COMPARATIVE OSTEOLOGY AND EVOLUTION OF THE LUNGLESS SALAMANDERS, FAMILY PLETHODONTIDAE

DAVID B. WAKE

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Eurycea longicauda, an adult female from Deputy Cave, Jennings County, Indiana.

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CONTENTS

COMPARATIVE OSTEOLOGY AND EVOLUTION OF THE LUNGLESS SALAMANDERS, FAMILY PLETHODONTIDAE

DAVID B. WAKE[1]

ABSTRACT: Lungless salamanders of the family Plethodontidae comprise the largest and most diverse group of tailed amphibians. An evolutionary morphological approach has been employed to elucidate evolutionary relationships, patterns and trends within the family. Comparative osteology has been emphasized and skeletons of all twenty-three genera and three-fourths of the one hundred eighty-three species have been studied.

A detailed osteological analysis includes consideration of the evolution of each element as well as the functional unit of which it is a part. Functional and developmental aspects are stressed.

A new classification is suggested, based on osteological and other characters. The subfamily Desmognathinae includes the genera *Desmognathus, Leurognathus,* and *Phaeognathus.* Members of the subfamily Plethodontinae are placed in three tribes. The tribe Hemidactyliini includes the genera *Gyrinophilus, Pseudotriton, Stereochilus, Eurycea, Typhlomolge,* and *Hemidactylium.* The genera *Plethodon, Aneides,* and *Ensatina* comprise the tribe Plethodontini. The highly diversified tribe Bolitoglossini includes three supergenera. The supergenera *Hydromantes* and *Batrachoseps* include the nominal genera only. The supergenus *Bolitoglossa* includes *Bolitoglossa, Oedipina, Pseudoeurycea, Chiropterotriton, Parvimolge, Lineatriton,* and *Thorius.*

Manculus is considered to be congeneric with *Eurycea,* and *Magnadigita* is congeneric with *Bolitoglossa.* Two species are assigned to *Typhlomolge,* which is recognized as a genus distinct from *Eurycea.* No new information is available concerning *Haptoglossa.* Recognition of a family Desmognathidae is rejected.

All genera are defined and suprageneric groupings are defined and characterized. Range maps are presented for all genera. Relationships of all genera are discussed.

Plethodontid salamanders have undergone an adaptive radiation characterized by structural, functional, and ecological parallelism. The relatively primitive desmognathines and hemidactyliines have remained close to the ancestral habitat, mountain brooks and streams in eastern North America. Evolutionary trends in the direction of abandonment of the aquatic larval stages and attainment of direct development are evident in desmognathines. The tribes Bolitoglossini and Plethodontini have direct development in terrestrial habitats. Terrestriality has stimulated evolution in these two successful groups and both have extended far beyond the ancestral range.

Paedomorphosis has played a significant role in influencing evolutionary patterns within the family. In hemidactyliines, paedomorphosis has led to paedogenesis in four genera. Paedogenesis is a highly specialized but regressive adaptation in these groups. Paedomorphosis has profoundly influenced terrestrial groups by allowing them to achieve reproductive maturity at early structural stages. The phenomenon has led to evolutionary progress and may have been the key to the success of the terrestrial groups.

Ancestral plethodontids probably arose from a stock close to that which gave rise to ambystomatids. The subfamily Desmognathinae is a specialized early derivative of this stock. Probable desmognathine remains from Cretaceous formations suggest that subfamilial differentiation was a Mesozoic event. The tribe Hemidactyliini is the most generalized group, both in structure and ecology, and is probably close to the ancestral familial stock. The tribe Bolitoglossini may have been the earliest derivative of the plethodontine stock. It ranges to western North America, Europe, and South America, and is the only salamander group that penetrates the tropics. In addition it is the only group of plethodontids that no longer occurs in eastern North America. The final derivative, the tribe Plethodontini, probably differentiated in early Tertiary times. The group has extended its range to western North America but still has relatively primitive representatives in Appalachia.

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INTRODUCTION

Despite considerable progress in studies of population genetics and the processes of speciation, biologists have made little headway in understanding the mechanisms of macro- and megaevolution. The goal of this comparative osteological study of the salamander family Plethodontidae is to elucidate problems relating to evolution above the species level. Salamanders are generalized, evolutionarily conservative tetrapods. They were chosen for study because available evidence indicates that evolutionary rates have been relatively slow in the group. The family Plethodontidae includes a large variety of adaptive types among its diverse species. Many intermediate adaptive stages are extant, thus facilitating analysis of major evolutionary events. Hopefully, this study will provide groundwork for comprehensive analyses of evolutionary patterns in the family Plethodontidae, as well as in other groups.

The amphibian order Caudata includes nearly 300 species of salamanders. Almost two-thirds of these comprise the family Plethodontidae. The family is distinguished from all others by absence of lungs combined with presence of a cutaneous depression (the nasolabial groove) extending from each nostril to the upper lip of transformed individuals. The most comprehensive treatment of the family is Dunn's (1926) pioneer monograph, which is now, unfortunately, badly out of date. While papers by Piatt (1935), Taylor (1944), Soler (1950), Tanner (1952) and others have provided additional information, the introduction to "The Salamanders of the Family Plethodontidae" (Dunn, 1926) has been the best source of information concerning structure and phylogeny. The most recent general reviews of theories of familial evolution are given by von Wahlert (1957) and Martof (1962).

A major adaptive radiation has been the outstanding feature of the phylogeny of the family. Primitive and generalized plethodontids live in semiaquatic habitats and pass through extended larval periods during their ontogeny. Some species are completely aquatic, but advanced species range from semiaquatic to terrestrial, with many of the intermediate stages still represented by living species. Many advanced species have abandoned the aquatic larval stage and undergo direct terrestrial development; they occupy a large variety of terrestrial habitats, from cold and barren highlands to heavily forested tropical lowlands. Some of the terrestrial species are arboreal, and a few are semifossorial, but most are surface dwellers that take daytime refuge in burrows or under surface cover.

Primitive species of plethodontids occur in eastern North America, primarily in Appalachia. Advanced species have spread to western North America, Europe, and Central and South America.

Because of the variety of adaptive types among plethodontid species, the family is veritably a "living laboratory." It is an ideal group in which to study patterns of vertebrate evolution, particularly speciation, mechanisms and patterns of adaptive radiation, and the origins of higher taxa.

This investigation has several objectives. Skeletal variation is analyzed, particularly to elucidate evolutionary relationships on generic and higher levels. Implications for taxonomy and phylogeny are emphasized and the biogeographic history of the family is reanalyzed on the basis of these data. A functional and evolutionary approach is employed to focus attention on factors involved in the invasion of new adaptive zones and subsequent adaptive radiations, that is, on major features of evolution in the family Plethodontidae.

The following brief sketches of the plethodontid genera are presented to provide general background information for the reader.

Salamanders of the genus *Desmognathus* (eight species), the dusky salamanders, are found in the eastern portion of North America from Quebec and Nova Scotia to the Gulf Coastal Plain. The stocky, agile members of this genus occur in a variety of habitats, but most are aquatic to semiaquatic in habits. The most aquatic species are the largest, and the smallest species are terrestrial and even semiarboreal. All are quick, alert forms, adept at leaping and climbing.

An aquatic genus, *Leurognathus* (one species), resembles the larger species of *Desmognathus* in habitus. It occurs in mountain brooks in the southern Appalachian Mountains.

A recently discovered genus, *Phaeognathus* (one species), is a primarily terrestrial form apparently restricted to a small area on the Coastal Plain of Alabama. The single species, an elongate form with very short legs, lives in burrows.

Gyrinophilus (three species) is a group of large, stout salamanders with elongated trunks and short, stocky tails. The species occur in springs, seepages, rivulets, and cave waters from Quebec to northern Alabama and Georgia. One species is permanently larval.

The strikingly colored (brownish to bright red, with dark spots) members of the genus *Pseudotriton* (two species) are very stout, short-legged species which occur in springs and seepages in eastern North American from New York to Florida, and west to Ontario, Ohio, and Louisiana.

The nearly aquatic salamanders of the genus *Stereochilus* (one species) have elongate trunks and relatively short, stout tails. The poorly known genus inhabits swampy and slow-moving waters on the Atlantic Coastal Plain from Virginia to Georgia.

The slender, active members of the genus *Eurycea* (twelve species) range over most of eastern United States, with isolated populations on the Edwards Plateau of Texas. The salamanders occur in a variety of habitats, from stream sides and swamps to springs, caves, and subterranean waters. Some species fail to metamorphose and achieve sexual maturity in a larval state. The genus *Manculus* (one species) is discussed separately in the data sections of this paper, but is considered by me to be congeneric with *Eurycea.*

The unpigmented, blind, cave-dwelling members of the genus *Typhlotriton* (one species) inhabit subterranean waters and water edge habitats in caves of the Interior Highlands.

Typhlomolge (two species) and *Haideotriton* (one species) are permanent larvae that are blind and unpigmented. The larger, spindly-legged *Typhlomolge* occurs in localized underground water systems at the edge of the Balcones Escarpment in Texas. *Haideotriton,* smaller and with shorter legs, is found in underground waters of southern Georgia and northern Florida.

Hemidactylium (one species) is a diminutive, highly distinctive inhabitant of swamps, sphagnum bogs, and neighboring woods. It has a basally constricted tail, only four toes, and is strikingly colored (clear white ventrally, with large black spots). The genus ranges from southern Canada to the southern Appalachian Mountains, with several disjunct southern and western populations.

Plethodon (eighteen species) is a large genus of terrestrial salamanders found in forest floor and woodland habitats. The salamanders vary considerably interspecifically, from relatively large, stout, short-bodied and long-legged species to relatively small, slender, elongate and short-legged species. The genus occurs in many areas of eastern and northwestern North America, and in the Rocky Mountains.

Ensatina (one species) is a stout-bodied, long-legged terrestrial salamander that ranges from southern British Columbia to southern California.

The genus *Aneides* (five species) is a group of terrestrial to arboreal salamanders found in the Appalachians, the high mountains of New Mexico, and along the West Coast of North America. Terrestrial members of the genus resemble generalized species of *Plethodon* and have cylindrical trunks and relatively short limbs and digits. Arboreal species have flattened bodies and relatively long limbs and digits. All species have enlarged jaw musculature.

The relatively short-bodied species of *Hydromantes* (five species) occur in terrestrial habitats in limestone areas in the mountains of California and in Europe. The salamanders are most commonly found under rocks and logs, and in caves.

Batrachoseps (three species) is a genus of small, attenuate salamanders with four toes and very long tails. All are terrestrial and utilize underground burrows. The animals are found along the West Coast of North America from northern Oregon to northern Baja California. There may be isolated populations in southeastern Alaska and on the Nevado de Colima, Jalisco, Mexico.

The seven remaining genera are collectively termed the neotropical genera in this paper. *Bolitoglossa* (fifty-two species) is a large, diverse, widespread group of terrestrial to arboreal species. Included are species that are among the largest *(B. robusta)* and smallest *(B. rufescens, B. orestes)* of terrestrial salamanders. Highland species usually have unwebbed to partially webbed hands and feet, while webbing is more extensive in lowland forms. The species occur from northeastern Mexico through Central America to central Bolivia, the mouth of the Amazon River in Brazil, and possibly as far southeast as southern Minas Gerais, Brazil (Wake and Brame, 1966).

The genus *Oedipina* (sixteen species) is a group of highly distinctive, elongate species with extremely long tails, very short limbs, and attenuated bodies. All are terrestrial. The genus ranges from southern Mexico through Central America to western Colombia and northern Ecuador.

Pseudoeurycea (twenty species) includes a rather variable group of terrestrial to semiarboreal salamanders found from northeastern Mexico to southern Guatemala. Although most of the species are of relatively moderate size, the genus includes species that are probably the largest terrestrial salamanders *(P. bellii, P. gigantea).*

A variable group of relatively diminutive salamanders is included in the genus *Chiropterotriton* (sixteen species). Members of the genus are largely arboreal, but some occur in forest floor habitats and others live mainly in caves. The genus is found from northeastern Mexico through northern Central America, and also in Costa Rica.

Lineatriton (one species) is a poorly known form from central Veracruz, Mexico. This terrestrial animal is a small, elongate form with extremely shortened limbs and a long tail.

Members of the genera *Thorius* (nine species) and *Parvimolge* (three species) are the smallest species of salamanders. These diminutive, attenuated salamanders are found in terrestrial and arboreal habitats in wooded highland areas. *Thorius* occurs in southern Mexico, north of the Isthmus of Tehuantepec, and *Parvimolge* is found in Veracruz, Mexico and in Costa Rica.

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MATERIALS AND METHODS

This study is based on a morphological analysis of plethodontid salamanders, with an emphasis on osteology. Materials have been prepared for osteological examination in a variety of ways. Preserved specimens have been measured and sexed, then cleared in potassium hydroxide, stained with Alizarin Red-S, and stored in glycerine. Measurements of size included in the text are the distance in millimeters from tip of snout to posterior angle of vent. Cleared and stained material has provided most of the skeletons used in the study. Many skeletons have been prepared by maceration and disarticulation, and many others by dehydration and subsequent cleaning by dermestid beetle larvae and sodium hypochlorite solution. Skeletons of every plethodontid genus have been utilized in the study, and include the following (number skeletonized, number cleared and stained; all measurements and locality information on file): *Desmognathus aeneus* 0, 2; *D. auriculatus* 1, 6; *D. fuscus* 1, 6; *D. monticola* 5, 7; *D. ochrophaeus* 1, 5; *D. ocoee* 0, 4; *D. quadramaculatus* 4, 12; *D. wrighti* 0, 1; *Leurognathus marmoratus* 0, 8; *Phaeognathus hubrichti* 1, 1; *Gyrinophilus danielsi* 1, 6; *G. palleucus* 0, 1; *G. porphyriticus* 2, 2; *Pseudotriton montanus* 2, 3; *P. ruber* 12, 10; *Stereochilus marginatus* 0, 3; *Eurycea aquatica* 0, 3; *E. bislineata* 2, 12; *E. longicauda* 2, 13; *E. lucifuga* 0, 1; *E. multiplicata* 0, 2; *E. nana* 0, 5; *E. pterophila* 1, 3; *E. tynerensis* 0, 1; *E. troglodytes* 0, 1; *Manculus quadridigitatus* 0, 9; *Typhlotriton spelaeus* 0, 8; *Typhlomolge rathbuni* 0, 1; *T. tridentifera* 0, 3; *Haideotriton wallacei* 0, 2; *Hemidactylium scutatum* 0, 6; *Plethodon cinereus* 2, 8; *P. dorsalis* 0, 3; *P. dunni* 3, 4; *P. elongatus* 2, 9; *P. glutinosus* 1, 11; *P. jordani* 5, 9; *P. larselli* 0, 1; *P. longicrus* 0, 1; *P. neomexicanus* 0, 3; *P. ouachitae* 0, 1; *P. richmondi* 0, 7; *P. vandykei* 0, 7; *P. vehiculum* 2, 8; *P. wehrlei* 0, 1; *P. welleri* 0, 6; *P. yonahlossee* 3, 10; *Ensatina eschscholtzii* 6, 7; *Aneides aeneus* 3, 10; *A. hardii* 0, 11; *A. ferreus* 3, 25; *A. flavipunctatus* 2, 13; *A. lugubris* 5, 12; *Hydromantes brunus* 0, 5; *H. genei* 0, 1; *H. italicus* 0, 1; *H. platycephalus* 0, 5; *H. shastae* 0, 1; *Batrachoseps attenuatus* 3, 26; *B. pacificus* 2, 25; *B. wrighti* 0, 10; *B. sp. nov.* (Monterey) 0, 22; *B. sp. nov.* (Bodfish) 0, 1; *Bolitoglossa adspersa* 0, 7; *B. borburata* 0, 1; *B. cerroensis* 0, 2;

B. colonnea 0, 1; *B. dunni* 0, 1; *B. engelhardti* 0, 2; *B. flaviventris* 0, 1; *B. helmrichi* 0, 1; *B. lignicolor* 0, 1; *B. marmorea* 0, 2; *B. mexicana* 0, 2; *B. morio* 0, 1; *B. nigroflavescens* 0, 1; *B. occidentalis* 0, 1; *B. orestes* 0, 1; *B. platydactyla* 0, 3; *B. robusta* 0, 1; *B. rostrata* 0, 2; *B. rufescens* 0, 3; *B. salvinii* 0, 2; *B. savagei* 0, 2; *B. striatula* 1, 1; *B. subpalmata* 6, 13; B. *schizodactyla* 0, 1; *Oedipina bonitaensis* 0, 4; *O. complex* 0, 1; *O. cyclocauda* 0, 1; *O. gracilis* 0, 2; *O. inusitata* 0, 5; *O. longissima* 0, 2; *O. parvipes* 0, 3; *O. poelzi* 0, 4; *O. pacificensis* 0, 1; *O. syndactyla* 0, 2; *O. uniformis* 0, 1; *O. sp. nov.* (Costa Rica) 0, 5; *Pseudoeurycea altamontana* 0, 1; *P. bellii* 0, 1; *P. cephalica* 0, 2; *P. expectata* 0, 1; *P. gadovii* 0, 1; *P. goebeli* 0, 1; *P. leprosa* 0, 3; *P. rex* 0, 1; *P. robertsi* 0, 1; *P. scandens* 0, 1; *P. smithi* 0, 2; *P. unguidentis* 0, 1; *P. werleri* 0, 2; *P. sp. nov.* (Mexico) 0, 1; *Chiropterotriton abscondens* 0, 3; *C. arboreus* 0, 1; *C. bromeliacia* 0, 2; *C. chiropterus* 0, 4; *C. dimidiatus* 0, 5; *C. multidentatus* 0, 5; *C. nasalis* 0, 1; *C. priscus* 0, 1; *C. xolocalcae* 0, 2; *Parvimolge richardi* 0, 1; *P. townsendi* 0, 2; *Lineatriton lineola* 0, 4; *Thorius dubitus* 0, 1; *T. macdougalli* 0, 3; *T. pennatulus* 0, 2; *T. pulmonaris* 0, 5.

