

LUNGLESSNESS IN PLETHODONTID SALAMANDERS IS
CONSISTENT WITH THE HYPOTHESIS OF A MOUNTAIN STREAM
ORIGIN: A RESPONSE TO RUBEN AND BOUCOT

CHRISTOPHER KING BEACHY* AND RICHARD C. BRUCE†

*Department of Biology, P.O. Box 42451, University of Southwestern Louisiana, Lafayette, Louisiana 70504-2451; †Highlands Biological Station, P.O. Drawer 580, Highlands, North Carolina 28741 and Department of Biology, Western Carolina University, Cullowhee, North Carolina 28723

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Abstract.—The salamander family Plethodontidae is characterized by the absence of lungs. In 1920, I. W. Wilder and E. R. Dunn proposed that lunglessness evolved as an adaptation for life in flowing streams. However, J. A. Ruben and A. J. Boucot recently suggested that protoplethodontids had no access to the mountainous terrain associated with fast-flowing stream habitats. They further suggested that plethodontids lost lungs for reasons other than ballast. We cite evidence contradicting Ruben and Boucot's geological interpretation. We contend that the Wilder-Dunn hypothesis remains a robust one and argue that the life-history pattern exhibited by the primitive members of the family (e.g., *Gyrinophilus*, *Pseudotriton*) suggests that lunglessness evolved as a rheotropic adaptation that promoted primarily larval, not adult, survival in streams. We review evidence on the life history, ecology, morphology, and physiology of larval salamanders that supports the Wilder-Dunn hypothesis.

Wilder and Dunn (1920) proposed that lunglessness in the salamander family Plethodontidae is an adaptation to mountain stream habitats that reflects the origin of the family in the Appalachian highlands. Ruben and Boucot (1989) recently challenged this hypothesis, arguing that late Mesozoic Appalachia—the hypothesized time and place of plethodontid origin (Wake 1966)—lacked the mountainous terrain that provided the selective environment for lung loss in aquatic environments. Their hypothesis had six elements. First, plethodontids may have evolved from semiterrestrial or terrestrial ancestors, similar to extant ambystomatids. Second, the origin of plethodontids occurred in warm, lowland environments. Third, loss of lungs was associated with selection for reduced head width, perhaps as a biomechanical adaptation. Fourth, decrease in head width resulted in decreased pulmonary efficiency, which required greater reliance on cutaneous respiration. Fifth, the shift in respiratory function was accompanied by a trend toward a more sedentary way of life. Finally, lungs were lost completely.

In this article, we review geological evidence contradicting Ruben and Boucot's claim that late Mesozoic Appalachia lacked upland environments. We then evaluate the evidence offered by Wilder and Dunn in support of their hypothesis. We argue that the strength of the Wilder-Dunn hypothesis lies in its emphasis on

the advantages of lunglessness for larval, rather than adult, survival in stream environments.

LATE MESOZOIC APPALACHIAN TOPOGRAPHY

In their review, Ruben and Boucot rejected the rheotropic adaptation hypothesis based on geological information (drawn primarily from Dunbar [1964]) that suggests that the entire Appalachian chain was reduced to a peneplane in the late Mesozoic era. If such a scenario were true, then no mountains existed in the late Mesozoic to provide plethodontids with their hypothesized ancestral habitat, fast-flowing cool streams.

Figure 1 of Ruben and Boucot's article (taken from Dunbar [1964]) is misleading, inasmuch as the authors claimed to present a history of the "evolution of Appalachian topography" (Dunbar 1964, p. 163). The figure actually represents the "evolution of the modern topography of the Middle Appalachian region" (Dunbar 1964, p. 403, fig. 256). This is an important distinction. Dunbar (1964, pp. 401-402) further stated that "nearly all the Appalachian region was peneplaned, the exception being a chain of monadnocks rising 2000 or 3000 feet along the border between eastern Tennessee and North Carolina, and scattered hills in northern New England" (Dunbar 1964, p. 402). These areas "show no evidence of ever having been reduced to a level summit." This history of Appalachian topography is corroborated by other authors (e.g., Stanley 1986). Thus, even granted that the Plethodontidae originated in the late Mesozoic, Ruben and Boucot's statement (1989, p. 163) that "Mesozoic Appalachian proto-plethodontids were most unlikely to have had access to fast-moving mountain brooks" is misleading.

