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# Rampant Homoplasy in Complex Characters: *Repetitive Convergent Evolution of Amphibian Feeding Structures*

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### Introduction

Were the Great Transitions in the history of life unique events in which a lineage of organisms evolved from a primitive to a more derived condition? Or during these transitions did separate but related lineages make similar transitions from a more primitive configuration independently? If so, how often might these independent similar transitions have taken place? Homoplasy, the independent evolution of similarity in a given phenotype in different taxa, has long been a central issue in evolutionary biology (see M. Wake, this volume). Arising from convergence, parallelism, or reversal to ancestral states, homoplasy has the potential to frustrate attempts to generate robust phylogenetic hypotheses and can lead to incorrect scenarios for the evolution of functional and biomechanical systems. In many cases, researchers have proceeded on the assumption that homoplastic features are overwhelmed by true phylogenetic signal, for example, in cladistic analyses. However, in some taxa the balance between signal and what might be called “noise” (i.e., homoplastic traits) is so close that cladistic analyses yield problematic results, especially in cases in which an entire clade is characterized by homoplastic traits. In clades in which many lineages, sharing only a remote common ancestor, have

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independently addressed the same fundamental problems using the same pathways, phylogenetic analyses of phenotypes may be positively misled by homoplasy. For example, resolution of the salamander tree of life using morphological data remained impossible for decades because of the many instances of species that remain aquatic as adults by essentially prolonging larval life (larvamorph taxa, including among others mud puppies and axolotls; Wiens et al. 2005). With the advent of molecular approaches for the generation of data used to test phylogenetic hypotheses, a new era of interest in homoplasy has arrived. Scenarios of phenotypic evolution can now be evaluated in a rigorous framework in which the primary data (i.e., DNA sequences) for phylogenetic inference are at least largely independent of the phenotypes of interest. Such analyses can fundamentally reshape our understanding of morphological and life history evolution, especially in cases in which highly nested clades have “reversed” to phenotypes characterizing ancestral taxa. With robust phylogenies in hand, the study of homoplasy can lead to new interpretations of the underlying mechanisms, and their relative frequencies, associated with major transitions in form and function.

Major evolutionary transformations such as the origin of feathers or the fin-to-limb transition are traditionally thought of as the result of a “one-off” series of events. This is a reasonable working hypothesis as we look back disadvantaged by the passage of time, extinction of lineages, and a paucity of organismal remains in the fossil record. Were we closer in time to those events and graced by a multitude of associated taxa, would we still find a singular “one-off” evolutionary series? Living plethodontid salamanders provide a laboratory to examine this question. Within this clade, any reasonable hypotheses of relationship indicate that similar feeding modes have evolved multiple times, representing independent experiments with evolutionary transitions. The comparative framework for examining such homoplasy enables one to ask broad questions about the importance of these transformations. For example, how do we measure the success or importance of a particular transformation? Answers to this question could include the number of species, breadth of phenotypic diversity, or uniqueness of habitat or distribution that have evolved in a given clade subsequent to that transformation. Both neotropical plethodontid salamanders

(e.g., *Bolitoglossa* and related taxa) and the temperate web-footed *Hydromantes* of Europe and western North America have evolved similar complex tongue projection mechanisms. Yet, these two lineages differ dramatically in species number with only 11 species of *Hydromantes* and more than 270 tropical salamanders (i.e., Bolitoglossini of Wake 2012). Any approach to reconstructing the evolutionary history of transitions requires a robust phylogeny. Plethodontids appear to have arisen in the Late Jurassic (Vieites et al. 2007), but the weak fossil record offers little of value regarding relationships within the family. Our approach here is to use the framework of recent phylogenetic hypotheses based on DNA sequence data to examine cases of previously proposed hypotheses of levels of homoplasy and evolutionary transitions in morphology.

### Evolution of Tongue Morphology in Plethodontid Salamanders

As early as the 19th century (Wiedersheim 1875) researchers were aware that different salamander taxa had tongues that were shot out of the mouth for a considerable distance to catch prey (fig. 22.1). Most frogs also project their tongue to catch prey, but it was apparent early on that different mechanisms were involved; in salamanders, the hyobranchial skeleton is a major element in the projected tongue and in the system controlling projection, whereas no skeletal element is projected in frogs. While salamanders in several families evolved effective mechanisms for tongue projection, members of the largest family, Plethodontidae, came under special scrutiny because of the high degree of specialization attained by many of its members (fig. 22.1).

The family Plethodontidae is by far the largest of the 10 families of Caudata (444 species out of a total of 671, AmphibiaWeb 2014), and accordingly there are abundant opportunities for homoplasy. The analysis of Lombard and Wake (1977) was unusual in that instead of atomizing morphology into characters, the tongue projection system was treated as an integrated functionally and morphologically complex character. The general biomechanical model of Lombard and Wake (1976) served as a point of departure, and historical treatments of feeding mechanisms and the then-prevailing phylogenetic hypothesis (Wake 1966) were

