Chapter 4

Terrestrial Feeding in Salamanders

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I. INTRODUCTION

A. Systematics

There are roughly 450 species of salamanders currently placed in 10 families (Fig. 4.1). Evidence exists for the monophyly of the Caudata and for the sister-group relationship of Caudata to Anura (Cloutier and Trueb, 1992; Larson and Wilson, 1991; Larson, 1991). However, relationships within the Caudata are unstable, and different results are obtained from DNA sequence analysis and from morphological characters (Larson, 1991). We use one of two similar phylogenetic hypotheses resulting from a combined data analysis (Larson and Dinnick, 1993). In this tree (Fig. 4.1), Sirenidae (aquatic, gilled, elongate, lacking hind limbs, and presumed to have external fertilization) is basal, followed by a branch leading to the sister-taxa Hynobiidae and Cryptobranchidae (which have external fertilization). The more derived salamanders form a monophyletic group (all have internal fertilization), but the base is unstable. Whereas earlier workers placed plethodontids as one of the most derived taxa, Larson’s (1991) DNA data place it as one of the most basal lineages, and only the combined data pull it up in the tree to the base of the derived taxa. The diverse and much studied ambystomatids and salamandrids are deeply nested and envisioned as highly derived.

Most terrestrial salamanders belong to the Plethodontidae, which includes about two-thirds of all species of salamanders. About three-quarters of the plethodontid species have no aquatic larval stage and develop directly from eggs laid on land (Wake and Hanken, 1996). Relationships within the Plethodontidae are discussed in Lombard and Wake (1986). Hynobiidae and Salamandridae are both relatively speciose and display

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diverse morphology related to feeding. Relationships of hynobiid genera are discussed in Zhao and Hu (1988) and those of salamandrids by Titus and Larson (1995). Only one genus of Ambystomatidae is recognized, but it is relatively speciose and the species display morphological variation with respect to feeding. Species relationships within Ambystoma were studied by Shaffer et al. (1991). Only a single genus is recognized for the Dicamptodontidae and the Rhyacotritonidae, and each contains four species. Relationships of the species of Dicamptodontidae are discussed by Good (1988) and of the Rhyacotritonidae by Good and Wake (1992).

B. Natural History

The vast majority of salamanders either have a terrestrial phase during which they feed on terrestrial prey or are terrestrial throughout life. The Cryptobranchidae, Sirenidae, Proteidae, and Amphiumidae, which are strictly to essentially aquatic, are emphasized in Chapter 3 and will not be discussed here. Together these four families include only about 16 species. Most members of the families Ambystomatidae, Dicamptodontidae, Hynobiidae, and Salamandridae metamorphose from aquatic larvae to terrestrial adults, but some remain aquatic as adults, either in a perennibranchiate (e.g., Ambystoma mexicanum, Dicamptodon copei) or in a fully metamorphosed state. The four species of the Rhyacotritonidae metamorphose, but they remain closely associated with water throughout life. The situation is complicated in the Plethodontidae, which is the largest family. The Plethodontidae includes the most terrestrial of salamanders, but adults of some taxa are fully aquatic, either perennibranchiate (e.g., Hiodontriton, Typhlonolge, and some species of Eurycea and Gymnophilus) or metamorphosed (e.g., Desmognathus marmoreus). All members of the plethodontid tribes Plethodontini and Bolitoglossini (together accounting for well over 50% of the living species of salamanders) undergo direct development (in encapsulated eggs) and are strictly terrestrial throughout life. A few salamandrids have a stage with larval-like morphology that develops within the oviduct and these, too, are fully terrestrial.

Terrestrial salamanders are strict carnivores, and the main prey are arthropods, especially insects (Lynch 1985; Keen 1979; Sites 1978; Kuzmin, 1991). Annelids are eaten by hynobiids (Kuzmin, 1991), ambystomatids (Bishop, 1941), and salamandrids (Roth, 1987). Some large salamanders eat other salamanders (Bishop, 1941; Hairston, 1987) and even such vertebrates as frogs, shrews, mice, lizards, and snakes (Dicamptodon, Bury, 1972; Gymnophillus, Bishop, 1941). Snails and isopods are widely eaten.

C. Feeding Modes and Terminology

This chapter deals not only with all terrestrial feeding, but also salamanders that use essentially terrestrial mechanisms when feeding under water, such as the desmognathine plethodontids. Prey capture typically is by the tongue, which is extended from the mouth and returns to the buccal cavity with the prey attached, a behavior known as tongue protraction or tongue protrusion. We reserve the term tongue projection for prey-capture mechanisms in which the tongue is fired from the mouth ballistically and reaches the prey under its own momentum, a mechanism known only in bolitoglossine plethodontids. Many terrestrial salamanders have weak jaws and teeth, particularly those that rely primarily on the tongue to bring prey into the buccal cavity. There are, however, species that have robust jaws: Dicamptodon, Ambystoma tigrinum, and some species of Batrachuperus have very large heads and strong jaws as adults, the desmognathine plethodontids have well-ossified skulls, powerful jaws, and unique jaw mechanics (Schwenk and Wake, 1993), and the plethodontid genus Aneides has strong jaws and very large, saber-like teeth (Wake, 1993; Staub, 1993). These species and others that typically use tongue protraction to capture prey will resort to capturing prey with the jaws, in a behavior known as jaw prehension, when the tongue fails to return prey to the mouth.
II. MORPHOLOGY

Salamanders have a generalized morphology with a relatively narrow head, well-developed eyes, and a short and broad neck. The head is flattened and is broader than high. The external nares are well separated at the front of a short face. The eyes are at the dorsolateral margin of the face, and head muscles lie behind them. There are varying degrees of eye frontality, but visual fields of the two eyes typically overlap to some degree (Roth, 1987). The mouth opening is large, characteristically extended to a point ventral to the eye.

At the margins of the mouth, generally small, bicuspoid, pedicellate teeth are found in opposing semicircular rows, one on the premaxillary and maxillary bones and the other on the dentaries. There are also palatal teeth on the vomer in various arrangements and highly varied in number among species; these teeth typically do not parallel the marginal teeth.

The tongue is typically large and fleshy, varying among species in the degree to which the margins are attached to surrounding tissues (from completely attached to entirely free). The surface of the tongue is covered with sense organs and the openings of numerous mucous glands, and it is soft and spongy in texture. Internally the tongue has an extensive musculature, including both extrinsic muscles that originate outside the tongue pad and intrinsic muscles that are associated with tongue retraction as well as molding of the tongue pad. General surface morphology of the tongue in relation to the mouth and teeth is illustrated for a variety of species by Bishop (1941) and Lombard and Wake (1977).

A. Skeleton

1. Skull and Jaws

Skulls of salamanders are weakly ossified and contain relatively few, thin bones. Premaxillary bones (single or paired) have rising, posteriorly oriented frontal processes that articulate with surrounding bones and provide support (Carroll and Holmes, 1980; see also Chapter 3, Fig. 3.3). Laterally the bones articulate with the much larger maxillary bones. The maxillaries have a frontal process that rises to articulate with surrounding bones (nasal, lacrimal, prefrontal, and frontal, depending on species). The premaxillaries and maxillaries have small, medially projecting, shelf-like processes that articulate with the expanded vomers to form the roof of the buccal cavity. The eyes lie lateral to the brain case, which is formed by a ventral parasphenoid, lateral orbitosphenoids, and dorsal, paired frons.

2. Hyolingual Skeleton

A hyolingual apparatus (also referred to as a hyobranchial apparatus, particularly in aquatic species) is associated with the tongue in all terrestrial salamanders and it varies substantially among taxa. The elements of the apparatus are cartilaginous to some degree, and in most taxa there is little or no bone, but the apparatus may ossify extensively in others.

