

previously. Our new phylogenetic hypotheses are based largely on new molecular datasets; because they are hypotheses, we are actively engaged in gathering additional data to test them. We need to develop other datasets and integrate our studies in such a manner as to effectively test and reject alternative hypotheses of plethodontid relationships until such hypotheses can generally be viewed as robust, even if they conflict with more classical hypotheses for the evolution of morphology and life-history evolution in this group. The newly discovered Asian plethodontid salamander, *Karsenia koreana*, also appears to be a direct developer. Given its placement in the phylogeny (Min et al. 2005), the case for a reversal in *Desmognathus* is even stronger; argument against reversal now requires the independent evolution of direct development in at least six clades (*Plethodon*, *Hydromantes* + *Ensatina*, *Karsenia*, *Aneides*, *Phaeognathus*, and *Desmognathus wrighti*).

What has become clear in this developing debate is the absence of relevant comparative ontogenetic and developmental morphological data for salamanders. Relatively few species have been studied, and even such common species as members of *Amphiuma* are imperfectly known. Direct development is best known from studies of a species that is only a marginal direct developer, *Desmognathus aeneus* (Marks 2000), and very little is known about the early ontogeny of the 328+ species of direct developing plethodontids, many of which may prove to be relevant to this controversy.

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## Re-evolution of the Larval Stage in the Plethodontid Salamander Genus *Desmognathus*

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Bruce (2005) presents provocative arguments in favor of an ancestral biphasic life-history mode for plethodontid salamanders, in particular for the genera formerly assigned to subfamily Desmognathinae Wake 1966: *Desmognathus* + *Phaeognathus*, the supergenus *Desmognathus* (sensu Chippindale et al. 2004). Bruce disputes the inferences of Chippindale et al. (2004) that a reversal from direct development to an aquatic larval stage occurred in *Desmognathus* (see also Bonett et al. 2005; Mueller et al. 2004). For decades, Bruce has played a leading role in studies of plethodontid life-history evolution (e.g., Bruce et al. 2000), and his disagreement with our conclusions is a cause for concern that must thoroughly be addressed.

The possibility that direct development is the ancestral state for supergenus *Desmognathus* (*Desmognathus* hereafter) has been discussed by several authors (e.g., Collazo and Marks 1994; Marks 2000; Titus and Larson 1996). The new and largely concordant phylogenetic hypotheses of Chippindale et al. (2004), Mueller et al. (2004), and Macey (2005) provide an opportunity to trace life-history evolution in plethodontids within a rigorous phylogenetic framework. Here, we address Bruce's arguments and show that the preponderance of evidence supports re-evolution of the aquatic larval stage in *Desmognathus*.

Bruce offers six key arguments in favor of biphasic development as the primitive condition for *Desmognathus*. We will address these in the order in which they appear in his paper. We

think that the issues can be distilled to four questions: (1) Is the family-level placement of plethodontids correct? (2) Is the phylogenetic position of supergenus *Desmognathus* within Plethodontidae correct? (3) Is the ancestral reconstruction for the evolution of direct development correct? (4) How strong is the evidence that competition in terrestrial environments drove the re-evolution of the larval stage?

#### 1. THE SISTER FAMILY QUESTION: AMPHIUMIDAE OR RHYACOTRITONIDAE?

Bruce raises concerns about the phylogenetic position of Plethodontidae and the possible implications of its placement for the ancestral reconstruction of direct development in the family. Larson and Dimmick (1993) and Larson et al. (2003) showed relationships among amphiumids, plethodontids, and rhyacotritonids to be uncertain, and the analyses of Mueller et al. (2004) and Macey (2005) omitted amphiumids. However, the analysis of Chippindale et al. (2004) found strong support for the relationships (Rhyacotritonidae (Amphiumidae + Plethodontidae)). This result also has been strongly supported in a more recent analysis of higher-level salamander relationships based on molecular and morphological data (Wiens et al. 2005). We think that the phylogenetic position of plethodontids has now been resolved, and that Chippindale et al. (2004) used the appropriate outgroup relationships (based on inclusion of nearly all salamander families in their phylogenetic analyses) for their ancestral-state reconstructions.