## Hydromantes Tongue Organization and Function

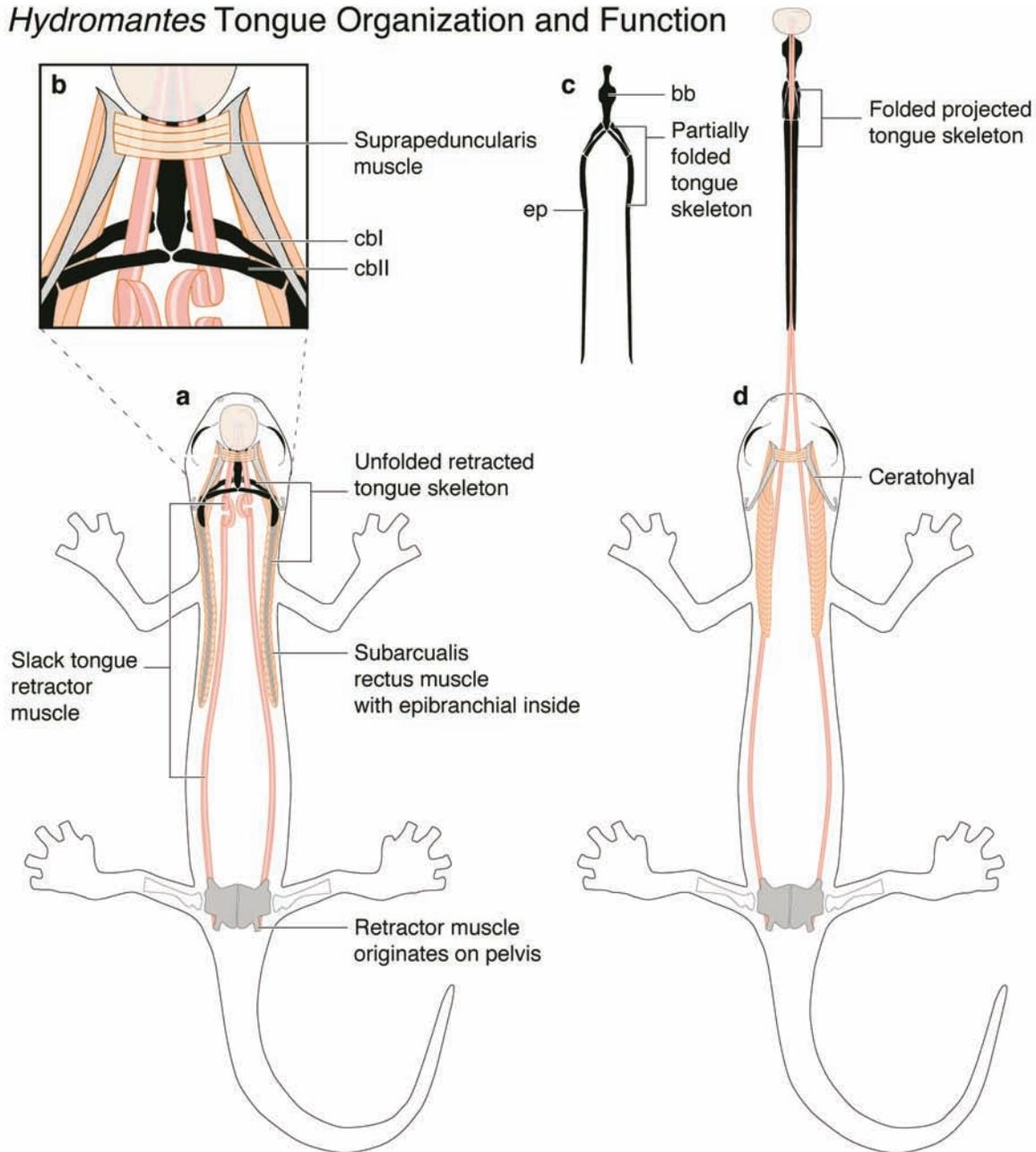


FIG. 22.1 Tongue organization and function in *Hydromantes*. a, Major skeletal and muscular elements with the tongue at rest. b, Detail of the major skeletal elements. c, Partly folded and projected tongue skeleton. d, Fully projected tongue with completely folded hyobranchial skeleton. Note the subarcualis rectus projector muscle originates on the ceratohyal, then sweeps back to enfold the epibranchial, the passage of the retractor muscle between the ceratobranchials, and the suprapeduncularis muscle, which is a major component of a muscular sheath that constrains and folds the hyobranchial skeleton during projection. bb, basibranchial; cbl, ceratobranchial I; cbII, ceratobranchial II; ep, epibranchial;

taken into account. Wake (1966) recognized four clades; a basal split separated Desmognathinae (a single, relatively small clade) from Plethodontinae (three large clades, Plethodontini, Hemidactyliini, and Bolitoglossini). Homoplasy was identified as a possibility by earlier

work, and Wake (1966) explicitly postulated that freely projectile tongues had evolved at least twice.

