; Corlett 1998; Fialho et al. 2000; Varela and Bucher 2002; Wotton 2002; Olesen and Valido 2003; Valido and Nogales 2003; Valido et al. 2003; Herrel et al. 2004a, b; Sazima et al. 2005; Valido and Olesen 2007; Rodríguez et al. 2008; Hansen and Müller 2009; Pafilis et al. 2009; Hong et al. 2011; Olesen et al. 2012; Piazzon et al. 2012; Schaerlaeken et al. 2012; Saint Pierre and Wright 2013; Bennett 2014; Brock et al. 2014; Crofts and Summers 2014; Gomes et al. 2014, 2016; Bochaton et al. 2015; Hopkins et al. 2015; Mateo and Pleguezuelos 2015; Rahman et al. 2015; Sagonas et al. 2015; Burgos-Rodríguez et al. 2016; Garrison et al. 2016; Gunethilake and Vidanapathirana 2016; Law et al. 2016; Nogales et al. 2016; Wotton et al. 2016; de Sena et al. 2017; Baeckens et al. 2017a; Colston 2017; Dollion et al. 2017; Giery et al. 2017; Karameta et al. 2017; Koch and Arida 2017; Moreno-Rueda et al. 2017; Pietczak and Vieira 2017; Sweeney et al. 2017; DeBoer et al. 2018; Hervías Parejo et al. 2018). Obviously, capturing different prey items is based on the modulation of movements of the trophic elements (i.e., Bels et al. 1994; Schwenk 2000; Lappin and German 2005; Hoese et al. 2008).

Briefly, most lizard species are viewed as predators that approach, kill, and eat living organisms (prey) in various ways (Schwenk 2000; Bels et al. 2019). Many species are mainly omnivorous and insectivorous exploiting prey, with highly different properties (i.e., size, volume, defence, shape and color, mobility, escape behaviors, and texture) (Herrel et al. 1997a, b, 2004a; Montuelle et al. 2009a, 2010, 2012a, b; Schaerlaeken et al. 2012). Some species have a more restricted diet such as carnivory (i.e., Secor and Phillips 1997; Kulabtong and Mahaprom 2014; Openshaw and Keogh 2014; D'amore 2015; McKinney et al. 2015; Uyeda 2015; Pianka 2017), ovophagy (Herrel et al. 1997b; Brock et al. 2014), myrmecophagy (i.e., Montanucci 1989; Lo Cascio and Capula 2011; Losos 2011; Randriamahazo and Mori 2012; Zuffi and Giannelli 2013), and even herbivory. Herbivorous lizards, such as the Galapagos marine iguana, are characterized by a highly specialized diet coupled with morphological and physiological specializations (Nagy and Shoemaker 1984; Wikelski et al. 1993; Wileski and Thom 2000; Wikelski and Wrege 2000; Wikelski and Romero 2003; Mackie et al. 2004; Hong et al. 2011; St-Pierre and Wright 2013). However, functional observations and data on the behavior of marine iguanas feeding under water remain scarce.

Lizards specializing in herbivory feed mainly on flowers and fruits with highly different properties. Some other species or indeed some individuals within populations can also be frugivorous occasionally, but this is not their primary food source. All lizards exploiting fruits can be seed dispersers (Traveset 1990, 1995; Valido and Nogales 1994; Willson et al. 1996; Wotton 2002; Valido et al. 2003; Godínez-Álvarez 2004; Rodríguez-Pérez and Traveset 2010; Gomes et al. 2016; Hervías et al. 2018). Especially on some islands, lizards are important vectors of seed dispersal, and this insular phenomenon could be explained by endemic lizard populations at high density

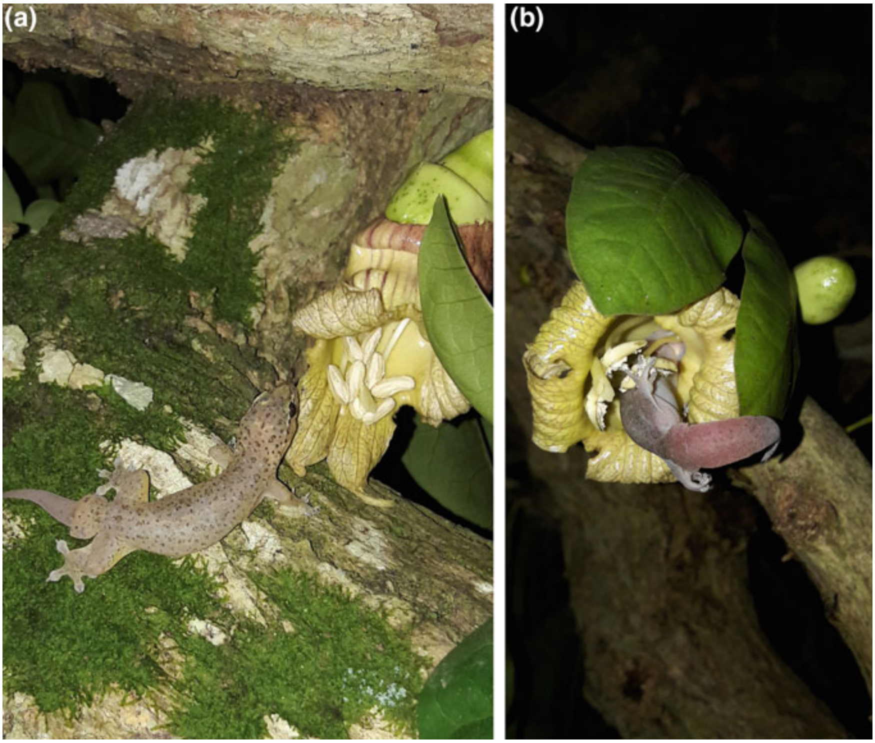


Fig. 13.2 Two pictures showing the approach **a** and complex feeding posture, **b** of the gecko *Gehyra mutilate* exploiting nectar of flowers of a bat-pollinated Calabash tree (*Crescentia cujete* L.). The last picture shows the postural demands required to eat the nectar with the tongue. The lizard enters the head into the flower to bring the nectar with the tongue. Photos courtesy of K. Tanalgo from Tanalgo and Hughes (2017)

(Olesen and Valido 2004). Other lizards, such as *Varanus salvator* and *Uromastyx aegyptia,* are for the most part herbivorous, but are also known to use scavenging behavior occasionally (Castilla et al. 2011; Fitzsimons and Thomas 2016). Some lizards also exploit nectar as a food resource (Fig. 13.2; Olesen and Valido 2003; Leal et al. 2017; Tanalgo and Hughes 2017). But exploiting liquid food is completely different than solid food (see below). Finally, and perhaps more importantly, diet of certain lizards can change along the lifespan (Mautz and Nagy 1987; James 1991; Rodriguez et al. 2008; Wotherspoon and Burgin 2016; Schulte et al. 2017; Toyama et al. 2018). For example, some scincids are insectivorous during the early stage of their life and then become omnivorous when adult (Ostrom 1963; Hawlena and Pérez-Mellado 2009). Other geckonids and iguanids are herbivorous when they are juveniles and become carnivorous or insectivorous once adults, or vice versa (Troyer 1984).

13.3 Functional Studies

The skull and hyo-lingual (e.g., tongue) systems of squamate lizards are often studied in separate conceptual and experimental contexts (Bels et al. 1994; Schwenk 2000; Alfaro and Herrel 2001). Such disparate approaches determine rather different explanations of the evolutionary pathways characterizing the squamate lineage. These can and must now be integrated into a general understanding of the evolution of the trophic system. On one hand, the skull is usually studied in the context of exploitation of food resources and other habitat constraints. In particular, a large number of studies within the last three decades investigated the effects of ecological parameters associated with microhabitat (i.e., fossorial) and diet (food preferences) on skull morphology. This is only briefly surveyed in this chapter. Functional studies of the tongue investigate not only its shape and the motor patterns associated with feeding and drinking (see below), but also in the context of vomerolfaction because the hyolingual apparatus plays a critical role in collecting chemical information transmitted to the Jacobson's organ (Gove 1979; Goosse and Bels 1992; Toubeau et al. 1994; Cooper 1997; Herrel et al. 1998b; Cooper and Vitt 2002; Baeckens et al. 2017b, c). Furthermore, the hyoid apparatus itself is investigated in the context of aggressive, territorial, and sexual behaviors (Bels 1990a, 2000; Font and Rome 1990; Lailvaux et al. 2015; Ord et al. 2015). For example, in *Anolis*, skull and throat movements during dewlap display depend on the shape and function of the hyoid apparatus (see, for example, Vanhooydonck et al. 2015; Reedy et al. 2017).

13.4 Skull Morphology

The skull of lizards is characterized by traits resulting from a trade-off among various ecological and behavioral constraints that have mutualistic or antagonist effects (i.e., diet, habitat, territorial, and aggressive behavior). If these effects play an important role in determining the morphological and functional properties of the skull (e.g., biting), they can also affect competition between species, and the successful establishment of an invasive species as suggested in *Anolis* (Dufour et al. 2018). Illustrating the effects of food/prey properties, feeding ecology and biomechanics are both associated with skull morphology in many lizard taxa with various diets (see, for example, Siqueira et al. 2013; Zuffi and Giannelli 2013; Garrison et al. 2016; Hernández-Salinas et al. 2016; Scali et al. 2016; Meyers et al. 2018). The majority of skull studies use morphological descriptions (Schwenk 2000), but more and more recent studies are based on various experimental methods, including bite force measurements and biomechanical modeling (e.g., Rayflied, this volume).

Linking proximal ecological factors with morphological traits of the lizard skull remains complex and still often discussed. Indeed, a large number of investigations show that dietary specializations play a key role in skull morphology and functional performance (e.g., biting force, gape angle). McBrayer (2004) reported that the skull is shorter and wider in sit-and-wait lizards than in active foraging species. Based on a morphospace created from more than 1000 lizard skulls (441 species from 17 lizard families), Stayton (2005) shows a basal morphological split between Iguania and Scleroglossa. Iguania seems to show primarily divergent evolution of skulls, whereas scleroglossan skulls are found to be primarily convergent.

However, a large number of studies demonstrate that skull morphology is the result of a trade-off among diverse ecological and behavioral constraints. For example, in their extensive analysis of the varanoid skull, McCurry et al. (2015) concluded that skull morphology mirrors "*its relationship to structural performance (von Mises strain) and interspecific differences in feeding ecology.*" These authors (McCurry et al. 2015) also emphasize the complex relationship between skull shape and feeding behavior in these omnivorous lizards (Loop 1974; D'Amore and Blumensehine 2009; Fry et al. 2009; Fitzsimons and Thomas 2016; Wilken et al. 2017): "*…Finite element modelling results showed that variation in cranial morphology resulted in large differences in the magnitudes and locations of strain in biting, shaking and pulling load cases*.". Such complex relationship between structural properties and the feeding behavior is confirmed by Moreno et al. (2008) who concluded that: "*the skull and associated musculature of V. komodoensis are particularly well-adapted to exert and resist forces generated during pull-back biting*." Similarly, in Tropidurinae, Kohlsdorf et al. (2008) explain that: "*expected adaptations leading to flat heads and bodies in species living on vertical structures may conflict with the need for improved bite performance associated with the inclusion of hard or tough prey into the diet, a common phenomenon in Tropidurinae lizards.…No phylogenetic signal was observed in the morphological data at any branch length tested, suggesting adaptive evolution of head shape in Tropidurinae. This pattern was confirmed by both factor analysis and independent contrast analysis, which suggested adaptive co-variation between the head shape and the inclusion of hard prey into the diet. In contrast to our expectations, habitat use did not constrain or drive head shape evolution in the group*."

Bite force capacity is typically estimated by having the lizards bite on two metal plates connected to a piezoelectric force transducer (Herrel et al. 2001a; McBrayer 2004). Bite force can be related to kinematics (e.g., gape angle) and a series of morphological skull properties (i.e., position of the teeth along the jaw apparatus, Meyers et al. 2018). The position of the bite along the mandible also influences the recorded data (Curtis et al. 2010; Lappin and Jones 2014). Functionally, bite force is one of the major traits to explain the relationship between skull structure and diet. Since the early time of research on the lizard skull, diet is considered a major driver of skull evolution and adaptation. Obviously, the mechanical properties of the food/prey play a determinant role in skull–food interactions, but the complexity of proximate and ultimate factors affecting skull properties still remains largely debated in the literature. In their review, Lappin and Jones (2014) concluded that: "*Bite-force performance is one form of in vivo data that has been used to evaluate predictions made by computer-based biomechanical models… Our results demonstrate that variations in methods for quantifying bite force, such as choice of biting substrate and whether bite out-lever is incorporated, can lead to significantly different and perhaps mis-*

leading in vivo results. Nevertheless, it seems widely assumed that in vivo results represent inherently accurate empirical data, to the extent that if model predictions match the in vivo data then the model is considered to be 'validated'…".

A large number of studies have linked skull properties with the associated musculature (i.e., adductor muscles) and discussed such links with food/prey characteristics. Indeed, in various lineages of lizards, dietary specialization plays a key role in determining skull morphological traits and functional performance (e.g., biting force, gape angle). Strong evidence based on biomechanical and functional studies has been recorded in many generalist and specialist lizard species (see, for example, Herrel et al. 1995a; 2001a, 2004a, 2016; Verwaijen et al. 2002; Huyghe et al. 2005, 2008; Vanhooydonck et al. 2005; Lappin et al. 2006; McBrayer and Corbin 2007; Herrel and Holanova 2008; Measey et al. 2011; Schaerlaeken et al. 2012; Sagonas et al. 2014; Des Roches et al. 2015; Jono 2015; Lopez-Darias et al. 2015; McCurry et al. 2015; Da Silva et al. 2016; Donihue et al. 2016; Toyama 2016; Wittorski et al. 2016; Dollion et al. 2017; Jones et al. 2017; Paluh and Bauer 2017; Powell et al. 2017; Valdecantos and Labra 2017). Specialized diets focusing on hard to bite items, such as durophagy and myrmecophagy, are among the strongest examples of diet that influence morphological and functional properties of the skull (Dalrymple 1979; Herrel and Holanova 2008; Schaerlaeken et al. 2012; Meyer et al. 2018).

Other omnivorous lacertids show a larger bite force than insectivorous species, but neither head shape nor size is different (Herrel et al. 2014). In addition, some morphological specialization in the skull and dentition, like the jaw-closing mechanism and the associated musculature can explain the differences in diet between omnivorous and insectivorous species (Montanucci 1968; Valido and Nogales 2003). Exploiting hard plant material in male and female *Uromastyx* produces similar high bite force (Herrel et al. 2014), and Metzger and Herrel (2005) conclude that: "*lizards specializing in food items imposing different mechanical demands on the feeding system show clear patterns of morphological specialization in their cranial morphology. True herbivores (diet of fibrous and tough foliage) are clearly distinguished from omnivorous and carnivorous lizards by having taller skulls and shorter snouts, likely related to the need for high bite forces.*" In their study of the chameleons *Bradypodion*, Dollion et al. (2017) concluded that: "*the cranial system in chameleons of the genus Bradypodion evolves under natural selection for the ability to eat large or hard prey. Moreover, significant differences in the ecomorphological relationships between the two sexes suggest that sexual selection plays a role in driving the evolution of bite force and head shape. These data suggest that ecomorphological relationships may be sex-dependent*."