The general morphology of the hyolingual apparatus is discussed in detail in Chapter 3 (see Figs. 3.4 and 3.6, as well as Figs. 4.2 through 4.4). In metamorphosed salamanders, an elongate basibranchial and a urohyal lie along the ventral midline. The urohyal is continuous with the basibranchial in embryos but the connection is lost before metamorphosis. Unlike the basibranchial, which is usually cartilaginous, the urohyal ossifies early. Paired arches extend posterolaterally and somewhat dorsally from the basibranchial: a hyoid and two branchial arches. The homologies of the arch
FIGURE 4.2. Hyobranchial apparatus of terrestrial salamanders. Ventral views, showing relation of apparatus to lower jaw. Note the radial loops and two pairs of epibranchials in the two hynobids shown, *Onychodactylus japonicus* and *Hynobius leechii*, the otoglossal cartilage in *Rhyacotriton olympicus* and *Ambystoma maculatum*, and the lingual plate in *Dicamptodon ensatus* and forked second radii in *Ambystoma texanum*. Compare the ossification of *Taricha granulosa* and the elongate basibranchial, radii, and epibranchials of *Chioglossa lusitanica* to the more generalized condition in *Salamandra salamandra*. Bone is stippled and cartilage is outlined. Scale = 5 mm. Abbreviations are explained in Chapter 3, Table 2.1. In some instances, an element has been interrupted or cut on one side to reveal the element dorsal to it. In other instances, the hidden element is indicated by a dotted line.
elements are debated and terminology varies among authors. All authors use the same terms for the first arch elements: a small hypohyal (proximal; absent in most taxa, possibly fused to the remaining element) and a much larger ceratohyal (distal). The proximal elements of the next two arches are called hypobranchials by some authors and ceratobranchials by others. A serial homologue of the hypohyal would be expected to be short, but this branchial element is characteristically long; the element may well represent both hypobranchial and ceratobranchial or the hypobranchial may be absent (Fig. 4.2). The more distal elements are termed either ceratobranchials or epibranchials. We use the term ceratobranchial for the more proximal of the paired branchial elements and epibranchial for the more distal element. There are only two branchial arches in terrestrial salamanders. Although the two proximal elements are universally present, there may be one (most taxa) or two (hynobiids) epibranchials (Fig. 4.2). When one epibranchial is present, the two ceratobranchials on each side connect to the single epibranchial, either directly or indirectly (in some taxa the second ceratobranchial connects at its distal end to the first ceratobranchial instead of the epibranchial). The articulated hyolingual skeleton of terrestrial salamanders includes the basibranchial, various skeletal pieces connected near its anterior tip (radii, otoglossal, lingual cartilage), and elements of the first two branchial arches. Ceratohyals lack articulations, other than with the hypohyal (when present); they are attached proximally to the suspensorium by the hyoquadrate ligament, and there are quasi-ligamentous connections of the flattened, distal blade to the lower jaw. When present the urohyal is an ossified triangular or crescentic element well separated posteriorly from the other elements and embedded in musculature.

Hynobiids have two epibranchials, but all other terrestrial salamanders have one (compare Onychodactylus and Hynobius in Fig. 4.2 to the others). The ceratohyals in hynobiids are continuous with one another across the midline by a slender, looped cartilage (radial cartilage; radial loop of Larsen et al., 1996) of uncertain homology (but sometimes termed hypohyal, and considered by other authors to represent the first radials) arranged in the form of a flat spring with the loop extending posteriorly and crossing at the midline. At its most posterior limit it may be attached to the basibranchial. The basibranchial in hynobiids is of moderate length in some species but very short in others, whereas it is relatively long in the other taxa. There are two pair of radii in most salamanders and in the ambystomatids, dicamptodontids, and rhyacotritonids. The last three families also have an unpaired, median otoglossal associated with the tongue pad. There

is a small interradial cartilage in most salamandrids that may be a homologue of the otoglossal. The first pair of radii has no muscles attached to it; we consider it to be the ontogenetic homologue of the hypohyals, as have other authors (Drüner, 1901). When only one pair
FIGURE 4.4. Hyobranchial apparatus of bolitoglossine plethodontid salamanders. Ventral views, showing relation of apparatus to lower jaw. Note that apparatus are entirely cartilaginous. The epibranchials of *Hydromantes platycephalus* are the longest of any salamander. The small, tapered first ceratobranchial in *Thorius narisovalis* disarticulates from the basibranchial during tongue protrusion. Bone is stippled and cartilage is outlined. Scale is 5 mm. Abbreviations are explained in Chapter 3, Table 3.1. In some instances, an element has been interrupted or cut on one side to reveal the element dorsal to it. In other instances, the hidden element is indicated by a dotted line.

of radii is present, it is the second. Some plethodontids lack radii and in others they are elongate. The most elongate radii occur in the salamandrid genera *Salamandrina* and *Chioglossa* (Fig. 4.2). These genera, as well as *Salamandra* and *Mertensiella*, have an epibranchial that results from the fusion of the epiibranchial and first ceratobranchial of other genera. The two epibranchials of hynobiids are attached to the ends of the first and second ceratobranchials. In general, differences among taxa with respect to the hyolingual apparatus are
mainly due to differences in proportions, which in turn reflect functional diversity, for example, differences in the length of the epibranchials among plethodontids (Figs. 4.3 and 4.4).

**B. Musculature**

The musculature associated with feeding is derived from the so-called branchiomeric series (Wake, 1993) and the somitic hypobranchial series. Detailed descriptions of muscles common to all salamanders are presented in Chapter 3 (see Chapter 3, Fig. 3.5). Among the branchiomeric derivatives are the jaw levators and depressors and the tongue protractors; the tongue retractors are somitic in origin. The neck is poorly differentiated, but epaxial somitic muscles are involved in raising the skull, and the levator scapulae (most families) and/or cucullaris (plethodontids) is associated with postural movements of the head. Details of tongue musculature relevant to feeding movements are discussed later in the context of tongue function (Section III,C,1,b).

**C. Sensory and Motor Systems**

1. **Vision, Olfaction, and the Brain**

Terrestrial salamanders locate prey by olfaction and vision, but vision predominates. The olfactory system is well developed but generalized. There is typically a rather elongate snout that houses the paired and cartilaginous olfactory capsules. Within each capsule is a large medial olfactory sac, lined with olfactory epithelium, and a small ventrolateral sac, lined with a specialized sensory epithelium (Dawley and Bass, 1989). The smaller sac is the vomeronasal organ. Plethodontids have a unique organ, the nasolabial groove, associated with each external nostril. The groove lies in the skin of the snout and extends to the margin of the jaw, where typically it opens broadly. In males, tissues associated with the groove swell and elongate during the courtship season (Eurycea) or throughout life (tropical plethodontids). The groove draws surface water into the nasal/vomeronasal sacs and is thought to be important in courtship behavior (Dawley and Bass, 1989), but it may also play a role in feeding.

The lateral eyes are large relative to larvae and to permanently aquatic species, and vision is good. The eyes are laterally oriented in species with more generalized terrestrial feeding, but in those species with highly protrusible tongues the eyes become frontally oriented and the animals are able to determine distance of the prey from the head with great accuracy. Visual behavior has been studied extensively, with special emphasis on its role in feeding (reviewed in Roth, 1987). The optic nerve projects to the well-developed midbrain, which has an enlarged optic tectum, the main center for the coordination of feeding in salamanders. Projections are both contralateral and ipsilateral, and ipsilateral projections are especially well developed in bolitoglossine plethodontids. The existence of this dual projection system contributes to visual acuity and the ability to accurately estimate distance.

2. **Tectobulbar Pathways, Brain Stem, and Innervation Patterns**

Descending pathways from the optic tectum and tegmentum to the bulbar portion of the brain stem are generalized in salamanders and less clearly differentiated from one another spatially than those of frogs. In sharp contrast with the situation in frogs, there is involvement by more cranial nerves in feeding, and motor nuclei are less condensed and overlap more extensively. As yet there has been little demonstration of interneurons in the reticular formation of the brain stem, and there is some evidence of direct innervation of motor neurons. There are few neurons in the motor nuclei, and their cell bodies are characteristically large (Roth, 1987).

The 4th, 5th, 7th, 9th, 10th, and 11th cranial nerves are all involved in feeding, as are the 1st and 2nd spinal nerves. The 4th nerve (abduscens) has well-differentiated lateral and medial subnuclei. The lateral serves extrinsic eye muscles, whereas the medial serves the retractor bulbii, muscles that function in part in aiding in swallowing.

The 5th nerve (trigeminal) innervates the jaw elevators and anterior constrictors of the buccal cavity, and the 7th nerve (facial) innervates the jaw depressors as well as throat constrictors. The 9th (glossopharyngeal) and 10th (vagal) nerves serve the tongue protractor muscles. The eleventh (accessory) nerve innervates musculature associated with movements of the head on the neck. The 1st and 2nd spinal nerves (which have trunks that unite to form the ramus hypoglossus) innervate the retractor muscles of the tongue, the muscles of the tongue pad, and the strap-like muscles paralleling the body axis that contribute to throat movements and throat stability.