However, the time of origin for plethodontid salamanders is a point of debate. The plethodontids are first found in the fossil record in the early Miocene, and some authors have estimated that the plethodontids are more recent than the Cretaceous (Naylor 1980; Carroll 1988). In contrast, there are data on ribosomal RNA evolution that suggest that the Plethodontidae is a much older lineage (Larson and Wilson 1989).

Late Mesozoic Appalachia apparently had mountainous areas and flat plains. The question of interest concerns the ancestral adaptive zone of the Plethodontidae. Did the plethodontids originate in the flat areas, and were they semiterrestrial or terrestrial as suggested by Ruben and Boucot? Or were the ancestral plethodontids semiaquatic or aquatic salamanders inhabiting upland environments, as originally proposed by Wilder and Dunn?

WILDER AND DUNN'S HYPOTHESIS

It has been convincingly argued (Dunn 1926) and subsequently supported (Wake 1966; Larson 1984) that the plethodontids originated and diversified in eastern North America, particularly Appalachia. Southern Appalachia supports more genera occupying more adaptive zones than any other geographical locale

(Wake 1966, 1987). The phylogenetic relationships of the major groups of the family have been reviewed by Wake (1966) and Larson (1984), and the inferred primitive forms are found in mountain stream habitats of southern Appalachia. This suggests that the ancestral plethodontids inhabited upland stream environments.

Wilder and Dunn (1920) argued that the lungless condition of these salamanders arose as an adaptation for a stream-dwelling existence. They cited Whipple's (1906a) contention that the lungs of salamanders function primarily as hydrostatic mechanisms and only secondarily as respiratory organs. In conjunction with the lungs, the ypsiloid apparatus aids in adjustment of position in the water. The ypsiloid apparatus is also absent in the Plethodontidae (Whipple 1906a). Whitford and Hutchison (1967) have demonstrated that the lungs of salamanders play a substantial role in respiration only at higher temperatures and that the skin is the primary mechanism of gas exchange.

In addition to the absence of lungs and the ypsiloid apparatus, other characteristics that have been proposed as adaptations to a mountain stream existence include the nasolabial groove and the condition of the otic apparatus. Whipple (1906b) suggested that the nasolabial groove is an adaptation to aid in buccopharyngeal respiration. Plethodontids can be observed extending their nares above the surface of the water, whereupon buccopharyngeal pumping is initiated. The nares are closed, and buccopharyngeal pumping does not occur when the salamander is completely immersed. Plethodontids with their nasolabial grooves blocked—and salamanders that lack nasolabial grooves—are unable to quickly clear their nares of water; buccopharyngeal pumping does not occur when the nares are blocked with water (Whipple 1906b). Buccopharyngeal respiration becomes more important upon loss of lungs but remains less important than cutaneous respiration. In addition to supplying any respiratory advantages, the nasolabial groove aids olfaction in adult plethodontids, according to recent evidence (Brown 1968; Jaeger and Gergits 1979; Dawley and Bass 1989); the nasolabial groove is undeveloped in larvae. Furthermore, its presence serves as evidence of the Plethodontidae as a monophyletic group, as emphasized by Dunn (1926).

The otic apparatus' was discussed by Reed (1920), who was struck by the retention of the columella, the otic structure of plethodontid larvae, in the adults of many plethodontid species. Dunn (1926) subsequently suggested that the otic apparatus was an adaptation of early plethodontid adults to habitats similar to those of larvae (i.e., mountain streams).

In addition to morphological evidence, there are comparative data that suggest lunglessness as a rheotropic adaptation (Dunn 1926; Wake 1966). In other salamander families, such as Dicamptodontidae (*Rhyacotriton*), Salamandridae (*Salamandrina*, *Chioglossa*, *Euproctus*), and Hynobiidae (*Onychodactylus*, *Ranodon*), there are forms with reduced or absent lungs. All of these salamanders occupy stream environments.

Given the weight of biogeographical, phylogenetic, morphological, and ecological evidence, Wilder and Dunn (1920) concluded that lunglessness in the family Plethodontidae is an adaptation to the fast-flowing streams of the southern Appalachian Mountains.