Bruce favors biphasic development as the ancestral condition for plethodontids, based in part on a presumed close relationship between Plethodontidae and Rhyacotritonidae. The latter family occurs in mountain stream habitats in western North America, has aquatic larvae, and exhibits some other features similar to those in plethodontids (e.g., lung reduction). However, new molecular analyses and combined molecular and morphological analyses overwhelmingly support amphiumids as the sister group of plethodontids (Chippindale et al. 2004; Wiens et al. 2005).

In this section of his paper, Bruce also asserts that the ancestral state reconstructions of Chippindale et al. (2004) assume that Amphiumidae is biphasic. He states that "life-history modes in amphiumids approach direct development." (p. X). This is a very reasonable view, especially given recent work by Gunzburger (2003). In fact, we presented and discussed ancestral state reconstructions in which amphiumids were treated alternately as biphasic and as direct developers. Both approaches yielded nearly identical results, with overwhelming support for a direct-developing ancestral *Desmognathus* using both maximum likelihood- and parsimony-based methods. In addition, treatment of amphiumids as direct developers supports the intriguing possibility (also suggested by analyses in which amphiumids were coded as biphasic) that direct development is the ancestral condition for Plethodontidae, and that there have been additional reversals to biphasic development in other lineages of plethodontids besides *Desmognathus*.

#### 2 AND 3. MORPHOLOGICAL HOMOPLASY AND PLETHODONTID PHYLOGENY: THE WHOLE IS GREATER THAN SOME OF THE PARTS

Bruce's sections 2 and 3 relate (directly or indirectly) to his concerns about the phylogenetic position of *Desmognathus* based

on the incongruence of new molecular results with certain morphological characters. Bruce has informed us (pers. comm.) that he does not question our phylogenetic conclusions, and he does adopt our new taxonomy in his paper. However, his discussion of character evolution suggests that he questions our placement of *Desmognathus* within Plethodontidae, and we wish to clarify some of the issues that he raises.

A critical point is that simply discussing the evolution of selected morphological characters provides a very limited view of the implications of the morphological data for the phylogeny, at least relative to performing a full-scale phylogenetic analysis. Bruce fails to mention that Chippindale et al. (2004) performed a thorough phylogenetic analysis of the available morphological data for plethodontid phylogeny. This analysis included 123 morphological characters (including both original observations as well as characters based on data in the literature), encompassing nearly all of those discussed by Bruce (i.e., toe number, tongue structure, tail autotomy, and number of larval epibranchials, but not the presence or absence of lateral line organs). Rigorous analysis of the morphological data fails to support the traditional basal position for *Desmognathus* within Plethodontidae. Indeed, a basal position for *Desmognathus* was supported by only a single character (three larval epibranchials) in the widely used phylogenetic hypothesis of Lombard and Wake (1986). Furthermore, although the morphological analyses do not support the placement of *Desmognathus* within plethodontines as the molecular data do, they do not support monophyly of plethodontines either.

On the other hand, phylogenetic analyses of mitochondrial genome sequences (Macey 2005; Mueller et al. 2004), combined and separate analyses of nuclear and mitochondrial data (Chippindale et al. 2004), and combined molecular and morphological data (Chippindale et al. 2004) show that *Desmognathus* is nested within Plethodontinae (*Aneides* + *Ensatina* + *Plethodon* + supergenus *Desmognathus*, sensu Chippindale et al. 2004; Macey 2005 also included *Hydromantes* in this group). With the exception of the biphasic species of *Desmognathus*, all plethodontines are direct developers. At least two of the three direct-developing members of supergenus *Desmognathus* (*Phaeognathus hubrichti* and *D. wrighti*) appear to be basal to the remaining species; the third direct-developing species (*D. aeneus*) may be as well (Chippindale et al. 2004; Titus and Larson 1996; note that Mueller et al. 2004 and Macey 2005 did not include this species in their analyses). The data sets are not completely independent: Chippindale et al. (2004) included 1,473 mitochondrial characters in some of their analyses, overlapping with the 14,040 used by Mueller et al. (2004) and then reanalyzed by Macey (2005). However, it is noteworthy that none of the analyses support either a basal position for *Desmognathus* or monophyly of the former Plethodontini (*Plethodon*, *Ensatina*, and *Aneides*). Instead, the available data favor nesting of *Desmognathus* within an otherwise exclusively direct-developing clade of plethodontids.