Skeletal material has also been available for the families Hynobiidae *(Hynobius)*, Cryptobranchidae *(Cryptobranchus, Megalobatrachus)*, Sirenidae *(Siren)*, Ambystomatidae *(Ambystoma, Dicamptodon, Rhyacotriton)*, Salamandridae *(Chioglossa, Cynops, Notophthalmus, Paramesotriton, Salamandra, Taricha, Triturus)*, Necturidae *(Necturus)*, Proteidae *(Proteus)*, and Amphiumidae *(Amphiuma)*.

Many specimens of most plethodontid genera have been dissected in order to study musculature and duct and nerve pathways. These specimens have been stored in seventy per cent ethyl alcohol and dyed with borax carmine-picric acid (for muscles and nerves) and toluidine blue (for cartilage). All observations have been made with a stereoscopic dissecting microscope with magnifications of from ten to ninety diameters.

Histological preparations of the tongues of *Batrachoseps pacificus, Bolitoglossa subpalmata, Chiropterotriton chiropterus, Ensatina eschscholtzii, Eurycea bislineata, Plethodon cinereus, Pseudotriton ruber,* and *Typhlotriton spelaeus* have been available. Materials were preserved in 8% formalin, Bouin's solution, or Zenker's solution, embedded in paraffin, and stained with Azan using standard techniques.

X-ray radiographs, mostly stereoscopic, have been prepared for many species, particularly of those not well represented in collections and not available for direct skeletal examination. Plates were exposed for from thirty seconds to ten minutes at instrument readings of twenty-five to forty kilovolts and five DC milliamperes. Much osteological information has been obtained in this manner. All radiographs are on file at the University of Southern California.

Extensive field experience in the Appalachian Highlands and eastern United States, on the Edwards Plateau of Texas, in the mountains of New Mexico, in the Pacific Northwest, in California, in Costa Rica, and in Peru has provided me with valuable background information concerning salamanders and habitats.

NON-OSTEOLOGICAL FAMILY CHARACTERS

Lunglessness was first reported among plethodontid genera by Wilder (1894). Subsequently it has been discovered that members of other salamander families (Hynobiidae, Ambystomatidae, Salamandridae) may have reduced lungs, and a few species of these families lack lungs, but lunglessness is apparently a universal character of plethodontid species.

A small depression, the nasolabial groove, extends from each nostril to the lip in all fully metamorphosed plethodontids. Associated with the groove is a system of glands, which, in many plethodontid genera, forms a swollen protuberance. The swelling is usually more obvious in males than in females, and may be drawn into a slender cirrus that extends ventral to the lower jaw.

The above characters, in combination, define the family Plethodontidae. The family is comprised of over one hundred and eighty species distributed among the following genera: *Desmognathus, Leurognathus, Phaeognathus, Gyrinophilus, Pseudotriton, Stereochilus, Eurycea, Typhlotriton, Typhlomolge, Haideotriton, Hemidactylium, Plethodon, Aneides, Ensatina, Hydromantes, Batrachoseps, Bolitoglossa, Oedipina, Pseudoeurycea, Chiropterotriton, Parvimolge, Lineatriton* and *Thorius.* The last seven genera are collectively termed the neotropical genera in this report. The species *Eurycea quadridigitata* is retained as the sole representative of the genus *Manculus* in the data sections only.

Plethodontid genera vary considerably in their ecological requirements. They may be grouped as follows (in part after Dunn, 1926; von Wahlert, 1957):

1. Primarily or strictly aquatic. *Leurognathus, Gyrinophilus, Pseudotriton, Stereochilus, Eurycea, Manculus, Typhlotriton, Typhlomolge, Haideotriton.*

2. Semiaquatic or semiterrestrial. *Desmognathus, Hemidactylium.*
3. Terrestrial. *Phaeognathus, Plethodon, Ensatina, Aneides, Hydromantes, Batrachoseps, Bolitoglossa, Oedipina, Pseudoeurycea, Chiropterotriton, Parvimolge, Lineatriton, Thorius.*

The above classification is over-generalized and there are many exceptions. *Desmognathus* alone has species that may be aquatic *(quadramaculatus),* semiaquatic *(monticola),* semiterrestrial *(ochrophaeus),* or almost terrestrial *(wrighti),* and several species of *Eurycea* are semiaquatic.

Life histories of only a few of the many plethodontid species are known, but the general mode of reproduction of most genera is understood (see Dunn, 1926; Noble, 1927 b, 1931; von Wahlert, 1957). Aquatic larvae are known to occur in *Desmognathus, Leurognathus, Gyrinophilus, Pseudotriton, Stereochilus, Eurycea, Typhlotriton, Manculus, Typhlomolge, Haideotriton,* and *Hemidactylium,* and all have been available for study. *Desmognathus* exhibits considerable interspecific variation in length of the aquatic larval period. According to Organ (1961 a) *D. quadramaculatus* has the longest larval period, and the period is successively shorter in *D. fuscus, D. monticola,* and *D. ochrophaeus.* Young of *D. aeneus* emerge from the egg in a semimetamorphosed condition, with gills, gill slits, nasolabial grooves, eyelids, and a greatly reduced dorsal tail fin (Valentine, 1963 a). Reduction of gills begins immediately, and transformation is completed in less than a week. Finally, Organ (1961 a, 1961 b) has shown that *D. wrighti* has no free living larval stage, and hatchlings lack gills and tail fins.

Most of the aquatic and semiaquatic genera have stream larvae with low dorsal fins, reduced gills, and well developed hind limbs. Pond larvae with high dorsal fins that extend onto the trunk and slowly developing, reduced hind limbs are found in *Hemidactylium* (Blanchard, 1923; Bishop, 1941), *Manculus* (Goin, 1951), and *Stereochilus* (Schwartz and Etheridge, 1954).

Paedogenesis, or retention of larval non-reproductive morphology throughout life, is characteristic of *Typhlomolge, Haideotriton, Gyrinophilus palleucus,* and certain species of *Eurycea (latitans, nana, neotenes, pterophila, troglodytes, tynerensis).*

Terrestrial direct development with no aquatic larval stage is characteristic of *Plethodon, Aneides, Ensatina, Hydromantes, Batrachoseps, Bolitoglossa, Pseudoeurycea, Chiropterotriton,* and *Parvimolge,* and is presumed to occur in the terrestrial genera *Oedipina, Lineatriton,* and *Thorius.* It is likely that *Phaeognathus,* a genus with terrestrial adults (Valentine, 1963 c; Brandon, 1965), also has direct development. It has long been stated as fact that *Hydromantes* and *Oedipus* (= the neotropical genera) are ovoviviparous or viviparous (Dunn, 1926; Noble, 1931). Recently Gorman (1956) has reported that *H. shastae* lays eggs, and has shown that earlier reports of ovoviviparity in the genus are questionable. Peters (1863) stated that *Bolitoglossa adspersa* bears living young, and he was followed by subsequent authors. Nicéforo María (1958), however, found that *B. adspersa* lays eggs. Brame and Wake (1963) reviewed literature reports and showed that there is no evidence of ovoviviparity or viviparity in neotropical salamanders.

Young males of all plethodontids have unilobed testes, but in certain genera an emptied lobe is moved forward and a second lobe appears caudally, separated from the first by a short, slender, nonfunctional region. A new lobe is added in the second, fourth, and sixth years of sexual activity in *Desmognathus,* with the new lobes becoming functional in the third, fifth, and seventh years (Humphrey, 1922; Organ, 1961 a). The maximum number of lobes is five (Humphrey, 1922).

Multiple testes are of common and apparently constant occurrence in old adult males of *Desmognathus, Leurognathus, Phaeognathus, Batrachoseps, Bolitoglossa, Oedipina, Pseudoeurycea, Chiropterotriton, Parvimolge, Lineatriton,* and *Thorius.* Other than in the above genera multiple testes have been encountered only in single specimens of *Typhlotriton spelaeus, Eurycea pterophila,* and *Aneides ferreus.*

Multiple testes may be used with caution as an indicator of relationships, and genera in which the character consistently occurs fall into two groups: (1) *Desmognathus* and its allies, and (2) *Batrachoseps* and the neotropical genera.

The remainder of this report deals primarily with osteological data. Detailed descriptions of the skeleton of *Aneides,* including illustrations of skulls and other features, have been presented previously (Wake, 1963). Original observations concerning osteological characters in additional genera are to be found in many papers, including in particular the following: Baird (1951), Cope (1859, 1866, 1869), Dunn (1926), Emerson (1905), Hansen and Tanner (1958), Hilton (1945 a, 1945 b, 1945 c, 1945 d, 1946, 1947 a, 1948, 1959), Joubert (1961), Kingsbury and Reed (1909), Moore (1900), Monath (1965), Noble (1921), Parker (1877, 1882), Piatt (1935), Reed (1920), Smith (1920), Soler (1950), Taylor (1944), Wiedersheim (1875, 1877), and Wilder (1925). Information presented here is limited to those elements that demonstrate significant intergeneric variation.

ANALYSIS OF VARIATION

Osteological Characters

Premaxilla

Cope (1866) first separated genera with two premaxillae from those in which the bones have fused, and these characters were adopted by most subsequent workers. Dunn (1926) concluded that premaxillae are primitively separated in plethodontids. His conclusion was probably based on the fact that separated premaxillae are the rule in fishes and early amphibians and are present in all members of the primitive salamander families Cryptobranchidae, Hynobiidae, and Ambystomatidae.

In 1943 Grobman reported the appearance during the ontogeny of *Gyrinophilus* of a suture between previously fused premaxillae. Larvae have a single premaxilla, but during metamorphosis a suture forms. In 1959 Grobman noted that a single premaxilla is present in the larvae of *Gyrinophilus, Pseudotriton,* and *Eurycea,* and stated "this may be considered primitive in the Salamandroidea although it is undoubtedly a specialized situation in comparison with the conditions prevailing in the hynobiids and remote ancestral stocks." Grobman suggested that fused premaxillae be regarded as the ancestral condition for these genera, and that fusion be considered less specialized than separation. The condition in *Gyrinophilus* was considered an advance over that of the other genera, in which the premaxillae remain fused.

Martof and Rose (1962) suggested that a single larval premaxilla is the rule in plethodontids, as earlier suggested by Grobman. They examined very small larvae of *Gyrinophilus, Pseudotriton, Eurycea, Desmognathus* and *Leurognathus* and found a single element with no evidence of two centers of ossification. Rose and Bush (1963) accepted the reasoning of Grobman (1959) that a single element is primitive in plethodontids and rejected Dunn's (1926) proposal that paired elements are primitive. They stated that fusion or separation of parts of the larval premaxilla, a single dentigerous rod with two frontal processes, should be considered advanced. Thus *Eurycea,* which usually retains a larval-like structure, was considered more primitive than *Pseudotriton,* in which the frontal processes fuse, and *Gyrinophilus,* in which the premaxillae separate.

Plethodontid larvae of all stages have a single premaxilla which consists of a curved, toothed *pars dentalis,* two tiny palatal processes, and two ascending and posteriorly directed frontal processes (Fig. 1). The latter arise separately and embrace the internasal fontanelle, and in all small larvae are separated for their entire length. This condition has been found in all larvae of *Desmognathus, Leurognathus, Gyrinophilus, Pseudotriton, Stereochilus, Manculus* and *Hemidactylium.* The condition is also common in *Typhlotriton* and *Eurycea,* but exceptional individuals of *E. nana* and *E. neotenes* have frontal processes that fuse posteriorly, behind the fontanelle. A single *Typhlotriton* larva has a single premaxilla with frontal processes that are broadly fused behind the fontanelle. The typical larval condition is found in all *Haideotriton* and *Typhlomolge.* The life history of *Phaeognathus* is unknown, and all remaining genera undergo direct development.

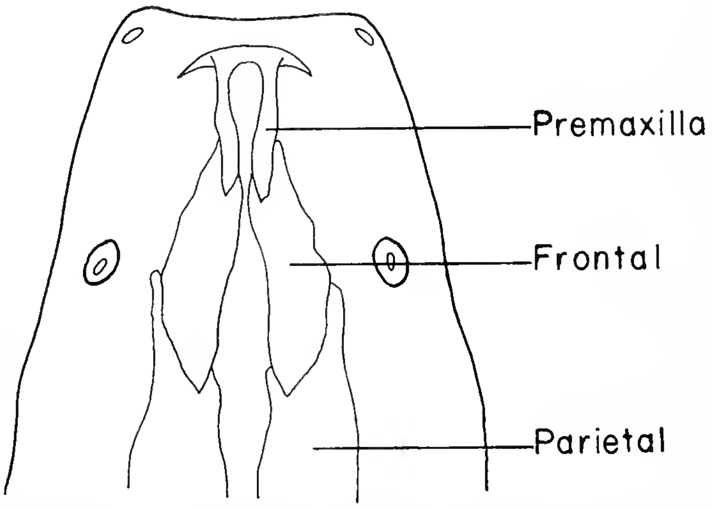


Figure 1. Anterior cranial elements of a small (23.9 mm.) larval *Gyrinophilus danielsi.* Drawn from a cleared and stained individual.

Despite numerous complexities and considerable variation two premaxillary conditions are recognizable in adult plethodontids. In most, a single premaxilla is present and the frontal spines may be separated, fused in front of the fontanelle, fused behind the fontanelle, fused in front of and behind the fontanelle, or fused for their entire length. This general situation is found in *Desmognathus, Leurognathus, Phaeognathus, Pseudotriton, Stereochilus, Eurycea, Manculus, Typhlotriton, Typhlomolge, Haideotriton, Aneides, Bolitoglossa, Oedipina, Pseudoeurycea, Chiropterotriton, Parvimolge, Lineatriton,* and *Thorius.* The other general condition in which two premaxillae are present in adults and separated for their entire lengths is found in *Gyrinophilus, Hemidactylium, Plethodon, Ensatina,* and *Hydromantes.* Grobman (1943) has shown that small *Gyrinophilus* have a single premaxilla, and Martof and Rose (1962) report a single premaxilla in small *Plethodon* and *Hemidac-*

tylium. One element is present in the smallest *Hydromantes* (27.5 mm. standard length) examined, but it is apparent that a suture is forming. Two premaxillae are present in all *Ensatina* examined (as small as 23.1 mm.), with no sign of fusion.