Lombard and Wake (1977) recognized eight functional feeding modes in plethodontids. Modes I (found in desmognathines, **DES** in the notation of Lombard and

Wake 1986: bold three-letter codes in figs. 22.2–22.4) and II (*Plethodon* and *Aneides*, **PLE**, both plethodontines) feature a relatively generalized morphology (seemingly less functionally specialized in I than in II), and represent what these authors termed an attached protrusible tongue. Mode III (*Ensatina*, **ENS**, a plethodontine) is biomechanically more specialized, with a more projectile tongue that is less firmly attached anteriorly (by elongated genioglossal muscles) to the lower jaw; its tongue was termed attached projectile. Mode IV (present-day tribe Spelerpini, then in the tribe Hemidactyliini and designated EUR now **SPE**) includes two subgroups, one highly specialized with freely projectile tongues (Mode IVa, **SPEa**) that utilizes a biomechanical system (folding option 1 of Lombard and Wake 1977)<sup>1</sup> necessitated by larval development and thought to constitute a constraint on functional specialization. These taxa all lack genioglossal muscles and the epibranchials are longer than in any taxa so far discussed. In two instances (*Stereochilus* and in one species currently deeply nested within *Eurycea*, *E. speleus*), a non-muscular attachment of the tongue to the lower jaw is retained (Mode IVb, **SPEb**); this attachment was thought to be ancestral in **SPE**, implying that freely projectile tongues (**SPEa**) have evolved more than once within spelerpines. Mode V (*Hemidactylum*, **HEM**) has a generalized morphology but with more components than other modes, and it also has a somewhat loose attachment (because of elongated genioglossal muscles) to the lower jaw. It was designated an attached projectile tongue. Mode VI (all of the tropical salamanders, i.e., the current bolitoglossines, encompassing more than 60% of plethodontid diversity, **BOL**) is a functionally highly specialized feeding system that utilizes folding option 2 and a tongue that is freely projectile (no genioglossal muscles). The epibranchials are very long. Mode VII (*Hydromantes*, **HYD**, then a bolitoglossine) is a highly specialized feeding mode featuring an extremely long (epibranchials greatly elongated), freely projectile tongue. While Lombard and Wake (1977) identified this mode as utilizing folding option 2, the two pairs of ceratobranchials are very short relative to the

basibranchials and the epibranchials and, as a result, folding may be a functionally inconsequential detail in this instance. The final mode (VIII, **BAT**, also a bolitoglossine) is found only in *Batrachoseps*, which has very long epibranchials and utilizes folding option 2, but at the same time has a tongue that is technically attached by means of extraordinarily elongated genioglossal muscles. Based on the phylogenetic hypothesis of Wake (1966), Lombard and Wake inferred (following Wake 1966) that tongue attachment of any kind was ancestral for plethodontid salamanders. Thus, attached projectile tongues had evolved at least three times and freely projectile tongues had evolved at least once within their hemidactyliines and twice within their bolitoglossines (fig. 22.2).

The hypotheses of Lombard and Wake (1977) were tested against a new phylogenetic analysis by Lombard and Wake (1986). The eight major tongue modes recognized were treated as operational taxonomic units; 30 characters, including 18 related directly to the adult feeding system, were evaluated. In an effort to conduct a “parsimonious analysis of a nonparsimonious system,” they were unable to reject the earlier hypotheses and concluded that freely projectile tongues had evolved homoplastically in plethodontid salamanders. Their “working hypothesis” phylogeny (their figure 4, modified and elaborated here as fig. 22.2) envisioned a basal split that separated **DES** from all of the others and a second split that separated **SPE + HEM** from (**PLE + ENS**) + (**BOL + HYD + BAT**). According to this hypothesis, attached projectile tongues and free projectile tongues each evolved three times. They argued that some degree of anterior freedom from the lower jaw was a likely precursor to being fully unattached (i.e., loss of the genioglossal muscles in particular), but they thought that extreme elongation of the muscle, as in *Batrachoseps*, was an unlikely precursor to loss of the muscle and assumed that each had evolved from an attached, protrusible tongue. Thus, because they postulated a sister taxon relationship of **BOL** and **BAT**, Lombard and Wake (1986) argued that free tongues had evolved independently in *Hydromantes* (**HYD**) and the tropical salamanders (*Bolitoglossa* and relatives, **BOL**). Either the genioglossus muscle had been elongated in the common ancestors of **BOL**, **HYD** and **BAT**, and subsequently had superelongated in **BAT**, and been lost in **BOL** and **HYD**, or it had been lost in the common

1. In folding option 1, ceratobranchial I is the more robust, lies in the plane of the epibranchial during projection, and carries the projectile force to the basibranchial. In folding option 2, ceratobranchial II is the more robust, lies in the plane of the epibranchial during projection, and carries the projectile force to the basibranchial.

