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Salamanders of the Family Plethodontidae

**with introductions by
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Emmett Reid Dunn and the Development of Scientific Studies of Salamander Biology

by David B. Wake*

Among the most important works in the historical development of ideas are those which, rather than providing conclusive answers to questions, organize data in a manner which facilitates and stimulates further investigation. Emmett Reid Dunn's *Salamanders of the Family Plethodontidae* is of this genre.

Dunn seems to have been the first major worker to recognize the overwhelming predominance of plethodontids among the living salamanders. His great contribution was to take a critical look at all known members of the largest family of salamanders and to provide an organized summary that has served as the point of departure for hundreds of diverse investigations. He also produced important generalizations concerning evolutionary processes.

When Dunn began his now classic studies, in the first quarter of this century, salamander biology was a neglected area. Taxonomy of the group was in dreadful shape, barely advanced from the work of Cope (1859, 1869, 1889). Voluminous morphological treatises emanating from Germany and England were characterized by extreme typological thinking, and little attention was given to other aspects of the biology of the group. Studies of ecology and evolutionary relationships not only were dormant, but were actually hampered by work of the late nineteenth century. While Boulenger made lasting contributions to the taxonomy of reptiles, his catalogue of salamanders (1882), one of his earliest publications, was literally regressive. He was particularly mystified by plethodontid salamanders, an almost entirely New World group with which Europeans had little contact. The monumental studies of Drüner (1901, 1904) on the hyobranchial apparatus of salamanders simply ignored plethodontids, and Wiedersheim's (1875, 1877) contributions were both scant and erratic. Newts were the biological stereotype of caudate amphibians, and plethodontids were oddities, frequently not accorded familial rank.

Timing is important in the success of scientists. When Stejneger, in 1913, advised Dunn to study salamanders, the herpetological community was ready for progress. Up until this time the field had been dominated by Europeans. As a group they seem to have had a mistrust of the analytical abilities of American scientists, especially Cope, and there was little

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appreciation of the diversity of American salamanders despite a moderately large literature. H. H. Wilder (1894) showed that plethodontids generally were lungless, Stejneger (1892, 1896) described the curious *Typhlotriton* and *Typhlomolge*, Moore (1899, 1900) made important contributions to plethodontid anatomy and taxonomy, Emerson (1905) contributed important anatomical data and meaningful interpretations, and I. W. Wilder (1913) began studies of plethodontid morphogenesis. The data base was broadening.

Familiar Virginia countryside provided the materials for Dunn's first researches on salamanders. A few notes were followed by the publication of a number of very important papers. From 1915 to 1925, Dunn published a series of papers which provided the basis for his monograph on plethodontids. Nearly half of the 64 papers which he wrote during this period were devoted to salamanders. Perhaps the most significant was published when he was only 23; this paper, co-authored with Fowler (1917), reviewed the important salamander collection in the Academy of Natural Sciences, Philadelphia. It included a summary of knowledge of plethodontid salamanders generally, and a number of novel and perceptive interpretations. This was the first really thorough and original consideration of the family since Cope's pioneering work of 1859.

In other papers, Dunn reviewed the amphibian and reptile collection of the Museum of Comparative Zoology at Harvard University (1918), and published a number of taxonomic papers. Especially notable is the revision of *Desmognathus* and *Leurognathus* (1917), which included much on natural history. He seems to have been the first to give detailed attention to sympatric species of salamanders, and the impact of this early work cannot be overemphasized. While not always explicit, his comments concerning the salamander component of communities provide important insight into factors leading to species diversity and interaction, and have stimulated many subsequent investigations.