**III. FUNCTION**

A. **Foraging, Prey Detection, and Localization**

Foraging has been studied in plethodontids by Jaeger and associates (Jaeger and Barnard, 1981; Jaeger...
Flower, 1927). Terrestrial salamanders forage actively and Gergits, 1979; Jaeger and Rubin, 1982; Jaeger et al., 1982), but only incidentally for other groups (e.g., Flower, 1927). Terrestrial salamanders forage actively at night under appropriate conditions of temperature and humidity, under suboptimal conditions the animals adopt a sit and wait strategy, remaining in burrows in the soil or other retreats with only the head exposed.

Capture of prey by salamanders involves a sequence of activities (Roth, 1987). Orientation is elicited by visual or mechanical stimuli and involves a turning movement of the head, which permits binocular fixation of the prey. The salamander next approaches the prey by walking to a point within reach of the tongue, which varies substantially in length among taxa. If the prey are not evasive, an olfactory test then may take place in which the salamander places its snout directly on the prey. Once within attack distance, binocular fixation of the prey may occur again. Finally, snapping occurs, and in this phase the mouth opens and the tongue seizes the prey, which is drawn into the mouth. Typically, prey capture is by lingual prehension, although forward lunging of the whole body may accompany tongue protraction.

Visual aspects of feeding have been studied in detail by Roth and associates (reviewed by Roth, 1987). Species differ greatly in the size of stimuli they prefer, which is correlated with natural food preferences. Species such as the plethodontid Hydromantes, which feed on insects, prefer smaller stimuli than Salamandra, which feeds mainly on worms. Both maximum and minimum size of response stimuli is much smaller in Hydromantes than in Salamandra. Salamandra feeds on prey moving at velocities from 0.5 to about 2 cm/sec, but bolitoglossine plethodontids have been recorded to feed on prey moving from 6 to 10 cm/sec. Motionless prey normally are ignored by terrestrial salamanders.

Salamanders typically forage at night and are able to use visual cues at extraordinarily low levels of light (Roth, 1976, Himstedt, 1982). Laboratory experiments demonstrate that they are able to feed visually at illumination levels equivalent to open areas on cloudy or rainy nights. Salamanders also feed from olfactory cues in the absence of visual stimuli, as in complete darkness. When light is present, odoriferous dead prey will be ignored for a long time, but if vision is ineffective the food is eaten quickly. Salamanders that live so deep in caves (e.g., Typhlotriton) that there is no light probably use a combination of smell and touch to obtain food.

Salamanders have both binocular and monocular depth perception. They do not use lens accommodation, but rather rely on disparities between direct ipsilateral and contralateral retinotectal projections. They apparently are able to make immediate calculations of depth and feed with great accuracy (Wiggers and Roth, 1991).

B. Prey Capture and Ingestion

Feeding involves mouth opening/closing, and tongue protraction/retraction. When prey are small relative to the salamander, jaws are not used in feeding, and marginal dentition does not contact prey. However, larger species feeding on larger prey (e.g., members of Dicamptodon and Ambystoma) do use their jaws. The role of vision in feeding is uncertain once the prey is localized. In general, the feeding act is so rapid that once feeding starts relatively little modulation of the strike itself is possible because of delays in response to sensory information (Thexton et al., 1977). Some species close their eyes during the strike, whereas others do not, and this variation occurs even among confamilial species (Roth, 1976; Larsen and Borneski, 1988; Larsen et al., 1989; Miller and Larsen, 1990).

In general, those species with the fastest tongues and the greatest degree of protraction are the most likely to keep the eyes open during the feeding cycle. Correspondingly, those that lunge forward strongly during feeding often close their eyes, presumably to protect them. Because prey are out of sight during tongue protraction and lunging, these movements are thought to be preplanned and executed without modification once begun.

C. Biomechanics and Functional Morphology

1. Lingual Feeding

a. Kinematics

Lingual feeding has been observed in all families of terrestrial salamanders. The published literature is dominated by information concerning ambystomatids, hynobids, plethodontids and salamandrids, and little information is available for the small families Rhacotritonidae and Dicamptodontidae. The prey object is first contacted by a protracted tongue pad that is delivered rapidly through a gaping mouth into the buccal cavity. The mode of protraction has been characterized as a lift and thrust mechanism (Beneski et al., 1995). Both a tongue cycle and a necessarily associated gape or mouth opening and closing cycle can be recognized. These combine to form the basis of a model of a generalized vertebrate feeding cycle, based on the premise that lingual prehension was ancestral in tetrapod feeding (Bramble and Wake, 1985). The four stages, first formally recognized in mammalian feeding (Hiemae,
The three-part cycle of ambystomatids involves rapid mouth opening, a period of stable positioning of the head during tongue protraction and retraction, and rapid mouth closing (Reilly and Lauder, 1989). The four-part cycle of other taxa includes an initial brief gape phase that opens the mouth only slightly, a second phase during which the mouth is held open just wide enough for tongue protraction, a third phase when gape is increased rapidly during tongue retraction, followed by mouth closure (Larsen and Beneski, 1988). Ambystomatids have modest abilities for tongue protraction and, the gape cycle has been simplified as a result. Beneski et al. (1995) and Larsen et al. (1996) characterize the ambystomatid feeding pattern as “lift and roll” in reference to the modest protraction of the tongue in the family and the extensive involvement of tongue pad ventral rolling over the rostral end of the protracted basibranchial and the extensive movement and “fitting” of the tongue pad onto the prey. Members of the other families have varying degrees of tongue protraction, but prey captured by tongue prehension often do not contact the teeth of the jaws. Some species, including even such highly proficient tongue-protracting forms as the plethodontid Ensatina, may use teeth and jaws with relatively large prey. The power stroke of the fourth phase of the generalized vertebrate feeding cycle is modified or absent in salamanders. The extreme degree of reliance on tongue prehension in terrestrial salamanders may account for the departures noted from the general model. Some studies have been conducted on salamandrids feeding without tongue prehension, using only jaws, and these differ from the generalized model in having a two-phase gape cycle: rapid mouth opening followed immediately by rapid mouth closing (Miller and Larsen, 1990). However, these exceptional cases are typically aquatic species feeding on land.

The typical strike in salamanders is accompanied by a forward lunge of the entire body toward the prey. This is the ancestral mode and it is widely retained. Lunging effectively increases the strike distance and may also increase the force of the strike. This may be of significance in forcing the tongue pad to conform to the prey surface, thus increasing the area of contact (Larsen et al., 1996). Furthermore, the lunge may continue as tongue retraction occurs so that teeth are quickly brought into contact with the prey item (Larsen et al., 1996). The lunge is absent in certain taxa that display high-speed tongue protraction, including bolitoglossine plethodontids (Larsen et al., 1989; Roth and Wake, 1985b) and the salamandrid Salamandrina (Miller et al., 1990), and is rarely present in some hemidactyline plethodontids with long tongues (e.g., Eurycea).

b. Protraction

Lombard and Wake (1976) studied biomechanics of tongue protraction in plethodontids and presented a theoretical model of folding of the hyobranchial apparatus. The model was based on assumptions dealing with the nature of materials (that the central main elements, the basibranchial and the ceratobranchials, do not bend during protraction or retraction), the stability of joints (there is no disarticulation during protraction and retraction), and other considerations (e.g., the system folds dorsally rather than ventrally). The model was used to formulate hypotheses concerning biomechanical events and was generated with specific reference to plethodontids. Members of this family are sufficiently different from other salamanders in hyobranchial structure that it is unclear if the biomechanical model has generality, but folding occurs to some degree in other taxa as well [e.g., the salamandrid Taricha; Findeis and Bemis (1990) and the hynobiid, Hydromantes; Larsen et al. (1996)].