#### 4. EVOLUTION OF DIRECT-DEVELOPING *DESMOGNATHUS*: THE PHYLOGENY MATTERS

In this section, Bruce discusses scenarios that might account for the evolution of direct development in genera *Phaeognathus* and *Desmognathus*. However, Bruce misses a key point. Given the overwhelming phylogenetic evidence that *Desmognathus* and

*Phaeognathus* are nested inside of plethodontines, any explanation for the evolution of direct development must also include *Plethodon*, *Aneides*, and *Ensatina* (and probably *Hydromantes* as well). Rather than making complex arguments to explain why direct development evolved convergently in these ecologically and morphologically diverse lineages, a simpler solution may be that this trait evolved in the common ancestor of all of these genera, and that there have been subsequent changes in body size, microhabitat specialization, and other traits among species sharing this developmental mode. This is what appears to have happened in the morphologically and ecologically diverse bolitoglossines, all of which are direct developers (Wake 1966). Thus, Bruce's comparison of miniaturization in the bolitoglossine genus *Thorius* to that in *Desmognathus aeneus* and *D. wrighti* merely highlights the repeated, extreme changes in body size in plethodontid lineages with direct development.

#### 5. THE ECOLOGICAL SCENARIO: OUT OF THE FRYING PAN, INTO THE COOL MOUNTAIN STREAM

We speculated that competition with terrestrial plethodontids (likely *Plethodon*) drove the reinvasion of aquatic habitats and subsequent radiation of *Desmognathus* (note that in this section we refer only to members of the genus *Desmognathus*), whereas Bruce suggests that competition with aquatic salamanders may have led to repeated evolution of direct development. Our scenario is consistent with our likelihood-based analysis of divergence dates in plethodontids. Radiation of *Plethodon* in Appalachia appears to have predated or overlapped with the radiation of biphasic *Desmognathus*. Bruce counters with an "out of the frying pan, into the fire" argument, invoking possible competition with or predation by spelerpine (sensu Chippindale et al. 2004) plethodontids in Appalachian stream habitats. Spelerpinae is a subfamily corresponding to the tribe Hemidactyliini (Wake 1966), but excluding the phylogenetically distinct genus *Hemidactylum*.

Given that our hypothesis of competitive interactions was highly speculative, we do not have compelling evidence that competition with spelerpines may be less important to species of *Desmognathus* than competition with other plethodontines. However, some lines of evidence are suggestive of this idea. First, both spelerpines and *Desmognathus* seem to reach their maximum local species richness in streamside habitats (Petranka 1998), which is not the expected pattern if competition between them was substantial. Second, there is extensive microsympatry among many species of *Desmognathus* and spelerpines along streams in eastern North America (e.g., members of the *Eurycea bislineata* complex and *Gyrinophilus porphyriticus*), suggesting that these lineages can coexist without competitively excluding each other (Petranka 1998). In contrast, there is considerable evidence for competitive interactions among terrestrial plethodontines (e.g., Hairston 1996), and Hairston (1981) suggested that some stream-associated Appalachian plethodontids (including members of the genus *Desmognathus*) might escape competition for nesting sites with terrestrial *Plethodon* by breeding in or near aquatic habitats. Furthermore, recent evidence (Baldwin 2002, unpubl. data; Baldwin and Chippindale, unpubl. data) indicates that *Pseudotriton*, one of the spelerpine genera that is sympatric with *Desmognathus*, colonized the Appalachian highlands very recently, long after the radiation of biphasic *Desmognathus*.

#### 6. EVOLUTIONARY REVERSALS AND BREAKING DOLLO'S LAW: CRIMES AND MISDEMEANORS

Bruce rests much of his case on "Dollo's Law" (or "principle"), the assumption that complex characters, once lost, cannot re-evolve (or at least not in their original forms). However, there is abundant evidence that Dollo's Law has been broken repeatedly. One clear example is the re-evolution of teeth on the lower jaw of the hemiphractine treefrog *Gastrotheca guentheri* (Duellman and Trueb 1986). Other recent examples (while not without controversy) also show the loss and re-evolution of complex features, such as hind limbs in snakes (Tchernov et al. 2000), wings in stick insects (Whiting et al. 2003), and shell coiling in gastropod molluscs (Collin and Cipriani 2003). Given these challenges to the generality of Dollo's principle, we seriously question its applicability to plethodontid salamanders.