Exceptional conditions are found in some individuals of *Typhlotriton, Chiropterotriton,* and *Thorius.* A tendency toward premaxillary separation seems evident in large, old adults of *Typhlotriton.* Average adults invariably have a single element, but with increasing size the toothed bar narrows on the midline. In one large adult (55.3 mm.) a distinct suture is present and two premaxillae occur. Curiously, there seems also to be a tendency toward fusion of frontal processes in large *Typhlotriton,* although the individual with two premaxillae had separated frontal processes as well. A single adult *Chiropterotriton xolocalcae* has two premaxillae which are joined by a single tooth pedicel, a situation also rarely encountered in *Plethodon,* which normally has separated elements. One adult *Thorius pennatulus* has two distinctly separated premaxillae. Ontogenetic series of these species have not been available for study.

Specialized species of *Batrachoseps* (*B. attenuatus, B. pacificus,* two *species nova*) have a single premaxilla. In *B. attenuatus, B. pacificus,* and one of the new species (Bodfish), the frontal processes arise separately, then fuse almost immediately and remain fused as far as the anterior margin of the fontanelle, where the processes separate and diverge. The processes fall short of the posterior margin of the fontanelle. A small fontanelle, often triangular but sometimes reduced to a tiny circle, is present immediately above the *pars dentalis* and below the point of frontal process fusion. In the other new species (Monterey) eleven of fifteen individuals have the condition discussed above, but the other four have frontal processes that remain separated. The most primitive member of the genus, *B. wrighti,* has a single premaxilla in small stages, but the frontal processes are separated. That there is ontogenetic variation is evident. Two small individuals (21.8 mm., 29.1 mm.) have a single premaxilla. A median depression is present in the toothed bar of slightly larger individuals (32.4 mm.), and at later stages (36.3 mm., 38.3 mm.) the single element of small individuals is separated by a suture into two distinct halves, connected by the pedicel of a single median tooth. As individuals become progressively larger (above 40 mm.), two premaxillae are present with no sign of fusion.

The larval and adult premaxillary conditions must be considered separately if a cogent theory is to be advanced to explain observed facts. In the Ambystomatidae two premaxillae are present in larvae of all genera. Maxillae appear earlier during ontogeny than in the plethodontids, and are moderately well developed before metamorphosis proper is under way. They are present in the permanently larval ambystomatids. In plethodontids maxillae do not form until late in metamorphosis, and no maxillae are present in the permanent larvae. In ambystomatids the premaxillae are attached to the skull proper by means of articulations with the frontals, the vomers, and the maxillae. In plethodontids the premaxilla projects forward from the skull proper, to which it is attached only by the tips of the frontal processes and by a tenuous articulation with the vomers (Fig. 1). Two premaxillae projected anteriorly from the skull proper, lacking lateral articulations, are considerably less rigid than a single structure resulting from fusion at the anterior extremity of the formerly paired structures. I suggest that the premaxillary condition observed in plethodontid larvae is an example of larval evolution, or caenogenesis (see DeBeer, 1958), which has resulted from selection operative at early larval stages of the ancestral stock. The larvae of plethodontids are carnivorous; they seize and manipulate prey by the closing of the premaxilla and dentaries on each other. The stronger the premaxilla, the more efficient would be the feeding process, and individuals having a single stronger structure would probably be favored over those with paired, weaker elements. The attainment of the single larval premaxillary condition has doubtless been of importance in the success of plethodontids.

Metamorphosis is a period of drastic molding and reorganization in plethodontids (Wilder, 1925). During metamorphosis several skeletal elements are lost, others are gained, and the remaining skull elements are extensively remodeled. In considering the evolution of plethodontids it is thus essential that the total metamorphic process be considered apart from the changes that take place in any given element. While this subject is considered in detail elsewhere (see below), it bears directly on the question of premaxillary evolution and is thus raised here.

It has long been customary to assume that one can find a more primitive condition in an earlier rather than a later developmental stage of a given species, and it is apparent that Grobman (1943) and Rose and Bush (1963) have followed this reasoning in their work. Such practices have been decried by DeBeer (1958) who states numerous objections and offers many alternative suggestions to explain commonly encountered phenomena. In the case of the plethodontid premaxilla it is clear that the metamorphic process must be considered apart from the element itself. One must distinguish between a primitive metamorphic pattern, and the presumed primitive nature of a retained larval character.

Metamorphosis in primitive salamanders (hynobiids, ambystomatids) results in paired, separated premaxillae. It is clear that such a condition is the end result of a primitive metamorphic pattern and should be considered primitive *regardless of the condition present in larvae.* Plethodontid larvae may be considered advanced over larvae of other families in the fused condition of their premaxillae. Premaxillary fusion in adult plethodontids is not primitive even though it is the condition of the larvae. There is considerable evidence that the primitive metamorphic pattern is retained in several primitive plethodontids, with resultant premaxillary separation. My interpretation of the events transpiring during metamorphosis in *Gyrinophilus,* for example, is that the primitive metamorphic pattern is retained (Fig. 2). The pattern is similar in *Hemidactylium, Hydromantes, Plethodon,* and presumably *Ensatina.* The metamorphic process is slowed in *Typhlotriton,* and is drawn out over a long period of an organism's life, but the premaxillae of the largest individuals may finally separate. In regard to premaxillae the exceptional *Typhlotriton* can be said to undergo delayed metamorphosis. Additional support is gained from the genus *Batrachoseps.* Four of the five species are specialized and demonstrate numerous paedomorphic tendencies, but the fifth, *B. wrighti,* is less specialized and more primitive. Delayed metamorphosis occurs in *B. wrighti* which results, in old adults, in two premaxillae while the other species never undergo premaxillary metamorphosis.

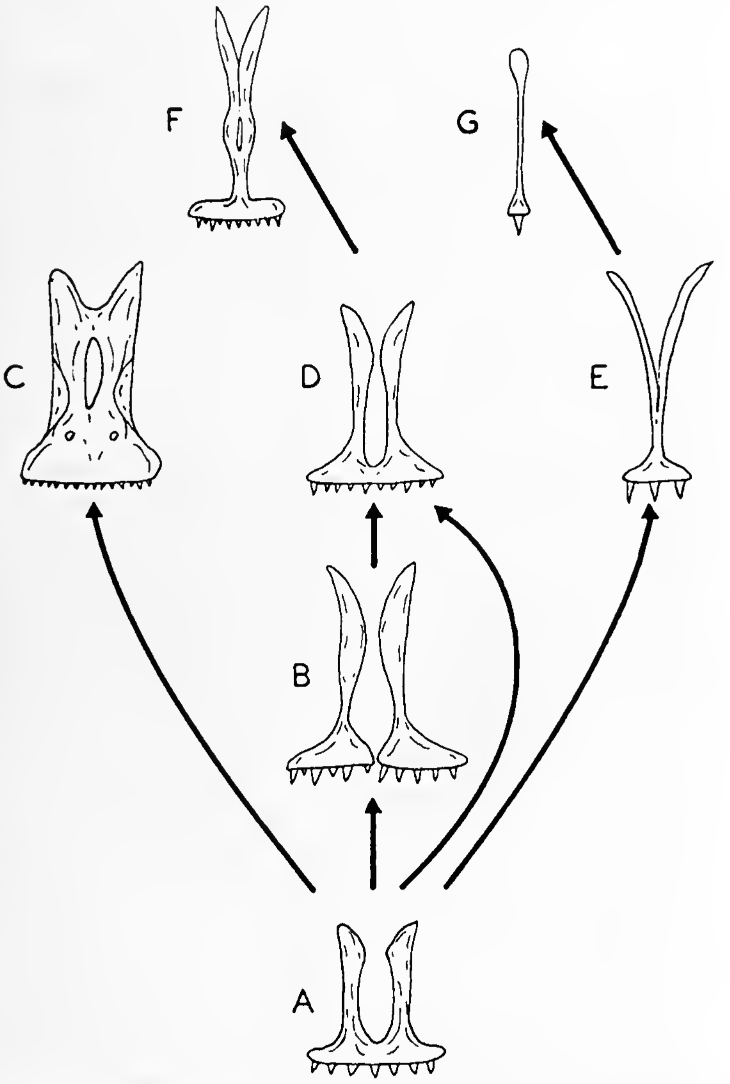


Figure 2. Trends in premaxillary evolution. A. Typical pattern of plethodontid larvae and embryos (*Gyrinophilus danielsi*), B. Adult pattern of primitive genera (*Gyrinophilus danielsi*), C.-G. Adult patterns of advanced genera (C. *Desmognathus monticola,* D. *Eurycea bislineata,* E. *Pseudoeurycea leprosa,* F. *Stereochilus marginatus,* G. *Oedipina parvipes*). Not drawn to scale.

The evidence cited above concerning *Typhlotriton* and *Batrachoseps* suggests that fused premaxillae in adults of these genera (and possibly in *Chiropterotriton* and *Thorius,* see above) is the result of paedomorphosis. Paedomorphosis also accounts for the fused premaxillae in *Typhlomolge, Haideotriton, Gyrinophilus palleucus, Eurycea pterophila, E. nana,* and *E. tynerensis.* It is probable that the fused premaxillae in *Pseudoeurycea, Chiropterotriton, Bolitoglossa, Oedipina, Parvimolge, Lineatriton,* and *Thorius* are due in part to paedomorphosis. All are affected by paedomorphosis in other ways (see below), and the premaxilla is relatively very small in the group. A simplification of parts has taken place in the neotropical genera, however, and it is possible that an evolutionary trend toward simplification has been operative in unison with a trend toward metamorphic delay or failure.

The skulls of *Pseudotriton, Desmognathus, Leurognathus, Phaeognathus, Stereochilus,* and *Aneides* appear to have been secondarily strengthened. All have solidly articulated skulls and all may have fused frontal processes. Fusion of premaxillae in adults of these genera is probably the result of selection in favor of increased strength of skull elements. A similar explanation can be advanced in regard to *Eurycea* and its derivative, *Manculus. Eurycea* may have arisen from an ancestor with a single premaxilla and a solid skull (Fig. 2). Skull weakening in advanced *Eurycea* is apparently a secondary event.

In the Plethodontidae it can be assumed that larval and embryonic premaxillary fusion is the rule. The primitive metamorphic pattern results in two premaxillae. I consider any modification of this primitive metamorphic pattern to represent an evolutionary advance, whether the result of paedomorphic influence or of selective pressures favoring the strengthened premaxilla which results from fusion. In this discussion I have limited the topic to fusion or non-fusion of the toothed portions of the premaxillae. Fusions of the frontal processes occur only in forms in which fusion of the toothed portions has occurred.

Several groups are recognizable on the basis of metamorphic effects on premaxillary structure, and details of their premaxillary anatomy are discussed below. The larval premaxilla is retained in relatively unmodified form in *Typhlomolge* and *Haideotriton.* The primitive metamorphic pattern is retained in *Gyrinophilus, Hemidactylium, Plethodon, Ensatina,* and *Hydromantes.* The final group includes genera that have some modification of the primitive metamorphic pattern, and may be subdivided as follows: (1) *Desmognathus, Leurognathus, Phaeognathus,* (2) *Pseudotriton, Eurycea, Manculus, Typhlotriton,* (3) *Stereochilus,* (4) *Aneides,* (5) *Batrachoseps,* (6) *Bolitoglossa, Oedipina, Pseudoeurycea, Chiropterotriton, Parvimolge, Lineatriton, Thorius.*

The skulls of *Haideotriton* and *Typhlomolge* are strongly depressed and the premaxillae are modified accordingly. The single *pars dentalis* is relatively broader than in larvae, and is a straight structure, posteriorly recurved only at the lateral tips. Frontal processes arise separately and extend almost directly posteriorly with little dorsal rise. The processes are very broad in *Typhlomolge,* narrower in *Haideotriton,* and in both embrace the internasal fontanelle. Frontal processes remain separate in the genera but may articulate behind the fontanelle. Palatal portions are poorly developed.

In *Gyrinophilus, Hemidactylium, Plethodon,* and *Ensatina* frontal processes embrace a moderate to large fontanelle but remain separated. The processes are longest in *Gyrinophilus* where they expand distally and articulate with each other behind the fontanelle. Post-fontanelle expansion is less well developed in the other genera. The processes may articulate posterior to the fontanelle in some species of *Plethodon* (see Wake, 1963), but not in *Hemidactylium* or *Ensatina.* A unique condition is encountered in *Hydromantes* in which the frontal processes are extremely short, especially in the American species. The slender processes abruptly terminate at about the anterior margin of the nasals, well anterior to the posterior end of the fontanelle. In addition the anterior portion of the snout is relatively deep in *Hydromantes* and the frontal processes are almost vertically oriented. The situation in *Hydromantes,* more than any other plethodontid, resembles that encountered in primitive salamander families (Hynobiidae, Ambystomatidae), and may reflect the relative antiquity of the genus and its proximity to the familial ancestral stock. It is not firmly established, however, that short frontal processes are primitive. In the above group palatal processes are generally moderately developed, but the palatal shelf of *Gyrinophilus* is relatively broad.

The premaxillae of *Desmognathus, Leurognathus,* and *Phaeognathus* have a characteristic structure, one not closely approximated by other plethodontids. Perhaps the most diagnostic features are the compactness, the close articulation of the premaxilla with surrounding elements, and the close association of the frontal processes and toothed bar. The skulls of all are depressed, especially *Leurognathus,* and it is impossible to distinguish between *pars dentalis* and *pars frontalis* where the two areas join. The lateral margins of the *pars dentalis* extend posteriorly and a little dorsally and become the lateral margins of either *pars frontalis.* The frontal processes of larvae resemble those of primitive plethodontid genera and have distinct shanks and blades. During ontogeny bone is added to the lateral margins of the shanks and the processes become relatively very broad. The distance across the shanks is only slightly less than the width of the toothed bar (Fig. 2). A small internasal fontanelle is embraced by the frontal processes and is increasingly reduced in size during ontogeny. In old adult *Leurognathus* the fontanelle is reduced to a tiny opening or is entirely closed (Moore, 1899). Frontal processes fuse behind the fontanelle in *Leurognathus, Phaeognathus,* and some *Desmognathus (fuscus, auriculatus, ochrophaeus, monticola),* while in other *Desmognathus (aeneus, ocoee, wrighti)* the processes articulate but do not fuse. The relatively primitive *D. quadramaculatus* has unfused processes for a long time (fused in individuals more than 80 mm.). The posterior tips of the frontal processes in this group of genera are lateral in position, and following fusion the posterior border is concave. The palatal shelves are relatively the broadest and best developed in the family.

Pseudotriton and *Eurycea* illustrate a tendency for fusion of the frontal processes posterior to the fontanelle. In the smallest *Pseudotriton* larva available (17.2 mm.) the frontal processes have already encircled the fontanelle and are in the process of fusing. In more advanced larvae and in all adults the frontal processes are solidly fused. Typical unfused frontal processes are found in *Manculus* and most *Eurycea (tynerensis, longicauda, lucifuga, multiplicata).* In the other *Eurycea* a trend toward fusion of frontal processes is evident. A single

E. nana, a single *E. pterophila,* and all available *E. aquatica* have fused processes. Rose and Bush (1963) report that three of five transforming *E. aquatica* and eleven of twelve adults had fused processes. Wilder (1924) reported that 4.5 per cent of 109 larval *E. bislineata* from Massachusetts had fused frontal processes. All *E. bislineata* larvae examined by me have unfused processes. Rose and Bush (1963) report unfused processes in eleven of twelve *E. bislineata* (size not specified) from Alabama, Mississippi, and Louisiana. My data indicate an ontogenetic trend toward process fusion in the species. Processes are fused in four of six adults (37.3 - 39.5 mm.) from North Carolina, but are separated in the two smallest individuals (36.9, 37.2 mm.). Frontal processes are partially to totally fused in three adults (37.4 - 44.4 mm.) from Indiana, but are not fused in one large adult (42.5 mm.). It is obvious that geographic and ontogenetic variation occurs. An unusual condition is evident in the frontal processes of *Pseudotriton* in that, following fusion, secondary growth occurs and a single process, usually with a bifurcated tip, grows posteriorly. Thus the postfontanelle portion of the frontal processes is large relative to other genera. Palatal shelves range from small *(Manculus)* to moderately large *(Pseudotriton)* in the group. The premaxilla of *Typhlotriton* closely resembles that of *Eurycea. Typhlotriton* may have paired premaxillae, however, and in a sense it joins this group of genera with *Gyrinophilus,* which it resembles in many other features.