It is difficult to appreciate the sorry state of plethodontid salamander taxonomy when Dunn began his work. Cope (1859) had laid the groundwork, but very little of consequence had been accomplished since. Starting with the co-authored paper with Fowler (1917), Dunn accomplished a thorough revision, not only of plethodontids but of all salamanders, in less than ten years. Emerson's (1905) early work was reaffirmed, and *Typhlomolge* was recognized as a plethodontid. *Spelerpes* was a name that had been variously applied to include from most to all of the free-tongued plethodontid salamanders. The name, preoccupied by *Eurycea*, disappeared, and the species associated with it were assigned to *Eurycea*, *Manculus*, *Pseudotriton*, *Gyrinophilus*, *Hydromantes* and *Oedipus*. *Ensatina* was recognized as a group distinct from *Plethodon*, and the species of *Plethodon* and *Aneides* were correctly sorted. Dunn began a long and frustrating association with neotropical plethodontids by describing some new species in 1921, and he described some new *Batrachoseps* from California in 1922.

Research was not limited to plethodontids, however. Many papers on reptiles appeared, and several important studies were published dealing with the taxonomy and evolutionary relationships of hynobiid, salamandrid and ambystomatid salamanders. *Rhyacotriton* was shown to be an ambystomatid (1920) and hynobiids were recognized as a distinct family. In 1923,

a major (still the most recent!) revision of the family Hynobiidae was published.

While from a casual glance at titles, taxonomy seems to have been emphasized, the contributions of Dunn to an understanding of the general biology of salamanders cannot be overlooked. Ecology and zoogeography played major roles in discussions of evolution of the different groups. With Inez Wilder (1920), Dunn presented a logical analysis of the significance of lunglessness in salamanders. Papers on the breeding habits of salamanders and on their sound-transmitting apparatus demonstrated his broad scope. These have had a lasting influence on the field of herpetology.

Dunn was not alone in his studies of salamander biology during these years. Major contributions were made by Camp, Grinnell, Van Denburgh, Ritter, Storer and others in the West. Camp's (1916) discovery of *Hydromantes platycephalus* focused critical attention on the composite *Spelerpes* of contemporary authors, and Storer's 1925 *Amphibia of California* presented much detailed information and carefully reasoned arguments concerning important aspects of salamander natural history. In the East, G. K. Noble was active, and his fertile mind produced ideas that had a most stimulating effect. The work of Wilder, Brimley, Piersol, Kingsbury, Reed, and others added greatly to the data base. In Europe, Bedriaga, Wolterstorff, Boulenger, and others were producing a series of papers on salamander biology. Thus the publication of Dunn's monograph on plethodontids was, in a sense, the culmination of a period of rather intense activity and much genuine progress. Dunn was clearly the leader of this disparate group, and made the most important and lasting contributions. It was thus fitting that he should be the author of the most comprehensive and influential treatment of a large family of amphibians or reptiles that has ever been written.

The monograph on plethodontid salamanders which Dunn produced consists of two distinct parts, the introduction and the species accounts. Both had profound impact. The introduction was one of the first truly analytical and synthetic treatments of an amphibian group, and the systematic section was the most detailed ever attempted for a group of amphibians or reptiles.

Dunn's views on various topics were challenged by Noble and others in the years following publication of this book, but it is safe to say that, by and large, the views of Dunn prevailed. In fact, they continue to exert a strong influence up to the present time. In the following paragraphs an attempt is made to view the major ideas of Dunn's monograph from the perspective of forty-six years.

Any consideration of *Salamanders of the Family Plethodontidae* must begin with the superb *Foreword*. Not only is it a remarkable literary accomplishment, but it has created something of a romantic tradition. Cerro de la Muerte, Whitetop, Grandfather, Orizaba and other Dunn collecting sites have attained a classic stature. The foreword distinguishes the book, giving it perspective and excitement. Others have tried, in recent years, to match Dunn's eloquence, but all pale by comparison.

Even today the fifty-seven page *Introduction* is awesome. It begins with a consideration of the diagnostic characters of the advanced families of salamanders, a contribution of major importance. The most curious

aspect of this discussion is Dunn's suggestion that plethodontids were derived from a salamandrid stock. The idea that plethodontids had been derived from ambystomatids had prevailed for many years, since Cope's work in 1859. Dunn's own data on the structure of the ear (1922b) seemed to contradict him. Perhaps he was strongly influenced by the incomplete studies of body musculature, and by the presence of such relatively free-tongued members of the Salamandridae as *Chioglossa*, a lungless form which does superficially resemble plethodontids. At any rate, in this area Dunn held sway by sheer weight of his authority for many years. Only recently has the ambystomatoid ancestry of plethodontids once again been accepted (see Regal, 1966, and Wake, 1966, following Laurent, 1947).