Eating hard materials such as snails and molluscs have a clear effect on the morphology and performance of the trophic systems in lizards. Head shape and bite force permit to the fossorial worm lizard *Trogonophis wiegmanni* to exploit gastropods. Compared to closely related species *Tupinambis merianae* that exploit snails in their diet, adults of the molluscivorous *Dracaena guianensis* do not show differences in head morphology and bite force. In contrast, juvenile *D. guianensis* have bigger heads and greater bite forces (Herrel and Holanova 2008), suggesting that a growth-related difference in jaw adductor muscles could be the cause of decrease of bite force in adult *D. guianensis.* Thus, it appears that developmental constraints can play a key role in the observed differences. These authors suggest that selection on the juvenile feeding traits drives the adult traits.

In amphisbaenian lizards, Baeckens et al. (2017a) concluded that: "*head size, and consequently bite force, increases the number and variety of gastropods that can be consumed by 'shell-crushing', but reduces the number and variety of prey items that can be consumed by 'shell-entering', and vice versa. This study implies that the cranial design of (molluscivorous) limbless burrowers may therefore not only evolve under constraints for efficient soil penetration, but also through selection for diet.*" In their comparative analysis of *Phrynosoma* lizards exploiting prey with various properties including hardness, Meyers et al. (2018) showed that: "*Maximal bite forces vary considerably among horned lizards, with highly myrmecophagous species exhibiting very low bite forces. In contrast, members of the short-horned lizard clade are able to bite considerably harder than even closely related dietary generalists. This group appears to be built for performing crushing bites and may represent a divergent morphology adapted for eating hard prey items. The evolutionary loss of processing morphology (teeth, jaw and muscle reduction) and bite force in ant specialists may be a response to the lack of prey processing rather than a functional adaptation per se*."

If food/prey is a major driver for explaining skull morphology, its function and its mechanical properties, a series of studies also shows the impact of other proximal environmental factors. In the monophyletic *Podarcis* species, for example, skull shape variation is influenced by a series of ecological constraints (i.e., terrestrial *vs* saxicolous species). This is also the case of fossorial lizards like gymnophthalmids, in which head shape and bite force are influenced by feeding on gastropods (Baeckens et al. 2017a). The data collected by Barros et al. (2011) demonstrate that head morphology in this lizard family is primarily shaped under the influence of microhabitat (e.g., mechanical resistance of the substratum) and is more constrained by their burrowing behavior, rather than diet which is phylogenetically conserved. Other rock-dwelling lizards from various lineages (i.e., Revell et al. 2007; Openshaw and Keogh 2014; Paluh and Bauer 2017) also show common traits such as dorsoventrally flattened head (and body) that may or may not be related to feeding behavior (Roitberg 1999; Revell et al. 2007; Goodman et al. 2008; Openshaw and Keogh 2014; Paluh and Bauer 2017; Pelgrin et al. 2017). For example, n *Tropidurus*, specialized species with flattened skulls differ in habitat use, morphology and prey size when compared to the generalist ectomorph. Pellegrin et al. (2017) concluded: "…*we hypothesized that specialization to habitat induces morphological modifications, which in turn may constrain lizard performance. Flattened species differed in habitat use, morphology and prey size when compared with the generalist ecomorph. Morphological modifications were related to specializations to rocky habitats and constrained the variety of prey items consumed*." Also, differences in maximal bite force between species and individuals (including sexual differences) show various results. In two lacertid species (*Lacerta oxycephala* and *Podarcis melisellensis),* bite forces mirror differences in absolute head size (Verwaijen et al. 2002), but in the dwarf chameleon *Bradypodion*, diet is not estimated as a major driver of variation in cranial morphology, even though these species show an important dietary overlap (Da Silva et al. 2016).

Differences between male and female skulls are often associated with sexual differences in behavior (Herrel et al. 1995b, 1999b, 2001b; Verwaijen et al. 2002; Herrel et al. 2007a, b; Vanhooydonck et al. 2010; Da Silva et al. 2014; Naretto et al. 2014; Wittorski et al. 2016; Dollion et al. 2017; Taylor et al. 2017). For example, Herrel et al. (2007a, b) showed that skull shape and bite performance differ between female and male *Anolis carolinensi*s. Males have larger heads due to larger jaw adductor muscles and bite harder. Dollion et al. (2017) demonstrated a link between skull morphology, bite force and diet among a large majority of *Bradypodion* species, but this link is influenced variably by sexual selection among the studied species. They concluded that: "…. *Sexual selection plays a role in driving the evolution of bite force and head shape. These data suggest that ecomorphological relationships may be sex-dependent.*"

As briefly reviewed above, the effects of many different environmental and historical factors on skull characteristics have been identified and interpreted in the context of phylogeny, as well as macro- and micro-evolutionary processes. However, we can conclude that diet is considered one major factor affecting skull morphology, performances, and function in lizards. Meyers et al. (2018) demonstrated that: "…*the influence of diet on morphology and performance in lizards may be more striking than previously thought*….". However, a series of lizard lineages and species remains to be studied to show the trade-off between several functions in the diversity of morphological and functional responses of the trophic system in these tetrapods.

13.5 The Hyo-Lingual System

Since the most recent revision of lizard tongue morphology (see Schwenk 2000 for revision), a large number of papers have compared the hyo-lingual system in various lizards (i.e., Schwenk 2000; Wassif 2001, 2002; Iwasaki 2002; Jarrar and Taib 2004; Herrel et al. 1999a, 2005; Koca et al. 2007; Abbate et al. 2009, 2010; Jamniczky et al. 2009; Cizek et al. 2011; Darwish 2012; Herrel et al. 2014; Zghikh et al. 2014; McMahan et al. 2015; Sabry et al. 2015; AL-Fartwsy et al. 2016; El-Bakry and Hamdi 2016; Yang and Wang 2016; Baeckens et al. 2017b; El Mansi and Fouda 2017; Sheren et al. 2018). Figures 13.3 and 13.4 provide typical examples of lingual morphology in iguanian and gekkotan lizards. The position of the tongue within the buccal cavity is rather different (See Schwenk 2000 for a description of the lingual morphology; Fig. 13.4).

Lingual prehension is used in a wide variety of lizard species with diverse tongue morphology (Fig. 13.5). The relationship between tongue morphology and feeding behavior has been studied in two main ways. On one hand, tongue morphology has been correlated with movements, and on the other hand, with adhesive mechanisms during prey capture that permit the fore tongue to pin the prey and/or move it toward the buccal cavity (Schwenk and Bell 1988; Schwenk 2000; Reilly and McBrayer

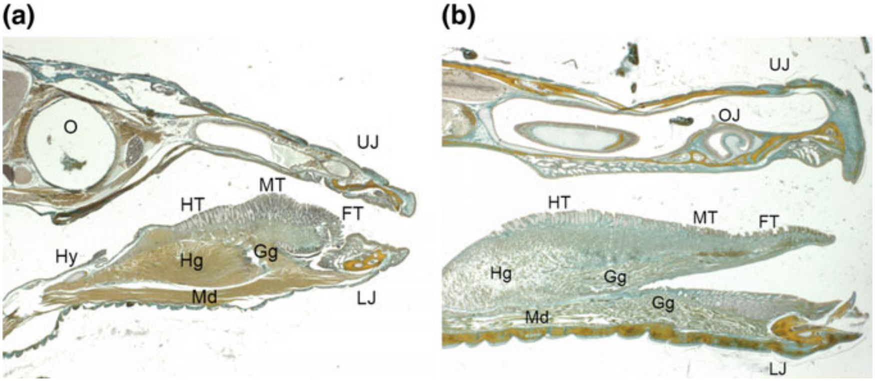


Fig. 13.3 Comparison of lingual morphology in *Anolis carolinensis* (**a**) and *Phelsuma madagascariensis* (**b**) FT: fore tongue; Gg: M. genioglossus; Hg: M. hyoglossus; HT: Hind tongue; Hy: hyoid; LJ: Lower jaw; MT: Mid-tongue; Md: M. mandibulohyoideus; O: orbit; OJ: Jacobson's organ; UJ: upper jaw

2007; Brau et al. 2016; Bels et al. 2019). The latter approach has been particularly well developed in chameleons and will not be covered in detail in this chapter (Zood 1933; Smith 1986; Schwenk and Bell 1988; Wainwright and Bennett 1992a, b; Herrel et al. 2001c, 2002, 2009; de Groot and van Leeuwen 2004; Anderson and Deban 2010; Lu et al. 2017; Singh et al. 2012; Fouda et al. 2015; Anderson 2016; Brau et al. 2016; Moulton et al. 2016; El Mansi and Fouda 2017; El Mansi and Fouda 2017; Lu et al. 2017). Schwenk and Bell (1988) suggest that: "*The extreme form of tongue protrusion we observed in an agamid lizard represents a functional intermediate between the plesiomorphic condition found in Sphenodon, Iguanidae, and Agamidae (most of the time), and the highly derived lingual projection of Chamaeleontidae. In this light, the chamaeleontid mechanism may be viewed as the end result of a three part transformation series…The transformation series above represents both a possible evolutionary sequence leading to the chamaeleontid projection mechanism and also a kinematic sequence exhibited by an individual chameleon during prey capture. Thus, the kinematic sequence of chameleon tongue projection recapitulates its phylogeny or evolutionary sequence*."

Comparative analyses show that lingual deformation during prey capture differs between iguanian and agamid lizards. Figure 13.6 shows deformation of the tongue a classical prey capture in *Pogona vitticeps* (Agamidae) and Fig. 13.7 in *Anolis carolinensis* (Iguanidae). Schwenk and Throckmorton (1989) proposed that tongue movement during protrusion differs between Agamidae and Iguanidae: "*In iguanids…the tongue is curled within the mouth so that the ventral pallets come to lie with their ventral surfaces directed dorsally. In agamids… the ventral pallets are placed ventral side on the tip of the mandible while the tongue deforms around them.*" In parallel, Smith (1988) confirmed that: "*the tongue in most agamids is derived relative to that in other squamates. In some features, such as the vertical connective tissue septa, agamids share primitive features with Sphenodon. Some conditions*

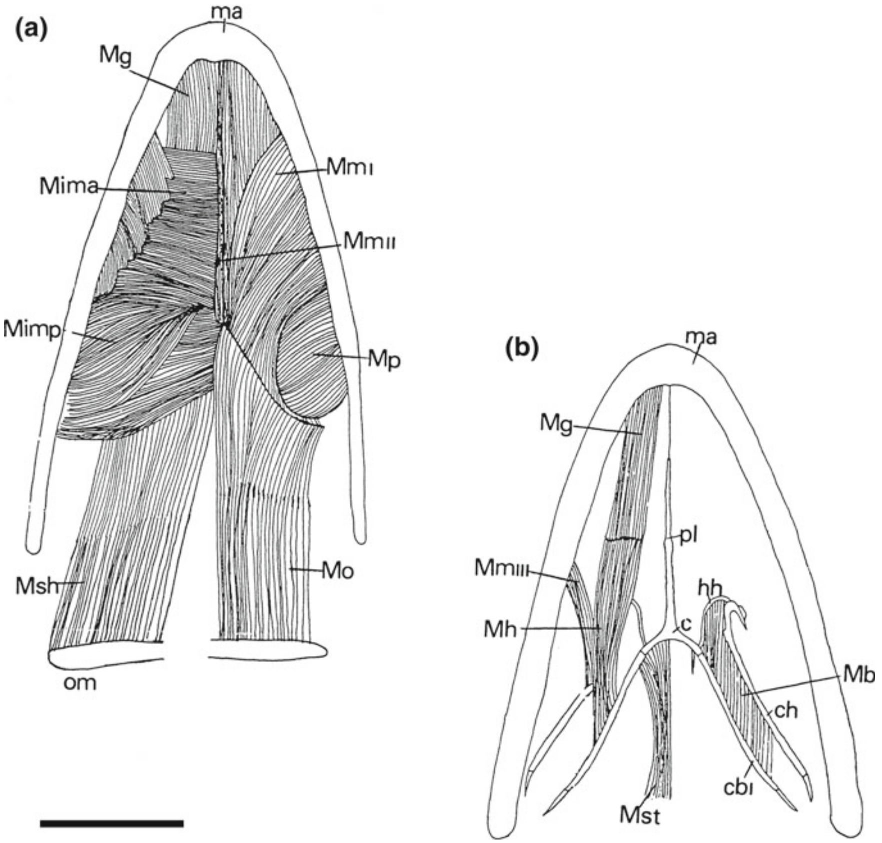


Fig. 13.4 Schematic ventral view of the extrinsic tongue hyo-lingual musculature and hyoid apparatus in *Phelsuma madagascariensis*. The muscles are presented layer by layer with the more superficial layers on the left in **a** and the more profound layer on the right in **b**. **a** Superficial muscular layers. **b** Profound muscular layers after removal of the layers presented in **a**. The elements of the hyoid apparatus are the following: c hyoid body; cbI ceratobranchial I; Ch ceratohyal; hh; hypophyal; pl lingual process. The ceratobranchials II are represented by the short element in the more profound layer in **b**. Ma mandible. Om: scapula. The represented muscles are: Mb m branchiohyoideus; Mg m. genioglossus; mh hyoglossus; Mima m. intermandibularis anterior; Mimp m. intermandibularis posterior; Mo m. omohyoideus;Mm I Mm II MnIII m. mandibulohyoideus I and m. mandibulohyoideus II; Mo m. omohyoideus; Mp m. pterygoideus; Msh m. sternohyoideus ; Mst m. sternothyroideus

Fig. 13.5 Lingual deformation during tongue protrusion in *Iguana iguana* during food capture

found in agamids are also found in anoline iguanids. Two genera, Uromastyx and and Leiolepis, differ significantly from other agamids in intrinsic tongue musculature. The functional significance of the unique tongue morphology is that agamids utilize a different mechanism of tongue protrusion from that of other lizards. This mechanism involves the production of force against the lingual process, leading to an anterior slide of the tongue." Relating muscular properties to its functional role in all feeding stages remains a key point. In *Pogona vitticeps,* Zghikh et al. (2014) concluded that: "*…Histoenzymology demonstrates that protractor and retractor muscles differ in fibre composition. The proportion of fast glycolytic fibres is significantly higher in the M. hyoglossus (retractor muscle) than in the M. genioglossus (protractor muscle), and this difference is proposed to be associated with differences in the velocity of tongue protrusion and retraction (5 ± 5 cm* s^{-1} *and 40 ± 13 cm* s^{-1}*, respectively), similar to Chamaeleonidae.*" However, combined morphological and biomechanical studies remain rather scarce. Therefore, more experimental studies are needed to confirm the "*form-performance*" link characterizing the hyo-lingual system of squamate lizards.