Perhaps *Stereochilus* should be grouped with *Pseudotriton, Eurycea,* and *Manculus.* The entire skull of *Stereochilus* is rather compressed and elongate, and the skull elements, including the premaxilla, are modified accordingly. In adults, frontal processes are fused and arise from the *pars dentalis* as a single element. The processes separate at a moderate distance from the toothed bar to encircle the relatively small fontanelle. In small adults the processes completely encircle the fontanelle and articulate with each other posteriorly. The processes are in contact for a considerable distance posteriorly but separate near their tips. In larger adults, the fontanelle is almost completely closed over. The frontal processes are completely fused anterior and posterior to the fontanelle and separate only at the posterior exeremity (Fig. 2). Palatal shelves are moderately large.

Hemidactylium has a larval premaxilla very similar to that of larval *Eurycea.* Adult premaxillae have relatively long toothed portions and broad, stout palatal shelves. In these features they resemble *Eurycea* and related genera. Resemblance to *Plethodon* is superficial, related to premaxillary separation in organisms of roughly similar size.

A single premaxilla occurs in all species of *Aneides,* but in other regards the element resembles the paired premaxillae of *Plethodon* (Wake, 1963). A distinct trend in the direction of increased strength of skull elements is evident in *Aneides,* and is reflected by the premaxilla. A single element appears to represent a specialization within the *Plethodon-Ensatina-Aneides* assemblage. An additional modification of the premaxilla occurs in large adult *A. lugubris,* possibly the most advanced and certainly the most specialized species. The frontal processes are very long, equaling or exceeding those in any other genus, and tend to fuse behind the fontanelle. Secondary bony growth in *lugubris* roofs the fontanelle.

The advanced species of *Batrachoseps* have a peculiar fusion of the frontal processes above the *pars dentalis* but below the fontanelle; this condition is not encountered in any genus discussed so far. The frontal processes are fused from their origin to the fontanelle in *Stereochilus,* but in *Batrachoseps* the processes arise separately, fuse for a very short distance, then separate and diverge posterolaterally around the fontanelle. Such a situation is found elsewhere among plethodontids only in the neotropical genera. In most plethodontids the fontanelle tends to be enclosed on all sides by the frontal processes, and a trend for fusion of the frontal processes posterior to the fontanelle is evident. In *Batrachoseps* and the neotropical genera fusion of the processes occurs in front of the fontanelle, if at all, and the fontanelle tends to be pushed posteriorly in reference to the premaxilla. The processes themselves are relatively shorter (relative to over-all skull dimensions) than in the more primitive genera, and there is a trend toward decrease in the over-all size of the premaxilla.

The neotropical genera resemble the advanced species of *Batrachoseps* in premaxillary structure more closely than do any other plethodontid genera. The most striking difference between the two groups is the great reduction seen in the neotropical species, particularly in the *pars dentalis.* While a general reduction in size of the premaxilla has taken place in *Batrachoseps,* the reduction is most evident in the palatal and frontal processes, and the *pars dentalis* remains a relatively large structure. In the neotropical species the *pars dentalis* is obviously very shortened relative to the total size of the premaxilla. This character separates the neotropical genera from all other plethodontids. Palatal processes tend to be poorly developed or absent in the entire group.

The *pars dentalis* is always relatively small in the neotropical genera, but in specialized species of several genera *(Chiropterotriton, Bolitoglossa, Oedipina)* and in all *Thorius* the portion is extremely reduced. The extreme is reached in *O. parvipes* in which the length is as great as the breadth and the structure is barely large enough to support a single tooth pedicel (Fig. 2).

In all *Parvimolge* examined the frontal processes arise separately and remain separated for their entire length. In all other neotropical genera at least some fusion is present.

Pseudoeurycea normally has separated frontal processes, but a single *P. leprosa* has processes that arise separately, then fuse, and finally separate to diverge at the fontanelle. In *P. smithi* the processes arise separately in small individuals, but are fused from the *pars dentalis* to the fontanelle in large adults (Fig. 2).

Frontal processes arise and remain separated in all *Chiropterotriton* examined with the exception of the specialized *C. abscondens* and *C. nasalis*. The processes of *abscondens* and *nasalis* have a common origin and remain fused until the fontanelle is reached at which point they separate and diverge.

Frontal processes are solidly fused from their origin on the *pars dentalis* to the somewhat posteriorly placed fontanelle in *Lineatriton*. At the anterior margin of the fontanelle the processes separate. The fontanelle is very narrow anteriorly, and the processes remain very close for about one-half the distance from the point of separation to the terminus. Most of the fontanelle is located posteriorly and is bounded by the anterior margins of the frontals.

The *pars dentalis* of *Thorius* is very small but gives rise to paired, extremely slender frontal processes. In most individuals the processes arise separately and remain separated for about two-thirds of their length before diverging around the posteriorly placed fontanelle. The processes may be fused for short distances in front of the fontanelle in *T. pulmonaris* and *T. macdougalli*.

The frontal processes of most *Bolitoglossa* are separated for their entire lengths, and are relatively long and well developed. In some species *(robusta, borburata)* the processes embrace the fontanelle, and are rather broadly expanded posterior to the fontanelle. In others the processes may arise separately, fuse at a point, then diverge around the fontanelle *(adspersa, orestes, savagei, subpalmata)*.

The most specialized premaxillary conditions are achieved in the genus *Oedipina*. The fontanelle has moved posteriad in reference to the premaxilla, and only the extreme anterior margin of the fontanelle is formed by the frontal processes. It is instructive to follow the ontogenetic changes in *O. poelzi*. In juveniles the frontal processes arise separately and remain separated. The processes are very close to each other for most of their length and diverge slightly only near the terminus. In small adult *O. poelzi* the processes are fused from their origin for about one-third of their length. The processes of old adults are fused from their origins for from one-half to three-fourths of their length. In general the frontal processes in all *Oedipina* are fused for one-third to three-fourths of their length, less in young and more in old individuals. *O. parvipes* illustrates the extreme condition in which a single, totally undivided frontal process arises from the midline of the *pars dentalis* and proceeds posteriorly to the anterior margin of the fontanelle, where it is only slightly expanded (Fig. 2).

In summary, primitive premaxillae that separate relatively early in ontogeny are found in five relatively primitive genera of plethodontids, and in the most primitive species of the advanced *Batrachoseps*. Premaxillary fusion occurs in forms with strengthened skulls; fusion thus may either be the result of a strengthening adaptation in the species, or of derivation from a stock in which such an adaptation had occurred previously. Secondary fusions of the frontal processes also occur in some of these forms. Fusions related to skull strengthening have arisen separately in groups containing the following genera:

1. *Pseudotriton, Eurycea, Manculus, Typhlotriton, Stereochilus.*
2. *Aneides.*
3. *Desmognathus, Leurognathus, Phaeognathus.*

Premaxillary fusion is characteristic of paedomorphic forms (retention of the larval premaxilla). It is difficult to trace the parallelism, but fusion must have occurred at least as many as four times:

1. *Gyrinophilus palleucus.*
2. *Typhlomolge, Haideotriton,* and paedomorphic species of *Eurycea.*
3. Neotropical genera.
4. Advanced species of *Batrachoseps.*

My ideas concerning morphological trends and relationships of premaxillary structure are illustrated in Figure 2. On the basis of total premaxillary structure it is possible to place plethodontid genera in the following groups:

1. *Gyrinophilus, Pseudotriton, Eurycea, Manculus, Typhlotriton, Typhlomolge, Haideotriton, Stereochilus, Hemidactylium.*

2. *Hydromantes.*
3. *Plethodon, Ensatina, Aneides.*
4. *Desmognathus, Leurognathus, Phaeognathus.*
5. *Batrachoseps, Pseudoeurycea, Chiropterotriton, Parvimolge, Lineatriton, Thorius, Bolitoglossa, Oedipina.*

It is significant that each of the above groups except 4 has at least one genus that includes species with the proposed primitive condition—unfused premaxillae. The fossil relative of *Desmognathus* and allies, *Prodesmodon,* had unfused premaxillae (Estes, 1964); all modern genera of Group 4 have greatly strengthened skulls and it is likely that the condition in *Prodesmodon* was primitive.

Maxilla

Facial lobes arise from the second quarter (from anterior) of the maxillary *pars dentalis* in most plethodontid genera, and the bulk of each lobe is anterior to the midpoint of the maxilla. The lobes of *Batrachoseps* arise from the anterior one-third of the *pars dentalis,* and the structures are well in advance of the midpoint. This forward movement is greater than in any other plethodontid, and is probably related to the general shortening of the snout characteristic of the genus. No obvious anterior movement of the lobes is seen in other species with greatly shortened snouts *(e.g., Bolitoglossa orestes).* The only other genera in which the anterior margins of the facial lobes approach the anterior tip of the *pars dentalis* are *Desmognathus, Leurognathus,* and *Phaeognathus,* in which the lobes are very large and extend posteriorly beyond the midpoint of the element.

Facial lobes of the remaining genera arise well posterior to the anterior tips of the maxillae. The lobes are primarily anterior to the midpoint of the *pars dentalis* and generally terminate anterior to that point in *Gyrinophilus, Pseudotriton, Stereochilus, Eurycea, Manculus, Typhlotriton,* and *Hemidactylium.* The lobes are of moderate size in most of these, but are relatively small in *Eurycea* and *Manculus.* In *Plethodon, Ensatina* and *Aneides* the lobes tend to arise from the central one-third of the *pars dentalis,* and usually extend past the midpoint. The lobes are relatively small in *Ensatina,* larger in *Plethodon,* and largest in *Aneides. Hydromantes* has a moderate-sized facial lobe lying anteriorly and terminating at about the midpoint of the maxilla. The relatively small facial lobes of the neotropical genera terminate at about the midpoint of the *pars dentalis.*

Desmognathus, Leurognathus, and *Phaeognathus* have greatly enlarged facial lobes. The genera lack prefrontals and the space normally occupied by the prefrontals has been invaded by the maxillae. Similar instances of bones enlarging into areas vacated by other elements have been discussed by Parrington (1956). The nasals are very small in these genera; the result of maxillary enlargement is that the facial lobes greatly exceed the nasals in size, a situation not found elsewhere among the plethodontids.

In primitive salamander families (Hynobiidae, Ambystomatidae) facial lobes arise from the anterior portion of the *pars dentalis* and terminate before the mid-point. The moderate-sized elements in a pre-midpoint position encountered in *Gyrinophilus* and others are generalized, and probably resemble the ancestral condition. The conditions in *Batrachoseps* (anterior movement), *Desmognathus* and its allies (enlarged size with very broad bases), and *Plethodon* and its allies (posterior movement) appear to be derived, specialized situations.

Nasals articulate firmly and extensively with the *pars facialis* of the maxillae only in *Desmognathus, Leurognathus, Phaeognathus,* and *Aneides lugubris.* Moderate articulation is found in *Gyrinophilus, Typhlotriton,* and *Stereochilus,* and rather limited articulations are found in a number of genera *(Pseudotriton, Eurycea, Plethodon, Aneides, Hydromantes, Batrachoseps, Bolitoglossa, Pseudoeurycea, Chiropterotriton, Parvimolge, Lineatriton).* In many of these latter genera articulation is limited, and may consist simply of a meeting at a single point. Primitively the space between the nasals and the maxillae is occupied by prefrontals, lacrimals, or both (Ambystomatidae, Hynobiidae), and extensive articulation is a specialized condition. In adult *Gyrinophilus,* nasals and maxillae are in contact, but prefrontals extend to the anterior margin of the nasals below the articulation. Nasals usually do not articulate with the maxillae in *Pseudotriton,* and prefrontals extend between the elements to the anterior margins of the nasals. This situation is also encountered in some *Eurycea,* and in *Manculus, Typhlotriton, Hemidactylium,* most *Plethodon,* and some *Aneides* and *Ensatina;* it is probably close to the ancestral plethodontid condition.

The maxillae are long, extending beyond the posterior margins of the eyes in *Desmognathus, Leurognathus, Phaeognathus, Stereochilus,* and *Typhlotriton,* and terminating at about the posterior margins of the eyes in some *Bolitoglossa (e.g., mexicana).* Maxillae are shorter in other genera and terminate between the centers and posterior margins of the eyes. In primitive salamanders (Hynobiidae, Ambystomatidae) the standard condition is elongate maxillae which extend beyond the eyes. The elongate condition in plethodontids may be a reflection of this ancestral pattern.

A process arises on the inner margin near the tip of each long *pars dentalis* of *Phaeognathus* and extends posteromedially toward the quadrate, terminating a short distance before the quadrate is reached. This process is large, stout and expanded, and has grown in the direction of the jugal ligaments, which are very short, dorsoventrally expanded and stout. Precursors of the process are evident as tiny projections extending out into the jugal ligaments in *Desmognathus* and *Leurognathus*. It is well known that osseous processes often develop at tension points, and the development of the processes in all three genera, and particularly in *Phaeognathus,* is an indication of the relatively great tension in the jugal ligaments and of the strength and rigidity of the skulls. The skull partially raises to open the mouth in these three genera, a unique situation in urodeles, and the development of processes is doubtless related to the new tensions resulting from this drastic functional modification.

Desmognathus, Leurognathus, and *Phaeognathus* have greatly enlarged palatal shelves that are broadly overlapped by the vomers. The shelves are considerably larger than in any other genus, and are approached in width only by *Stereochilus. Gyrinophilus* and *Pseudotriton* resemble *Stereochilus,* but have relatively narrower shelves. Palatal portions of the maxillae of all other genera are narrower than in the above genera. The shelves are subject to considerable ontogenetic and interspecific variation, however, and in very large adults of several genera *(e.g., Aneides, Plethodon)* may be relatively broad. Primitive salamanders seem to have relatively narrow palatal shelves, but broad shelves are found only in relatively primitive plethodontids. Most specialized and advanced plethodontids, such as the neotropical genera, have narrow palatal shelves.

Several unique maxillary specializations are encountered in the genus *Aneides*. These will be discussed more fully in a forthcoming paper (see also Wake, 1960; 1963).

The American species of *Hydromantes (brunus, platycephalus, shastae)* have high, sharp-pointed facial lobes with relatively narrow bases, while the European species *(genei, italicus)* have low, rounded, broad-based lobes.

As maxillae appear during metamorphosis, they are, of course, absent from the paedogenetic groups.

On the basis of total maxillary structure it is apparent that the plethodontid genera fall into two major groups; the first contains the genera *Desmognathus, Leurognathus,* and *Phaeognathus,* the second contains the remaining genera.

Septomaxilla

Small paired septomaxillae are primitively present in plethodontids but are absent in some advanced groups and in those species which fail to complete metamorphosis *(Typhlomolge, Haideotriton, Gyrinophilus palleucus,* and paedogenetic *Eurycea).*

Septomaxillae are greatly reduced in *Desmognathus, Leurognathus,* and *Phaeognathus,* and appear as tiny crescentic ossifications with relatively great dorsoventral dimensions. Maxillae and nasals are well separated from the septomaxillae. Other temperate genera have relatively large septomaxillae, and the bones are particularly well developed in *Hemidactylium, Plethodon, Ensatina,* and *Batrachoseps.*

In *Gyrinophilus, Pseudotriton, Stereochilus, Eurycea, Manculus, Typhlotriton,* and *Hemidactylium* the septomaxillae are particularly well separated from the maxillary facial lobes, with the least separation in *Hemidactylium*. Septomaxillae may be slightly covered by lateral portions of the nasals in these genera.

Maxillary facial lobes overlap the septomaxillae slightly to considerably in *Plethodon,* and extensively overlap the bones in *Aneides*. Septomaxillae are well separated from the facial lobes in *Ensatina,* but in *Ensatina* and in *A. aeneus* specialized lateral nasal processes may overlap the septomaxillae.