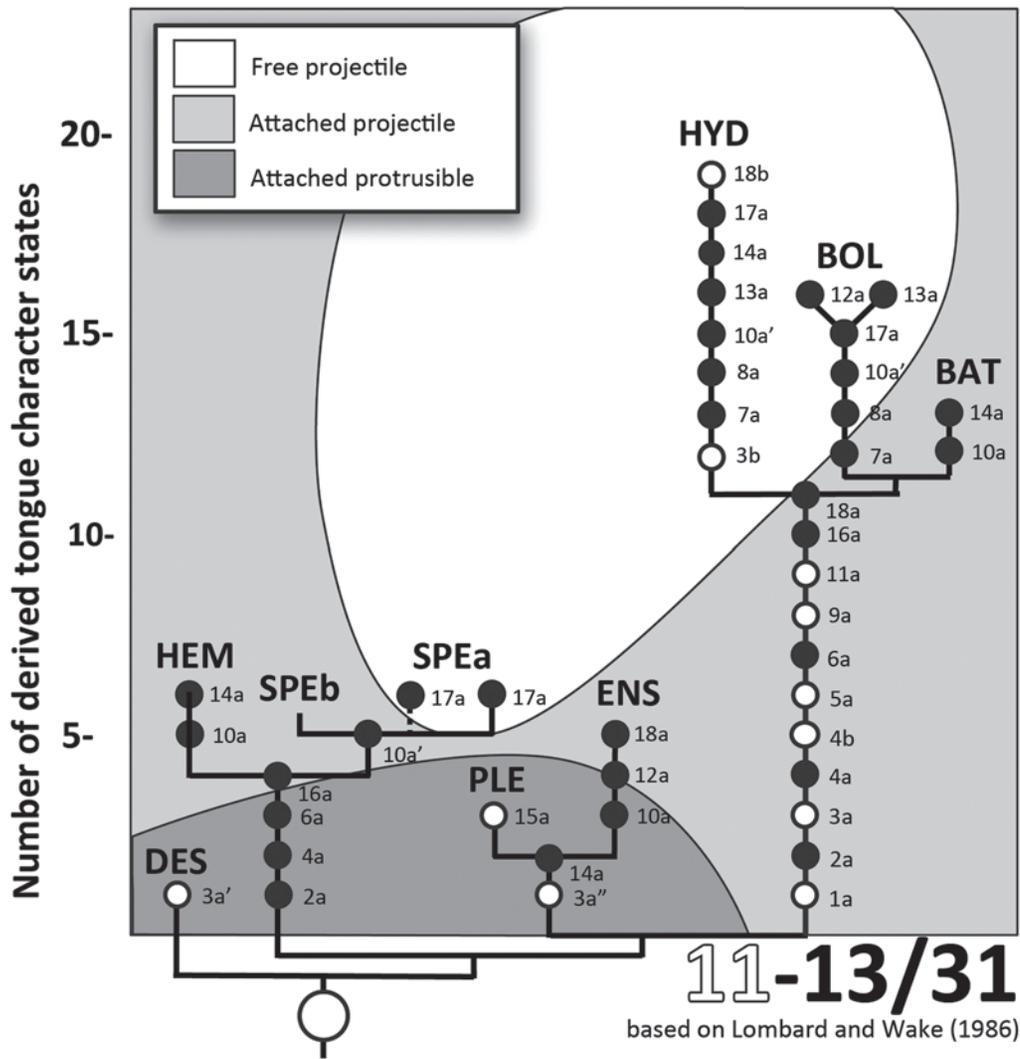


FIG. 22.2 Ground-plan diagram illustrating tongue and lineage evolution in salamanders of the family Plethodontidae, derived from Lombard and Wake (1986, figs. 4 and 7). Three general adaptive zones are recognized, based on use of the tongue in feeding: attached protrusible tongues, apparently close in structure and function to the ancestral state for the family (zone of heavy shading); attached projectile tongues (zone of light shading); and free projectile tongues (zone with no shading). Numbers at lower right indicate the number of uniquely derived character states (open circles on phylogeny), number of individual homoplastic characters, and number of homoplastic character states (closed circles on phylogeny). The characters are indicated in the phylogeny by integers and the character states by lowercase letters, from character lists in Lombard and Wake (1986); as in that work, the characters were ordered a priori and only presumptive derived states are shown. Uniquely derived synapomorphies indicated by a larger open circle on the stem signify four derived character states of the tongue unique to plethodontids.

ancestor and regained in **BAT** (a more parsimonious but seemingly less likely possibility because it required reacquisition of a muscle inferred to have been lost previously).

Lombard and Wake (1986) presented a ground-plan diagram (their figure 7, reproduced in revised form here in fig. 22.2) to illustrate tongue and lineage evolution. **SPEa**, **BOL**, and **HYD** all having free projectile tongues (open triangles in the unshaded zone of diagram). The

diagram was arranged so that both the phylogenetic relationships as well as the degree of specialization were displayed (as measured by numbers of apomorphic character states directly related to adult tongue features). The degree of specialization was displayed as character states thought to be convergently derived plus those thought to be uniquely derived, based on transformation arguments determined a priori. Their phylogeny (their figure 4) recognized four clades: desmognathines,

hemidactyliines, plethodonines, and bolitoglossines, as proposed by Wake (1966). However, the interrelationships of these four were revised relative to Wake (1966). The desmognathine clade, **DES**, was not further subdivided. The hemidactyliine clade was divided into two subclades, *Eurycea* and relatives, our **SPE**, with alternative pathways for the basal morphological state into two derived states **SPEa** and **SPEb**, and *Hemidactylium* alone, **HEM**. The plethodonine clade was divided into two subclades, *Plethodon* and relatives (e.g., *Aneides*), **PLE** plus *Ensatina*, **ENS**; and the bolitoglossine clade was divided into three subclades, the tropical genera, **BOL**, *Hydromantes*, **HYD**, and *Batrachoseps*, **BAT**. The extent of homoplasy in character states (the characters were ordered, in that ancestral and derived states were identified; many characters were multistate) in relation to phylogeny of the eight feeding modes is mapped on the phylogeny. For the 18 adult tongue characters, there are 11 non-homoplastic derived states: four are autapomorphies and seven are synapomorphies, six of which characterize the clade including **HYD**, **BOL**, and **BAT**. *Hydromantes* (**HYD**) had an additional eight derived states, six of them homoplastic and two autapomorphic. Their hemidactyliines are characterized by four homoplastic character states and **SPEa** and **HEM** each by two additional derived states, all homoplastic. Overall, 13 of the 18 tongue character states were homoplastic, and there were 31 occurrences of homoplastic states. In many ways, the analysis of tongue evolution of Lombard and Wake (1986) only served to bolster previous arguments by Wake (1966) for a close relationship among the tropical plethodontids, *Batrachoseps*, and *Hydromantes*.