Typically, the fore tongue surface always touches the prey/food and pins it down on the ground, and then retracts backward toward the buccal cavity through various mechanisms (Schwenk and Bell 1988; Urbani and Bels 1995; Schwenk 2000; Reilly and McBrayer 2007; Montuelle et al. 2012a; Brau et al. 2016; Bels et al. 2019). But this lingual role in feeding is balanced by its role in vomerolfaction, drinking, and specialized behavior (i.e., eye lapping). Overall, fore tongue traits (i.e., degree of forkedness, musculature, papillae) are simultaneously related to both feeding and for-

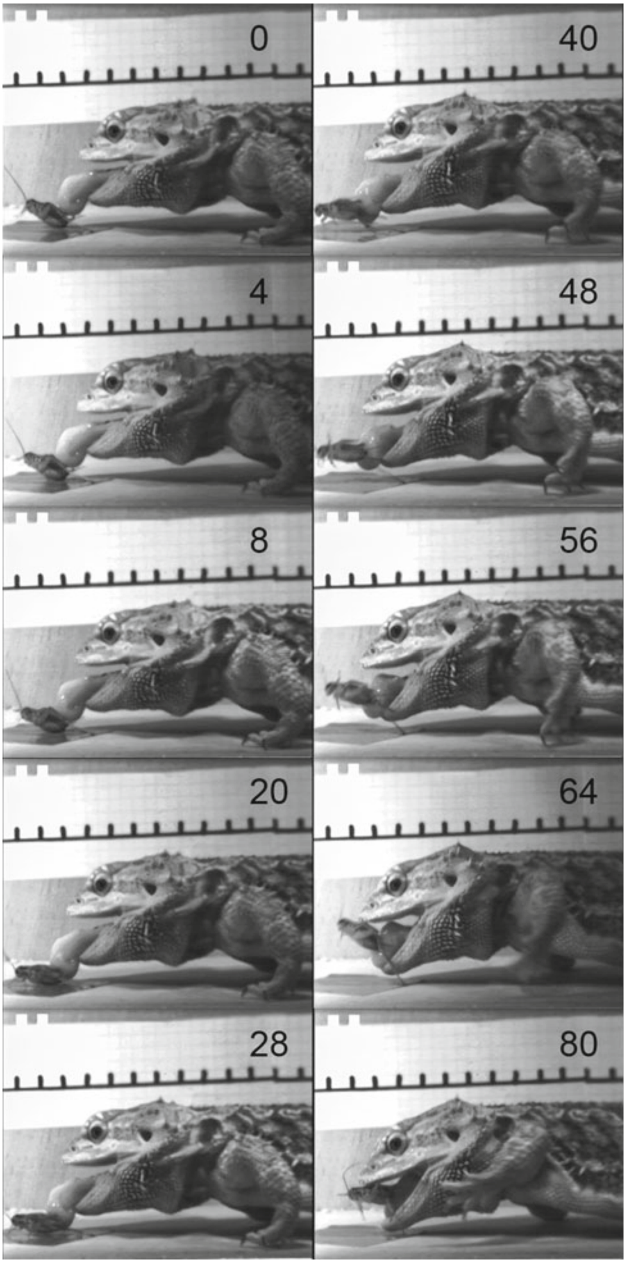


Fig. 13.6 Lingual deformation during tongue protrusion in *Pogona vitticeps* during prey capture. The tongue is maximally protruded contacts and pins the prey on the substratum from tile 0 (contact) to 28 ms. Active retraction and tongue recovering its shape and position in the buccal cavity from time 40 to 80 ms. The contact between the prey occurs from time 28 to 40 ms. The prey is pin and slightly moves forward on the substratum during lingual prehension. Time is given in ms

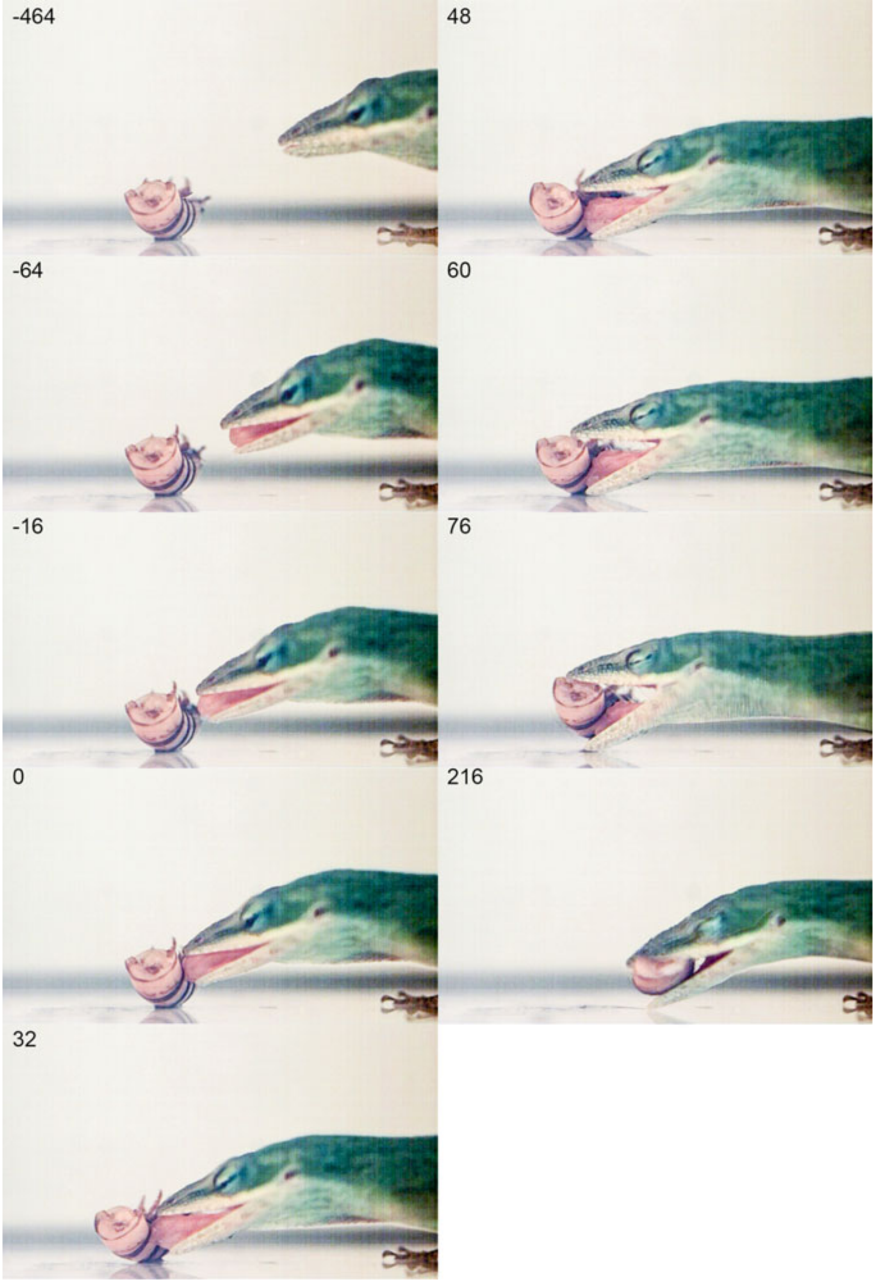


Fig. 13.7 Lingual protrusion and retraction (with food) in *Anolis carolinensis* capturing piece of insect (mealworm). The time is given in ms. This series of frames shows that the tongue is not protruded so far as shown in *Pogona vitticeps* (Fig. 13.6) and *Iguana iguana* (Fig. 13.5)

aging behaviors (e.g., vomerolfaction). Several authors have discussed the evolution of squamates by functionally linking tongue morphology with its use for vomerolfaction and prey capture (Bels et al. 1994, 2019; Schwenk 2000; Reilly and McBrayer 2007). Reilly and McBrayer (2007) suggested that: "*…From the primitive pattern of tongue and jaw prehension and visual prey recognition in Sphenodon, lizards have radiated into five basic trophochemosensory patterns (Iguania, Gekkota, Scincoidea, Lacertoidea, Anguimorpha)…*". Similarly, Baeckens et al. (2017b) concluded that for Lacertidae: "*interspecific variation indicating that the chemosensory system of lacertids has undergone substantial change over a short evolutionary time. Although our results imply independent evolution of tongue and vomeronasal-organ form, we find evidence for co-variation between sampler and sensor, hinting towards an 'optimization' for efficient chemoreception. Furthermore, our findings suggest species' degree of investment in chemical signalling, and not foraging behaviour, as a leading factor driving the diversity in vomeronasal-lingual morphology among lacertid species.*"

Obviously, the overall shape of the mid- and hind tongue and their surface properties (papillae), in particular, have been tentatively discussed in relationship with food/prey transport (see below). But this role still remains rather unknown: How does the tongue move under the prey? How does its surface interact with the complex structures of the prey? Do prey characteristics modulate these movements? And if so, how? Based on lingual morphology, several authors have speculatively discussed the role of the tongue in these phases. In their study of lingual morphology in *Iguana iguana*, Abbate et al. (2008) reported that: "*Each surface plays successive roles during food ingestion, intrabuccal transport, and swallowing* (Delheusy et al. 1994; Iwasaki 2002). *The mucous inter-papillary spaces would serve to ensure the adherence between the tongue and the food, the smooth epithelium could facilitate movements of the prey toward the pharynx, and conical papillae of the hindtongue present a rough surface which could act on the prey during the swallowing phase* (Herrel et al. 2005). *Different functional roles could be hypothesized for the three tongue areas: the tongue tip could have a role related to the movements of the prey immediately after the capturing, while the middle papillae and the hindtongue could have an important role concerning the swallowing phase.*" In their morphological study of the tongue in *Uromastyx aegyptia*, Al-Ahmady Al-Zahaby et al. (2017) showed that: "… *The distribution and orientation of the muscle fibers prove that the tongue is able to catch the prey by biforked tip and facilitate the swallowing behaviour.*"

The hyoid apparatus is the main element of the trophic system used in lizard display (Bels et al. 1994; Smith 1986; Schwenk 2000). The motor pattern of all of the display behaviors is related to a similar motor pattern primarily based on the contraction of the M. branchiohyoideus (M. ceratohyoideus) relating the ceratohyal and the ceratobranchial of the hyoid apparatus in a first-order lever. The diversity of the hyoid morphology produces diverse visual signals (Fig. 13.8) as has been largely described in the literature (van Geldern 1919; Gnanamuthu 1937; Avery and Tanner 1971; Smith 1982, 1988; Font and Rome 1990; Bels 1990, b, 2000; Bels et al. 1994, 1995; Meyers et al. 2002b; Rosen et al. 2004; Ord et al. 2015; Hagman and Ord

Fig. 13.8 Example of visual signal produced by movement of the hyoid apparatus in *Iguana iguana*

2016). Bels (2000) suggested that the display signal is related to the hyoid elements at two levels: (i) the shape of the hyoid system and (ii) and the molecular components of the hyoid apparatus. He shows that the calcification of the ceratobranchials II in Iguanidae probably plays a key role in its deformation and consequently on the visual signals. These data need to be confirmed through analysis of the calcification process of these hyoid elements in lizards with highly different shapes of dewlap and throat signals (see also, Font and Rome 1990) (Fig. 13.8).

Following these observations, Ord et al. (2013) investigated the relationship between the hyoid anatomical properties and dewlap performance in iguanid lizards. They calculated the ratio between the length of the ceratohyal and that of the ceratobranchial II (fulcrum ratio), which they compared to dewlap performance such as dewlap speed. Supporting the role of the diversity of hyoid anatomy on the visual signals (Bels 2003), these authors show that change in anatomical properties (e.g., length) of the hyoid elements led to differences in dewlap speed among *Anolis* species from various islands. The properties (i.e., fiber typing) and contraction velocity of the muscle M. branchiohyoideus (see Fig. 13.3) may play a key role in production and variation of this signal (Font and Rome 1990). In their histochemical study of this muscle in *Anolis carolinensis*, Rosen et al. (2004) concluded that: "…*males had a greater percentage of tonic fibers than females, whereas females had a greater percentage of SO fibers than males. The high proportion of FOG fibers in the anole ceratohyoideus makes it similar to other relatively fatigue-resistant muscles used in movements of moderate speed and duration. Although the precise role of tonic fibers in dewlap extension is not known, the greater percentage of these fibers in the* *male ceratohyoideus might be required to stabilize or maintain extension of the large dewlap apparatus in males.*"

13.6 Food Capture

Prey capture is a complex behavior defined as "…*the apprehension and subjugation of a prey item and ingestion is its movement from the environment into the oral cavity*…" (Schwenk 2000). Various ways have been used to describe prey capture in lizards and identify the motor actions of the trophic system during capture of living prey. Kinematic profiles and variables (Figs. 13.9 and 13.10) have been recorded in numerous lizard species catching various types of prey to compare kinematic profiles among various prey items (i.e., Moermond 1981; Smith 1984; Schwenk and Throckmorton 1989; Bels 1990b; Bels and Goosse 1990; Delheusy and Bels 1992; Goosse and Bels 1992; Delheusy et al. 1995; Herrel et al. 1995a, 1997a, b, 2000, 2008; Urbani and Bels 1995; Smith et al. 1999; Kardong and Bels 2001; Mcbrayer 2004; Lappin and German 2005; Meyers and Herrel 2005; Schaerlaeken et al. 2007; Schaerlaeken et al. 2012; Montuelle et al. 2009a, b, 2012a, b; Anderson and Deban 2010; Zghikh et al. 2014; Fitzsimons and Thomas 2016; Moreno-Rueda et al. 2017). Traditionally, the studies of prey capture involve kinematics (Figs. 13.9 and 13.10) and/or functional methodology (e.g., electromyography EMG) which provides a description of the sequential actions of the postcranial, cranial, and lingual elements, as recently revised by Bels et al. (2019). Here, we report only a brief description of the two modes of typical prey capture in lizards: lingual prehension and jaw prehension within the various lizard taxa (see Bels et al. 2019, for review).

Briefly, tongue-based prehension in lizards shows three modes of lingual action for a large diversity of food mainly including living and mobile prey. Tongue pinning, tongue active retraction (translational tongue protrusion, sensu Reilly and McBrayer 2007), and ballistic tongue projection are fully described in the literature through a series of kinematic variables (Smith 1982, 1984; Schwenk and Bell 1988; Schwenk and Throckmorton 1989; Bels 1990a, b; Kraklau 1991; Wainwright et al. 1991; Delheusy and Bels 1992; Bels et al. 1994; Urbani and Bels 1995; Smith et al. 1999; Herrel et al. 1995a; Bels 2003; Meyers and Herrel 2005; Schaerlaeken et al. 2007; McBrayer et al. 2007; Anderson and Deban 2010; Montuelle et al. 2010; Brau et al. 2016; Bels et al. 2019). These variables are used to characterize the FAP or MAD. Preliminary comparative analysis shows that lingual prehension in neonate and adult iguanian lizard *Pogona vitticeps* presents a large number of similarities (Bels et al. 2019). However, lingual prehension along the life of the lizards and the factors that can influence the motor pattern (i.e., scaling, environmental factors, cognition) largely remain to be investigated.