Maxillary facial lobes tend to overlap slightly or just contact the posterior margins of the septomaxillae of *Hydromantes,* but extensively overlap the septomaxillae of *Batrachoseps.*

Septomaxillae are of rather irregular occurrence in the neotropical genera, but have been observed in at least some individuals of all genera. There is a well marked evolutionary trend toward reduction and loss of the bones in these genera. When present the septomaxillae are small and well separated from the maxillary facial lobes and the nasals. Septomaxillae are best developed in some species of *Chiropterotriton,* and Rabb (1956) stated that presence of septomaxillae distinguished *Chiropterotriton* from *Pseudoeurycea.* In a later paper Rabb (1960) wrote that septomaxillae are present only in those species north of the Isthmus of Tehuantepec, but my observations conflict somewhat with his. The bones are present in the following species (N=north of Isthmus; S=south): *C. arboreus* (N), *C. bromeliacia* (S), *C. chiropterus* (N), *C.*

multidentatus (N), and *C. priscus* (N). Septomaxillae are absent in: *C. abscondens* (S), *C. dimidiatus* (N), *C. nasalis* (S), and *C. xolocalcae* (S).

Septomaxillae, not previously reported in *Pseudoeurycea,* are present in some individuals of *P. cephalicus* and *P. werleri,* and Rabb *(in. litt.)* says the bones occur in western populations of *P. leprosa.* Very small septomaxillae are present in *Parvimolge townsendi,* but the bones are absent in *P. richardi.* Septomaxillae are reduced to tiny splinters of bone in *Lineatriton. Bolitoglossa* normally lacks septomaxillae, but small remnants are present on either side of one *B. rufescens,* on one side of another, and on one side each in one individual each of *B. mexicana, B. platydactyla,* and *B. rufescens.* Small septomaxillae are present in some *Oedipina inusitata,* but are absent in other species. Septomaxillae are absent in most *Thorius,* but are present on one side in one *T. pennatulus.* Hilton (1946 b) reported some indication of septomaxillae in the same species.

Generally septomaxillae are well developed in primitive plethodontids. The bones are either reduced or lost in three separate evolutionary lines: (1) *Desmognathus* and its allies (always present, but reduced); (2) the paedogenetic species (absent because species fail to metamorphose); (3) the neotropical species (either true evolutionary reduction and loss or the result of paedomorphosis).

Nasal

The nasals of plethodontids are subject to considerable interspecific and intergeneric variation, but it is difficult to group genera on the basis of nasal structure. The primitive nasal condition is probably close to that seen in *Gyrinophilus, Plethodon,* and other genera in which relatively large nasals only slightly overlap the frontal processes and usually only slightly, if at all, articulate with the maxillae. The bones are somewhat variable in shape, but are usually quadrangular or broadly triangular. Anterior borders of the bones slope posterolaterally. Posterior margins are irregular, but often terminate in poorly to well defined points. Similar conditions are encountered in the primitive Ambystomatidae. Since nasals appear during metamorphosis they are absent in the paedogenetic species. Martof and Rose (1962) report the appearance of nasals earlier in the ontogeny of *Pseudotriton* than *Gyrinophilus.* The elements also appear relatively early in *Eurycea,* at a stage approximating that of *Pseudotriton.* Nasals of *Desmognathus* and *Leurognathus* appear late during metamorphosis.

Nasals in *Desmognathus, Leurognathus,* and *Phaeognathus* are small and narrow, with a characteristic shield-like shape. The nasals are much smaller than the maxillary facial lobes and slightly overlap the premaxillary frontal processes. Lateral portions of the nasals are in very close contact with the maxillary facial lobes.

Pseudotriton adults have nasals that broadly overlap the premaxillary frontal processes and may meet in the midline. Grobman (1959) stated that nasals develop in contact during metamorphosis and tend to separate during ontogeny; my observations conflict with his and support Martof and Rose (1962) who said in regard to the nasals "they are closer in adults than in earlier stages." Examination of eight cleared and stained *P. ruber* ranging in size from 44.8 to 75.6 mm. indicates that nasals arise far apart and tend to grow slightly mediad during ontogeny. Only one individual (73.0 mm.) had the nasals in median contact. Grobman (1959) considered the *Pseudotriton* condition to be primitive for the family, but such a situation is not seen in more primitive families. Nasals are in contact medially in hynobiids, but the bones are distinctly different from those of *Pseudotriton* and are overlapped by the premaxillary frontal processes. Recent work by Lebednika (1964) indicates that medial portions of the nasals of hynobiids represent vestiges of the postfrontal bones of fishes. No evidence of postfrontal contribution to the nasals of plethodontids was found, and the condition in *Pseudotriton* is probably specialized. Skulls of *Pseudotriton* are relatively solid, rigid structures; secondary medial growth of the nasals is clearly related to a strengthening trend.

A parallel to the condition in *Pseudotriton* is seen in large *Ensatina,* and to a lesser extent in *Gyrinophilus.* The nasals undergo medial growth and overlap the frontal processes. Similar, but less extensive, medial growth is encountered in other genera as well.

All anterior elements of *Manculus* are reduced, and those of *Thorius* are very small and variably shaped. The strikingly reduced nasals of *Thorius* are in the form of slender crescents lying far posteriorly at the anterior margins of the orbits. Some of the large-nostriled species of *Chiropterotriton (e.g., nasalis)* have tiny, crescentic nasals.

Prefrontal

Prefrontals are primitively present in plethodontids, but since the bones appear during metamorphosis they are absent in *Typhlomolge, Haideotriton,* and the paedogenetic species of *Eurycea* and

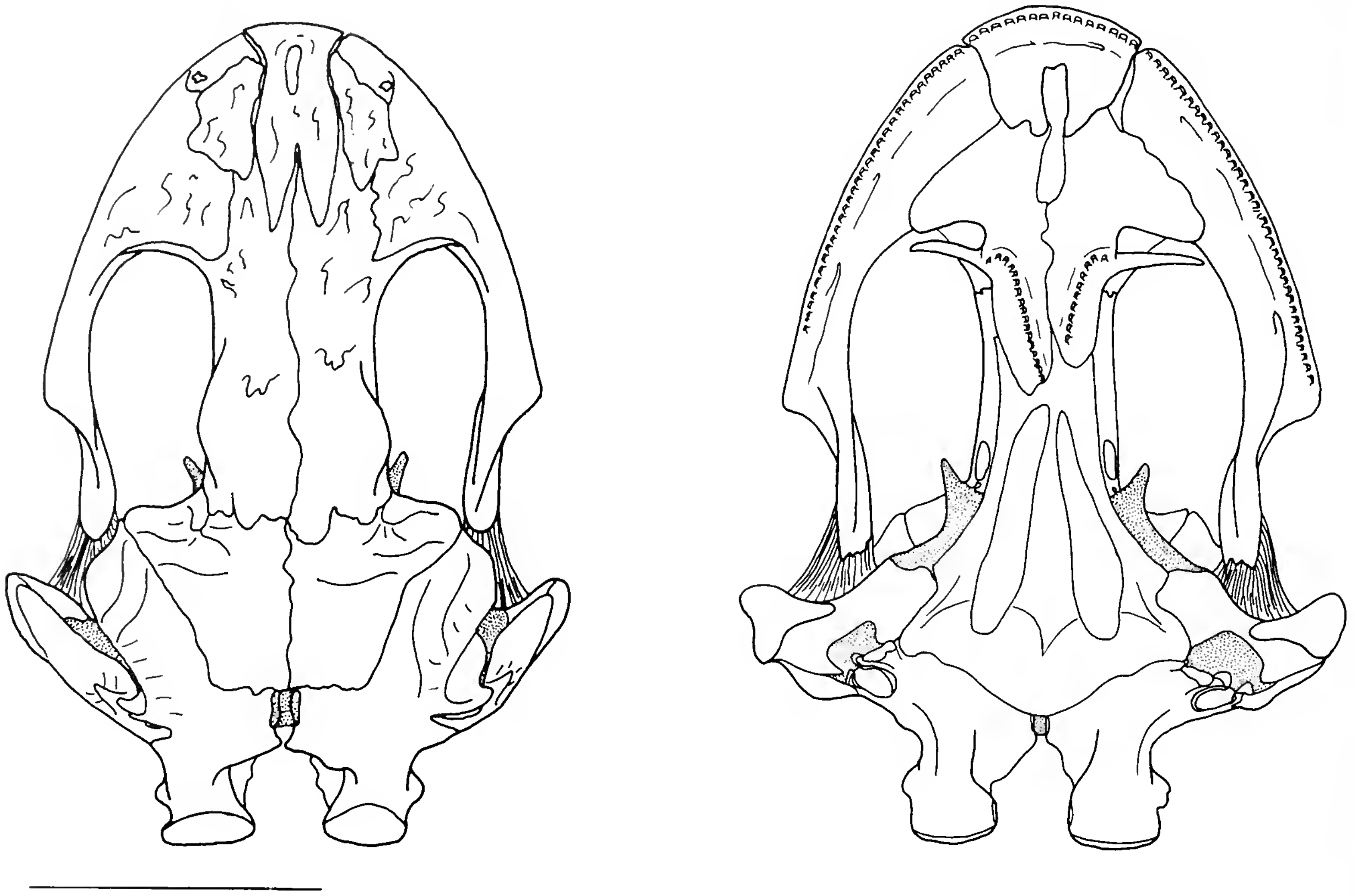


Figure 3. Dorsal and ventral views of skull of adult female *Phaeognathus hubrichti.* Cartilage stippled. Jugal ligaments lined. Posterior patch of vomerine teeth outlined. Line equals 5 mm.

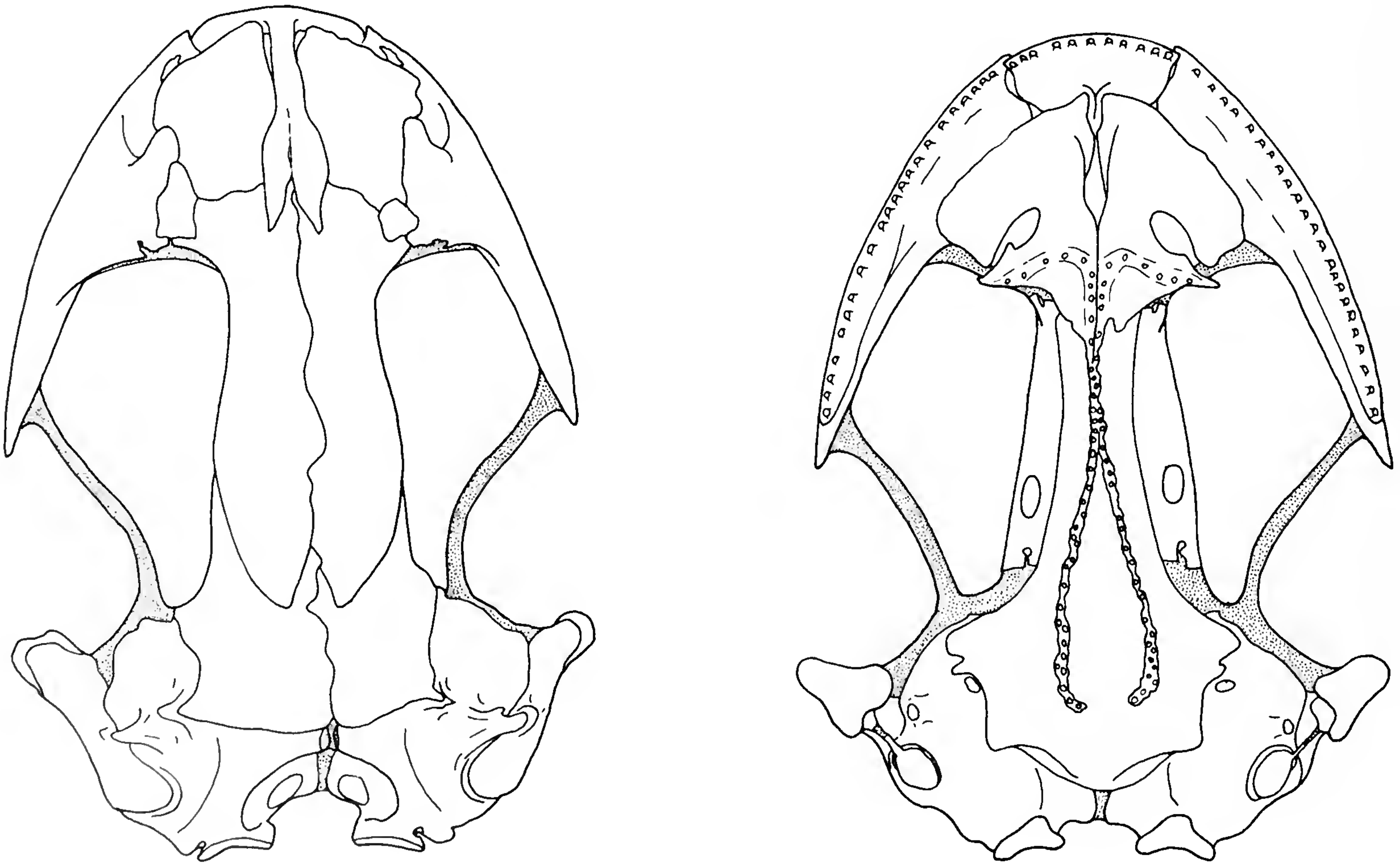


Figure 4. Dorsal and ventral views of skull of adult male *Stereochilus marginatum.* Cartilage stippled. Line equals 5 mm.

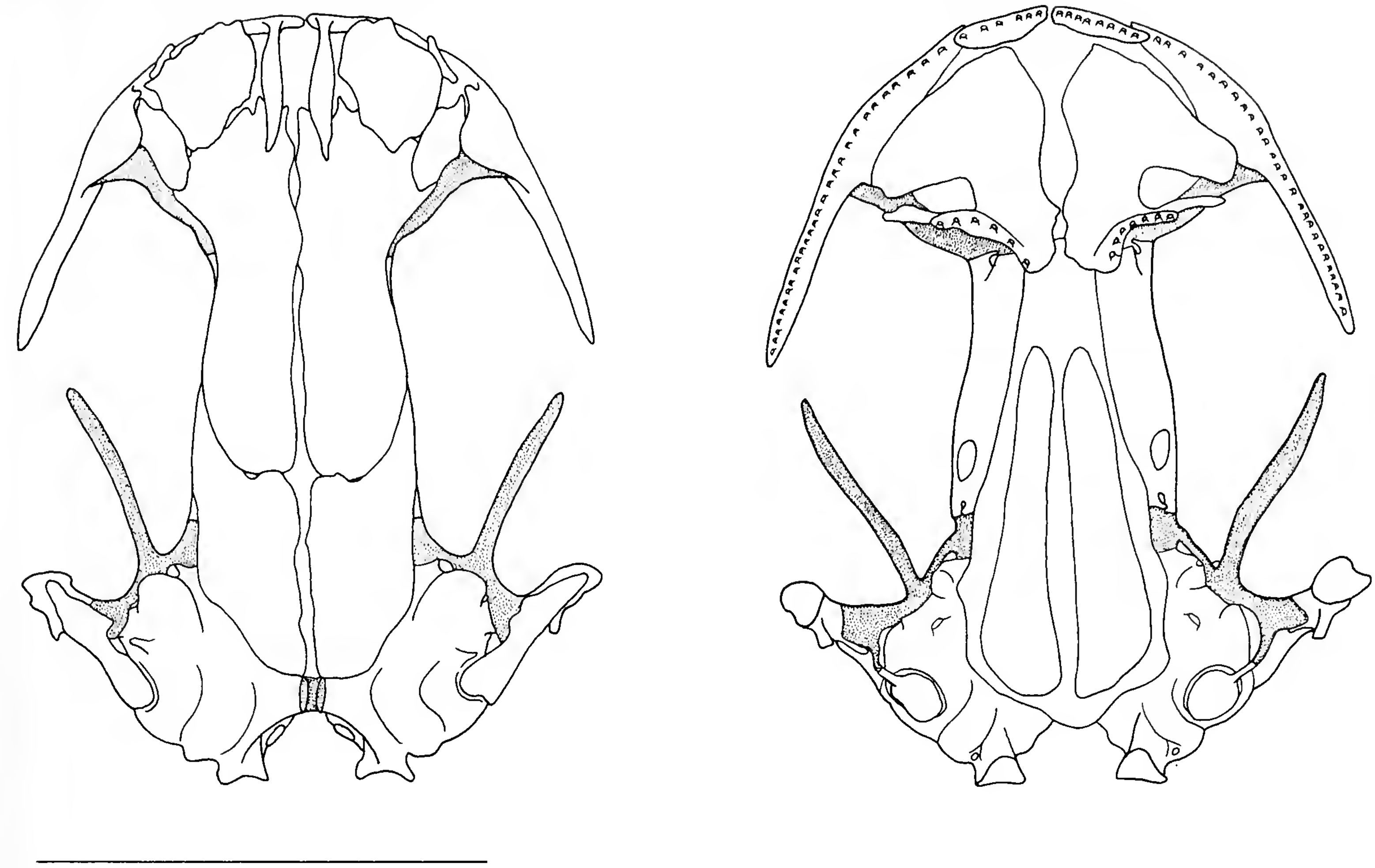


Figure 5. Dorsal and ventral views of skull of adult male *Plethodon jordani*. Cartilage stippled. Posterior patch of vomerine teeth outlined. Line equals 5 mm.