Recent advances in evolutionary developmental biology may explain why Dollo's Law may be broken so frequently. Numerous complex phenotypic traits appear to be controlled by regulatory or "master switch" genes (e.g., Carroll et al. 2001; Rogers et al. 2002; Wilkins 2001). These genetic control systems provide a potential mechanism by which expression of complex features may be turned off and then on again during development and over evolutionary time. Furthermore, based on analyses of mutation rates, Marshall et al. (1994) estimated that key genes controlling organismal structure and function can remain intact for millions of years, even if they are not expressed. It seems reasonable that gene reactivation or altered timing of regulatory gene expression could enable a return to a biphasic lifestyle in some plethodontids. We also question the extent to which invoking Dollo's Law is applicable in the case of *Desmognathus*, given that some larval traits may be expressed in the embryos of direct-developing plethodontids. For example, the embryonic hyobranchial apparatus of *Plethodon cinereus* retains key features associated with a larval lifestyle, albeit in a reduced form (Dent 1942). Thus, the re-acquisition of the larval stage in *Desmognathus* may not require the re-evolution of all larval traits.

We agree with Bruce that more detailed study of development in plethodontids (using both embryological and molecular genetic approaches) would be valuable, given that most inferences about the morphology and development of embryos have been based on data from only a tiny fraction of the extant species, in the absence of a rigorous phylogenetic framework. However, we caution that the morphology of embryos and larvae may be subject to just as much homoplasy as the adult morphology, and may not be perfect indicators of the evolutionary history of traits or taxa (e.g., Wiens et al. 2005).

#### BRUCE'S CONCLUSIONS

Bruce concludes, in part, by stating that reconstruction of ancestral states on Macey's (2005) "total evidence" mitochondrial genome tree is consistent with a biphasic ancestral state for *Desmognathus*. However, we believe that his interpretation is in error with respect to simple parsimony. According to our calculations (using MacClade v. 4.02; Maddison and Maddison 2000), an ancestral *Desmognathus* with aquatic larvae requires a minimum of five steps on Macey's total-evidence tree (if all taxa are shown). If re-evolution of biphasic development within *Desmognathus* is allowed, then only three steps are required, mak-

ing this the more parsimonious hypothesis. We obtained an identical result using Macey's (2005) alternate, transversion-only parsimony tree. Furthermore, Mueller et al. (2004) and Macey (2005) examined only two of the three direct-developing species of *Desmognathus*, and excluded *D. aeneus*. This omission potentially biases their results against finding direct development to be ancestral within *Desmognathus*. Addition of *D. aeneus* to their analyses likely would require a sixth step for the ancestral *Desmognathus* to be biphasic, given the many other studies that indicate that this species is a basal member of the genus *Desmognathus* (e.g., Chippindale et al. 2004; Titus and Larson 1996). Thus, contrary to Bruce's conclusions, the most parsimonious explanation for the distribution of developmental modes in plethodontids requires a reversal to the aquatic larval stage in *Desmognathus* for all of the phylogenies discussed here.

#### OUR CONCLUSIONS

Bruce (2005) has challenged our conclusions regarding the loss of direct development and re-acquisition of the larval stage in plethodontid salamanders. Specifically, he has raised doubts about (1) the phylogenetic placement of plethodontids within salamanders, (2) placement of the supergenus *Desmognathus* within plethodontids, (3) reconstruction of direct development as the ancestral state in *Desmognathus*, and (4) our ecological scenario for why this reversal has occurred. We have argued that the placements of plethodontids and the supergenus *Desmognathus* are very strongly supported by our analyses, and the contradictory morphological evidence mentioned by Bruce had already been taken into consideration. Furthermore, his argument against our ancestral reconstruction is based largely on a principle (Dollo's Law) that has been challenged both by new empirical evidence (e.g., Tchernov et al. 2000; Whiting et al. 2003) and a new understanding of the evolution and expression of regulatory genes (e.g., Carroll et al. 2001; Marshall et al. 1994). Our hypothesis that competitive interactions drove this evolutionary reversal is (admittedly) highly speculative, but no more so than the alternative hypothesis proposed by Bruce.