LUNGLESSNESS AS A LARVAL ADAPTATION

Those extant plethodontids that are inferred to be most similar to the ancestral forms are the aquatic and semiaquatic members of the subfamily Plethodontinae (tribe Hemidactyliini) and the subfamily Desmognathinae (Wake 1966; Larson 1984). These groups are limited in range to eastern North America and are most diverse in the southern Appalachians. With three exceptions, the species of these groups are characterized by a larval stage in the life history.

Ruben and Boucot (1989) totally overlooked the importance of larval forms. We submit that consideration of larval physiology, morphology, ecology, and life history lends support to the hypothesis that lunglessness is mainly a larval adaptation.

Although plethodontid larvae lack lungs, they have external gills, which are the primary respiratory surface in gilled salamanders (Guimond and Hutchison 1972). Salamandrid and ambystomatid larvae have lungs as well as gills; in these salamanders, lungs are used as hydrostatic organs in pond environments, which allows animals to maintain their position in the water column. Plethodontid larvae are benthic, usually living under rocks or in leaf packs on the stream bottom where lungs might provide disadvantageous buoyancy.

It is likely that selection for lunglessness would occur in the larval rather than the adult stage of the life history. Although phylogenetic relationships within the Desmognathinae and Hemidactyliini are not entirely clear, it is believed that the species that most closely represent the ancestral condition are hemidactyliines with lengthy larval periods, for example, *Gyrinophilus porphyriticus*, *Pseudotriton ruber*, *Pseudotriton montanus*, and *Stereochilus marginatus* (Wake 1966). These species have larval periods of 2 or more years, as do several species in the closely related genus *Eurycea* and some desmognathines (table 1). This contrasts sharply with the short larval periods (3–9 mo) of rapid-growing biphasic ambystomatids and salamandrids.

We suggest that the length of the larval period was an important factor in the evolution of lunglessness because of the deleterious effects of downstream displacement of larvae by the water current (stream drift). The role of stream drift in the biology of aquatic organisms has been explained under two alternative hypotheses: the colonization hypothesis of Müller (1954), which treats downstream drift as a process requiring compensatory upstream movements to avoid population displacement, and the production hypothesis of Waters (1972), wherein drift is viewed as a density-dependent response to excess productivity. Larval plethodontids undergo drift, but its function is uncertain (Bruce 1986). However, plethodontids usually inhabit small, low-order streams and are less common or absent in larger, higher-order streams and rivers. The larvae are more aquatic than the adults and thereby more susceptible to stream drift. Species with brief larval periods would be expected to drift less during their larval life than species with extended larval periods. Because prolonged exposure of stream-dwelling salamanders with larval periods of 2–5 yr to stream drift might have deleterious effects, both on larval survival and on general population stability,

TABLE 1
LARVAL PERIODS OF PLETHODONTID SALAMANDERS WITH BIPHASIC LIFE CYCLES

Taxon	Larval Period (mo)	Reference
Subfamily Desmognathinae:		
<i>Leurognathus marmoratus</i>	10–36	Martof 1962; Bruce 1985a
<i>Desmognathus quadramaculatus</i>	24–48	Organ 1961; Bruce 1988
<i>Desmognathus welteri</i>	24	Juterbock 1984
<i>Desmognathus monticola</i>	9–10	Organ 1961; Bruce 1989
<i>Desmognathus ochrophaeus</i>	9–10	Organ 1961; Tilley 1973a, 1973b; Bruce 1989
<i>Desmognathus fuscus</i>	9–10	Wilder 1913; Organ 1961; Danstedt 1975; Juterbock 1990
Subfamily Plethodontinae, tribe Hemidactyliini:		
<i>Gyrinophilus porphyriticus</i>	36–60	Bishop 1941; Bruce 1980
<i>Pseudotriton ruber</i>	30	Bishop 1941; Bruce 1972, 1974
<i>Pseudotriton montanus</i>	18–30	Bruce 1974, 1978
<i>Stereochilus marginatus</i>	15–27	Bruce 1971
<i>Eurycea bislineata</i>	24–36	Wilder 1924; Duellman and Wood 1954
<i>Eurycea wilderae</i>	12–24	Bruce 1982a, 1982b, 1985b
<i>Eurycea junaluska</i>	24	Bruce 1982b
<i>Eurycea guttolineata</i>	3–15	Bruce 1982a
<i>Eurycea longicauda</i>	3	Anderson and Martino 1966
<i>Eurycea quadridigitata</i>	6	Semlitsch 1980
<i>Eurycea multiplicata</i>	8	Ireland 1976
<i>Eurycea lucifuga</i>	12–15	Banta and McAtee 1906
<i>Hemidactylium scutatum</i>	1–2	Blanchard 1923
<i>Typhlotriton spelaeus</i>	29–30	Brandon 1971; Rudolph 1978

the advantage of lung loss would be greatest to the primitive species that have the longest larval periods.