A lunge phase (Fig. 13.11) is usually included in the MAP of lizard prey capture. All lizards approach and pause before lunging toward the prey as stated by Montuelle et al. (2008): "…*The approach is initiated from up to almost 20 cm away from the prey and the animals engage in the actual strike at distances varying from 2 to 10*

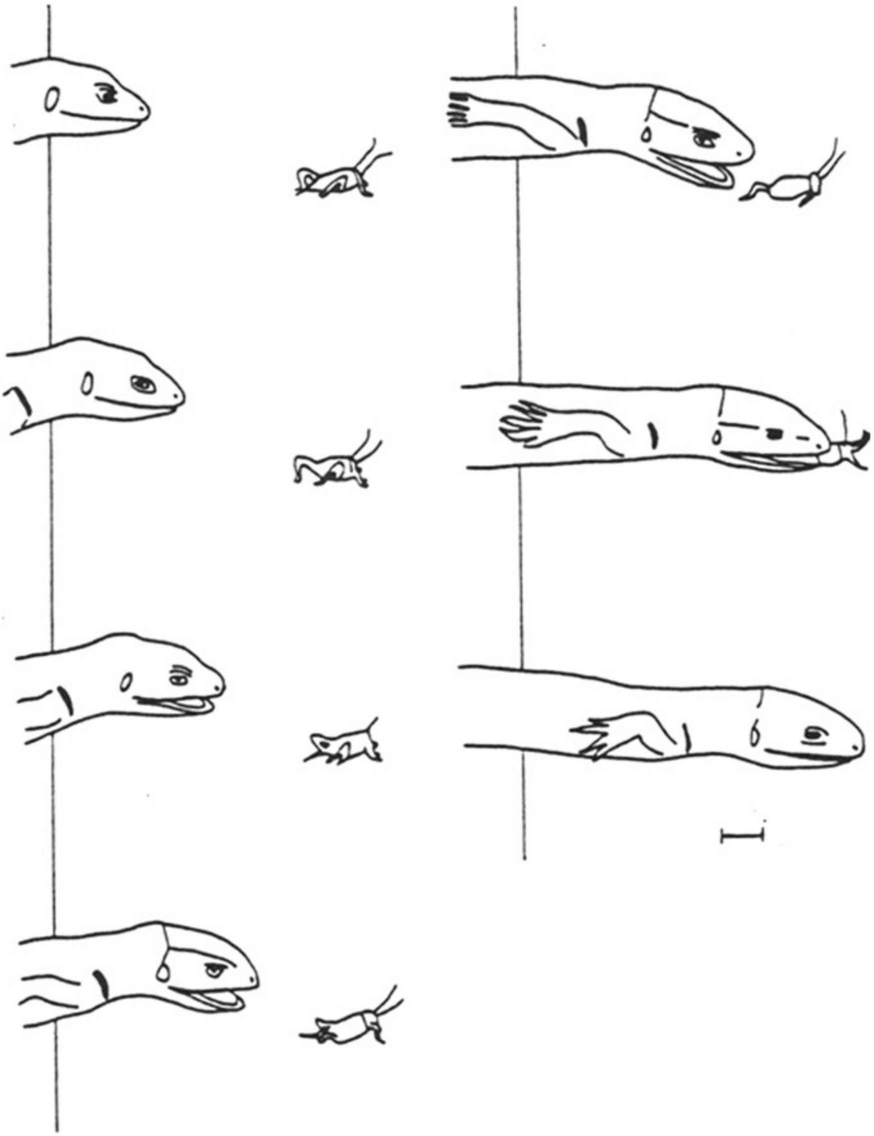


Fig. 13.9 Typical lunge phase in *Lacerta bilineata* preying on mobile insect

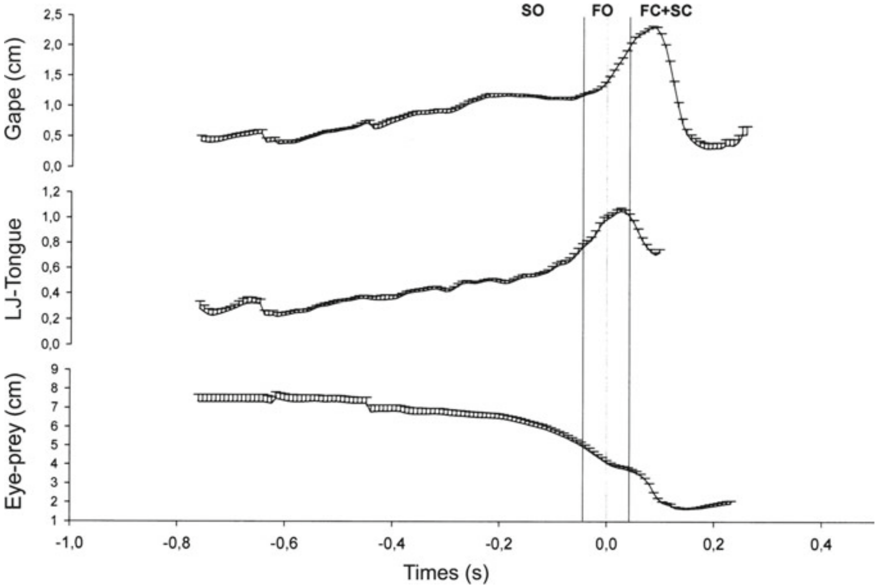


Fig. 13.10 Typical prey capture kinematic profiles (mean ± ESM N = of capture *Acheta domesticus* (25.11 ± 1.53 mm) in *Pogona vitticeps*. The head gape and tongue profiles are similar in all iguanians chasing these anoxious prey items; Gape distance is the distance between tips of lower and upper jaws (cm) LJ-Tongue is the distance between the tip of the lower jaw and the tip of the dorsal surface of the tongue contacting the prey (cm); Eye–prey is the distance between the corner of the eye and a point on the body of the prey (cm). FO Fast opening; FC Fast closing; SC Slow closing; SO Slow opening

cm. When strike initiation distance is reached, the predator pauses to configure its body and strikes at a speed around 50 cm s^{-1}*…*". Frazetta (1983) suggests to distinguish three phases of the attack on prey by lizards using jaw prehension: (i) the rush or the chase "*…where the attacker dashes up to the prey—or pusues it—to within lunging distance*" (Frazzetta 1983), (ii) the lunge or delivery, and (iii) the seizure or grasp (jaw prehension per se). Often, the preparatory phase is primarily described and not quantified. Montuelle et al. (2009a) compare this phase during lingual and jaw prehension in *Gerrhosaurus major*: "*…In prey capture sequences involving the use of the tongue, the lizard stopped closer to the prey compared with those involving the jaws. During the preparatory phase, a distinctive body configuration was associated with each prehension mode… During tongue prehension sequences, the body remained close to the substratum with the vertebral column in an extended horizontal position; in contrast, during jaw prehension the forelimbs were extended, thus elevating the head and neck…*". Several environmental factors likely influence this preparatory phase.

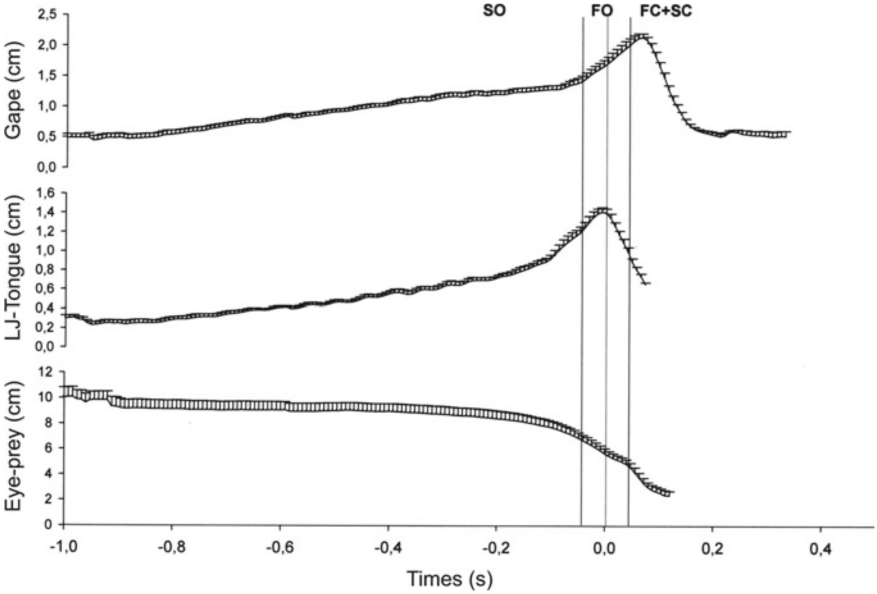


Fig. 13.11 Typical prey capture kinematic profiles of mice capture in *Pogona vitticeps*. FC Fast closing; FO Fast opening; LJ Lower jaw; SC Slow closing; SO Slow opening. See Fig. 13.10 for explanations

13.6.1 Motor Pattern and Evolution

One key point that appears since the early functional studies of prey capture in lizards is the link between the behavioral dichotomy of tongue versus jaw prehension with phylogeny. The evolution of predatory behavior in squamates is linked with the trade-off between the roles of the tongue during prey capture and prey detection (Bels et al. 1994; Cooper 1996; Schwenk 2000; McBrayer et al. 2007; Reilly and McBrayer 2007). Three major hypotheses have been proposed to explain the evolution of predatory capture strategies in lizards. A first hypothesis suggests a dichotomy between the Iguania (Iguanidae, Agamidae, and Chameleonidae), which use tongue-based prehension and visual detection, and the Scleroglossa (all other families), which use jaw-based prehension and vomerolfaction (Schwenk and Throckmorton 1989; Schwenk 2000, 2001; Vitt et al. 2003). In this hypothesis, jaw prehension is considered the derived condition, whereas tongue prehension is the ancestral condition, and the tongue in scleroglossan lizards has been modified to be used primarily for chemoreception (Iwasaki 2002). According to this hypothesis, Gekkota uses jaw prehension (Montuelle and Williams 2015) although these lizards mainly use nasal olfaction for prey detection (Vitt et al. 2003). Tongue prehension in scleroglossan lizards (Urbani and Bels 1995; Smith et al. 1999; Montuelle et al. 2009a) is considered to be a secondarily derived condition (Schwenk 2000), but one that is not considered homologous to tongue prehension in Iguania. Indeed, Schwenk (2000) stated that "*…lingual feeding in scleroglossans is probably not homologous to lingual feeding in iguanians (and Sphenodon), but was reinvented from a jaw feeding ancestor…*". This hypothesis was suggested before the identification of ventral tongue prehension in Cordylidae (Broeckhoven and Mouton 2013) and numerous recent studies demonstrating lingual prehension in Scleroglossa lizards (references).

A second hypothesis is built upon the phylogenetic relationships based on molecular characters (Vidal and Hedges 2005, 2009). In this hypothesis, molecular evidence rejects the dichotomy between the Iguania and the Scleroglossa, and accordingly, the suggested ancestral mode of food acquisition is jaw-based prehension, with tongue-based prehension evolving in the Iguanian clade. Vidal and Hedge (2005) stated that: "*As the iguanians are the only squamate lineage using tongue prehension of food, and are highly nested within squamates, we can robustly infer that they have lost the jaw prehension trait used by all other squamate lineages, and have secondarily acquired their* tongue prehension trait…". These findings are supported by Townsned et al. (2004) who explained that: "*iguanians and* Sphenodon (*or some possibly distant ancestor to* Sphenodon) *are inferred to have acquired lingual prey-prehension techniques independently.*" These authors also suggested that: "*…Even if lingual prehension is assumed to be the ancestral lepidosaurian condition, it is possible that the similar feeding behavior and tongue morphology of* Sphenodon *and iguanians represent homoplasy rather than homology.*"

A third hypothesis is based upon combining morphological and functional characteristics of the lingual system in prey capture and vomerolfaction (Bels 2003; McBrayer et al. 2007; Reilly and McBrayer 2007). In this hypothesis, ancestral squamates are proposed to have the ability to use lingual-based and jaw-based prehension, depending on the properties of the prey (see Fig. 10.5 in Reilly and McBrayer 2007; see Bels et al. 2019 for discussion). This is based on the observation of prey capture in the sister group of squamates: *Sphenodon* (Gorniak et al. 1982). In this hypothesis, the Iguania would have lost jaw-based prehension, and retained only tongue-based prehension with an evolutionary transformation. In details, Reilly and McBrayer (2007) considered that Iguania developed "*translational tongue protrusion*" that is "*…derived tongue protrusion system that is morphologically and kinematically different from tongue prehension…*" (Reilly and McBrayer 2007, p. 306). This mode of prey/food capture is unique because "*contraction of specialized tongue muscles (hyoglossus, genioglossus, verticalis, circular fibers) pushes (translates) the tongue along a long (>50% tongue length), tapered lingual process (hyobranchial rod) to protrude the entire tongue beyond the jaws*" (Wagner and Schwenk 2000). For these authors, this modality of tongue movement is different compared to the ancestral tongue prehension that is retained in Scincoidea and Gekkota. However, all kinematic studies show that arboreal and terrestrial Gekkota only use their jaw for solid (prey) food (see, for example, Delheusy et al. 1995; Delheusy and Bels 1999), but their tongue for liquid (i.e., nectar). The Gekkotan tongue is proposed to be morphologically specialized for drinking (see below) and eye licking or wiping, although Reilly and McBrayer (2007) also noted that: "*…this (eye licking) is the primary function of the tongue and may actually conflict with direct aerial chemosensory and* *feeding function*." The ancestral mode of tongue prehension with dorsal surface of the fore tongue is retained in Gerrhosauridae (Urbani et al. 1995; Montuelle et al. 2012a) and Scincidae (Smith et al. 1999). Reilly and McBrayer (2007) discussed the question of the role of the tongue in this latter group. Tongue prehension is completely lost in three families of the Autarchoglossa (Lacertiidae, Teiidae, and Xantusiidae), in which tongue-based prehension capabilities probably diminished with the enhancement of vomerolfactive abilities to check their habitat, including finding prey and conspecifics.

This hypothesis supports the conclusion of Bels (2003) who described four modes of prehension in lizards (Bels et al. 2019): (i) tongue pinning, (ii) tongue active retraction, (iii) ballistic tongue, and (iv) jaw prehension. Reilly and McBrayer (2007) suggested that the ancestral character state involves jaw prehension with fast opening. "*Tongue active retraction*" (Bels 2003; Bels et al. 2019) and "*translational tongue protrusion*" (Reilly and McBrayer 2007) correspond to a similar motor pattern (MAP, Figs. 13.10 and 13.11). Prey capture can be defined as a FAP or MAD defined in classical ethology (Tinbergen 1952; Bels 2003).

Without active retraction of the prey, the prey/food is only pressed on the substratum and the jaws advance onto the prey when the gape is at its peak opening (Bels 2003). Tongue pinning occurs as a capture mode per se (Bels et al. 2019) and always occurs as soon as the mass of the tongue touches the prey (Fig. 13.5), but also likely occurs in any other modes of lingual prehension (Fig. 13.3 in Bels 2003; as shown in Figs. 13.6 and 13.7), since it allows the tongue to adhere to the prey. The role of the tongue in squamate ancestors probably was either to press the prey/food on the substratum and/or to slightly retract it into the buccal cavity (references). The properties of the selected prey probably play a key role in the tongue movement in relationship with its muscular characteristics (see Figs. 13.3 and 13.4).