The theory of plethodontid origin, from a stream dwelling species which had lost its lungs as a rheotropic adaptation, has never been seriously challenged, nor has the idea that "Appalachia" was the likely area of origin and diversification of the family. While Dunn's ideas on these and other points may sound didactic and incomplete in the light of present knowledge, they were original, synthetic and highly influential. Speculations concerning time of divergence and diversification seem much too recent, but, in fact, we have little more information now than in 1926 concerning the fossil history of plethodontids.

Great advances have been made in the area of what Dunn termed "Habits," and this section of the monograph has little value for modern workers. The only major error, however, is the still repeated statement that *Hydromantes italicus* and *Bolitoglossa uderspersa* bear living young. It is now known that both lay eggs, and there is not a shred of evidence that any plethodontid gives birth to living young.

Dunn's approach throughout the *Introduction* is thoroughly evolutionary. His conception of evolutionary processes was surprisingly modern in some respects, yet in other ways he clearly represented the general level of evolutionary thought of the period in which he worked. Ecological interactions, habitat, and regional patterns of distribution were stressed in discussions of speciation and species relationships. After commenting on the little ecological segregation shown by the species of *Eurycea* he observed (p. 28), "without ecologic segregation there must be competition; with competition there must be either migration or extermination." Dogmatic, perhaps, but in this and other similar statements Dunn reveals himself to be a perceptive, problem-oriented scientist with a clear set of operational principles. Dunn would feel quite comfortable with current research, which often stresses competitive interactions, life history strategies, evolutionary morphology, and other topics that are natural developments of the kinds of problems which interested him.

The section entitled "Generalizations" includes five main evolutionary points. The first two (the precedence in time of function over form, and the recognition of parallelism as a major factor in evolution within lineages) are accepted as being almost self-evident today, but they were subjects of controversy at that time. Orthogenesis is treated in a modified and cautious manner, simply applying the term to the existence of separate character states of an apparent morphological continuum in different species. We no longer refer to Jordan's or Osborn's "Laws," but we certainly recognize the

importance of geographic factors in speciation, and concern ourselves with studies of dispersal, colonization and competitive interactions leading to adaptive radiations. It is these processes to which Dunn refers. It was work such as his, organization of data in an evolutionary framework, which led to the development of a general evolutionary synthesis in the 1930's.

The bulk of the monograph consists of detailed species accounts of all recognized genera and species of plethodontids. Dunn recognized 72 species; 44% (31) of these were neotropical species of the genus *Oedipus*. My latest estimate is 204 species, of which 70% (142) are neotropical species. Thus the total number of known species has nearly tripled, and the number of tropical species recognized has increased more than four times! In North America such novelties as *Phaeognathus hubrichti*, the permanently larval species of *Eurycea* and *Gyrinophilus*, *Haideotriton wallacei*, and several very distinctive as well as cryptic species of *Batrachoseps*, *Desmognathus* and *Plethodon* have been described since the appearance of Dunn's monograph. Representatives of all currently recognized neotropical genera were known to Dunn, but he had no idea as to the extent of species diversity in the tropics.