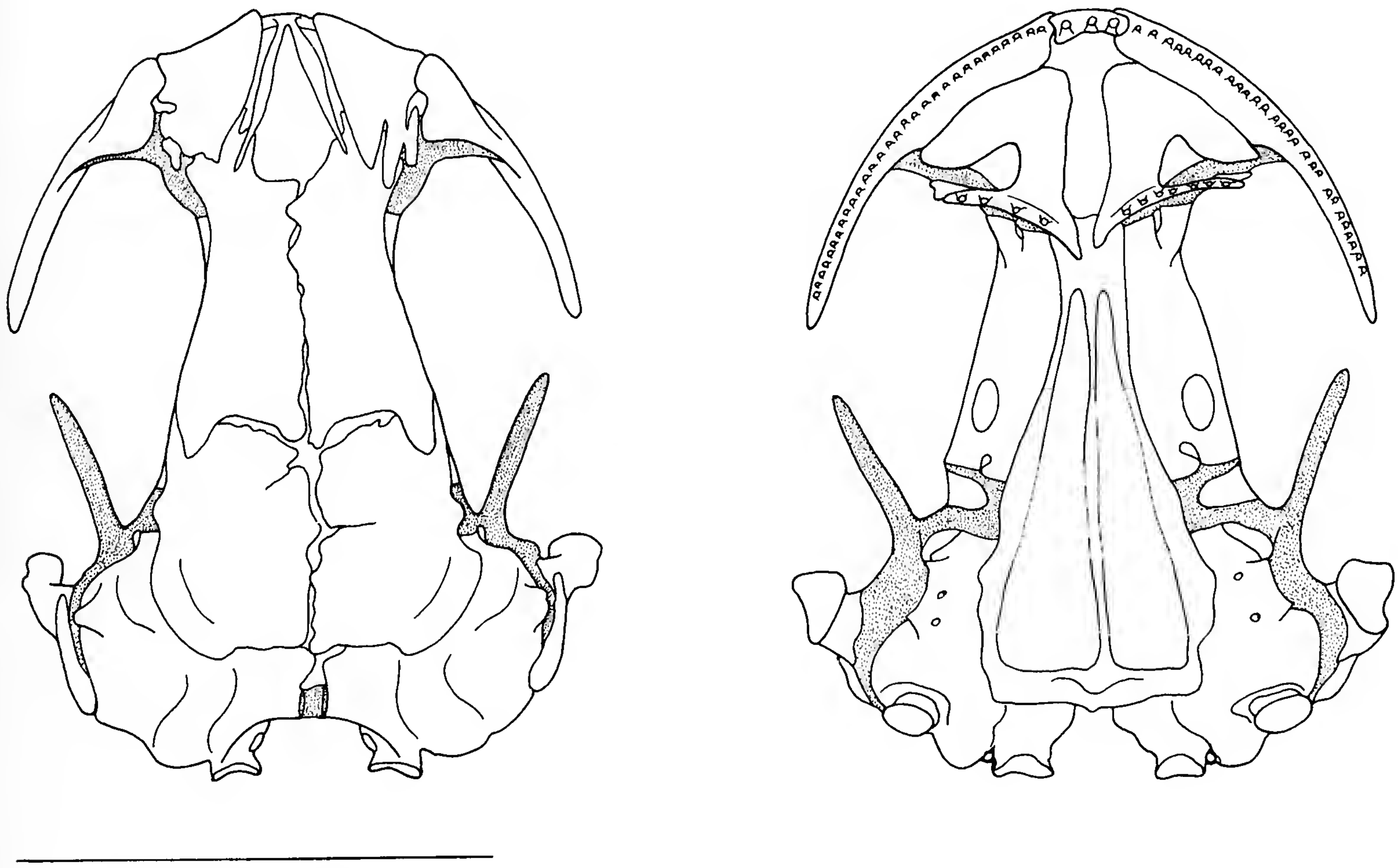


Figure 6. Dorsal and ventral views of skull of adult female *Bolitoglossa subpalmata*. Cartilage stippled. Posterior patch of vomerine teeth outlined. Line equals 5 mm.

Gyrinophilus. The bones also have been lost in other genera including *Desmognathus, Leurognathus,* and *Phaeognathus,* in which the prefrontal area is invaded by the maxillary facial lobes and the expanded anterior portions of the frontals.

All *Hydromantes* lack prefrontals; the prefrontal region is invaded by relatively large nasals and, in the American species, by enlarged maxillary facial lobes.

Prefrontal loss in *Batrachoseps* and various neotropical genera is associated with trends toward reduction and simplification of general skull structure as well as paedomorphic trends. The bones are absent in all species of *Batrachoseps* except *B. wrighti*. Prefrontals are absent in small *B. wrighti,* but appear during ontogeny and are present as very small dots of ossified tissue in adults over 45 mm. (large for the species). Enlarged nasals occupy some of the prefrontal region in *Batrachoseps.*

Among the neotropical genera prefrontals are present in all *Pseudoeurycea* (moderate-sized), *Parvimolge* (small), and *Lineatriton* (small). Prefrontals are inter- and intra-specifically variable in *Thorius,* and are represented by tiny slivers of bone in some, but appear to have fused with the nasals in others.

Rabb (1960) stated that prefrontals are present in species of *Chiropterotriton* which occur north of the Isthmus of Tehuantepec, but absent in species south of the Isthmus. Prefrontals are present in all northern species that I have examined, but are also present in the southern *C. nasalis,* and present or absent in the southern *C. abscondens*. The bones are absent in the southern *C. bromeliacia* and *C. xolocalcae*.

Prefrontals are present in primitive *Bolitoglossa,* but in a number of advanced species they may be lost *(colonnea, orestes, robusta),* or fused with the nasals *(adspersa, cerroensis)*. Hansen and Tanner (1958) report greatly reduced prefrontals in *B. occidentalis* and *B. rufescens,* but the bones are absent in my material. Intraspecific variation occurs in some species *(savagei, subpalmata),* and the bones may either fuse with the nasals or remain discrete.

Prefrontals are absent in all species of *Oedipina,* and the nasals and maxillary facial lobes have grown into the vacated area.

The remaining plethodontid genera have relatively well developed prefrontals. The highest development is achieved in *Aneides,* in which the specialized members of the *lugubris* group have very large prefrontals which interlock with the maxillary facial lobes (see Wake, 1963).

Route of the Nasolacrimal Duct

Eye glands are associated with the lower eyelids of metamorphosed salamanders, and the secretions of the glands are conducted to the external nares by the nasolacrimal ducts (Noble, 1931). The secretion is apparently an eye lubricant, and the excess drains through the ducts (Noble, 1931). Since eyelids, eye glands, and nasolacrimal ducts develop during or just before metamorphosis, all are absent in *Typhlomolge, Haideotriton,* and the paedogenetic species of *Gyrinophilus* and *Eurycea.*

Nasolacrimal ducts of hynobiid and primitive ambystomatid *(Dicamptodon, Rhyacotriton)* salamanders pass through horizontally oriented foramina in the lacrimal bones, elongate, longitudinally oriented elements located between the nasals and the maxillary facial lobes. Near their anterior ends the ducts pass through evacuations or grooves in the septomaxillae, and open in the nasal cavities. Relations of the ducts to bony elements have changed in advanced ambystomatids, in salamandrids, and in plethodontids. Larsen (1963) has suggested that intercalation of a lacrimal between the prefrontal and the maxilla reduces stability of the maxilla on the neurocranium and that the lacrimals have been lost in higher groups due to selective pressures acting to fix firmly the maxillae to surrounding elements. Lacrimal loss has led to relatively extensive prefrontal-maxillary articulations in primitive plethodontids. In addition the prefrontals of genera such as *Ambystoma* have taken over the function of the lacrimals, and the ducts pass through the prefrontals.

The primitive nasolacrimal duct route of plethodontids is best seen in *Gyrinophilus,* in which the ducts extend from the eyes through the tissue of the *canthus rostralis* to the anterior ends of the nasal capsules. Anteriorly the ducts proceed ventrad and open in the nasal cavities. The ducts leave no or only slight impressions on the underlying bones. Similar routes are followed in *Stereochilus* and *Typhlotriton.*

Ducts of the remaining plethodontid genera have wholly or in part abandoned the primitive dorsal integumentary routes for routes closer to the cranial elements. Each prefrontal of *Pseudotriton* has a narrow anterolateral projection, similar to that of *Gyrinophilus,* which extends between or slightly ventral to the maxillary facial lobe and the nasal. The prefrontals differ, however, in that those of *Pseudotriton* have tips which are slightly to considerably evacuated. In addition each prefrontal has a distinct, lengthwise dorsal groove or trough. Nasolacrimal ducts pass from the eyelids over the prefrontals and along the depressions or grooves to the anterior margins of the prefrontals. The ducts proceed ventrad through foramina, the walls of which are formed by the evacuated prefrontal tips on three sides, and by integument on the fourth.

Paths of the ducts in *Plethodon, Ensatina,* and *Aneides* (except *A. lugubris*) are similar to those in *Pseudotriton*. Relatively large prefrontals, evacuated anteriorly, extend from the orbits nearly to the nares; the ducts extend dorsally and anteriad across the bones, then ventrad through the anterior evacuations. The ducts pass posterior and then ventral to characteristic lateral nasal lobes in *Ensatina,* and the foramina are formed of nasal and prefrontal material. An extensive maxilla-nasal articulation effectively separates the prefrontals from the narial region in *Aneides lugubris*. The anterior cranial elements of the species are covered with dense osseous accretions, and the ducts enter foramina running lengthwise in the accretions and proceed to the anterior ends of the prefrontals. There the ducts enter grooves in the thickened lateral margins of the nasals, and enter the nasal cavities at the anterior ends of the bones.

The prefrontals in *Eurycea* and *Manculus* are moderate to small and lie farther back than in the genera discussed above. The bones are primarily associated with the anterior orbital margins, and, although they extend between the maxillae and nasals, are walled off from the osseous nasal apertures by lateral processes of the nasals. In both genera the prefrontals have pronounced anterior concavities, and, in some *Eurycea,* distinct laterally placed foramina. The concavities and/or foramina may be associated with small lateral concavities of the nasals, mid-dorsal concavities of the maxillary facial lobes, or both (see also Wilder, 1925). The nasolacrimal ducts extend across the prefrontals, and, in some instances, dorsal to the posterior portions of the facial lobes, before entering the foramina. The point at which the ducts run ventrad is relatively posterior to that found in *Pseudotriton*.

Processes of the nasals articulate with the maxillary facial lobes in *Hemidactylium,* but the prefrontals are similar to those of *Eurycea* and bear pronounced anterolateral concavities. The ducts pass over the prefrontals, through the prefrontal concavities, then under lateral nasal processes.

Prefrontals play no role in the route of the nasolacrimal ducts in the remaining genera of middle lattitudes. Prefrontals of *Batrachoseps wrighti* are extremely reduced, and do not extend between the nasals and maxillae. The ducts pass across the maxillary facial lobes and through foramina in the interspace between the maxillae and nasals. Duct routes are similar in other species of *Batrachoseps,* but small posterolateral nasal concavities are usually associated with foramina which are otherwise integumentary.

Prefrontals are absent in *Hydromantes,* and the ducts extend across the maxillary facial lobes, then through foramina formed by concavities in the posterolateral boundaries of the nasals and facial lobes.

In *Pseudoeurycea, Parvimolge, Lineatriton,* and primitive species of *Chiropterotriton* and *Bolitoglossa* the ducts pass dorsally over the prefrontals and enter foramina formed by anterior prefrontal, dorsal maxillary, and posterolateral nasal concavities. Nasals are reduced in size in *C. nasalis,* and the prefrontals bear distinct, fully enclosed foramina on their anterior extremities. In those *Chiropterotriton* and *Bolitoglossa* which have lost prefrontals, and in all *Oedipina,* the nasals and maxillae usually articulate extensively, and the ducts pass dorsad initially, then move ventrad through concavities in the posterolateral nasal margins. Slightly to moderately concave dorsal margins of the maxillary facial lobes also contribute to the foramina.

An extreme of the trend described above is reached in *Thorius,* in which the prefrontals are greatly reduced and play no role in the nasolacrimal duct routes. The nasals have been forced posteriorly by the shortening of the snout and enlargement of the nostrils, and now form the anterior margins of the orbits. Nasal-maxillary articulation is slight. The ducts initially extend anteriad from the eyelids in a dorsal position, but very soon enter partially closed foramina in the posterior orbital margins of the nasals and proceed ventrad to the nasal capsules.

Presumably the most specialized plethodontid condition is that encountered in *Desmognathus* and allied genera. Wilder (1913) was unable to find nasolacrimal ducts in *Desmognathus,* and the ducts appear to be absent in *Phaeognathus* and *Leurognathus* as well.

On the basis of the arrangement of the anterolateral cranial elements, and the route of the nasolacrimal ducts, the following generic groupings are evident:

1. *Gyrinophilus, Stereochilus, Typhlotriton.*
2. *Pseudotriton.*
3. *Plethodon, Ensatina, Aneides.*
4. *Eurycea, Manculus, Hemidactylium.*
5. *Hydromantes, Batrachoseps, Bolitoglossa, Oedipina, Pseudoeurycea, Chiropterotriton, Parvimolge, Lineatriton, Thorius.*
6. *Desmognathus, Leurognathus, Phaeognathus.*

The above groupings reflect the general trends from primitive dorsal to advanced ventral nasolacrimal duct routes. This is a morphological trend that may reflect phylogeny. It is likely that the tendency for posterior movement of the nasolacrimal duct foramina has proceeded in parallel along several phylogenetic lines, with parallelism most evident between groups 3, 4, and 5.