Hypotheses generated from the model were tested in various ways. The fundamental part of the model is that the skeletal parts of the tongue are folded into a kind of bundle, formed together with protractor and retractor muscles, other connective tissue, and nerves. This compact unit is protracted from the mouth, to some degree in a ballistic manner, carrying the attached tongue pad at its tip. The cylindrical epithelial sheath surrounding the bundle is heavily pleated when at rest, and as the bundle is protracted it unpleats. The folding of the apparatus is initiated with the contraction of the protractor muscles, the subarcualis rectus I, which originate on the ventral side of the anterior blade-like portion of the ceratohyals and extend to
FIGURE 4.5. Kinematic profiles for the bolitoglossine plethodontid salamander *Hydromantes platycephalus*. The panels are, from top to bottom, tongue reach and gape distance, gape distance, jaw deflections, and head angle, all presented on the same time axis. Gape distance is presented in both the first and the second panels, on different ordinates, to illustrate the vast differences in excursion between the tongue and jaws. This prey-capture event was performed with small prey and lacks a distinct second phase of mouth opening, which often occurs during tongue retraction.
form a complex, pinnate muscle wrapped around the tapered epibranchial. The protractor muscles are differentiated in the plethodontids into an anterior, parallel-fibered portion and a distinct, posterior, bulb-like muscle, which is greatly enlarged in relation to that found in members of other families. The hyolingual apparatus contains two triangular units, formed by the medial basibranchial and the ceratobranchials on either side, so in order to form a compact bundle without bending, it folds in three dimensions as it is protracted, moving along a morphological track having the geometrical form of a tractrix. This form has favorable attributes. It appears to act as an accelerator of movement and contributes to the rapidity of protraction. It also acts as a brake for the returning apparatus.

The three-dimensional expansion of a tractrix is known geometrically as a bugle body, and it exists, in a limited degree, in the floor of the mouth. The sides of the bugle body are formed by the medial margins of the ceratohyals. The bottom is formed by intermandibularis muscles and the top by a strap-like, unpaired suprapeduncularis muscle (the last muscle unique to the Plethodontidae). The structural element thus formed, called the cylinder by Lombard and Wake (1977), controls the direction of tongue protraction. In species that are most proficient in tongue protraction, members of the plethodontid tribe Bolitoglossini, the cylinder is well formed and incorporates a number of muscles that serve different functions in other taxa. These muscles include the anterior fibers of the subarcualis rectus I, the geniohyoideus medialis, anterior fibers of the rectus cervicis superficialis, and the heboypsiloideus. According to the biomechanical model of Lombard and Wake (1976, 1977) movement of the cylinder from side to side within the mouth is possible. The cylinder appears to rest in the floor of the mouth attached posterolaterally to the mandible by a slender and poorly defined mandibulo-hyoid ligament and anteriorly by the geniohyoidius lateralis. Thus there appears to be a kind of “firing platform,” and a relatively large contraction of the left geniohyoideus lateralis is hypothesized to direct the tongue toward the right.

The biomechanical model also hypothesizes that a mechanical linkage between parts of the hyolingual apparatus accomplishes at least a partial rotation of the tongue pad during protraction. The very action of folding is biomechanically coupled to rotate the tongue pad around the tip of the basibranchial so that the fleshy, mucous-covered pad contacts the prey. A ligament-like bundle of connective tissue extends from the anterolateral part of the first ceratobranchial into the substance of the tongue pad. This fiber bundle extends anteriorly from each side, coalescing at the ventral midline of the anterior tip of the basibranchial and then variously attaching to a flexible tip of the basibranchial, to a detached anterior part of the basibranchial known as the lingual cartilage, or extending dorsally around the tip of the basibranchial and then fanning out posteriorly into the substance of the tongue pad. When the skeleton folds as it is protracted, the fibers become taut and the tongue pad is pulled forward to rotate around the tip of the basibranchial in such a fashion that the sticky dorsal surface is presented to the prey.

The cylinder of plethodontids is lined along its inner surface by serous glands, which apparently lubricate the bundle within it during protraction. Protraction can result in the bundle being rapidly propelled forward and can be so great as to result in the skeletal elements, totally evacuating the cylinder as well as the bulb formed by the subarcualis rectus muscles. Momentum of the projectile carries the epibranchial cartilages fully out of the mouth in species of the genus Hydromantes and other bolitoglossine species we have observed. In these taxa the tongue is fired ballistically from the mouth as a projectile (Fig. 4.6; Deban et al., 1997).

Auxiliary protraction mechanisms function in other, nonplethodontid taxa. The subhyoideus connects the posterolateral parts of the ceratohyals to the mandible (see Fig. 3.5B). When these paired muscles contract, the ceratohyals are moved forward as a first stage in tongue protraction. The subarcualis rectus are presumably firing at the same time so the two-stage protraction involves (1) the anterior movement of the ceratohyals carrying with them the entire tongue apparatus, and (2) the independent protraction of the articulated hyobranchial apparatus and attached tongue pad relative to the first segment (Findeis and Bemis, 1990; Miller and Larsen, 1990). This has been termed the “mobile ceratohyal system” by Findeis and Bemis (1990), who contrast it with the other main evolutionary trend involving a “stable ceratohyal system” in plethodontids (which we believe is the ancestral condition).

Another auxiliary system found in salamandrids (Chioglossa and Salamandrina) involves the rotation of elongated radii (Fig. 4.2) in an arc around the tip of the strengthened, mineralized basibranchial, which is “T” shaped in cross section (Ozeti and Wake, 1969). This action carries the tongue pad forward, effectively flipping the free posterior flap of the pad well out of the mouth.

c. Prehension and the Tongue Pad

The tongue pad varies considerably in shape among terrestrial salamanders. In general, it is attached firmly to somewhat loosely at the front, has varying degrees of freedom along the sides, and has the greatest
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FIGURE 4.6. Photograph of *Hydromantes genei* capturing a housefly, showing projection of the hyolingual apparatus. The projectile includes the retractor muscle and the bundle of cartilages wrapped in a cylindrical membrane of connective tissue and epithelium. The tongue pad has enveloped the fly, but is not extended so maximal reach for the tongue would be considerably longer than is apparent in this photograph. The epibranchial has left the borders of the mouth. The bends near the distal tip of the projectile indicate the positions of the end of the basibranchial and the epibranchial—ceratobranchial joints.

degree of freedom posteriorly. The posterior part of the tongue may be extended into two limbs that are loose and form relatively long strands during full protrac-
tion. This is especially true in some salamandrids and some plethodontids. In two plethodontid clades the
tongue has lost its anterior attachment (the genioglos-
sus muscles are absent) and the tongue has a mush-
room-like shape. In these species the pad typically be-
comes relatively small and round; these groups show
the greatest distance of tongue protrac-
tion.

Shaping of the tongue pad may be facilitated by the
contraction of muscles inside the tongue pad that arise
from the tip of the basibranchial and fan out into the
posterior part of the tongue (hyoglossus), extend to the
tips of the radii (basiradialis), extend between the tips
of the radii (interradialis), or extend from the tips of the
radii into the tongue pad (radioglossus). For the pleth-
odontid salamanders, Lombard and Wake (1977) pro-
posed three functional classes of tongue pad muscles:
rotators (genioglossus, circumglossus, basiradialis, and
intraglossus), molders (interradialis and hyoglossus),
and restorers (rectus cervicis profundus). Families dif-
er substantially with respect to relative numbers, sizes,
and proportions of skeletal elements and muscles pres-
ent, and the tongue pad varies significantly among
taxa; however, this diversity has not been the subject of
detailed comparative analysis.

The surface of the tongue is rotated by a combina-
tion of skeletal and muscular movements so that the
glandular dorsal surface covered with relatively sticky
mucous contacts the prey. The tongue pad shape
is transformed and expanded during protrac-
tion so that
it is relatively large and expansive when it contacts
the prey. In those taxa having an otoglossal cartilage,
movement of this element during protrac-
tion is postu-
lated to carry the glandular field of the tongue pad dor-
soanteriorly so that it contacts the prey (Larsen et al.,
1996). In ambystomatids, the tongue pad is rotated for-
ward as protrac-
tion occurs via the connection between
the first radii and the hypohyals.