Behavioral specialization can modify the lingual motor pattern. This is evident in the study of Cordylidae showing that prey selection drives a major change in lingual movement. In this lizard family, Broeckhoven and Mouton (2013) concluded that: "*the consumption of termites in O. cataphractus has resulted in the evolution of a novel lingual prehension mode, during which the ventral surface of the tongue is used to apprehend prey. This is in contrast to other lizards, which use the dorsal surface of the tongue to contact prey. Moreover, we demonstrated that this novel lingual prehension mode is accompanied by distinct morphological elaborations of the tongue surface.*" However, the question of evolution of ventral tongue prehension in Cordilydae remains to be debated. Towsend et al. (2004) present one novel scenario on the evolution of capture per se (not feeding) in lepidosaurians based on their phylogenitc study. They suggest the prey/food capture is "*more labile*" along the squamate tree (Towsend et al. 2004). For these authors: "*Lingual feeding evolved at least twice, once either in the lineage leading to* Sphenodon *or in a common ancestor of* Sphenodon *and squamates (allowing uncertainty in the outgroup designations), and once in an ancestor to Iguania.*"

13.6.2 Lingual Adhesion

The properties of the mucus secreted by the fore tongue that contacts the prey are probably critical for successful prey capture. In the iguanian *Oplurus cuvieri*, Delheusy et al. (1994) confirmed that: "…*The epithelium of the papillae is composed of cells filled with secretory granules. Each surface plays successive roles during food ingestion, intra-buccal transport, and swallowing. The mucous interpapillary spaces would serve the adherence between the tongue and the food.*" A strong adhesion between the fore tongue and the prey is required during the retraction phase in all lizard species using lingual prehension. Tongue–prey adhesion in lizards can be explained by various mechanisms such as interlocking with self-adjustment between prey surface and tongue for physical crosslinks, suction mechanism, and wet adhesion (Schwenk 2000, Herrel et al. 2000; Vitt et al. 2003; Higham and Anderson 2013).

Only a few experimental analyses provide data to explain prey–tongue adherence, however, and most focus on chameleons. Herrel et al. (2000) explained that: "*It is generally thought that chameleons, like other iguanians, rely on serous and mucous secretions and on interlocking to hold the prey on the tongue after capture* (Bramble and Wake 1985; Bels et al. 1994)." In addition, they confirmed that: "*suction plays an important role in the mechanics of chameleon tongue prehension…. Clearly, a suction process is enabled by the rearrangement of the intrinsic tongue musculature in chameleons so that the tongue pad can be withdrawn to form a pouch-like structure. Interestingly, an evolutionary precursor for this unique arrangement of the intrinsic musculature (a modified arrangement of the fibres of the m. hyoglossus) may be present in agamid lizards (K. Schwenk, personal communication; note that this depends on the nature of the relationship between chameleons and agamids). The withdrawal of the tongue pad and the subsequent formation of a pouch not only create suction forces on the prey, but also increase the adhesive properties of the tongue considerably, presumably by increasing the contact surface area and possibly by reorientating the tongue papillae (resulting in increased interlocking).*"

Recently, a dynamic model for viscous adhesion has been proposed for prey capture in chameleons (Brau et al. 2016). This model is based on measurements of the viscosity of the mucus produced at the fore tongue (tongue pad), although this secretion remains to be biochemically characterized. In this model, the viscosity of the fore tongue secretion is about 400 times larger than that of human saliva. Using this model, the maximum prey mass that can be held by the fore tongue is calculated as follows (Fig. 13.12):

$$m_{\mathrm{p}}^{*} = \rho V^{*} = \frac{9}{64\pi^{2}} \frac{\eta^{2} \Sigma^{4}}{k d^{2} h_{0}^{4}}$$

In this equation, V = the prey volume; ρ = typical prey density; $\eta = 0.4 \pm 0.1$ Pa. The morphological parameters, k, Σ, and m_t depend on the snout-vent (SVL) length, L_{SVL}. For Chameleons, Brau et al. (2016) estimate SVL between 50 and 200 mm,

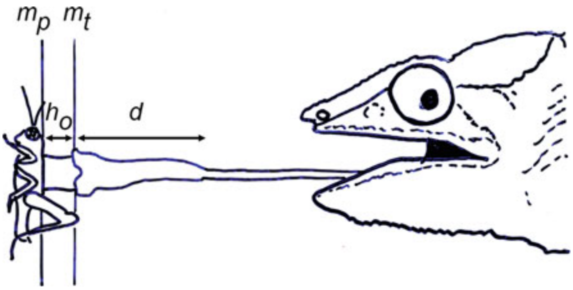


Fig. 13.12 Chameleon schema of prey capture (modified from Brau et al. 2016) used to build the model proposed by Brau et al. (2016). h_0 the initial thickness of the mucus; m_p prey mass; m_t tongue mass; *d* distance

and h_0 the initial thickness of the mucus layer = 50 ± 10 mm. The authors suggest that $k = 223\ (\pm 60)\ L_{SVL}$, $\sum = 4.8\ (\pm 1.2)\ 10^{-3}\ L^2_{SVL}$, and the mass of the tongue $m_t = 0.45\ (\pm 0{:}09)\ L^3_{SVL}$ (MKS units). The retraction force applied on the prey at a distance linearly scaling with chameleon L_{SVL} is $d = 0.2\ (\pm 0.1) L_{SVL}$.

Using these parameters, the equation can be written as a function of the animal body size:

$$V^{*1/3} = (1.2 \pm 0.6) L^{1.4}_{\mathrm{SVL}}$$

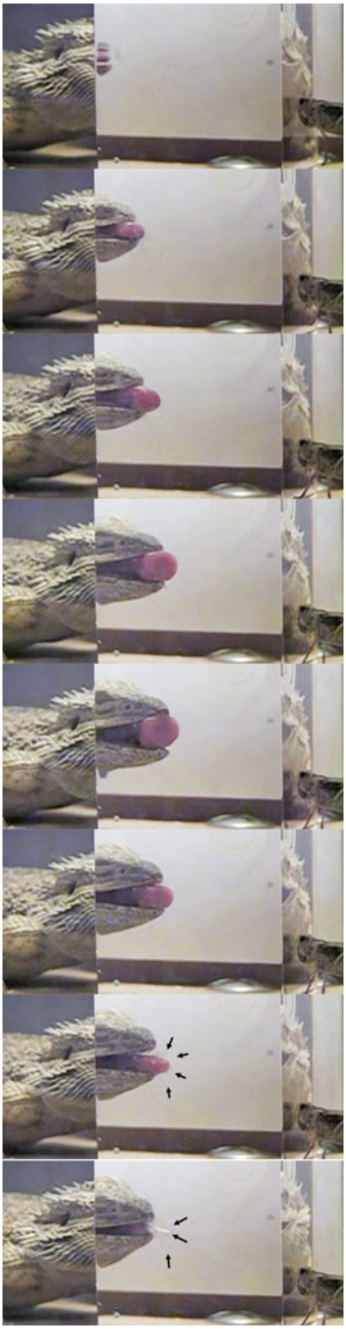
Because the mass of the captured prey reported for various chameleon species is always under that calculated with this model, Brau et al. (2016) concluded that: "…*Viscous adhesion alone is therefore largely sufficient to allow capture of very large prey.*"

The dynamic model based on viscoelasticity of the mucus remains to be tested in all other lizards using tongue prehension (Fig. 13.13). The role of tongue retraction for carrying the prey into the oral cavity can be hypothesized to be rather similar in all iguanian lizards (and possibly scleroglossans using lingual prehension), although it may also be affected by differences in morphological features such as the nature of secretion, the number of cells along the tongue papillae, the number and type of muscle fibers, etc. Comparative analyses of the surface of fore tongue suggest that production of various secretions can play a key role in such viscous adhesion. But how the tongue retracts the prey into the buccal cavity in Cordylidae and Scincidae remains to be investigated. Even more so, in the case of lizards using the ventral surface of the tongue to capture food (Broeckhoven and Le Mouton 2013), does viscoelasticity vary between dorsal and ventral surface?

13.6.3 A Scenario…

Townsend et al. (2004) explained that: "*lingual prehension is assumed to be the ancestral lepidosaurian condition, it is possible that the similar feeding behavior and tongue morphology of* Sphenodon *and iguanians represent homoplasy rather than*

Fig. 13.13 Series of frames showing the deformation of the fore tongue during its expansion on the prey in *Pogona vitticeps*. The prey is presented to the lizard through a prism permitting images of the tongue at prey contact to be obtained. Only the dorsal surface of the fore tongue contacts the prism to show its potential deformation (instead of the prey). The mucus (black arrows) is produced by the fore tongue as soon as lingual contact occurs between the tongue and the prey. The arrows indicate the mucus produced by the lizard tongue



homology." Figure 13.14 proposes a schematic evolution scenario of prey capture in lizards based on morphological, functional, and behavioral data within the context of a recent phylogenetic relationship proposed for lizards (Reeder et al. 2015). In accordance with previous hypotheses (Bels 2003; Reilly and McBrayer 2007), we suggest that prey/food is captured either by lingual or prehension in ancestral lepidosaurians probably depending on prey/food properties. The MAPs of jaw opening present an opening–closing profile and head movement (lunge, see Figs. 13.8 and 13.9) toward the prey/food. The opening phase is controlled with regular gape increase at various speeds (called FO, Fig. 10.3, Reilly and McBrayer 2007) associated with various amplitudes of tongue protrusion, if any in the case of strict jaw prehension. This condition is proposed to be illustrated by several families including Scincidae, Cordylidae, and Gerrhosauridae. In Agamidae and Iguanidae, this condition is also retained with the tongue used to pin the prey and limited active retraction at various degrees (translational tongue protrusion, Reilly and McBrayer 2007). In all of these lizards, the tongue is slightly protracted to pin the prey on the substratum (Urbani and Bels 1995; Bels 2003) or is able to retract the prey/food as in Scincidae (Smith et al. 1999), Agamidae (i.e., *Acanthosaura* sp., Bels et al. 2019), and even *Anolis* (Fig. 13.6; Montuelle et al. 2008).

The movements of the tongue outside of the buccal cavity can be understood to be in agreement with the morphological properties of the tongue in Agamidae (Smith 1982) and the scenario proposed by Schwenk and Bell (1988), who suggested that "*protrusion with hyoid protraction and limited lingual translation caused by extrinsic muscles; little or no activity of verticalis musculature; only tongue tip curls ventrally (the primitive state).*" Active tongue retraction (translational lingual protrusion, Reilly and McBrayer 2007) is probably related to some morphological and functional innovations as demonstrated by Reilly and McBrayer (2007). This is also supported by Reilly and McBrayer (2007) who stated that "…*the key innovation of lingual translation varies within Iguania.*" In most lizards that capture food with tongue prehension, the dorsal papilose surface of the tongue always touches the prey/food. However, some Cordylids have recently been reported to be able to use the ventral surface of their tongue (Broeckhoven and Le Mouton 2013). In contrast, all iguanian lizards used the dorsal surface of the tongue to drink and to collect chemical information from the substratum. Dynamic viscous adhesion probably limits the prey/mass selected by the lizards, but this mechanism appears to be sufficient for all prey selected as demonstrated in chameleons (Brau et al. 2016). This suggestion of the ancestral condition is not problematic, because both modes of prehension are variably present in the closest outgroups to lepidosaurs (i.e., birds, turtles, and crocodilians).

During lizard evolution, the functional constraint associated with the ability to detect chemicals via chemoreception has a strong effect on tongue morphology and its functional and behavioral performance (Toubeau et al. 1994). In Lacertidae, Baeckens et al. (2017b) demonstrated: "*co-variation between sampler and sensor, hinting towards an 'optimization' for efficient chemoreception*" and concluded that "*species' degree of investment in chemical leading factor driving the diversity in vomeronasal-lingual morphology signalling, and not foraging behavior.*" In some

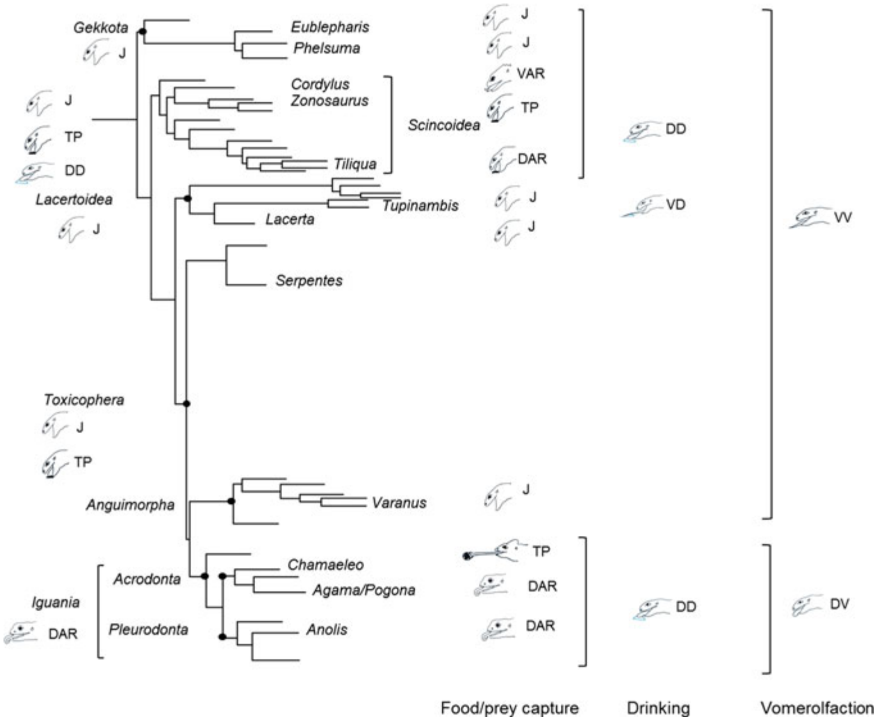


Fig. 13.14 Schematic cladogram showing a proposed evolutionary scenario in lizards. All lizards use their tongue for food transport (and reduction when it occurs). Some species (i.e., *Tupinambis* sp. and *Varanus* sp.) with a highly modified lingual morphology can use their tongue for prey transport at various degrees and are also characterized by inertial feeding (see text for explanations). Probably, the lizard ancestors were able to catch food/prey by using the jaws only or by pinning their food on the substratum (Bels 2003; Bels et al. 2019). They may be able to use "tongue prehension" (Fig. 10.5, p. 314, Reilly and McBrayer 2007) as recorded in *Tiliqua* sp. (Smith et al. 1999). Tongue pinning is a component of the lingual action on the food/prey in all modes of lingual prehension (ventral and dorsal lingual prehension). As soon as the tongue touches the prey on the substratum, the lizard uses active lingual prehension (transational tongue protrusion) can be viewed as a derived mode of the ancestral pinning with possible prey lingual retraction when jaws close on the prey (Bels 2003; Reilly and McBrayer 2007). Except *Tupinambis* sp. (and probably *Varanus* sp.) with highly modified tongue, all lizards use the dorsal surface of their protruded tongue to collect any liquid (water and nectar). Probably, the ancestral mode of drinking was based on this movement including lingual protrusion and fore tongue deformation to reach the liquid (i.e., drops of liquid). In contrast, vomerolfaction is related to contact of the ventral lingual surface on the substratum (the role of tongue flicking in air remains to be investigated, see Goosse and Bels 1992), except in all Iguania that use the dorsal surface of their tongue to collect chemicals. We suggest that lingual movement during tongue pinning, drinking, and vomerolfaction show similar MAP in the lizard ancestors (see text for more explanations). DAR Dorsal Active Retraction; DD Use of dorsal surface of the fore tongue in drinking; DV Use of dorsal surface of the fore tongue in vomerolfaction; J jaw capture; TP tongue pinning; VAR Ventral Active Retraction; VD Use of ventral surface of the fore tongue in drinking; VV Use of ventral surface of the fore tongue in vomerolfaction

families, the anatomical specialization of the tongue modifies the deformation and elongation process and reduces its ability to catch any food/prey items (Smith 1982; Reilly and McBrayer 2007). In such cases, the tongue only plays a functional role during drinking (Bels et al. 1993). In contrast to Reilly and McBrayer (2007) who stated that "*…The ground geckos, the Eublepharidae, are unique among the Gekkota in having lost tongue prehension….*", all Gekkonidae have lost lingual prehension but use their tongue for exploiting liquid food like nectars (Fig. 13.1; see below). Living prey and other solid foods (i.e., fruits) are captured with jaw prehension (Delheusy and Bels 1999). As suggested by Vitt et al. (2003) and Reilly and McBrayer (2007), several behavioral and functional constraints (i.e., noctuarity, eye licking/wiping) probably play a key role in explaining the loss of lingual prehension in Gekkonidae. This evolutionary scenario remains to be explored in association with comparative analysis of tongue morphology and performance in many families of lizards.