### Reanalysis of the Evolution of Tongue Morphology in Plethodontids

The revolution in phylogenetic inference enabled by DNA sequence data has led to significantly revised perspectives on relationships within the Plethodontidae (e.g., Chippindale et al. 2004; Mueller et al. 2004; Min et al. 2005; Vieites et al. 2007; Vieites et al. 2011; Wake 2012). For this discussion, we use the higher-level taxonomy recently formalized by Wake (2012) based on analyses of Vieites et al. (2011), whose inferred phylogenies use molecular data alone. Two subfamilies, Plethodontinae (including the Desmognathinae of Wake 1966)

and Hemidactyliinae (including Bolitoglossini of Wake 1966) are recognized. Otherwise the most significant, and surprising, change is the discovery that *Hydromantes* (**HYD**) is not a close relative of **BOL** and **BAT**; it is instead nested within the Plethodontinae, in a subclade with *Karsenia*, and with **ENS**, **PLE**, and **DES**. The Asian plethodontid *Karsenia*, only recently discovered (Min et al. 2005), was not included in previous analyses. While *Karsenia* has yet to be studied in detail with respect to tongue morphology, the anatomy of the hyobranchial skeleton (Buckley et al. 2010) and preliminary dissections (by DBW) show that it can be included as a part of **PLE**, an already possibly paraphyletic assemblage that retains what may be the ancestral morphology for plethodontids. The 18 tongue characters identified by Lombard and Wake (1986) were plotted on recent phylogenetic hypotheses of Vieites et al. (2011). One of these is presented here as figure 22.3, the “reference phylogeny” (fig. 1A of Vieites et al. 2011), which shows *Batrachoseps* and *Hemidactylium* as sister taxa. Homoplasy in individual characters is surprisingly much more extensive than what was reported in the original analysis (Lombard and Wake 1986). For the “reference phylogeny” there are now only four unique states, each autapomorphic (i.e., no unique synapomorphies at the taxonomic level analyzed). The number of individual homoplastic states has increased from 13 to 20 (65%), and the total number of homoplastic states across all taxonomic units has risen from 31 to 52 (nearly 60%). An alternative phylogeny (fig. 2C of Vieites et al. 2011), which differs mainly in having a sister taxon relationship between *Batrachoseps* and Bolitoglossini, shows somewhat less homoplasy (20 homoplastic states but 47 instances of homoplasy) (fig. 22.4). A primary reason for the great increase in homoplasy is the assignment of *Hydromantes* to the Plethodontinae. **HYD** now displays 17 homoplasious states related to feeding compared with six in the 1986 phylogeny. In the “reference phylogeny” (fig. 22.3) **BOL** has 13 homoplasies, and in the alternative phylogeny (fig. 22.4) six homoplasies, compared with six in the 1986 phylogeny.

These analyses use the ordered characters of Lombard and Wake (1986). We also conducted a parsimony analysis of unordered characters to determine if homoplasy might be reduced. The answer is that homoplasy is reduced, but not by much, in relation to figure 22.3. The number of unique states is increased to five, one of