The mechanism of tongue protrac-
tion in pleth-
odontids is somewhat simplified in relation to the other
group that has been studied in detail, the ambystoma-
tids (Reilly and Lauder, 1989, 1990b). In the ambysto-
matids the ventral throat constrictors (intermandibu-
laris and interhyoideus) and two longitudinal muscles
geniohyoideus and genioglossus) are active during
protraction. The constrictors and the geniohyoids are
implicated in provision of a lift vector to the hyolingual apparatus. The subarcualis rectus I provides a separate forward and upward vector, and when well protracted the geniohyoiids and genioglossus provide a third forward and ventral vector to the protraction. The combined effect of these three vectors is a resultant horizontal vector that advances the entire hyolingual system, and flipping of the tongue pad is attributed in part to the action of the genioglossus.

d. Retraction

The articulated hyolingual skeleton has one retractor muscle attached to it at the anterior border of the first ceratobranchial. This is a muscle with several names, but is usually termed the sternohyoideus or the rectus cervicis lateralis (in some taxa the muscle is not well differentiated from the rectus cervicis superficialis). It arises from the sternum and is an anterior continuation of the rectus abdominis series. However, this muscle appears to be a secondary retractor, and the main retractor is a muscle that extends forward under the ventral surface of the hyolingual skeleton and passes through the triangular gap between the first and the second ceratobranchials and the basibranchial. From this position the paired muscles extend forward and then bend abruptly dorsally to enter the tongue pad, where they typically attach to a mass of connective tissue long known by the German term *Schenenplatte* (“tendon plate”). This muscle is also known by various names, including the abdominohyoiodeus and the rectus cervicis profundus. This muscle arises from the lateral margin of the sternum, from a tendinous inscription lateral to the sternum that separates it from the rectus abdominis profundus, or as a direct and continuous anterior extension of the last named muscle, which in extreme cases (Plethodontidae) represents an undivided muscle that arises from the posterior border of the ischium and proceeds uninterrupted into the tongue pad. Retraction of the tongue appears to be exclusively the result of the action of the two different segments of the rectus cervicis series. In the most proficient tongue protractors, the bolitoglossine plethodontids, the rectus cervicis lateralis muscle is absent in two of the three major lineages, and retraction is exclusively by the rectus cervicis profundus. The omohyoideus is also missing in these taxa, and the heboestoeopsoideus, which is part of the general retractor system in most taxa, is incorporated into a muscular cylinder through which the tongue is folded as it is protracted.

e. Speed and Distance of Lingual Feeding

The effectiveness of lingual feeding has not been studied in most taxa. As a generalization, species demonstrating true tongue projectility are the fastest, the most accurate, and have the greatest range. The fastest tongue recorded to date is that of *Bolitoglossa occidentalis*, which takes less than 10 msec from the start of electrical activity in the subarcualis rectus I muscles to the time the tongue strikes the target.

Maximum tongue extension (form tip of snout) has been measured in a number of species. In six species of *Ambystoma* the largest average distance was 2.4 ± 0.3 mm (*A. californiense*) and the smallest was 0.3 ± 0.4 mm (*A. mabeei*) (Beneski et al., 1995). Hynobids can extend their tongues only a few millimeters beyond the tip of the snout, but as much as 7% of snout–vent length (Larsen et al., 1989, 1996). However, *Hynobius kimurae* was found to protract its tongue 4–6 mm beyond the symphysis (J. Larsen, personal communication), and in our laboratory a large (6 to 7 cm snout–vent length) *Salamandrella keyserlingii* has protracted its tongue 6.6 mm, thus some hynobids are apparently far more proficient than those reported to date. Salamandrids are apparently the most variable with respect to maximal tongue extension. *Pachytriton brevipes*, an aquatic species that lacks a defined tongue pad (Ozeti and Wake, 1969), retracts rather than protracts the hyolingual apparatus during terrestrial feeding (Miller and Larsen, 1990), thus in essence performing an aquatic, suction-feeding behavior on land (see Chapter 3 for details of this behavior, including Fig. 3.2). In most species of salamandrids, tongue protrusion is relatively short, from 1.1 to 2.7 mm (average extension beyond snout), the latter distance in *Tylototriton verrucosus* (Miller and Larsen, 1990). *Salamandrina terdigitata* has a complex tongue protraction involving an initial protraction of the hyolingual apparatus from the mouth and then flipping of the pad (Ozeti and Wake, 1969; Miller and Larsen, 1990). The average maximal tongue extension recorded by Miller and Larsen (1990) for this species is 7.4 mm, or 20% of snout–vent length (4.7 mm is reported in the paper, but a printer’s error reversed the digits; J. Larsen, personal communication). *Chioglossa lusitanica* probably has the longest tongue extension of the salamandrids, based on its morphology (Ozeti and Wake, 1969), but it remains largely unstudied. Maximum tongue extension is variable in plethodontids; distances are about 7% of snout–vent length in species with attached tongues (*Desmognathus quadramaculatus* and *Plethodon glutinosus*), about 15% in a species with an attached protrusible tongue (*Ensatina eschscholtzii*), and 30–44% in *Bolitoglossa occidentalis* (Thexton et al., 1977; Larsen et al., 1989). This species is capable of firing the tongue effectively for at least 17 mm from the head, or as much as 44% of the snout–vent length of the salamander (Thexton et al., 1977). *Hydromantes italicus*, a larger species, is reported
to be capable of capturing prey 40 mm from the head, and the intermediate-sized Bolitoglossa subpalmata can project its tongue 30 mm (Roth, 1987). Adult Hydro-

mantes supramontis can project the tongue accurately to a distance of about 80% of snout-vent length (over 60 mm from the head) (Fig. 4.6; Deban et al., 1997).

The prey-capture success rate has been measured in only a few species, but is higher in the proficient tongue protractors than in more generalized species. *Salamandra salamandra* was successful in only 39% of attempts (Luthardt-Laimer, 1983) compared with above 50% in the generalized plethodontid genera *Plethodon, Eurycea,* and *Batrachoseps.* The very long tongued bolito-
glossine genera *Bolitoglossa* and *Hydromantes* “rarely miss,” although no exact figures are available (Roth, 1987). These last two genera may engage in “stalking” in the laboratory to move slowly into range (Roth, 1987; personal observation).

The total length of the kinematic cycle is variable among the different taxa studied. The mean gape cycle (in species with tongue protrusion) ranges from 92.8 to 115.7 msec in hynobiids (Larsen et al., 1996), 78 to 214 msec in ambystomatids (Beneski et al., 1995), 100 to 238 in salamandrids (Miller and Larsen, 1990), and 87 to 110 in plethodontids (Larsen et al., 1989; Beneski and Larsen, 1988). Gape cycle time is apparently rather similar across a wide array of morphologies.

Speed of the tongue strike (tongue protraction, equivalent to phase II of Beneski and Larsen, 1988) varies greatly among taxa. The fastest tongues are found in *Bolitoglossa,* which has a mean duration of phase II of 5.0–7.7 msec, with *Ensatina* at 11.6 msec being only a little slower (although we have measured one individual *Ensatina* at ca. 7 msec from the time the tongue left the mouth until it touched the prey). *Pseudotriton ruber,* a hemidactyline with a free tongue, has a protraction time of as little as 11 msec (Deban, 1997). The plethodontids with attached tongues are slower still: *Plethodon glutinosus* takes 19.3 msec and *Desmognathus quadramaculatus* takes 37.3 msec to protract the tongue (Larsen et al., 1989). Roughly comparable times are reported for other taxa (different papers use slightly different methods of reporting). Ambystomatids range from 16 msec for *Ambystoma mabeii* to 87 msec for *Ambystoma cingulatum* (Beneski et al., 1995). Maximum tongue protrusion in *Ambystoma tigrinum* is reported by Reilly and Lauder (1989) to take 45 msec, and by Dockx and De Vree (1986) to take 39.6 ± 11.0 msec. Hynobids are reported to range from 25.1 msec for *Hynobius kimurae* to 36.0 msec for *H. nebulosus* by Larsen et al. (1996) [27.4 msec and 36.0 msec for the same species by Larsen et al. (1989)]. Among salamandrids, tongue protrusion times are reported by Miller and Larsen (1990) to range from 22.0 msec in *Salamandra salamandra* to 111.9 msec in *Paramesotriton hongkongensis.* Dockx and De Vree (1986) report 84 ± 21.7 msec for tongue protrusion in *Salamandra salamandra,* and Findeis and Bemis (1990) report a range of durations from 80 to 140 msec for *Taricha torosa.*

### f. Physiology

Electromyographic (EMG) investigations of tongue movement (Thexton et al., 1977; Reilly and Lauder, 1990b) in two very different taxa (a bolitoglossine plethodontid with a highly protractible, free tongue and an ambystomatid with a weakly protrusible, attached tongue) show that the protractor (subarcularis rectus I) and the retractor (rectus cervicis) have essentially synchronous onset and similar motor patterns. Because electrical signals are delivered to the protractor and retractors simultaneously, the activity of the system is thought to be controlled by the peripheral organ-

*...*
a second peak during the retraction phase. Buccal muscles in the floor of the mouth are active throughout the cycle, but tend to peak early and then taper off. The main retractor muscle (rectus cervicis profundus) peaks at the time retraction begins and activity continues until after mouth closing. We take the coactivity of antagonistic muscles as a sign of fine control over tongue and jaw movements and the prolonged activity of the buccal floor muscles as an indication that they are performing a stabilizing function.