13.7 Reduction and Transport

Studies in various lizard species with divergent trophic systems (e.g., skull and hyolingual system) demonstrate that patterns (FAP or MAP) of the intraoral food reduction and transport cycles show many motor similarities, but at the same time, many are modulated by food/prey properties (Throckmorton 1980; Smith 1982, 1984, 1986, 1994; Schwenk 1988; Bels and Baltus 1988, 1987; Schwenk and Throckmorton 1989; Delheusy and Bels 1992; Bels et al. 1994; Delheusy et al. 1995; Urbani and Bels 1995; Herrel et al. 1996, 1997a, b, 1999c, 2001a, b; Kardong et al. 1996; Delheusy and Bels 1999; Elias et al. 2000; Reilly et al. 2001; Montuelle et al. 2009b; Zghikh et al. 2014; Fitzsimons and Thomas 2016). Here, we only discuss the evolution of the transport cycle and not the number of cycles, which can vary between and within species in relationship with to prey properties (i.e., movement of the prey into the buccal cavity when crushing/killing, contact between the prey and the tongue, prey volume, and size).

Figure 13.15 shows a typical cricket processing sequence by the agamid *Acanthosaura capra* showing that the position of the prey is the key factor that separates reduction and transport (Bels and Baltus 1987; Herrel et al. 1996). During reduction cycles, the prey is maintained between the teeth, whereas during transport cycles, it is moved by the protraction–retraction of the tongue through the buccal cavity toward the esophagus. A division of intraoral process into phases (reduction, intraoral transport, swallowing) has been reported in many species (Schwenk and Throckmorton 1989; Kraklau 1991; Herrel et al. 1997a, b; Delheusy and Bels 1992; Urbani and Bels 1995; Smith 1984; Bels and Baltus 1987; So et al. 1992). Sckwenk (2000) compares reduction (chewing) in iguanians and scleroglossans, and his detailed comparative analysis in relationship with morphology (e.g., dentition, tongue) concludes that: "*In most pleurodont and some acrodont species, chewing takes the form of simple puncture-crushing in which the food item is repeatedly crushed between upper and lower teeth with simple, vertical movements of the jaws…*". It can be assumed that reduction cycles (crushing cycles in *Agama stellio*: Herrel et al. 1996, 1997a, b; chewing cycles in Schwenk 2000) derive or are a simple modulatory cycle response of food/prey transport.

The motor pattern of the reduction and transport cycle has been conserved but is also modulated in response to change in prey type (Bels et al. 1994; Schwenk 2000; Herrel et al. 2001a, b). Herrel et al. (2001a) explain that: "*Despite the large variability observed within and among species, some elements of the feeding cycle in lizards do appear to be conserved and corroborate parts of the* Bramble and Wake (1985) *model* (Fig. 13.2)." In each cycle, the movements of the jaws and hyo-lingual apparatus show the classical division in slow opening (SO), fast opening (FO), fast closing (FC, and slow-closing-power stroke (SC-PS) as suggested for transport in all tetrapods (Bels 2003). The SO stage is often divided into SO I and SO II. Except in *Phelsuma madagascariensis* which exhibit long SO II phases between transport cycles, prey transport does not show a consistent SO II stage (Fig. 13.16). Herrel et al. (2001a) emphasize that: "*…in all species examined slow opening phases are present, but this is clearly food type dependent and SO phases do not always occur in every cycle* (e.g., see Delheusy and Bels 1992; Herrel et al. 1999a; Herrel and De Vree 1999; Schwenk 2000). *During this phase the fitting of the tongue to the prey occurs (ensuring an effective subsequent backward prey transport), hence this phase is related to, and might even be determined by, anterio-dorsad tongue movements* (see Bramble and Wake 1985; Herrel et al. 1997a)". In their extensive review of kinematics of gape cycle, McBrayer and Reilly conclude that: "*… all species had some transport gape cycles containing both the SO and FO phases, and overall, it was the predominant pattern observed in 79 kinematic models of prey transport in lizards…. An SO phase has been observed in at least some gape cycles in most lizards investigated to date* (reviewed in Schwenk 2000), *and the outgroup to lizards, rhynchocephalians, show a slow opening phase in reduction and repositioning movements (Figs.* 13.6, 13.7, 13.8 and 13.9, Gorniak et al. 1982; *simple transport cycles have not been analyzed in this taxon). … Therefore, lizards… not only retain the pleisomorphic open-close transport cycle but also commonly insert an SO phase during prey transport.*"

All studies based on X-ray films and EMGs demonstrate that the hyo-lingual protractor and retractor muscular activities produce movements of the tongue and the hyoid apparatus during prey transport. These lingual movements are based on a series of trophic muscles (associated or not with dorsal epaxial muscle activity) allowing synchronization with jaw opening and closing (Smith 1982, 1984, 1986; Herrel et al. 1997a, b, 1999a, b). In both phases, the tongue plays the key role to move the food/prey within the buccal cavity (Bels and Goosse 1990; Herrel et al. 2001a, b). Bels and Goosse (1990) determined the role of the tongue through the description of hyo-lingual movements during intraoral food (locust) transport in *Anolis equestris*: "*When the food item (locust) is within the buccal cavity of the lizard, its mechanical reduction begins. During the SO and the main part of the FO stages, the hyoid elements move forward…. The movement of ceratobranchials I and ceratohyals is more rapid during the FO stage…. The ceratobranchials I move further anteriorly than the ceratohyals so that the two elements seem to be crossed in*

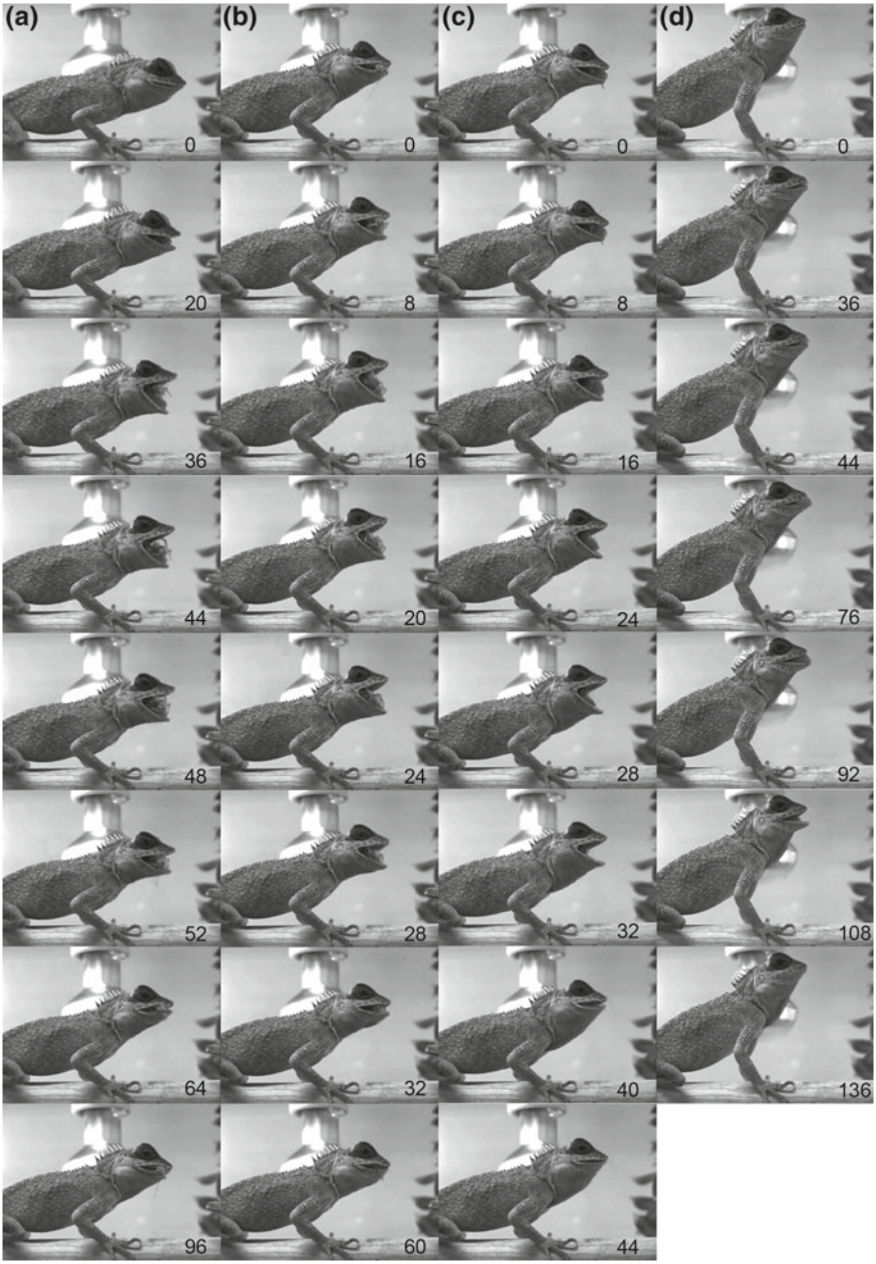


Fig. 13.15 During a typical feeding cycle in *Acanthosaura capra*, the captured prey is repositioned by the tongue **a** reduced, **b** transported, **c** and swallowed **d** lingual cyclic movement (protraction—retraction) within the buccal cavity is related to different modulation of lingual deformation. The lizard changes the body posture along the transport and the swallowing cycle. Time is given in ms

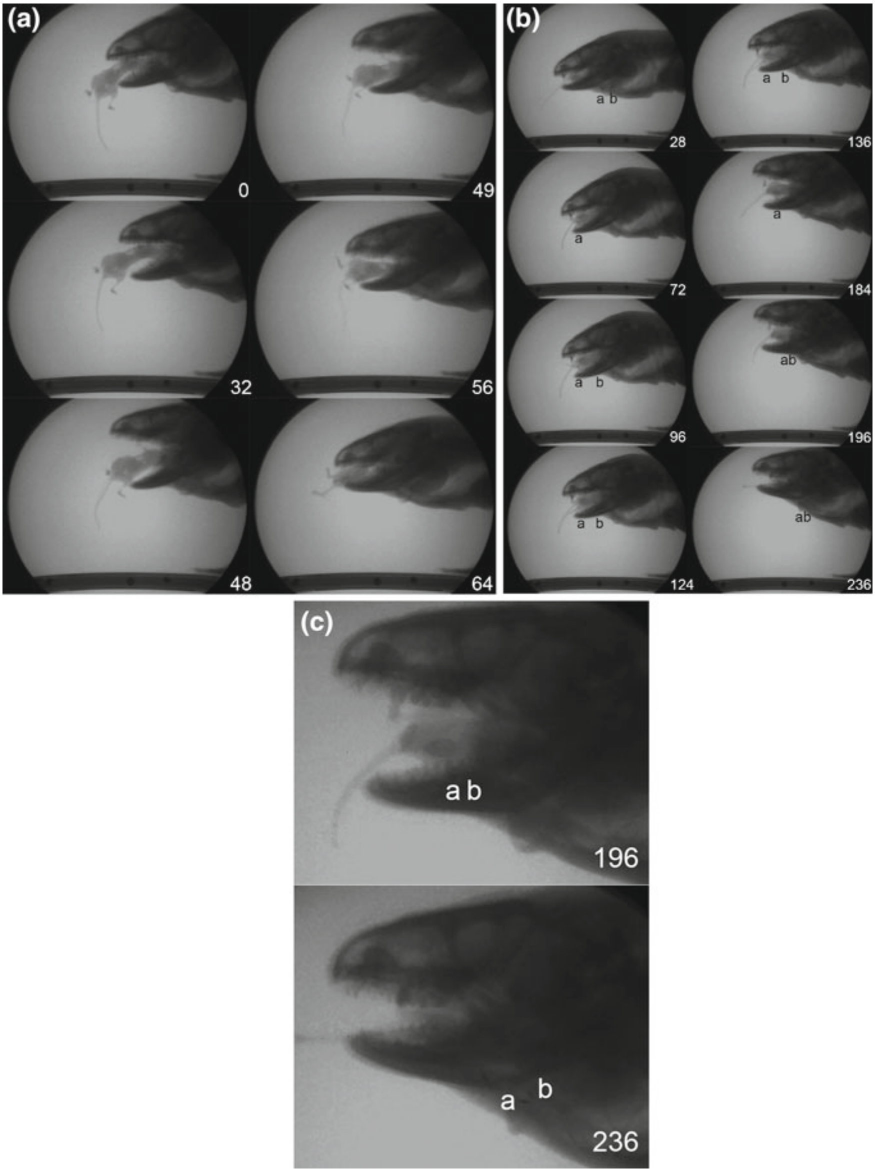


Fig. 13.16 X-ray series of frames depicting mice transport in *Tupinambis merianus*. **a**. The tongue does not play any major role in food movement. **b**. The tongue acts on the movement of the prey as demonstrated by relative movements of markers placed into fore (a) and mid (b) tongue. **c** The two last frames of the transport cycle depicted in **b** show lingual deformation demonstrated by the movements of the intra-lingual markers at the end of this cycle. During this cycle, the prey begins to enter into the esophagus showing the difficulty to separate last transport cycle and first swallowing cycle

their mid-portion…. The hyoid body is therefore forced upward …The hyoid elements cease to cross as they move backward at the beginning of the FC stage… The force exerted by the ceratobranchials I against the hyoid body should be greater than that exerted by the ceratohyals because the contracting m. ceratohyoideus and/or m. mandibulohyoideus I protract(s) the ceratobranchials I against the ceratohyals. This produces a forward and upward force acting on the tongue. The forward component results in the protraction of the lingual process and the tongue and the upward component elevates the lingual process… The tongue is then elevated during the FO stage …At the same time, the intrinsic musculature of the tongue would act to produce the hump-backed shape…."