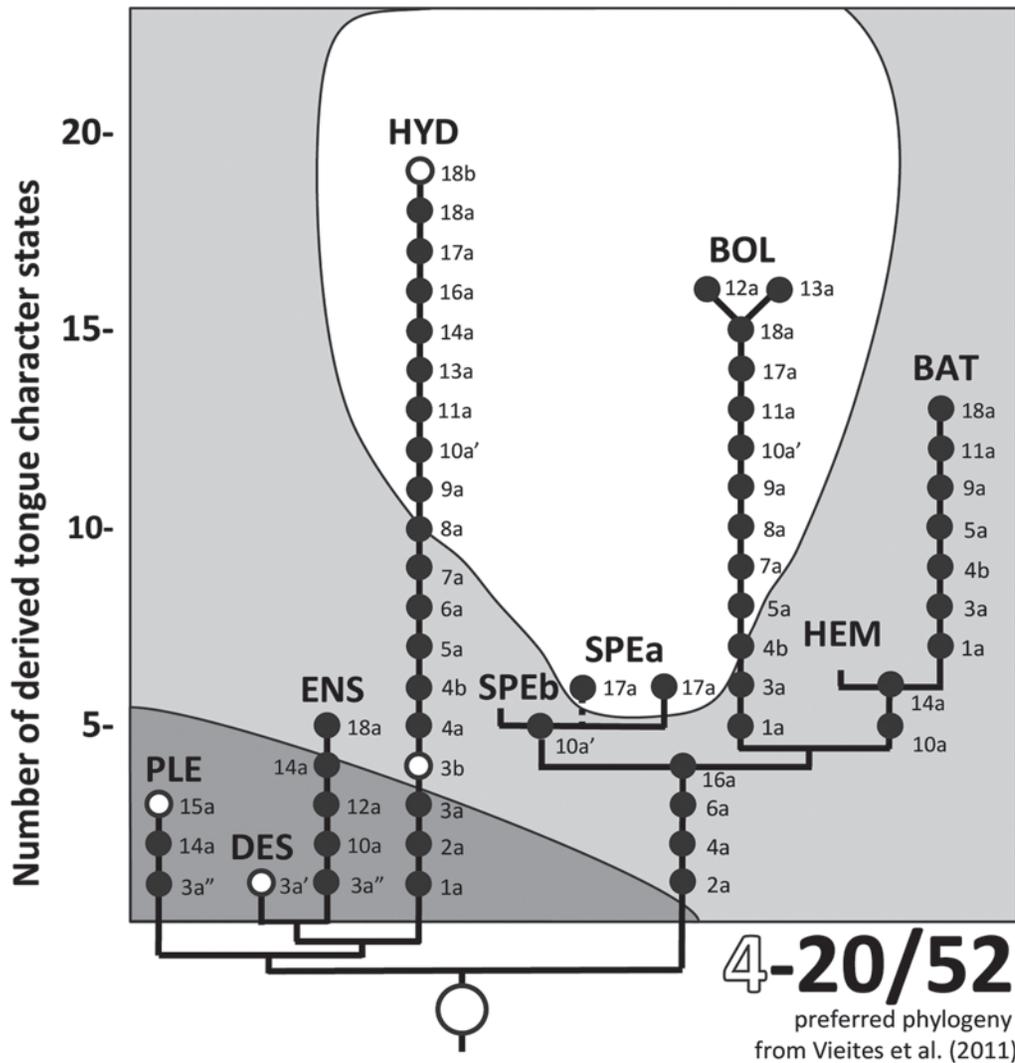


FIG. 22.3 Ground-plan diagram derived from figure 22.2, but using the “reference phylogeny” of Vieites et al. (2011, fig. 1A). Relative to figure 22.2 the number of uniquely derived states is greatly reduced and the number of individual homoplastic states and total number of homoplastic states across the phylogeny is greatly increased.

which is a synapomorphy for the Plethodontinae. There is a net reduction in the total number of homoplastic character states, from 52 to 48, and a reduction from 20 to 19 individual homoplasious characters; we consider these numbers to be inconsequential, especially in light of the fact that alternative phylogenetic hypotheses reduce the number of steps to 47 (while maintaining the number of homoplasious characters at 20). The additional uniquely derived fifth character is number 3 of Lombard and Wake (1986), the condition of the radii at the anterior ends of the basibranchial, a complex, multistate character with seven derived states. There are two equally parsimonious arrangements of

this rather “messy” character, and we have selected 3a”, a detached, distally expanded condition, to represent the synapomorphy in this instance. The point of this exercise is only to show that either ordered or unordered characters require essentially the same levels of homoplasy, all much higher than previously inferred.

The greatest similarity between taxa with independently evolved freely projectile tongues is found in *Hydromantes* and *Bolitoglossini*. Characters involved in this example of homoplasy are provided in table 22.1 and noted as whether lost or elaborated (changed proportionally).