In Bolitoglossa strain gauges were used to measure force of tongue impact with the prey (Thexton et al., 1977). At relatively short distances, force varies considerably, probably indicating differences in motivation and concomitant muscle activity level. However, at distances exceeding 10 mm from the snout (animals have a maximal head-body size of about 44 mm), force fell off dramatically as a function of distance from the snout, finally failing to register at the greatest distance (19 mm). This supports the idea that there is a ballistic phase (at the end of muscular protraction) to long-distance tongue projection in the species most proficient in tongue projection.

2. Jaw Feeding

Use of the jaws to capture prey is unusual in terrestrial salamanders, but it does occur, at least in members of the families Ambystomatidae and Salamandridae (Larsen and Guthrie, 1975; Miller and Larsen, 1990). We have also observed it infrequently in various terrestrial species of the Plethodontidae in circumstances when the tongue fails to apprehend the prey. In addition, we have observed the semi-aquatic plethodontid Desmognathus quadramaculatus and the hynobids Salamandrella keyserlingi and Batrachuperus persicus using jawprehension in water and the fully aquatic plethodontid Desmognathus marmoratus using either tongue or jaw prehension in water (see also Schwenk and Wake, 1993). Kinematics of the gape profile of salamanders using jaw prehension differs from either the generalized four-part or the specialized three-part pattern of other taxa and consists of a bell-shaped, two-part gape profile. The action is relatively rapid (on the order of 60 msec) and resembles that of fully metamorphosed ambystomatids that feed underwater without using tongue protraction (Reilly and Lauder, 1989). While the standard pattern of feeding in salamanders involves participation of the tongue in apprehending the prey, species such as Pachytriton brevipes, which effectively lacks a tongue pad (Ozeti and Wake, 1969), and other mainly aquatic salamanders feeding on land (Miller and Larsen, 1989) can use jaw prehension, although not very effectively. Jaws are used in aggressive encounters in salamanders (Staub, 1993), and it is evident that biting without tongue protraction is possible. Nonetheless, we expect that salamanders feeding in terrestrial situations typically will display a pattern of feeding that involves tongue prehension (Bramble and Wake, 1985).

D. Prey Processing

Prey immobilization is significant when the prey are too large to be fully engulfed at the time of capture. Large-bodied salamanders are capable of eating long and slippery (e.g., earthworms in ambystomatids) and even very large prey (e.g., mice in dicamptodontids) relative to body size. In these species, strength of the jaw-closing muscles is important, as well as size and strength of the marginal tooth-bearing bones. The mouth is closed at the end of the strike and if the prey protrudes from the mouth there may be a delay of a few milliseconds to several seconds before processing and/or swallowing proceeds. This process has been most thoroughly studied in ambystomatids and is described later. Dicamptodontids have heads that are the largest of terrestrial salamanders both absolutely and relatively, and they seize (it is not recorded if this is by lingual prehension or jaw prehension) prey such as mice and hold them in the buccal cavity until the prey suffocates before further processing proceeds. Two groups of plethodontids have special prey-processing features. Aneides includes species (e.g., A. lugubris) that have greatly enlarged adductor muscles, jaws and marginal teeth (Wake, 1963). These may well be associated mainly with aggressive behavior (e.g., Staub, 1993), but they also enable these species to eat larger food than co-occurring species of similar size (Lynch, 1985). Desmognathine plethodontids engage in a unique behavior, cranial ventroflexion or head tucking (Dalrymple et al., 1985; Larsen and Beneski, 1988; Schwenk and Wake, 1993), that is enabled by the presence of a number of morphological modifications of the head and neck regions, including a ligamented tendon extending over either side of the skull from a specialized ridge on the atlas to the lower jaw. This behavior is characteristically performed after lingual capture of the prey and involves a sharp ventroflexion of the head relative to the neck with the prey caught in the jaws. Head tucking may occur as a final component of mouth closing following capture, or without mouth opening, and it represents an extreme form of a static pressure feeding system (Olson, 1961) in salamanders. The result is the penetration of the prey by the teeth and the effective immobilization of the prey. Both Aneides and the
desmognathines have enlarged quadrapectoralis and an additional muscle (often termed gularis) that contribute to their ability to deliver a strong bite.

Prey transport has been studied most extensively in *Ambystoma tigrinum* (Reilly and Lauder, 1990a, 1991b; Gillis and Lauder, 1994), and only fragmentary information is available for other taxa (Dockx and De Vree, 1986; Thexton et al., 1977). Four phases of intraoral prey transport are recognized in metamorphosed ambystomatids feeding on worms on land (as well as in the water as larvae): preparatory, fast opening, closing, and recovery. Transport per se is accomplished during fast opening and closing. Electromyographic recordings reveal that the preparatory phase involves electrical activity in muscles of the buccal floor (both the longitudinal genioglossus and geniohyoideus, and the transverse intermandibularis and interhyoideus) and then there is a short period of electrical silence before a fast opening of the mouth that is accompanied by simultaneous activity of all muscles studied, even antagonists such as the mandibular depressors and adductors (Reilly and Lauder, 1991b). Reilly and Lauder (1990b) divided the preparatory phase into two parts. In the first part the prey item is pressed against the roof of the mouth by the elevated hyoid apparatus. Gape increases slowly but is never great during phase one. During the second phase, which is shorter in duration, the gape is held constant. Then the fast opening phase occurs, followed quickly by a closing phase, and in each cycle of opening and closing between 4 and 8 mm of prey is transported. Intraoral transport of the prey occurs at the beginning of mouth opening, as the rectus cervicis contract, thus retracting the hyobranchial apparatus and moving the tongue pad (to which the prey is sticking) posteriorly into the pharynx. The muscle that protracts the tongue during prey capture, the subarcualis rectus I, is also active during this time, and Reilly and Lauder (1991a) postulate that it may act antagonistically to the retractors so as to stabilize the interaction of the articulated hyobranchial apparatus and the ceratohyal and to enable the system to function as a whole in aiding the rapid posterior movement of the tongue. There is no inertial component to prey transport. The mouth closes as the prey moves backward. During recovery, hyobranchial protraction carries the tongue forward under the prey, for now the prey is held by the combination of palatal and marginal teeth.

The intraoral prey transport system in *Ambystoma* is very similar during aquatic and terrestrial feeding. However, electromyographic patterns differ between prey capture and transport (reviewed by Lauder and Gillis, 1997). Variation in feeding kinematics is event specific rather than reflecting the environment in which it occurs (Gillis and Lauder, 1994). Reilly and Lauder (1991) hypothesize that prey transport in terrestrial feeding retains an ancient (extending to fishes) motor pattern associated with suction feeding by larvae. The facts that prey transport behaviors are similar in fishes and salamanders and that they are faster and involve less excursion than prey capture have been used to hypothesize that the prey transport system of terrestrial salamanders may have been directly inherited from the aquatic transport behavior based on suction in aquatic ancestors (Gillis and Lauder, 1994; Lauder and Gillis, 1997).

Many salamanders, especially plethodontids but also members of other families, eat small prey that are ingested fully on capture. In these species the marginal dentition does not contact the prey, and transport within the buccal cavity differs from the pattern seen in ambystomatids. Frequently the mouth is not opened again, but evidence shows that the tongue is repositioned and then retracted further, moving the prey into the pharynx. Thexton et al. (1977) recorded two to three bursts of activity in the rectus cervicis muscles following prey capture in the diminutive plethodontid *Bolitoglossa occidentalis*. This implies that the tongue is being protracted and retracted repeatedly with the mouth closed, and that swallowing follows.

### E. Modulation of Feeding Behavior

Little attention has been given to modulation of feeding behavior under different conditions. Substantial modulation is possible under different circumstances, especially with respect to differences in prey (Deban, 1997; unpublished observations). The species that have been most intensively studied to date are *Salamandra salamandra* (earlier work reviewed by Roth, 1987; see also Reilly, 1995) and *Ensatina eschscholtzii* (Deban, 1997); other species studied less intensively include various salamandrids (e.g., Miller and Larsen, 1990) and plethodontids (*Hydromantes italicus*, Roth, 1987; *Plethodon cinereus*, Maglia and Pyles, 1995).

