



## The Abundance and Diversity of Tropical Salamanders

David B. Wake

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## LETTERS TO THE EDITORS

THE ABUNDANCE AND DIVERSITY OF TROPICAL  
SALAMANDERS

In a recent stimulating discussion of temperature adaptations of amphibian embryos, Bachmann (1969) suggests that salamanders are genetically restricted by a lack of adaptability to any but moderately low temperatures. He states that this supposed lack of adaptability corresponds to the "very restricted" distribution of salamanders and is accordingly "striking." Bachmann is quite aware of the limits of his salamander data, from only seven species of the exclusively north temperate families Proteidae, Ambystomatidae, and Salamandridae, and I do not wish to criticize that aspect of his paper. Rather, I will examine some of his premises, explicit and implicit, concerning salamander abundance and diversity.

One of the most persistent myths in the biological literature is the view that salamanders are strictly a north temperate group, which has few or no tropical representatives (e.g., Bentley 1966). The basis for this view is the fact that eight of the nine families, including all of the most familiar species, are restricted to extratropical regions in the Northern Hemisphere. Ambystomatids on the Mexican Plateau and salamandrids in the mountains of Formosa and North Vietnam live like more northern relatives and are generally considered to be members of the temperate fauna. There are no tropical species in the Old World. The ninth family, Plethodontidae, has north temperate representatives in both the Old and New Worlds, but, in addition, one subdivision, the tribe Bolitoglossini, has undergone an extensive neotropical radiation. The neotropical representatives comprise over 40% of all living species of salamanders! Recent estimates (based on Brame 1967 and unpublished data) find 316 species of salamanders, including 194 plethodontids of which 132 are residents of the neotropics. The tropical species are concentrated in two major areas, southern Mexico to Guatemala, and Costa Rica to northern South America (table 1), but the ranges extend to about 20°S latitude (Wake 1966).

Available information indicates that a major adaptive radiation has occurred in the neotropics, but this must be viewed relative to the diversification seen in all salamanders. The range of diversity within tropical salamanders is great, and ways of life not seen elsewhere have evolved (Wake 1966). Species live in a wide variety of habitats, but the more primitive ones live in upland, terrestrial situations. Numerous lowland invasions have occurred, and many species successfully occupy the tropical lowland forests from Veracruz to the mouth of the Amazon. Lowland in-

TABLE 1  
 NUMBERS OF FAMILIES, GENERA, AND SPECIES OF SALAMANDERS FOUND  
 IN ZONES OF 5° LATITUDE IN THE WESTERN HEMISPHERE

Zone	Families	Genera	Species
Above 50° N .....	4	8	12
45°-50° N .....	4	14	24
40°-45° N .....	6	18	44
35°-40° N .....	7	22	63
30°-35° N .....	7	24	58
25°-30° N .....	6	12	33
20°-25° N* .....	3	4	17
15°-20° N* .....	2	10	74
10°-15° N* .....	1	5	34
5°-10° N* .....	1	4	44
0°-5° N* .....	1	2	10
0°-5° S* .....	1	1	5
5°-10° S* .....	1	1	2
10°-15° S* .....	1	1	1
15°-20° S* .....	1	1	1

\* Zones in which all or most species may be considered tropical.

vaders almost invariably occupy either burrowing or arboreal niches, possibly because ways of life more typical of temperate salamanders are not possible in the highly competitive lowland environments. The genus *Bolitoglossa* includes over 60 species. It is the group most active in lowland invasions, and its range is nearly equivalent to that of the entire tropical assemblage.

Within this great range of diversity, group differentiation is weak and generic borders are difficult to define, suggesting that the tropical radiation is a relatively recent event (see Wake 1966). Until a few years ago (Taylor 1944), all of the tropical species were included in a single genus. Nearly 80% of the tropical species have been discovered during the past 40 years. As a result, most authors have not incorporated current information in their general work, and even basic herpetological sources do not give a clear picture of the number and diversity of the tropical species (e.g., "the salamanders are a north temperate group and have invaded the tropics only in Central America and northern South America; this invasion has been made only by one group [*Bolitoglossa* and its allies of the Plethodontidae]" Goin and Goin 1962). The standard reference has been Dunn (1926), who recognized only 30 species of tropical salamanders and placed them in a single genus. In view of the phenomenal success of tropical salamanders, relative to the ancient lineages of extratropical regions, one would expect them to be the subject of intensive study, but they have been largely ignored except by taxonomists. This is perhaps the result of ignorance concerning the extent and possible significance of the radiation. Especially intriguing is the basic problem of how a specialized lineage of an ancient, generalized group was able to invade and occupy the tropics, and there undergo an extensive radiation in the presence of a highly differentiated fauna including many potential competitors.

Certainly a key factor in the success of tropical salamanders has been the abandonment of the aquatic larval stage and the acquisition of direct

terrestrial development (Wake 1966). Bachmann's conclusions may well hold true for the generalized species with aquatic larvae, for their ecology sharply restricts their geographic distribution. But his premises are wrong in regard to those temperate and tropical salamanders with terrestrial development, for they have freed themselves from some constraints of the more generalized way of life and have broad ecologic and extensive geographic distributions. To his credit, Bachmann recognized the need and desirability of studying these species, although none was available to him. Despite the lack of such data, Bachmann has made a worthwhile contribution, and my objection simply is to his willingness to apply findings from studies of the generalized, temperate species to the tropical species, based on the false premises that the latter are restricted in distribution and are few in number.

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DAVID B. WAKE

MUSEUM OF VERTEBRATE ZOOLOGY  
UNIVERSITY OF CALIFORNIA  
BERKELEY, CALIFORNIA 94720  
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