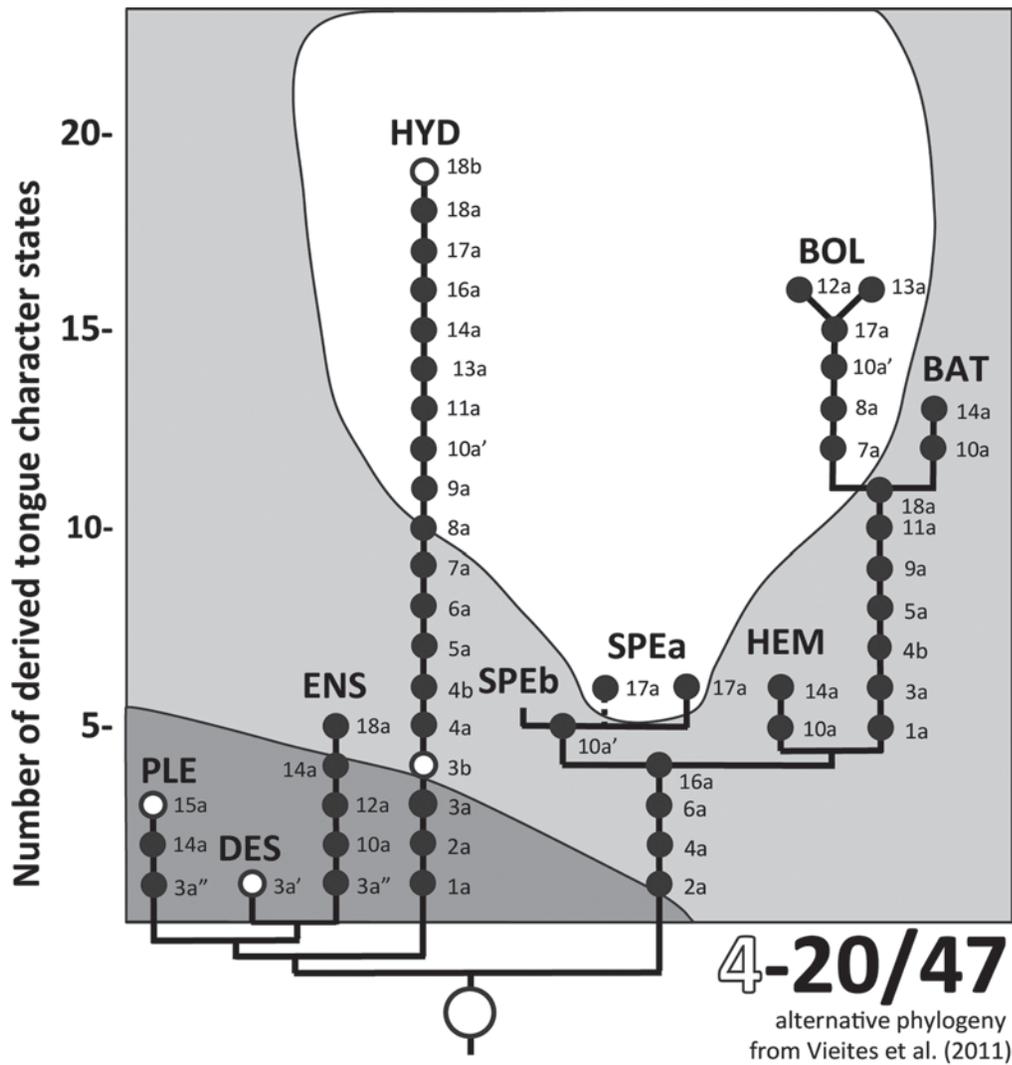


FIG. 22.4 Ground-plan diagram as in figure 22.2, except using an alternative phylogenetic hypothesis (Vieites et al. 2011, fig. 2C).

## Discussion

Homoplasy is extraordinarily extensive in the evolution of the tongue of plethodontid salamanders. But the phenomenon is present more broadly if one extends the comparisons to other families of salamanders (Wake and Deban 2000). Highly projectile attached tongues are found in the Hynobiidae (*Onychodactylus*) and Salamandridae (*Salamandrina*, *Chioglossa*) (Özetli and Wake 1969). While all three genera have an aquatic larval stage, they are all also lungless, which appears to be a necessary, but not sufficient, precondition for the evolution of truly specialized tongue projection. The mechanisms of projection differ greatly from those found in plethodontids (e.g., the salamandrids flip a

greatly elongated tongue pad using rotating radii), and one must count three additional instances of convergent evolution of projectile tongues.

The phylogenetic hypothesis of Lombard and Wake (1986) had a number of implications for interpreting the ecological setting of the extreme specializations of tongues of plethodontids, the evolution of freely projectile tongues, which enable “stealth” feeding by firing the tongue without movement of the body. Two constraints were envisioned (Roth and Wake 1985; Deban and Marks 2002): (1) the hyobranchial apparatus of nonplethodontids fulfills two functions—lung ventilation and tongue protraction—that are in conflict; and (2) the larval hyobranchial apparatus plays a critical role in larval biology and must be remodeled at metamorphosis.

**TABLE 22.1** Characters shared between *Hydromantes* (Plethodontinae, Hydromantini) and *Bolitoglossa* (Hemidactylinae, Bolitoglossini) apparently due to convergence in feeding mode.

Form of convergence	Character number	Character description
Loss	1a	Urohyal
	7a	Lateral slip of rectus cervicis superficialis muscle
	8a	Omohyoid muscle
	10a'	Genioglossus muscle
	11a	Circumglossus muscle
	13a	Basiradialis muscle (lost in some Bolitoglossini)
	17a	Cutaneous attachments of tongue pad to floor of mouth
Proportional change	2a	Basibranchial expanded
	4b	Epibranchial increased in length, ceratobranchials decreased in length
	5a	Folding pattern of hyobranchial skeleton
	6a	Rectus cervicis profundus muscle lengthened and folded anteriorly
	9a	Muscular complex aiming cylinder
	12a	Intraglossus muscle attaching to glossal ligament
	16a	Suprapenduncularis muscle discrete

Source: Character numbers follow Lombard and Wake (1986).

With respect to the first, the lungless plethodontids are freed from lung ventilation constraint, permitting extreme specialization. With respect to the second, loss of the larval stage permits early and extensive remodeling and a high degree of specialization (e.g., abandonment of the less efficient folding option necessitated by the need for effective larval function). Because it was long assumed that ancestral plethodontids had larvae and that lungs evolved in some connection to aquatic habitat, skeletal folding option 1 (of Lombard and Wake 1977) involved less evolutionary change than did option 2.

Our analysis indicates that close phylogenetic relationships are not revealed by highly derived tongue morphology, patterns of force transmission (via ceratobranchial I or II), or the form of projectile tongue (attached vs. free). However, this statement needs qualification with respect to the alternative phylogeny (fig. 22.4) in which seven synapomorphic character states support the topology derived from molecular data. This finding lends support to that topology (in which **BAT** and **BOL** are sister taxa), which was only slightly less favored relative to the “reference phylogeny” by Vieites et al. (2011).

The increased homoplasy observed through reanalysis of the tongue morphologies of Lombard and Wake (1986) in the new phylogenetic contexts reveals that the independent evolution of freely projectile tongues by **HYD**, **SPE**, and **BOL** involves a greater number of changes than previously thought, especially since **HYD** and **BOL** are resolved as members of different major clades. Unlike the analysis of Lombard and Wake (1986), we can now better determine which characters might be shared due to shared evolutionary history and which are due to convergence. Those characters shared by **HYD** and **BOL** that are classified as convergent fall into two classes: loss, and proportional changes of existing structures (table 22.1). We consider it significant that none of these changes involves gaining novel structures. Rather, once the stage is “set,” further specialization is readily attained.