The greatest modulation occurs in newts that feed both on land (using tongue protraction) and in the water (using suction feeding). Miller and Larsen, 1990). *Bolitoglossa occidentalis* showed little evidence of modulation in early studies (Thexton et al., 1977; Larsen et al., 1989), but our observations show a high degree of modulation of the timing and extent of tongue movements in several species of bolitoglossines. Among ambystomatids, some species (e.g., *Ambystoma tigrinum*) are apparently highly stereotyped in tongue protraction, whereas others (*Ambystoma macrodactylum*) show evidence of some modulation (Larsen and Guthrie, 1975).
When tested with two distinctly different kinds of prey (waxworms and termites), *Ensatina eschscholtzii* modulated both the timing and the magnitude of tongue and jaw movements with respect to different prey. When feeding on waxworms, the larger prey, feeding took less time and tongue and jaw movements attained a higher velocity than when feeding on termites (Deban, 1997). In *Plethodon cinereus*, maximal tongue extension was as great as 17% of snout-vent length when feeding on adult *Drosophila* (mean 10.4%), but as little as 1% (mean 4.5%) when feeding on larval *Drosophila* (Maglia and Pyles, 1995). In *Ensatina*, distance of protraction correlated with distance of the prey from the head, not prey type. In both species, prey capture is completed more quickly on large than on small prey.

IV. DIVERSITY AND EVOLUTION

A. Origins and Outgroups

Extant out-group taxa for the order Caudata include the orders Anura and Gymnophiona, both of which differ profoundly with respect to feeding mechanisms from all salamanders. There has been a general consensus that the three orders of living amphibians (Lissamphibia) were derived from a temnospondyl labyrinthodont stock; one widely accepted hypothesis is that lissamphibians might be a sister taxon of the temnospondyl group Dissorophoidea (Bolt, 1977). Another alternative is that lissamphibians are derived from a lepospondylous ancestral stock, perhaps somewhere in the microsaur radiation (Laurin and Reisz, 1996). A further alternative is that lissamphibians do not form a monophyletic group with respect to fossils (Carroll and Holmes 1980). Regardless of phylogenetic considerations, living salamanders have a hyobranchial apparatus that is more generalized in morphology and more similar to known fossils (whether temnospondyl or lepospondyl) than either frogs or caecilians, and we (in accord with Lauder and Reilly, 1994) consider salamanders to be an appropriate model for the first terrestrial feeding system.

B. Phylogenetic Diversity

Six families of salamanders have species that metamorphose and feed on land: Hynobiidae, Rhacotritonidae, Dicamptodontidae, Ambystomatidae, Salamandridae, and Plethodontidae. The last three families have been studied in greatest detail with respect to feeding mechanisms and the last two display great diversity.

1. Hynobiidae

There is a general consensus that hynobiids are the most basal of the terrestrial taxa of the Caudata (Larson and Dimmick, 1993), and certain features of their feeding mechanism retain apparent ancestral states. The most evident of these is the retention of two branchial arches, with two epibranchials. All other terrestrial salamanders have a single epibranchial, supported by two ceratobranchials. There are, however, indications that hynobiids do not retain the ancestral structure, because they have a unique feature, the radial loop. The ceratohyals are connected to the basibranchial by means of elongated, attenuate hypohyal derivatives arranged in the form of a flat spring (Fig. 4.2). This arrangement is associated with a modest degree of tongue projection, which occurs with great speed (Larsen et al., 1989, 1996; unpublished data). The tongue pad itself has been described as “sac-like” (Larsen et al., 1996) and lacks differentiated musculature, and the basibranchial is extended forward in the radial loop, pulling it along as the hyobranchium is protracted. The extent of protraction is apparently limited by the structural connection of the the hyoid arch to the basibranchial, a connection that exists to a more limited extent in other terrestrial salamanders that do not protract their tongues so far. Tongue projection is accompanied by a strong forward lunge of the entire body of the salamander, so the effective strike distance is relatively great. Apart from the radial loop, which represents the first radii of other families, the structural arrangement of the tongue in hynobiids is generalized. The second basibranchials are ossified, whereas the first remain cartilaginous, suggesting that the second basibranchials are the main force-transmitting elements from the protractile musculature to the tongue pad. There is a well-developed subhyoideus muscle in hynobiids, and the subarcualis rectus I muscle is wrapped around both first and second epibranchials. These two muscles, working together, serve to protract the hyobranchial apparatus, but functional morphology of the musculature has not been well studied (Severtsov, 1971).

A pair of “cornua” are found at the anterior end of the basibranchial in many hynobiids (Cox and Tanner, 1989); these are paired anteriolaterally directed projections continuous with the anterior end of the basibranchial, and they are drawn out into long processes in *Onychodactylus* (Fig. 4.2). Cornua resemble the radii of plethodontids, but phylogenetic analysis suggests that the resemblance is homoplastic.

The hynobiid condition has been proposed to be the most basal salamander feeding mechanism, based on the combination of its morphology and the fact that it
displays a generalized four-part feeding cycle (Larsen et al., 1996; Beneski et al., 1995). However, the specialized nature of the radial loop precludes the possibility that it retains the ancestral morphology or function entirely.

2. Rhyacotritonidae

The Rhyacotritonidae has only recently been recognized as a distinct taxon that is relatively basal phylogenetically within the Caudata. Rhyacotritonids have a generalized hyobranchial morphology (Fig. 4.2). The first radii are present but not elongate as in the hynobiids. There is an otoglossal cartilage, an unpaired, dorsal, medial element that either joins the tips of the two second radii or lies freely between them. The articulated elements of the hyolingual skeleton remain cartilaginous, and there is only a single pair of very short epibranchials. The musculature is also generalized. The family resembles the Hynobiidae and the Salamandridae in having a subhyoideus muscle, which may function in a two-phase tongue protraction system.

3. Dicamptodontidae

The four species comprising this family are large, robust animals, three of which have a terrestrial stage. The tongue is unique and largely unstudied. It combines elements of the tongues of hynobiids, rhyacotritonids, and ambystomatids. The first radii are drawn into an attenuated loop that recalls the situation in hynobiids but is less extreme. The second radii are joined by a thin cartilaginous plate (Fig. 4.2) that appears to be the homologue of the otoglossal cartilage of rhyacotritonids and ambystomatids and supports the relatively enormous tongue pad that is used to capture prey of a wide range of sizes. There is no subhyoideus muscle. The single pair of epibranchials are short and ossified near their proximal ends.

4. Ambystomatidae

This is a large family of North American salamanders that has been relatively well studied. Both otoglossal cartilages and two pairs of radii are present. However, in contrast to the situation in hynobiids, rhyacotritonids, and dicamptodontids, the first radii are neither attenuate nor drawn into a radial loop that is continuous with the hyoid arch, but their distal tips are loosely connected to the free anterior ends of the ceratohyals. The second radii may be forked and elongate in the subgenus Linguaelapsis (Fig. 4.2).

Ambystomatids lack a subhyoideus muscle. They have a muscle termed the genioglossus lateralis that lies in the same general area as the subhyoideus but that has an entirely different origin and innervation (Piatt, 1940). This muscle may be used to move the ceratohyals medially, thus orienting the tongue.

5. Salamandridae

Basal salamandrids have two pairs of radii. The first radii are typically rather short and tapered, with free distal ends. The first radii are apparently lacking in Salamandra and Chioglossa, in which the second radii have moved to the distal tip of the basibranchial and rotate around it as the tongue pad is flipped. The radii are moderately long and robust in Salamandra, but very long and attenuate in Chioglossa (Fig. 4.2). In both genera the basibranchial is stout and is the only part of the articulated hyobranchial apparatus that is mineralized. In Salamandra it is T shaped in cross section. In other salamandrid genera the second radii are located behind the first radii, and an interradial cartilage (possibly a homologue of the otoglossal of other taxa) extends between them.