Vomer

Vomers of two distinct types are encountered in larval and paedogenetic plethodontids (Fig. 7):

1. Vomers in shape of inverted L's with rounded corners and varying amounts of expansion; articulation between bilateral counterparts limited to extreme anterior tips; elements very widely separated posteriorly; small anterior processes attach vomers to premaxilla. *Gyrinophilus, Pseudotriton, Stereochilus, Eurycea, Manculus, Typhlotriton, Haideotriton, Typhlomolge, Hemidactylium.*

2. Vomers in shape of upper quarter circles, with small posteromedial projections; virtually complete articulation of bilateral counterparts along midline; no anteriorly directed processes, and no attachment of vomers to premaxilla. *Desmognathus, Leurognathus.*

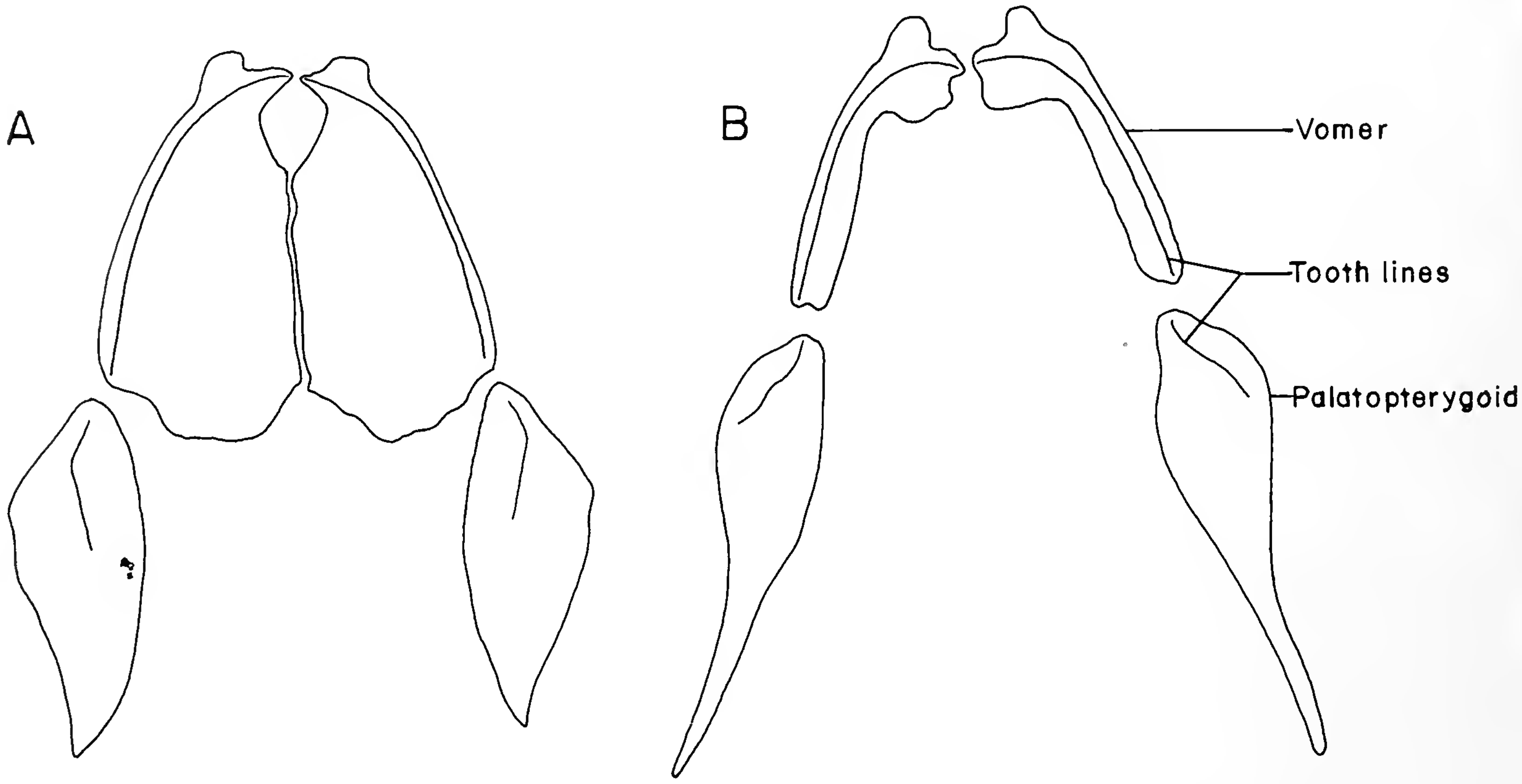


Figure 7. Vomers and palatopterygoids in larval plethodontids. A. Desmognathine pattern (*Desmognathus quadramaculatus*), B. Plethodontine pattern (*Gyrinophilus danielsi*). Not drawn to scale.

Larval ambystomatid vomers resemble condition 1, and it apparently is the more generalized and primitive of the two plethodontid conditions. The larval vomers of *Desmognathus* and *Leurognathus* articulate extensively with each other. The most plausible explanation for this articulation is that it is a strengthening compensation for the loss of suspensorial articulation of the palatopterygoids (which see), with which the larval vomers articulate posteriorly.

Plethodontid genera may be placed in three groups on the basis of adult vomerine structure. *Gyrinophilus, Pseudotriton, Stereochilus, Eurycea, Manculus, Typhlotriton,* and *Hemidactylium* form one group that is characterized by: (1) presence of sharply arched vomerine tooth series, (2) bony vomerine growth posteriolateral to the tooth series (Fig. 8). Fontanelles are open and of moderate size in all genera, and vaulting is moderately to well developed in all but *Typhlotriton.* Preorbital processes are present primitively. The vomerine tooth series originate on the processes and proceed anteriomediad almost to the midline where the series sharply turn and proceed initially posteromediad, finally posterolaterad, to terminate below the posterior portions of the parasphenoid. Such a pattern is characteristic of *Gyrinophilus, Pseudotriton, Stereochilus,* and *Typhlotriton.* All four have well developed and stocky preorbital processes that extend beyond the lateral margins of the internal nares, but fall far short of the vomerine body margins. Anterior and posterior portions of the tooth series are continuous in the four genera. The bilateral series are joined for a short distance at about the level of the anterior margins of the orbitosphenoids in *Stereochilus*. Lateral margins of the vomerine bodies are projected a little posteriad, below the preorbital processes, in *Stereochilus* and are drawn into spinous, posterolaterally projecting processes that are diagnostic of the genus; preorbital processes are also directed rather strongly posterolaterad, and thus are not overlapped by the body processes.

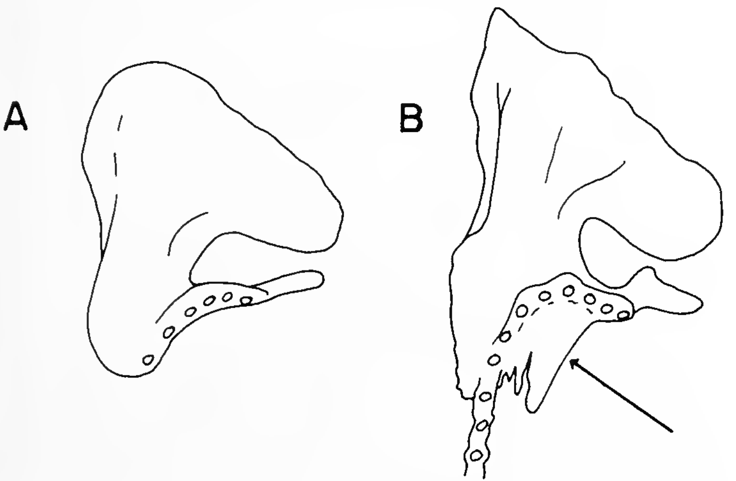


Figure 8. Vomers of adult plethodontines. A. Plethodonine and bolitoglossine pattern (*Plethodon jordani*), B. Hemidactyliine pattern (*Pseudotriton ruber*). Arrow indicates bony growth behind tooth series. Not drawn to scale.

In contrast to *Stereochilus* with its compressed skull, *Typhlotriton* has a broad, flat skull. In old adults the vomerine series of teeth are very sharply arched and the posterior portion of each series curves back on itself as it leaves the vomer proper. Thus the series are very widely separated in the interorbital region, and in the largest individuals come to lie, for a short distance, along the orbitosphenoids rather than the parasphenoid. The series are usually sinuous, however, and curve back below the parasphenoid, where they extend to the posterior end of the parasphenoid. At the latter point the series proceed medially and approach each other on the midline. The pattern in *Typhlotriton* is unique both in the degree of separation of the series and their posterior extent. The body of each vomer is also unusual in the genus and bears a posteriorly directed process that forms the lateral margins of the nares.

Eurycea and *Manculus* have short preorbital processes that fall short of the lateral edges of the internal nares. Metamorphosing individuals have tooth patterns similar to those described above, but adults normally have the posterior patches separated by toothless gaps from the arched anterior series (usually continuous in *E. aquatica;* Rose and Bush, 1963).

Hemidactylium has slender, toothless preorbital processes that extend to the lateral margins of the internal nares. The anterior tooth series are arched anteromedially, but to a lesser extent than in other members of the group. In very small individuals (16 mm.) the anterior and posterior tooth series are continuous, but in adults there is a toothless gap.

The posterior portions of the tooth series, or the posterior tooth patches, are widely separated past the parasphenoid midpoints in all members of the group. The posterior teeth are in relatively narrow series or patches which contain from two to six diagonal rows at the point of maximum width.

Plethodon, Ensatina, Aneides, Hydromantes, Batrachoseps, Bolitoglossa, Oedipina, Pseudoeurycea, Chiropterotriton, Parvimolge, Lineatriton, and *Thorius* form a second group. The farthest anterior extent of the vomerine tooth series is at the extreme lateral extremity of each series, or slightly medial to that point, rather than near the midline. The anterior tooth series extend along the lateral and posterior margins of the vomers, and there is no posterolateral vomerine growth beyond the series (Fig. 8). Anterior and posterior toothed areas are normally widely separated, particularly in adults. Fontanelles are normally moderate to very large, and vaulting is moderately to well developed. Relatively slender preorbital processes that extend to at least the lateral margins of the internal nares are present in all genera of this group except *Batrachoseps, Thorius,* some species of *Aneides (ferreus, flavipunctatus, lugubris),* and some *Chiropterotriton (bromeliacia, dimidiatus, nasalis).* Small processes are evident in some *Batrachoseps,* but are virtually absent in most. The longest preorbital processes occur in *Ensatina,* where they extend beyond the lateral margins of the vomerine bodies.

The posterior tooth patches may be continuous with the anterior tooth series in very young individuals (*e.g., Ensatina* at 23.1 mm.), but toothless gaps are normally present in adults. The posterior patches vary from very well separated in *Hydromantes* and *Batrachoseps,* to moderately or slightly separated in most genera, to closely appressed but unfused in *Thorius* and some species of *Bolitoglossa.* In genera such as *Pseudoeurycea* and *Chiropterotriton* the tooth patches may be in contact anteriorly but well separated posteriorly. In general, patches in genera of this group contain more teeth than those of the former group, and vary from three to four rows at maximum in some species of *Pseudoeurycea,* to as many as ten to twelve rows in some species of *Bolitoglossa* and *Plethodon.*

Parasphenoids in the first two groups of genera extend dorsally above the vomers proper to points equal to, or somewhat in advance of, the anterior orbitosphenoid margins. The area of overlap is relatively great, and at no point do the parasphenoids and vomers articulate squarely. This is also the condition encountered in primitive salamander families. In the third group *(Desmognathus, Leurognathus, Phaeognathus)* parasphenoids are greatly shortened in old adults, and articulate squarely with vomerine posterior margins at points near the orbitosphenoid midpoints. This articulation is considerably more rigid than in other groups, and is a specialized condition associated with the trends toward skull strengthening in the third group. The specialization involves not only parasphenoid shortening, but also relative vomerine lengthening. Thin portions of the parasphenoids in *Desmognathus* may extend fairly far anteriorly, dorsal to the vomers.

Vomerine tooth pattern is highly distinctive in the third group. In young *Desmognathus* and many adults the anterior teeth are in short, arched series that do not extend onto the preorbital processes. Anterior vomerine teeth are lost in the larger individuals, especially males, of some species *(e.g., D. monticola, D. quadramaculatus).* Anterior teeth are in relatively long, straight series in *Phaeognathus,* with slight anterolateral curves; the series form relatively very small angles with the skull axes, and are located considerably more posteriorly than in other plethodontid genera. The slender preorbital processes of *Phaeognathus* are toothless. Teeth are usually absent in *Leurognathus,* but may be present in some populations (Martof, 1962). In toothed individuals of *Desmognathus* and *Leurognathus,* and in *Phaeognathus,* considerable amounts of bony posterolateral growth occur beyond the tooth series in a manner similar to that encountered in genera of the first group.

Vomerine bodies are relatively small and very flattened in *Phaeognathus* and *Leurognathus,* but the somewhat larger elements of *Desmognathus* are slightly vaulted. The vomerine bodies are broadly overlapped dorsally by the palatal shelves of the premaxillae and maxillae in *Desmognathus* and *Leurognathus,* but the vomers overlap the premaxillary palatal shelves in *Phaeognathus.* Fontanelle closure was reported in *Leurognathus* by Moore (1899), and was employed as a generic character by Dunn (1926) and Noble (1931). Distinct fontanelles are present in young individuals and in small adults, however, and are progressively closed over with increasing size. Dunn (1926) has stated that fontanelle closure is related to the fact that the highly aquatic *Leurognathus* has lost the internasal glands, which aid in food capture in terrestrial habitats. Fontanelles in *Desmognathus,* and to a lesser extent in *Phaeognathus,* may be closed over secondarily by medial growth of the fontanelle borders. These genera differ further from *Leurognathus* in that dorsal growth of the vomerine bodies forms bony walls around the posterior and posterolateral portions of the fontanelles, while the processes are absent in *Leurognathus* because skull depression places the premaxillae and vomers essentially in contact.

The internal nares have shifted laterally in *Leurognathus,* and the preorbital processes are very closely applied to the vomer bodies, with only narrow lateral narial slits. Nares are in the normal position in *Desmognathus* and *Phaeognathus.* Preorbital processes of *Phaeognathus* and, especially, of *Leurognathus* are long and extend laterally beyond the vomerine bodies. The processes are shorter in *Desmognathus,* and lateral margins of the bodies grow posterolaterad to extend below the tips of the processes. Preorbital processes tend to articulate with the antorbital portions of the frontals in all three genera, a situation not encountered in the other generic groups.

Posterior vomerine patches are well separated from the anterior series and slightly separated from each other in adults of the third generic group. The patches are well developed, and have five or six diagonal rows of teeth. The anterior series and the posterior patches are continuous in late larvae and metamorphosing individuals in *D. quadramaculatus.* At these stages the anterior series are highly arched, and the apices are anteromedial in position. From each apex the series slope laterally and terminate before the medial margins of the internal nares are reached; in the other direction the series extend posteromediad, then posterolaterad, and finally terminate on the posterior, ventral surfaces of the parasphenoids. The general pattern closely resembles that seen in adult *Stereochilus.*

Frontal

Frontals primitively are large and occupy most of the interorbital area. Ambystomatid and hynobiid frontals are long, and extend beyond the posterior margins of the orbitosphenoids, and such a condition is probably primitive in the plethodontids. The evolutionary trend in plethodontids appears to be toward a decrease in frontal size, associated with an increase in the relative size of the parietals. Plethodontid genera may be grouped as follows on the basis of this character:

1. Frontals long, extend beyond posterior margins of orbitosphenoids. *Desmognathus, Leurognathus, Phaeognathus, Gyrinophilus, Pseudotriton, Stereochilus.*
2. Frontals short, fall short of posterior margins of orbitosphenoids. *Eurycea, Manculus, Typhlotriton, Typhlomolge, Haideotriton, Hemidactylium, Plethodon, Ensatina, Aneides, Hydromantes, Batrachoseps, Bolitoglossa, Oedipina, Pseudoeurycea, Chiropterotriton, Parvimolge, Lineatriton, Thorius.*

The genera may also be grouped on the basis of presence or absence of distinct lateral processes on the posterior margins of the frontals:

1. Frontals with medially sloping posterolateral margins; no distinct lateral processes. *Desmognathus, Leurognathus, Phaeognathus, Gyrinophilus, Pseudotriton, Stereochilus, Typhlomolge, Haideotriton.*
2. Frontals with relatively straight or only slightly medially sloping posterolateral margins; poorly to very well developed lateral processes which overlap parietals on posterior margins. *Eurycea, Manculus, Typhlotriton, Hemidactylium, Plethodon, Ensatina, Aneides, Hydromantes, Bolitoglossa, Oedipina, Pseudoeurycea, Chiropterotriton, Parvimolge, Lineatriton, Thorius.*

Many exceptions are found among species of the genera of the last group, but every genus has at least some species that fit the category. The best developed processes are found in *Eurycea, Manculus, Hemidactylium,* and the neotropical genera, and the processes are apparently all that remains of the greatly reduced frontals of *Batrachoseps.* In *Typhlotriton* the posterolateral borders slope medially, and the small posterior processes are located more medially than in other genera. There is no indication of lateral processes in ambystomatids or hynobiids, and the posterolateral borders slope medially. Lack of lateral processes appears to be primitive in plethodontids. The lateral processes may compensate for general skull weakening, since they tend to be better developed in forms with weakly developed skulls *(e.g., Manculus).*

Frontals of *Batrachoseps* and *Oedipina* have well developed anteromedial spinous projections that extend beside and below the premaxillary frontal processes. Anterior expansion of the frontals is marked in *Hydromantes,* and is also evident in various species of many other genera.