Regarding modulation of the transport cycles, Herrel et al. (2001a) showed that: "*Some elements of the feeding cycle appear to be conserved across lizards. Notably, we see hyolingual protractor activity during slow opening, jaw opener and dorsal epaxial muscle activity during fast opening, bilateral contraction of all jaw closer groups during fast closing, and bilaterally simultaneous, co-activation of all jaw closers during the slow close phase* (Smith 1982, 1984, 1986; Herrel et al. 1997a, b, 1999a, b). *The limited amount of information available for jaw and hyolingual muscle activation patterns suggests that the overall amount of variation is larger for the jaw closer muscles compared to the hyolingual muscles. However, as quantitative data on hyolingual muscle activation patterns are scarce* (Herrel et al. 1997a, unpublished) *this should be confirmed by further research.*"

Food/prey properties are also known to modulate several characteristics of feeding cycles, including bite force (reduction) and jaw–tongue kinematics. For example, Metzger (2009) showed that prey mass has a more significant effect than prey hardness or mobility. His data confirmed that the SO phase of the gape cycle plays a key role in the contact ("*physical conformation*", Metzger 2009) of the lingual surface with the food. Herrel et al. (2001b) discuss this modulation and concluded that: "*Although most lizards respond to changes in the structural properties of food items by modulating the activation of the jaw and hyolingual muscles, some food specialists might have lost this ability. Whereas the overall similarity in motor patterns across different lineages of lizards is large for the hyolingual muscles, jaw muscle activation patterns seem to be more flexible. Nevertheless, all data suggest that both the jaw and hyolingual system are complexly integrated. The elimination of feedback pathways from the hyolingual system through nerve transection experiments clearly shows that feeding cycles are largely shaped by feedback interactions.*"

Furthermore, other analyses show differences among species. For example, in their comparative analysis of two closely related scincid species with highly different morphologies and diets (omnivorous *Tiliqua scincoides* and herbivorous *Corucia zebrata*), Herrel et al. (1999c) emphasize that both species respond to mobility and toughness of the food. For example in *C. zebrata,* the SO stage and the total duration of the cycle decrease while transporting leaves of endive. In *T. rugosa,* gape distance decreases and FC shortens for transporting grasshoppers. This demonstrates that these lizards are able to recruit jaw closers differently in response to the mechanical resistance of the food. For example, in the case of tough vegetables like endive, lizards recruit their jaw muscles maximally. In *T. rugosa*, the intensity of the jaw muscle recruitment is similar when feeding on endive and snails, but a very strong recruitment of the jaw closers is also recorded for mice and grashoppers. In this case, prey mobility is suggested to be the main factor affecting muscular recruitment. Herrel et al. (1999c) suggest that "*…a quick killing of a potentially mobile prey is undoubtably the best way to assure that it will not escape. Indirect support for this is the observation that T. rugosa responds to grasshoppers by decreasing the gape distance, and thus the duration of the FC, during intraoral transport cycles. By decreasing the time that the prey is not in contact with the jaws (*i.e. *during FOs and FCs) the chances that a mobile prey can escape are likely to be reduced…*".

In contrast, Herrel and De Vree (1999) showed only few food-type dependent differences in the herbivorous *U. acanthinurus* eating locusts and endive which are food items with large differences in terms of toughness, size, shape, and intra-buccal mobility. By comparing data from *U. acanthinurus* with the insectivorous *Pogona vitticeps* transporting grasshoppers, these authors explained that contact properties between the tongue surface and the prey can be a possible explanation for the differences recorded in the transport cycle stages. The medial fore tongue surface in *P. vitticeps* (see also Zhgikh et al. 1014) is covered by plumose papillae showing numerous secretory cells (Schwenk 2000), whereas this surface is covered by dense papillae in *Uromastyx acanthinurus*. This suggests that the tongue may fit better under the prey in the insectivorous *Pogon*a. Interestingly, these authors also argue that prey reduction is not retained in the herbivorous *Uromastyx*.

The effects of tongue movements on the modulation of the transport cycle dynamics have also been investigated in teiid and varanid lizards with their highly specialized tongue related to vomerolfaction (Elias et al. 2000; Schaerlaeken et al. 2012). These lizards use three types of prey transport modalities: (i) "pure" inertial transport performed during the beginning of the transport sequence (no tongue involvement), (ii) inertial transport with extension–retraction cycles of the tongue when the prey was positioned along the jaws, and finally (iii) a series of so-called "normal tongue-based" cycles when the prey was in the most posterior position in the buccal cavity. Based on high-speed films, Elias et al. (2000) show that the tongue is used variably along the transport sequence of killed mice, and that these cycles are "*…with little or no inertial movement of the head.*" By using X-ray films allowing visualization of the hyoid and some lingual movements, Schaelaeken et al. (2011) demonstrate that varanid lizards are able to modulate hyoligual movements in relationship to prey types. They found that transport of mice, as studied by Elias et al. (2000), required greater and longer feeding movements (e.g., gape distance, maximal jaw opening velocity, total hyoid displacement, durations of SO and FO stages).

13.8 Swallowing

Swallowing is the last phase of the feeding sequence (see review by Schwenk 2000) and involves pharyngeal packing and compression. This feeding stage remains not well studied although clear differences have been recorded in the jaw and lingual

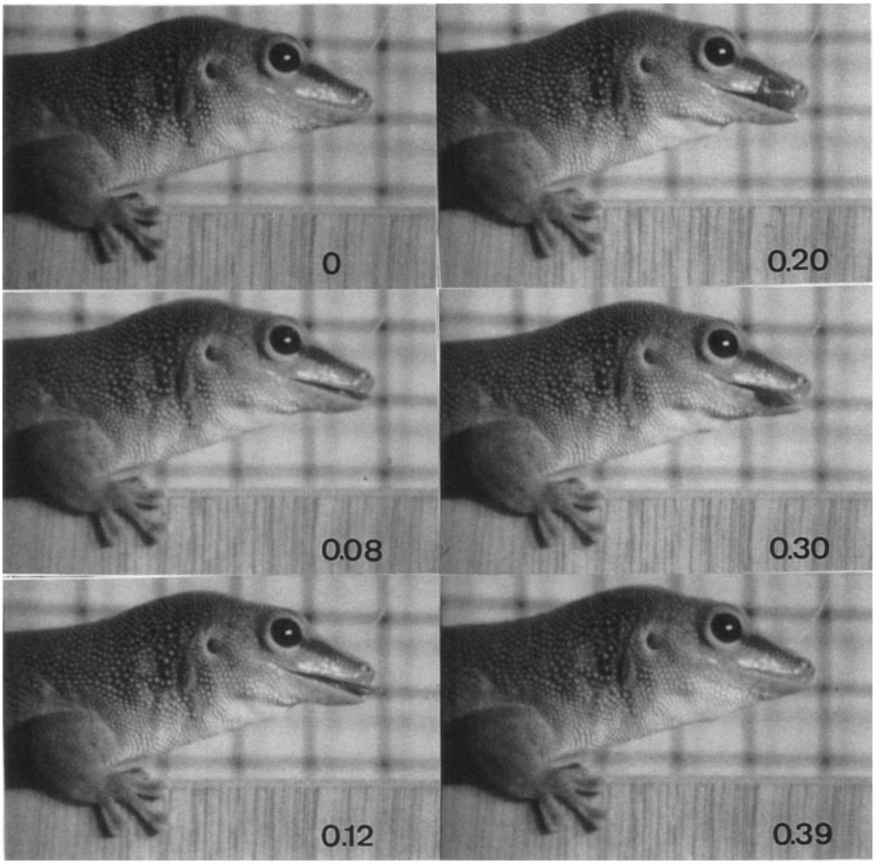


Fig. 13.17 Series of frames depicting movement of the tongue out of the buccal cavity in *Phelsuma madagascariensis*. These movements at the end of the swallowing phase likely probably facilitate pushing of the prey into the esophagus. Time is given in s

kinematic profiles determining the MAP of this phase (Fig. 13.17). Interestingly, this MAP seems to be conserved in species with various lingual morphologies. The tongue plays a key role during this feeding stage but its role remains to be determined and probably is modulated by the food/prey properties and the amount of space between food/prey and buccal cavity (Fig. 13.18). Tongue protrusion–retraction cycles and deformation move the food into the pahrynx and the digestive tract. Clear differences are present in jaw and tongue movements when comparing intraoral transport and swallowing cycles (Schwenk 2000). A swallowing cycle is often characterized by a decrease in the importance of the FO phase, and an increase in the duration of the SO phase associated with pronounced tongue movements (Fig. 13.18).

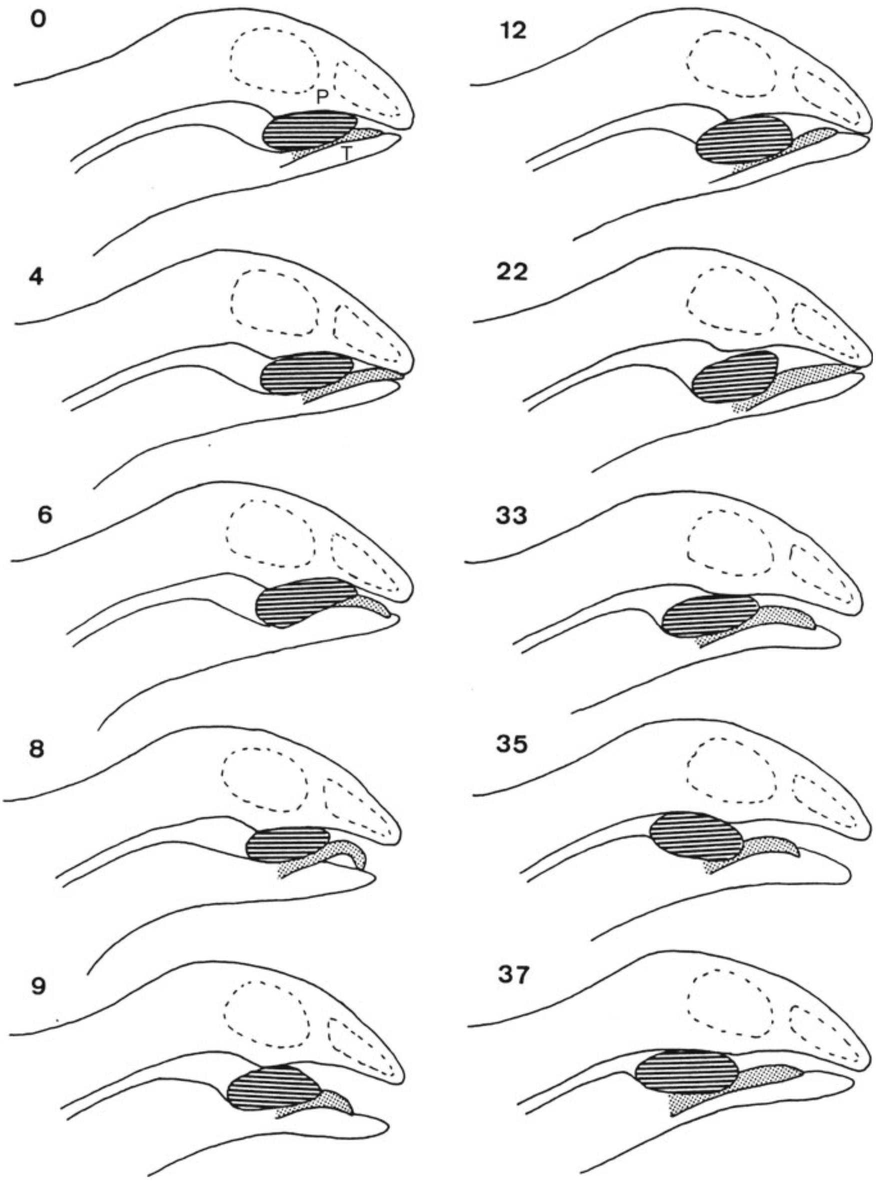


Fig. 13.18 Series of X-ray frames depicting two lingual and jaw cycles determining the MAP of swallowing in *Lacerta viridis*. The tongue deforms to move beneath the food and to facilitate its movement into the pharynx (frames 0–9) and into the esophagus (frames 12–37). Frames are separated by 0.004 s. P Prey; T tongue

Fig. 13.19 Like the majority of lizards, *Anolis carolinensis* uses the dorsal surface of the tongue to collect water

13.9 Drinking

Drinking is the principal behavior for intake of liquid food (e.g., nectar) and water (Fig. 13.19). In their extensive study of drinking strategies in living organisms, Kim and Bush (2012) define drinking as "…*We loosely define drinking as fluid uptake required for the sustenance of life. …Finally, we note that drinking need not involve water; for example, many insects and birds ingest fluid primarily in the form of nectar, which serves also as their principal source of energy…*". All lizards occupying non-xeric terrestrial and arboreal habitats adopt several postures to be able to uptake water and many species exploit nectar as a source of food and water. In xeric lizards, postures are used to collect the limited water from the environment (Malik et al. 2014; Yemmis et al. 2016; Cotman 2018). Cotman (2018) concludes: "*Although many species exhibit an accompanying behaviour—that is, active body movements—the actual process of water collection remains passive. The behaviour can instead be regarded as positioning the body surface towards the source from which water is obtained or to assist gravity-mediated water collection.*"

In the majority of lizards, water moves into the buccal cavity and the dorsal surface of the tongue plays the key role to acquire water in any kind of environment (Peterson 1998; Schwenk and Greene 1987; Sherbrooke 1990, 1993, 2004, Sherbrooke et al. 2007; Bels et al. 1993; Wagemans et al. 1999; Veselỳ and Modrỳ 2002). In experimental conditions, lizards with various lingual morphologies approach the source of water, position the head a few millimeters (5–15 mm) above the substrate and the water source, and rhythmically protract and retract the tongue in and out of the buccal cavity to collect the liquid (Fig. 13.20). In all lizards studied, drinking behavior is divided into two phases: immersion and emersion. During immersion (Fig. 13.21), water is collected and moved to the pharyngeal cavity through buccal compartments (Bels et al. 1993) (Fig. 13.22).

During emersion, water enters the digestive tract (Bels et al. 1993; Wagemans et al. 1999). The salient point is the role of the tongue during this behavior. Except *Tupinambis* and *Varanus* (see below), the liquid (water or nectar) is collected by the fore tongue alone. In all lizards studied, the tongue not only collects the liquid but also moves this liquid to the pharynx and the entrance of the esophagus. In contrast to the Sclerologossa, in the iguanians *Anolis* and *Oplurus* (Wagemans et al. 1999), the tongue is only slightly protruded (Fig. 13.20) when compared to the degree of tongue protrusion involved in prey capture (Delheusy and Bels 1992; Delheusy et al. 1994; Montuelle et al. 2008). This difference between iguanians and scleroglossans is even more marked for chameleons, which protrude the tongue only very slightly when drinking, compared to enormous tongue projection that occurs during food capture (Wainwright and Bennet 1992a, b; Herrel et al. 2000; Brau et al. 2016).