Tongue pad musculature is relatively complicated in the Salamandridae, and several muscles occur that are not found in other families (e.g., radioglossus) whereas others are larger than in other families (e.g., basiradialis). The most complicated tongue pad is found in Salamandra, in which tongue pad flipping is thought to be accomplished by rapid rotation of the radii by the basiradialis muscles (Özetli and Wake, 1969)

Salamandrid genera were divided into two functional groups based on tongue structure and use of the tongue in feeding by Özetli and Wake (1969). Most genera have a “water tongue” and they have been known as “Wassermolchen” in the German literature (Wolterstoff and Herre, 1935). In these genera the hyolingual apparatus is used for suction feeding in the water and for tongue prehension on land. Characteristically the skeleton of the hyolingual apparatus is relatively heavy and well ossified. At least one genus, Pachytriton, is permanently aquatic, has no tongue prehension ability, and has a very reduced tongue pad. Paradoxically, Pachytriton has a terrestrial eft stage (common in other newts) in which tongue prehension likely occurs (Thiesmeier and Hornberg, 1997), prior to the return as an adult to a permanently aquatic existence in which tongue prehension is impossible. The most terrestrial salamandrids, Salamandra, Mereniella, Chioglossa, and Salamandra, have “land tongues.” They either do not enter water or feed in water using terrestrial behaviors and they have specialized tongues used for prehension of prey. Typically the hyolingual apparatus is either entirely cartilaginous or only the basibranchial is ossified. A significant part of tongue protraction in Chioglossa and Salamandra is accomplished by flipping and extension of the large tongue pad (Miller and Larsen, 1990).
Salamandrids have a subhyoideus muscle (see Fig. 3.5 in Chapter 3) that is used to protract the ceratohyals and the tongue in general (Findeis and Bemis, 1990). Some salamandrids have some lateral muscle fibers arising near the genioglossus (e.g., Özefi and Wake, 1969), and these may be homologues either of the genioglossus lateralis of ambystomatids or possibly the geniohyoideus lateralis of plethodontids.

6. Plethodontidae

Ototoglossals are absent in the Plethodontidae, and some taxa have a medial unpaired "lingual cartilage" (Fig. 4.4). Rose (1996) has shown that the lingual cartilage may have some connection with the hypohyals of experimental animals treated with thyroxin. Wake (1966) argued that the cartilage is derived from the anterior extension of the basibranchial that lies in front of the attachment of the radii. Out-group taxa that have an anterior extension also have either a pair of first radii attached to it or bear a pair of cornua. It is possible that the anterior extension represents the fusion of the lingual cartilage to the basibranchial; perhaps the lingual cartilage should be considered a homologue of a long missing basihyal. The first radii of out-group taxa that have two pairs of radii lack muscular attachments, and because the single radii of plethodontids have muscular attachments they are best considered to be homologues of the second radii of other taxa. An alternative interpretation is that the radii of plethodontids may be homologues of the cornua of hynobiids, because in many plethodontids the radii are homoecontinuous with the cartilage of the basibranchial, although in others they are articulated with the basibranchial, as are the second radii in members of other families. If, as argued earlier, the first radii represent hypohyals of out-group taxa, the lingual cartilage represents the basihyal, the distal (with respect to distance from the midline) element found in rhyacotritonids represents the epihyal, and portions of the middle ear complex are derived from the arch as well, all components of the entire hyoid arch are present in the Caudata, but not in any single taxon.

There is no subhyoideus muscle in plethodontids. A well-developed geniohyoideus lateralis may play an important role in controlling lateral to medial movements of the ceratohyal and thus direct the firing of the tongue, but this has not been demonstrated behaviorally (Lombard and Wake, 1977).

Feeding mechanisms in plethodontids have been studied extensively, and summary discussions of feeding in a phylogenetic context accompanied by evolutionary scenarios are presented by Roth and Wake (1985b), Lombard and Wake (1986), and Wake and Larson (1987). Phylogenetic analyses (Jackman et al., 1997) support the hypothesis (Wake, 1966; Lombard and Wake, 1986) that the freely projectile tongues of the superfamilies Hydromantes and Bolitoglossa are derived independently. Both are derived independently of the even more phylogenetically remote members of the tribe Hemidactyliini, which also have evolved freely projectile tongues. Thus, within the Plethodontidae there are three lineages that have evolved highly specialized tongue projection mechanisms. The hemidactyline tongue is folded according to one of two hypothetical possibilities (Lombard and Wake, 1976, 1977), called option 1. This folding pattern involves holding the first ceratobranchial and epibranchial coplanar during folding. It results in a relatively bulky projectile that is postulated to have more limited projectability than is involved in option 2 (Wake, 1982). This option has been hypothesized as a necessary consequence of the retention of an aquatic larval stage and associated larval suction feeding in hemidactylines (Wake, 1982). In contrast, bolitoglossines, which all have direct terrestrial development and no aquatic larval stage, all use option 2 folding, in which the second ceratobranchial and the epibranchial are held coplanar. This option results in a slimmer projectile that is less limited in length than in hemidactylines. There are two modifications of the option, that of Hydromantes, which has apparently optimized for distance by having evolved extremely long epibranchials, and that of the supergenus Bolitoglossa, which also has elongated epibranchials but substantially shorter than in Hydromantes, and is apparently optimized for speed (Larsen et al., 1989).

C. Feeding Biology and Evolution

1. Ecology and Selective Regime

The evolution of terrestrial feeding in salamanders has proceeded in a great diversity of habitats and microhabitats, and in the absence of information about close sister taxa of Caudata it is impossible to reconstruct the habitat occupied by the first terrestrial feeders. However, it seems likely that early salamanders had a biphasic life cycle, involving feeding in water and on land, and that courtship and mating probably occurred in the water. Accordingly, feeding most likely entailed suction feeding both as larvae and as adults, and tongue protrusion, apprehension, and capture on land. The most specialized terrestrial feeding mechanisms tend to be associated with species that do not spend much time in the water, or that are entirely terrestrial. The exception to this generalization is the family Hynobiidae, in which species with aquatic larvae and semiaquatic habits as adults have a hyolingual system that is fast and biomechanically specialized (e.g.,
Larsen et al., 1996). In the hemidactyliine plethodontids and in salamandrids such as Chioglossa and Salamandrina, tongues are also highly specialized for speed and distance of protraction, and these forms all have aquatic larvae. However, all are lungless or have reduced lungs, and this appears to be a necessary, but not sufficient, precondition for the high specialization of the tongue (Roth and Wake, 1985b). Rhacotritonids, whose tongue and feeding are relatively unstudied but which have a generalized morphology, also have reduced lungs. The greatest specialization in tongue speed and protrusion is found in the bolitoglossine plethodontids, all of which lack an aquatic larval stage. These species have diverged far beyond the ancestral home of not only salamanders as a group but of plethodontids, and occur in a great diversity of terrestrial habitats and microhabitats, including waterless caves, cavities in trees, epiphytes, scrublands, and other settings in which foraging is restricted by environmental considerations. Whatever the environment in which tongue specialization evolved, it is a highly effective feeding strategy.

2. Homoplasy

Homoplasy is common in the evolution of terrestrial feeding mechanisms of urodèles and has been discussed extensively (e.g., Wake, 1966, 1982; Lombard and Wake, 1986). What has attracted the greatest attention is tongue protrusion. While some degree of tongue protrusion occurs in all salamanders that metamorphose and have a terrestrial feeding stage, long-distance tongue protrusion has evolved independently along very different biomechanical pathways within at least three families (Hynobiidae, Salamandridae, and Plethodontidae).

In hynobiids, tongue protrusion is associated with modest increases in length of the two pairs of epibranchials and with the flat spring arrangement of the hyoid loop, which is attached to the articulated lingual skeleton in some way. However, the basibranchial remains short. Paired, relatively elongate cornua appear in Onychodactylus (Fig. 4.2), and while these may represent retained ancestral elements homologous to the second radii of other taxa, phylogenetic analysis suggests homoplasy. Tongue protrusion is never as great as in the other two families, but the tongue is fast and maneuverable. Larsen et al. (1996) argue that the radial loops and the attachment of the ceratohyals to the suspensorium constitute a functional constraint that mechanically limits the extent of tongue protrusion. Whether there has been homoplasy within the Hynobiidae awaits a modern phylogenetic analysis of the family and further morphological studies.

V. OPPORTUNITIES FOR FUTURE RESEARCH

Research effort has been unevenly distributed with respect to salamander clades. Biomechanical models of tongue protraction have been produced and tested for plethodontids and ambystomatids, but are largely lacking for other taxa. Detailed morphological studies date to the early part of this century and do not include several families, including Dicamptodontidae, Hynobiidae, and Rhacotritonidae. However, comparative anatomical studies of some of the larger families, including Ambystomatidae, Plethodontidae, and Salamandridae, are relatively complete. What is needed is a broad and integrated comparative anatomical analysis of the musculoskeletal system of all the families, with special attention given to the establishment of homologies.

Quantitative studies of kinematics are limited to only a few species and in general have been conducted in artificially controlled conditions and with limited, sometimes unnatural, prey. The modulation of behavior has been investigated in only a handful of species, even though most species feed on a diversity of prey and under a variety of conditions. Diet and foraging are in need of further study in most taxa. Two families, the Dicamptodontidae and the Rhacotritonidae, have been especially understudied with respect to kinematics.

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