The new phylogenetic inferences for Plethodontidae provide the surprising insight that the many synapomorphies proposed by Lombard and Wake (1986), especially those thought previously to unite **HYD**, **BAT**, and **BOL**, evolved convergently. The extent of homoplasy is further underlined because no new synapomorphies related to tongue morphology are revealed by the

new phylogenies. The insight gained by the realization that homoplasy is more extensive than previously understood is that many morphological components must be integrated to produce the extreme freely projectile tongues observed in **HYD** and **BOL**. Evolutionary specializations required to produce a freely projectile tongue follow such predictable pathways of morphological change over evolutionary time that homoplasy seems inevitable.

Freely projectile tongues are one of several specializations that together comprise a key innovation of tropical salamanders—lunglessness, direct development, and feeding specialization. This complex of traits characterizes the entire clade **BOL**, containing more than 280 species, 90% of which are crowded into the narrow geographical boundaries of Middle America. These species represent more than 60% of plethodontids and more than 40% of all salamanders. They all have the extreme set of feeding specializations characteristic of **BOL**, but one subclade, *Thorius*, has evolved even further. In *Thorius*, comprised of more than 25 species, all miniatures, the hyobranchial skeleton disarticulates during projection, thus attaining freedom from the constraint of folding and achieving the highest level of specialization. We believe that this added specialization is facilitated by the reduction of anatomical structures associated with miniaturization. While **HYD** and **SPE** contain numerous species, neither approaches the “success” in number of species of **BOL**, although **HYD** is the most widely distributed of the plethodontid clades, occurring in both western North America and southern Europe. **SPE** has only 35 species, but because it has retained the more generalized folding option 1 and larval life history, some of its species have been able to exploit habitats such as ponds and streams in caves by remaining permanently larvamorph. The contrast with tongue projecting species in other families is striking: *Chioglossa* is monotypic, *Salamandrina* contains two species, and *Onychodactylus* contains seven.

Studies of great evolutionary transitions, the primary focus of this edited volume, emphasize morphological transformations, usually based on fossil evidence. While paleontologists are all well aware of the limitations of the fossil record, the lesson from our study of tongue evolution is that morphological transitions that give the appearance of being unique events may lead to an oversimplified interpretation. Do the findings of

our study represent a special case, an exception to the general rule, or, instead, are great transformations likely to often involve homoplasy, leading to independently evolving, but related, lineages transitioning to the apparently “same” new functional states? We suggest that homoplasy is so common that one ignores it at one’s peril.

Homoplasy is a deep problem for those developing phylogenetic hypotheses from morphological data. Once a robust phylogeny is developed, homoplasy might well be interpreted as error in coding of states of characters. However, we view homoplasy as an opportunity to gain insight into the mechanisms underlying morphological change, of any kind, but especially those relating to increased biomechanical, physiological, and behavioral performance. Whereas convergence in the evolution of freely projectile tongues in three independent clades of plethodontids can be interpreted as an indication of response to natural selection, one instead might profitably ask what underlying genetic and developmental mechanisms establish a biological framework in which convergence is expected, and almost inevitable (e.g., Wake 1991; Wake et al. 2011). Evolution of functional systems follows avenues of least resistance. In our example, the evolution of freely projectile tongues appears facilitated by convergent losses of multiple anatomical structures coupled with proportional changes in otherwise unmodified musculoskeletal elements. We have no understanding of the genetic mechanisms associated with the homoplastic events we have documented, but recent studies of genetic “hotspots,” where loci of repeated evolution are located, may provide a path forward for understanding this phenomenon (Martin and Orgogozo 2013). These authors treat such hotspots as “loci of evolution” and state as a truism that specialized genes drive the evolution of specialized traits. Perhaps evolution has a limited directionality, following avenues of least resistance facilitated by specialized genes associated with particular phenotypes and special patterns of selection. Existing variational potential is reworked, rather than evolving novel structures. Repeated independent evolutionary events such as these can potentially point to underlying genetic signals and developmental networks, and lead to new avenues of research. As evolutionary biologists, we celebrate homoplasy as an opening to a new world of opportunity.

## Acknowledgments

We are honored to participate in this celebration of our friend and colleague, Farish Jenkins. One of us (DCB) owes much to Farish, from whom he learned what it means to truly teach and mentor. Together, the three authors of this manuscript represent a special confluence: DBW was REL's PhD advisor, who in turn was DCB's undergraduate instructor, who in turn was a PhD student of DBW's former student Jim Hanken and worked closely with Farish. We celebrate the frequent interconnectedness of our and our colleagues' careers and also recognize that single individuals such as Farish have powerful impacts on all of our careers across decades-long timescales. This manuscript benefited from comments by David Buckley and Stephen Deban. We also thank Marvalee Wake and Neil Shubin for comments on the manuscript. We thank Stephen Deban for permitting us to modify his artwork into our figure 22.1. The National Science Foundation provided support to one of us (DBW) for the molecular phylogenetic work on which our reanalyses are based.

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