Plethodontid larvae, like other stream-dwelling salamander larvae, show morphological adaptations (in addition to lung loss) that correlate with a stream existence (Valentine and Dennis 1964; Duellman and Trueb 1986). Relative to pond-dwelling larvae, stream dwellers have small gills, a shallow caudal fin, and dorsoventral depression. These characteristics streamline the larvae. The larvae also have a muscular tail and, unlike pond larvae, hatch with well-developed, muscular forelimbs that enhance crawling against a stream current.

Upon metamorphosis, plethodontids lose their gills and are left only with cutaneous and buccopharyngeal respiration. They usually become more terrestrial. However, *Leurognathus marmoratus* is aquatic in cold mountain streams in the Appalachians (Martof 1962), and *Stereochilus marginatus* is highly aquatic in warm swampy habitats in the southeastern Coastal Plain (Bruce 1971). Other streamside plethodontids may remain submerged for long periods, particularly females brooding their eggs in several species of *Desmognathus*, *Gyrinophilus*, and *Eurycea*. Thus, many metamorphosed plethodontids, lacking lungs, derive

sufficient oxygen via the skin and buccopharynx over a broad range of aquatic habitats.

The idea that lunglessness represents a larval adaptation is not new. It was Wilder and Dunn (1920, p. 64) who suggested that "the advantage of a lungless condition in such a habitat is obvious, which may be demonstrated by observations upon the activities of various Plethodontidae in the streams in which they lay their eggs and *spend their larval* and, to a less extent, their adult life" (*italics added*).

CONCLUSIONS

Plethodontids exhibit a unique suite of ecological, cytological, morphological, and physiological characteristics that differentiate them from other small ectothermic vertebrates. These include slow growth, lengthy life cycles, and long generation times (Hairston 1987); large genomes (Hally et al. 1986; Sessions and Larson 1987) that suggest low cell-division rates (Horner and Macgregor 1983); lunglessness; and low metabolic rates (Whitford and Hutchison 1967; Feder 1983).

These characteristics probably represent an integrated set of traits that reflect the original adaptation of plethodontids to streamside habitats in stable, humid forest environments of upland regions of eastern North America. The basic life-cycle pattern shown by the more primitive members of the family suggests that lunglessness evolved as a rheotropic adaptation to promote larval survival in flowing streams.

Until Ruben and Boucot's (1989) criticism of Wilder and Dunn's (1920) hypothesis, it had been generally accepted that lunglessness in plethodontid salamanders is the result of selection to reduce buoyancy in flowing mountain streams. As an alternative hypothesis, Ruben and Boucot suggested that late Mesozoic Appalachia lacked the upland environments required for such selection and suggested that plethodontids lost their lungs for reasons other than ballast.

We have cited evidence contradicting Ruben and Boucot's suggestion. Late Mesozoic Appalachia had hilly or mountainous terrain, and phylogenetic evidence suggests that the ancestral plethodontids had a mode of life suited to mountain streams as originally suggested by Wilder and Dunn. Moreover, it is uncertain whether the plethodontids arose before, during, or after the Cretaceous.

We further submit that lunglessness arose as primarily a larval, not adult, adaptation. Since larval plethodontids lack lungs and are otherwise morphologically adapted to life in streams, it seems reasonable to hypothesize that selection against lungs occurred in just such an environment but in the larval stage as an adaptation to reduce buoyancy in well-oxygenated stream environments where cutaneous and branchial respiration could provide for the respiratory needs of the animals. This argument is strengthened by the observation that the larval period is prolonged in many living plethodontids. If we assume that lungless plethodontid larvae are a sister taxon to lunged ambystomatid larvae, then the loss of lungs in the former and their retention in the latter is consistent with the basic habitat dichotomy between the two families.

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Associate Editor: Joseph Travis