Desmognathus and *Leuognathus* were separated from all other groups by Dunn, and this division is reflected in the modern taxonomy, which usually places these genera (with *Phaeognathus*) in a subfamily Desmognathinae. Other genera were placed by Dunn in two "natural" groups. *Plethodon*, *Ensatina*, *Aneides*, *Hemidactylum* and *Batrachoseps* formed the *Plethodon* group. *Hemidactylum* was thought to have reverted to the water and re-evolved a larval stage, and *Batrachoseps* was said to be a degenerate *Plethodon* derivative. The first three genera are still grouped together, in a tribe Plethodontini, but *Hemidactylum* is now thought to be closer to the *Eurycea* group of genera (tribe Hemidactyliini). *Batrachoseps* is now grouped with *Hydromantes* and the neotropical Bolitoglossini. Dunn was impressed with the free tongue as a feature uniting members of his *Eurycea* group, which he considered to be the generalized and central stock of the family. Although he had earlier resurrected Cope's *Manculus*, it was here placed in the synonymy of *Eurycea*. *Hydromantes* and *Oedipus* were thought by him to form a natural subgroup within the *Eurycea* group. The close association of *Oedipus* and *Hydromantes* has been recognized by most subsequent workers, with some including *Batrachoseps* in this subgroup (Wake, 1966).

It is with reference to the neotropical assemblage that the greatest departures from Dunn's thinking have occurred. It is now thought that "free" tongues have evolved twice in the family quite independently (Wake, 1966). Thus ancestors of the neotropical species (with *Batrachoseps* and *Hydromantes*) are sought among hypothetical attached-tongued ancestors of all plethodontines. Of course, increasing the number of known neotropical species from 31 to 142 was bound to modify thinking, but Dunn seems to have been quite confused by this group. He was reluctant to admit their great diversity, and failed to detect the extensive parallelism which has occurred. Four groups within *Oedipus* were recognized. The primitive group was thought to contain three subgroups. Each of these subgroups contains species belonging to at least two presently recognized genera, including *Bolitoglossa*, *Pseudoeurycea*, and *Chiropterotriton*. A second group included

four diminutive species which are currently assigned to the genera *Thorius*, *Parvimolge* and *Chiripoterotriton*. Another group included fully webbed, lowland species of *Bolitoglossa*, and the final group contained the elongate, worm-like species of the genera *Lincatrion* and *Oedipina*. Taxonomy of this group remained chaotic until 1944, when Taylor sorted the species in a realistic way. However, Dunn never did accept Taylor's arrangement despite the fact that he had nothing better to offer.

The name *Oedipus* was preoccupied, for it had been assigned to a group of fossil orthopterans. When Taylor (1940) reassigned the salamanders of that genus to *Bolitoglossa*, Dunn was unhappy and refused to accept this decision. In part this may have been a genuine difference of opinion among scientists. *Oedipus* had been used in only one publication in the early 1800's, and had been almost immediately synonymized. However, one feels that other, more personal factors were also involved. Dunn and Taylor were often adversaries. Further, Dunn had a classical bent, and he rather enjoyed being the author of *Oedipus rex* and *Oedipus complex*. Even late in his life, Dunn considered making an appeal, with K. P. Schmidt, to the International Commission on Zoological Nomenclature to suppress *Bolitoglossa* in favor of *Oedipus*.

In the years following publication of this monograph, many modifications of Dunn's ideas took place, and this trend continues. New data continue to accumulate, and a continual reevaluation is required. Nonetheless, this book is still the point of departure for studies of plethodontids.

Some of Dunn's views were challenged almost immediately by Noble (1927), who questioned some points relating to habitat preferences, secondary sexual characters, color pattern and species relationships. Dunn (1927) responded, and the questions were never fully resolved. Noble did add new data, but his assertive style of argument weakened his work. Dunn withstood this essentially lone challenge with ease. The 1930's witnessed a great surge in studies of plethodontid salamanders, with Schmidt, Stuart, Bishop, Taylor, Blanchard and others contributing. Some of these workers acknowledged Dunn's direct influence, but certainly he was largely responsible for the sharply increased interest in the group. Dunn continued to contribute, but his interests shifted to other groups. His last major paper on salamanders appeared in 1941.

After nearly half a century, *Salamanders of the Family Plethodontidae* retains a freshness and vibrancy that makes it essential, basic reading for a beginning student of this group. It is the bibliographic source for plethodontids up to 1926. But it is not only a useful reference for the devotee of plethodontids, it is also a book which stimulates and even inspires. It sets a standard.

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