We conclude by posing the following question: what additional evidence would be required for Bruce to accept that there was re-acquisition of the larval stage in *Desmognathus*? Initially, we found this result hard to believe ourselves, and we even agree (in principle) that a few more independent origins of direct development might be more likely than a reversal. However, in the case of *Desmognathus*, the probability that repeated origins of direct development explains the phylogenetic pattern is extremely low. Given our maximum likelihood reconstructions on the tree based on combined nuclear DNA, mitochondrial DNA, and morphological data, multiple origins of direct development would have to be >77,000 times more likely than a single loss. We think that the available evidence points towards a loss of direct development and re-evolution of aquatic larvae as the more likely explanation. We invite Bruce (as one of the leading authorities on plethodontid life-history evolution) to identify what specific evidence could convince him of the veracity of our conclusion.

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## ARTICLES

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### Nomenclatural Notes on the Generic Nomen *Luperosaurus* Gray, 1845 (Squamata: Gekkonidae)

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Gray (1845) occupied the nomen *Luperosaurus* (p. 145, and later, on p. 283, in the index) and subsequently *Luperosaurus* (p. 163) for a genus of Southeast Asian gekkonid lizards. The root ‘Lyper,’ Greek for ‘difficult’ or ‘vexing lizard’ is presumably for sharing characters of *Amydosaurus* Gray, 1845 (synonymous with *Lepidodactylus* Fitzinger, 1843 and *Ptychozoon* Kuhl and van Hasselt, 1822). The type species of the genus is *Luperosaurus Cumingii* Gray, 1845, by monotypy. The content of *Luperosaurus* has been reviewed by Boulenger (1885), W. C. Brown and Alcalá (1978), Russell (1979), and R. M. Brown and Diesmos (2000), and the latter nomen appears in checklists compiled by Kluge (1991, 1993, 2001), Rösler (2000), Welch (1994), Welch et al. (1990), and Wermuth (1966), but none of these reviews or lists give reference to the other original spelling (*Lyperosaurus*) of the generic nomen. In the most recent checklist of constituent species of the genus, Kluge (2001) recognized eight species within the genus, including *Luperosaurus browni* Russell, 1979 and *Luperosaurus yasumai* Ota, Sengoku, and Hikida, 1996, from the

Sundas, *Luperosaurus iskandari* R. M. Brown et al., 2000, from Sulawesi, and *brooksii* Boulenger, 1920, *cumingii* Gray, 1845, *joloensis* Taylor, 1918, *macgregori* Stejneger, 1907 and *palawanensis* W. C. Brown and Alcalá, 1978, from the Philippines (Brown and Alcalá 1978).

Although the lack of citation of the nomen *Luperosaurus* by Boulenger (1885:181), in the next monograph of the lizard collection of the British Museum (Natural History) can be interpreted that the name is a *lapsus calami*, argument against include its inclusion on p. 283 of the index of the work by Gray (1845), which notes its usage on p. 163 (where it is spelled *Luperosaurus*). Although the manuscript of the original work does not exist at The Natural History Museum, London, Gray’s annotated copy of the printed work (kindly examined by C. J. McCarthy at my request) has no corrections or remarks concerning these nomen.

Article 24.2.3 of the International Code of Zoological Nomenclature (International Commission of Zoological Nomenclature, 1999, hereafter, The Code) states that if more than a single original spelling for the same taxon exists, the first author to cite them together can select one spelling as correct (the First Reviser Principle), whereupon the other original spelling is incorrect and therefore unavailable. No such selection has ever been made. In accordance with Article 24.2.3 and Recommendation 24a of The Code, which states that the selection should be the one that “best serves stability and universality of nomenclature,” I here select, as First Reviser, the nomen *Luperosaurus* Gray, 1845 as valid for the taxon, instead of *Lyperosaurus*. The spelling *Lyperosaurus*, with this action and in conformance with that article, has no nomenclatural status.

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