The iguanian *Oplurus cuvieri* appears to be capable of drinking with its snout submerged in a large volume of water, and, in such circumstances, to use a buccal pumping mechanism (Wagemans et al. 1999) similar to that recorded for some varanids (Smith 1986) and snakes (Kardong and Haverly 1993; Berkhoudt et al. 1995; Cundall 2000). But the fore tongue always enters in contact with liquid in all lizards. The use of both mechanisms (lingual loading versus suction) for gathering water in squamates is seemingly related to the volume of water available, but this remains to be tested by using a similar experimental approach to that employed by Cundall (2000) for snakes.

High-speed and X-ray films provide data to elucidate the drinking mechanism. Two mechanisms appear to be used by lizards. The first mechanism has been mainly revealed in lizards with highly different lingual morphologies using the fore tongue to gather water into the buccal cavity (Fig. 13.21). Water (and probably any other liquid) is collected by the dorsal surface of the fore tongue. Two major mechanisms seem to play in water collection: (i) presence of a film thickness of water on the tongue surface and (ii) capillary imbibition of water into the papillae (Kim and Bush 2012). These authors suggest the following formula to calculate the volume of the liquid (water) layer:

$$e = l\mathrm{Ca}^{2/3}\,(l = \text{the length of the tongue in contact with the liquid})$$

with

$$\mathrm{Ca} = u\,\mu/\sigma^{\sim 10-4}$$

(u = tongue velocity; μ = liquid viscosity; σ = surface tension)
and the water intake rate is:

$$Q = el^2 f^{\sim 0.5}$$

(f (Hz) = the recorded licking frequency during one immersion phase).

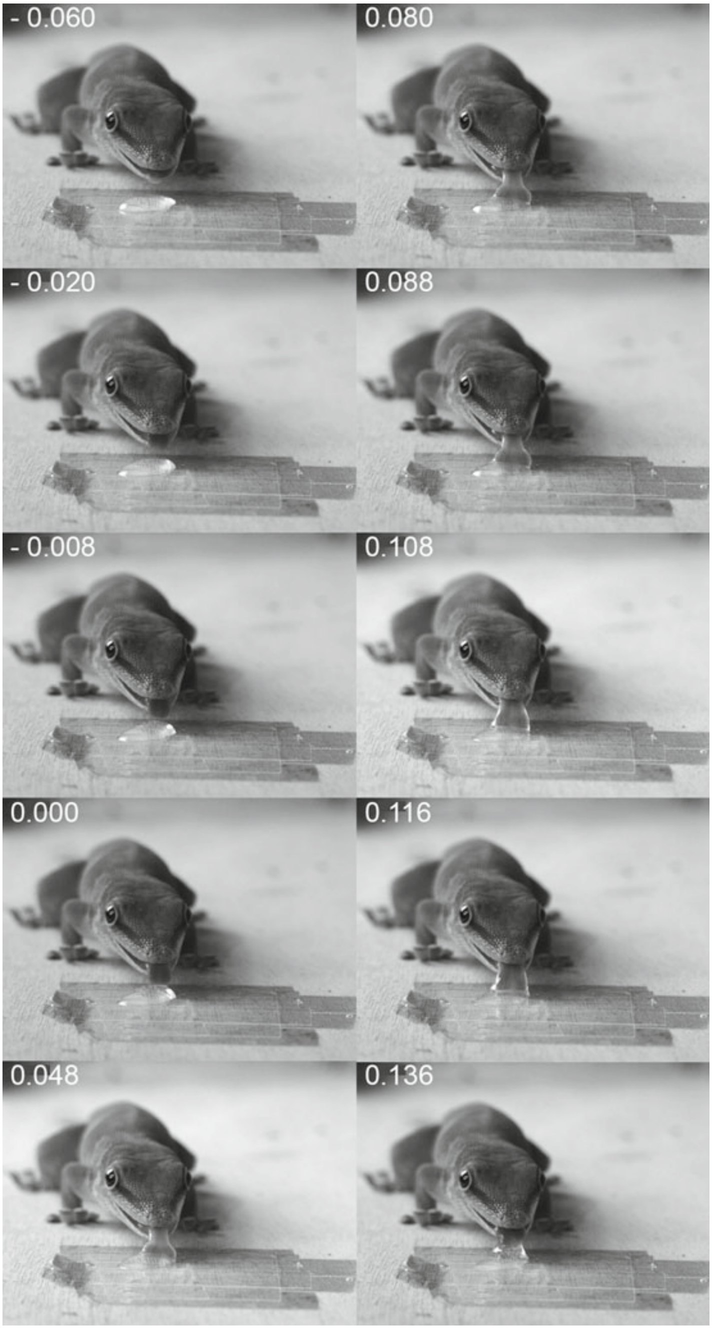


Fig. 13.20 Drinking sequence showing lingual movements in *Phelsuma madagascariensis*. The tongue is expanded when moved out of the buccal cavity and contacts the liquid (time: 0.00–0.88 s). Only the dorsal surface of the fore tongue acts to transport water to the buccal cavity. Time is given in s

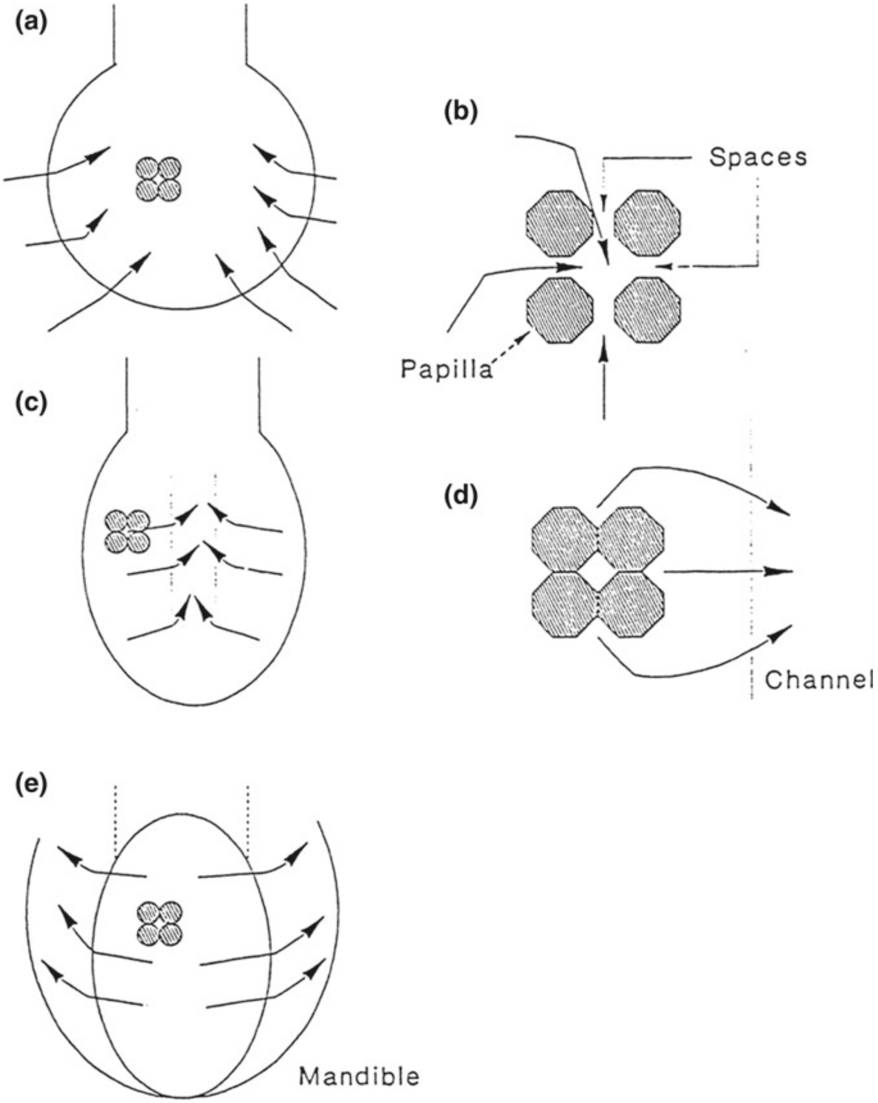
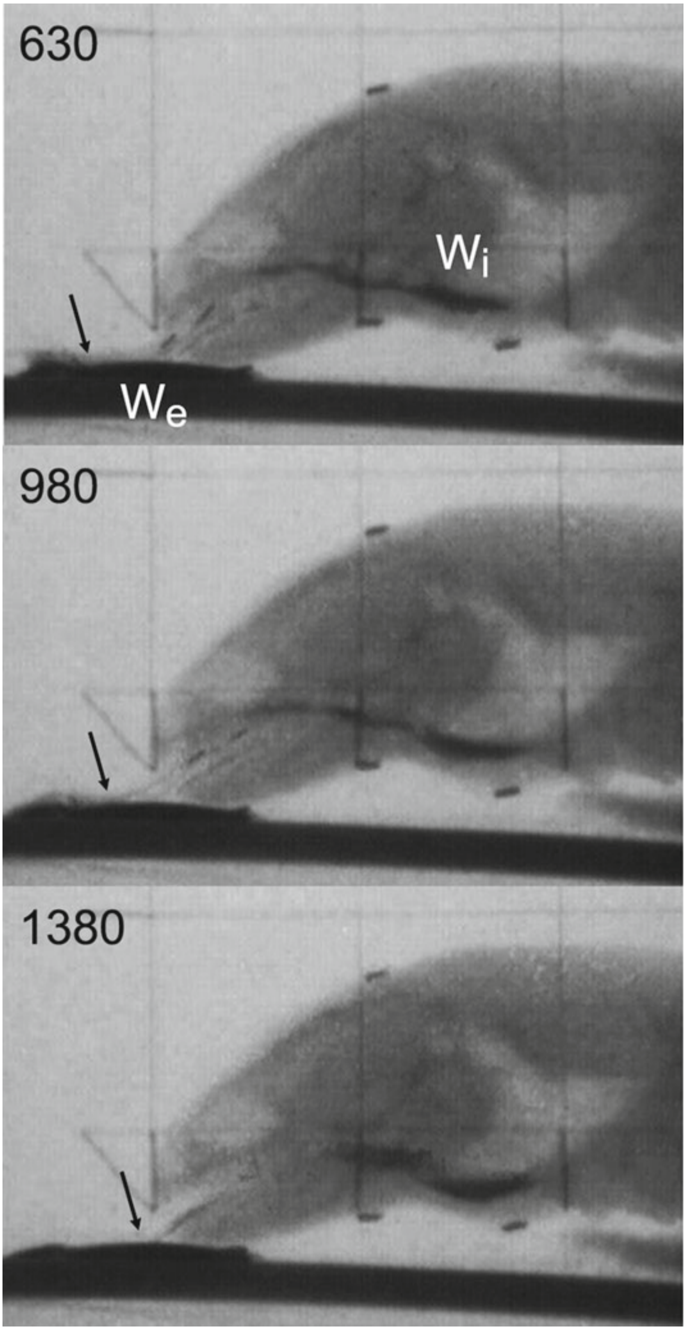


Fig. 13.21 Schematic illustration of the drinking mechanism in lizards. Papillae are represented in gray. **a** A coating film is produced as suggested by Kim and Bush (2012). **b** Opening the spaces between the papillae occurs during tongue contact with the film (drop) of water on the substratum to enhance water filling of the tongue by facilitating capillary imbibition. **c** During tongue retraction out of the buccal cavity, the tongue returns to a less expanded shape and water of the film is entrained in the middle of the tongue. **d** In the meantime, interpapillary spaces are reduced, and the amount of water in these spaces is added to the water film on the tongue. **e** As soon as the tongue in the buccal cavity and jaws closes, the liquid fills the buccal compartments as determined in *Lacerta viridis, Oplurus cuvieri*, and *Anolis carolinensi*s (Bels et al. 1993; Wagemans et al. 1999). The arrows indicate the possible movement of water


630
W_i
W_e
980
1380

◂**Fig. 13.22** Series of X-ray frames illustrating the role of the tongue to gather water into the buccal cavity in *Tupinambis merianae*. These frames are only used to illustrate the mechanism of drinking recorded in lizards with highly specialized tongue. Time (ms) corresponds to the position of the tongue in one opening–closing cycle during the immersion phase. Two small markers are present in the tongue of the lizard (black boxes) to show the complex protraction–retraction movements of the tongue. One marker is also positioned on the head and two markers on the throat of the lizard. These last markers show that water is pushed into the pharyngeal cavity with the movement of the tongue as in previous studies (Bels et al. 1993). The arrows indicate the postion of the fore tongue. *We*, external water in the environment; *Wi*, water in the buccopharyngeal cavity

As soon as the tongue contacts the water, the fore tongue enlarges (Fig. 13.20). This change can modify the papillar organization. The papillae probably expand away from each other, opening spaces between them and then favoring imbibition of the fore tongue. When the tongue retracts, it recovers its initial shape and water flows into a central canal in the tongue. The tongue retracts into the buccal cavity and fills the first buccal compartment just at the level of the Jacobson's organ as shown in Lacertidae (Bels et al. 1993) and Iguaniade (Wagemans et al. 1999). As soon as water has filled the pharyngeal compartment, the lizard begins the emersion phase allowing water to be swallowed (Bels et al. 1993).

The mechanism used by Teiidae remains to be explored. In this lizard, the fore tongue is not used to collect water, but regular movements of the tongue on the water surface create a fluid movement from outside to the buccal cavity (Fig. 13.22; Bels et al. in prep.).

13.10 Conclusion

This chapter summarizes the main data and hypotheses related to the evolution of feeding behavior in lizards. This review provides a rationale for why future investigations of our empirical knowledge of feeding in these tetrapods are needed at all the levels, from evolutionary ecology to sensory functional biology. The chapter attempts to show the generalities *vs* specialities of the trophic system in relationship with ecological demands through the diversity of lizards although a large number of questions remain to be investigated. Kinematic studies in various species with various types of food/prey provide the opportunity to discuss the combined effect of historical and ecological constraints on the feeding behavior in lizards. Our knowledge on feeding provides one of the best models of morpholigcal, functional, and behavioral evolution as demonstrated by Schwenk (2000), Bels (2003), Reilly and McBrayer (2007) and Bels et al. (2019). The question of evolution of the adhesive model permitting to successful catch food must now be added to the suggested evolutionary hypothesis. This mechanism remains to be deeply studied because it is a key point to explain the success of the feeding behavior in lizards using the tongue to capture their food. Also clearly chemoreception and feeding plays a functional trade-off on tongue morphology and use that still must be investigated. Neuro-ethological studies of feeding are very scarce and probably are now needed to understand the actions of the nervous system that give rise to prey selection and capture behaviors. Further attentions to both behavioral and neurobiological issues are needed to provide deep insight into our understanding of the evolution of the functioning of the sensory and nervous systems in generating and controlling behavior in lizards, from capture to swallowing. Finally, the studies of skull and hyo-lingual morphology related to ecological constraints including food/prey properties are now well studied in some species to extract micro- and macro-evolutionary trends in a changing ecological word.

Acknowledgements We thank very much K. Tanalgo (Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, P. R. China) for permission to use photographies of gekkos exploiting nectar (Fig. 13.2). We also thank Kiisa Nishikawa and one anonymous reviewer for their help to improve our chapter.

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