Notable frontal reduction occurs in two genera. In *Batrachoseps* frontals are narrow and are very widely separated posteriorly. The elements are essentially in contact between the anterior margins of the orbits, but rapidly diverge posteriorly, and leave much of the dorsal portion of the brain uncovered by bone. The frontals of *Thorius* are also reduced, and leave middorsal gaps that are considerably smaller than those of *Batrachoseps.*

The most distinct group of plethodontid genera based on frontal structure contains *Desmognathus, Leurognathus,* and *Phaeognathus,* in which the bones are dense, stout, relatively thick, and enlarged. Anterior expansion is great. Ventrolateral extensions of the expanded regions have invaded the antorbital regions between the maxillary facial lobes, and the maxillary palatal shelves and vomerine preorbital processes. This feature is one on which Cope's (1866) family Desmognathidae was based. The antorbital processes are specializations associated with skull solidification and strengthening, and are found in no other plethodontid genera. The expanded anterior portions of the frontals have grown into the area vacated by the prefrontals, and are extensively overlapped by the maxillary lobes in a firm, extensive articulation. Posteriorly, along the orbital margins, distinct lateral ridges are present.

Parietal

Generic groupings are recognizable on the basis of parietal structure. The first group includes *Plethodon, Ensatina, Aneides,* and *Hydromantes.* In these genera the parietals are relatively flattened with broad, concave, posterior depressions (some large *Aneides*), slight depressions *(Aneides, Plethodon, Ensatina),* or essentially no depressions *(Hydromantes).* In all four genera the orbital edges of the parietals are laterally rather than ventrally directed, and the bones have no lateral aspects. The orbitosphenoids are moderately to slightly overlapped by the depressed posterior portions except in *Hydromantes.* The general condition in these genera is similar to that found in primitive salamanders, and is perhaps close to the ancestral condition of the family.

The second group includes *Gyrinophilus, Pseudotriton, Stereochilus, Eurycea, Manculus, Typhlotriton, Typhlomolge, Haideotriton,* and *Hemidactylium.* Parietals of this group have posterior depressions that vary from marked to shallow, and the bones have distinct lateral aspects with ventrally directed edges that significantly overlap the orbitosphenoids in metamorphosed individuals. Posterior depression is marked in *Hemidactylium, Stereochilus, Eurycea,* and *Manculus,* but is poorly developed in *Gyrinophilus, Pseudotriton,* and

Typhlotriton. The relatively smooth parietals of *Typhlomolge* and *Haideotriton* resemble those of larvae of the other genera, but are somewhat better developed. Lateral processes and distinct, obliquely oriented crests are present posteriorly in *Typhlomolge.* The posterolateral margins of the parietals are raised to form portions of the parietal-otic crests in *Pseudotriton, Gyrinophilus, Stereochilus,* and some species of *Eurycea (aquatica, bislineata).*

A third group includes *Batrachoseps, Bolitoglossa, Oedipina, Pseudoeurycea, Chiropterotriton, Parvimolge, Lineatriton,* and *Thorius.* The parietals of these genera are either smooth or have slight posterior depressions. Well developed, lateral parietal spurs are present in all genera, and are diagnostic of the group (this structure is well illustrated by Wiedersheim, 1877, Fig. 9b, in *Batrachoseps*). The spurs are small lateral processes that are directed sharply ventrally over the area of the ascending processes of the suspensoria. It is possible that the spurs may have arisen as compensations for the generally weakened condition of the dorsal roofing bones in members of this group. The spurs appear to be neomorphic developments in these genera, and are probably not morphologically related to the lateral portions of the parietals of *Eurycea* and *Manculus* which may, in very small species, resemble the spurs.

Genera of the final group *(Desmognathus, Leurognathus, Phaeognathus)* have highly specialized parietals that differ markedly from those of the other groups. Parietals are divisible into two sections. The anterior sections are high and very flat, and are on the same level as the frontals. Neither frontals nor anterior portions of parietals are covered by musculature. The anterior portions articulate very firmly with the frontals. Pronounced lateral ridges are present, and each bone proceeds ventrad and slightly mediad from the ridge; thus there is a distinct lateral aspect to each bone. The posterior portions of the parietals have been impressively molded by the strong ligaments that extend from the atlas vertebrae to the mandibles (Fig. 9), and are in the form of deep, concave, almost U-shaped troughs that are directed anterolaterad, into the orbits. The parietals and anterior portions of the occipito-otics are drawn into anterolateral orbital extensions of the troughs. The distinction between anterior and posterior portions of the parietals is strong in *Desmognathus* and *Leurognathus,* but is less well marked in *Phaeognathus,* in which the anterior portions are relatively lesser proportions of the bones and the parietals form significantly greater amounts of the troughs.

In *Pseudotriton* and some *Aneides* (*lugubris* group) the parietals tend to fuse medially in large individuals, and a median crest forms. Parietals are separated by medial spaces in larvae and paedogenetic adults. Separation in adults of non-paedogenetic species *(Hydromantes, Batrachoseps, Thorius, Eurycea multiplicata, Bolitoglossa platydactyla)* may be due to paedomorphosis. A huge

Figure 9. Skull, cervical vertebra and first trunk vertebra of adult female *Desmognathus ochrophaeus* (46.7 mm.). Note atlas-mandibular ligament, shape of cervical vertebra, and pterygapophyses extending posterolaterally above postzygapophyses of trunk vertebra; all are characteristic features of the subfamily Desmognathinae.

space separates the parietals of *Batrachoseps* (smaller in *wrighti* than in other species), and moderate spaces are present in *Thorius*. The statement by Cope (1889) that the parietal bones of *Oedipina* are "two small oval lateral scales" and are unossified is incorrect. The bones are well ossified and completely roof the posterior portions of the brain in *Oedipina*.

Orbitosphenoid

Orbitosphenoids are absent in *Typhlomolge* and *Haideotriton*, and in small larvae of other genera. They are present in large larvae, and in the paedogenetic species of *Eurycea*. Well developed orbitosphenoids are present in adults of other genera, except in *Thorius*, in which the elements are small and do not articulate dorsally with the frontals and parietals.

The optic fenestrae are always enclosed in bone and are located from near the midpoints of the bones (in some *Aneides*), to very near the posterior margins. The fenestrae in *Typhlotriton* have been reduced to minute foramina which reflect the reduced nature of the visual system, including the drastic reduction of the optic nerves, in the genus.

Parasphenoid

Plethodontids may be placed in two groups on the basis of parasphenoid structure. The first group contains *Desmognathus, Leurognathus,* and *Phaeognathus*. The parasphenoids are shortened and fall short of the anterior margins of the orbitosphenoids. In addition the anterior portions are truncate and strongly concave to U-shaped. The bones articulate along their anterior margins directly with the vomers in moderately firm sutures. The posterior portions of the parasphenoids are very broad with large posterolateral processes that articulate directly with the enlarged quadrates.

The parasphenoids are not notably shortened in the second group (all other plethodontid genera), and extend to the anterior margins of the orbitosphenoids or beyond. The anterior portions are moderately concave (but never U-shaped) to almost flat. Anteriorly the bones overlap the vomers, and posteriorly parasphenoids fail to articulate with the quadrates. Broad, posterolateral wings, which fall short of the quadrates, are present in *Stereochilus,* and somewhat smaller processes are present in *Pseudotriton*. In *Gyrinophilus* rounded processes are present, but they are less well developed than in *Pseudotriton*. The processes are faintly indicated, or absent, in all other genera.

Anterior portions of the parasphenoids are particularly broad in *Typhlotriton,* and, while less broad, are noticeably expanded in *Gyrinophilus, Pseudotriton, Stereochilus, Eurycea, Manculus,* and *Hemidactylium*. Broad anterior parasphenoid tips are typical of plethodontid larvae, and are found in adult *Typhlomolge* and *Haideotriton*. A tendency toward tip narrowing is evident in the remainder of the genera, but the tips may be slightly expanded in some species of *Pseudoeurycea* and *Chiropterotriton,* and relatively broad in large species of other genera *(e.g., Bolitoglossa robusta, Plethodon yonahlossee)*. An extreme of reduction is achieved by *Chiropterotriton abscondens,* in which the anterior tips are narrowed to sharp, shortened points in front of which the orbitosphenoids articulate.

Broadened posterolateral parasphenoid processes are found in primitive salamanders (hynobiids, ambystomatids) in which they do not ordinarily articulate with the quadrates. The condition encountered in *Stereochilus* appears to be the most primitive in the family, and two major types of modifications have occurred. Hypertrophy of the processes has taken place in the first group of genera, and reduction and eventual loss of the processes occurs in most members of the second group. The truncated anterior parasphenoid tips encountered in the first group are unlike those found in other salamander families, and the moderately long, overlapping tips of the second group of genera are apparently close to the primitive condition. Furthermore, the broad or expanded parasphenoid tips of some genera *(e.g., Typhlotriton, Gyrinophilus)* resemble those characteristic of hynobiids, ambystomatids, and salamandrids, and probably represent the primitive plethodontid condition.

Occipito-Otic

Otic capsules of plethodontids are considerably variable in size, but genera cannot be grouped on that basis alone. In some the otic capsules are noticeably large *(Ensatina)*; in others they are greatly reduced *(Oedipina)*. Most genera have capsules of moderate size.

Distinctive otic crests allow some groupings to be made. *Desmognathus, Leurognathus,* and *Phaeognathus* have posteromedial-anterolaterally oriented crests that extend along the posterior margins of the otic-parietal depressions. The crests are prominent and relatively high, and are formed exclusively of otic capsular material. No other genera have crests even remotely similar.

Double crests, usually separated, are found in *Gyrinophilus, Pseudotriton, Stereochilus,* and some species of *Eurycea (aquatica, bislineata)*. The anterior crests are formed of parietal and otic projections, and more posterior, lateral crests are formed of otic and squamosal projections. The crests are about equal in over-all height and extent, and are relatively isolated with rather limited bases. In all four genera the crests tend to be spine-like, and are directed laterally or slightly posterolaterally. Otic and parietal contribution is about equal in the anterior crests of *Gyrinophilus* and *Stereochilus*, but parietal participation is sharply decreased in *Pseudotriton* and *Eurycea.* Otic and squamosal participation is about equal in the lateral crests of *Gyrinophilus* and *Stereochilus,* while squamosal participation is sharply increased in *Pseudotriton* and *Eurycea.* The crests reach a maximum development in *Pseudotriton* and *Gyrinophilus.* In *Gyrinophilus* one or two small projections may be present in the region between the two crests, and the crests may be joined to form high, curved lamina in large *Pseudotriton* (*circa* 90 mm.).

Distinctive high, wing-like otic crests are present in most species of *Aneides* (Wake, 1963). The crests are extensive and are oriented in a posterolateral-anteromedial direction. Posteriorly the crests are continuous with long, low, posteriorly directed squamosal crests.

Moderate crests similar to those in *Aneides* are present in *Pseudoeurycea smithi.* The crests have parietal rather than squamosal participation, and small, accessory, anterior crests proceed over the anterior semicircular canals perpendicular to the main crests. Slight otic crests are present in some other species of *Pseudoeurycea (bellii, goebeli).*

Small anterolaterally oriented crests, or anterolaterally directed small projections, are found in some individuals of *Plethodon, Ensatina, Batrachoseps, Chiropterotriton,* and *Bolitoglossa.* Unique, laterally oriented and dorsoposteriorly directed crests are present in *Plethodon elongatus* (Wake, 1963).

All crests are apparently specializations related to provision for additional space for the origin and insertion of enlarged amounts of mandibular adductor musculature, and are most prominent in forms in which the jaw musculature is greatly enlarged. No otic crests have been observed in *Manculus, Typhlomolge, Typhlotriton, Haideotriton, Hemidactylium, Hydromantes, Oedipina, Parvimolge, Lineatriton,* or *Thorius,* and crests are absent in most species of *Batrachoseps, Eurycea, Chiropterotriton,* and *Bolitoglossa.*

Occipital Condyles

Plethodontid genera may be placed in two groups on the basis of occipital condyle structure. Sessile condyles, attached directly to the lateral margins of the foramen magnum, are characteristic of primitive salamanders (hynobiids, ambystomatids), occur in most plethodontid genera, and are doubtless primitive in plethodontids. Occipital condyles of *Desmognathus, Leurognathus,* and *Phaeognathus* are borne on the distal tips of moderately long, cylindrical pedicels or stalks. Stalked occipital condyles were first noted by Cope (1866) and were one of the characters on which his family Desmognathidae was based. Mandibles of these three genera are held largely immobile, and skulls move on condylar-atlas joints. The stalked condyles increase the distance between the skull proper and the vertebral column, and provide space for vertical skull movement.

Suspensorium

Plethodontids differ from other, more primitive salamanders in lacking bony pterygoids as adults. Pterygoids have been replaced by cartilaginous pterygoid processes of the suspensoria, which extend anterolaterally toward the maxillary tips. The processes are shortest in those forms in which the maxillae are longest, and are particularly short in *Desmognathus, Leurognathus,* and *Phaeognathus.*

Cartilaginous portions of the suspensoria are relatively large in most plethodontid genera, and the ossified portions (quadrates) are limited to distal regions and do not articulate with the occipito-otics or the parasphenoids. The quadrates communicate with the skull proper by means of large, cartilaginous, basal suspensorial portions. This situation is similar to that commonly encountered in primitive salamanders, and is evidently primitive in plethodontids. In large adults of some genera *(e.g., Pseudotriton, Aneides*) there is a tendency for thin, bony, dorsomedial quadrate processes to develop, but the processes do not reach to the otic capsules.

Ossified portions of the suspensoria are extensive in *Desmognathus, Leurognathus,* and *Phaeognathus,* but the cartilaginous portions are small. The quadrates extend below the squamosals to articulate broadly and firmly with the otic capsules and with posterolateral parasphenoid processes. Crania raise in opening the mouths of these three genera, and forces between the crania proper and the quadrates are much greater than in more generalized forms in which the quadrates serve simply as points of suspension of the mandibles. In most plethodontid genera the quadrates serve as the fulcra for mandibular motion; in *Desmognathus* and its allies the articulars serve as fulcra for cranial movement.

Palatopterygoid

Palatopterygoids are present in larval and paedogenetic plethodontids, but disappear during metamorphosis. Larval plethodontids may be placed in two groups on the basis of palatopterygoid structure. Palatopterygoids are large and elongate in *Gyrinophilus, Pseudotriton, Stereochilus, Eurycea, Manculus, Typhlotriton, Typhlomolge, Haideotriton,* and *Hemidactylium*. The bones are expanded anteriorly, but are usually drawn into relatively narrow, elongate, posterior processes which articulate directly, or almost articulate, with the quadrates. The condition in these genera is similar to that encountered in primitive salamanders, and probably represents the primitive plethodontid condition.

Palatopterygoids are small and teardrop-shaped, and have posterior points in *Desmognathus* and *Leurognathus*. The bones are separated from the quadrates by distances that approximate the total lengths of the palatopterygoids. This condition appears to be advanced within the family.

Squamosal

The squamosals are most highly developed and strongest in those species of various genera in which head and jaw musculature is well developed (*e.g., Desmognathus* and allies, *Aneides lugubris, Gyrinophilus, Pseudotriton, Pseudoeurycea smithi*). Genera with reduced skeletal elements and head muscles (*e.g., Manculus, Batrachoseps, Chiropterotriton, Thorius, Oedipina*) have thin, narrow, splint-like squamosals. Squamosal processes contribute to the otic-squamosal crests in *Gyrinophilus, Pseudotriton, Stereochilus,* and *Eurycea,* and the squamosals may have relatively large, dorsal raised regions in *Desmognathus, Leurognathus,* and *Phaeognathus*. Posterior squamosal crests are present in large *Aneides*. In general variation is closely related to function, and is more significant evolutionarily on the interspecific than on the intergeneric levels.

The squamosals bear small, well-developed, slender, cylindrical processes in all *Thorius* (Tanner, 1952). The processes arise above the midpoints of the anteroventrally sloping, posterior squamosal edges and proceed almost directly posteriorly in horizontal planes. The quadratopectoralis musculature, which in other genera attaches to the quadrates, has shifted to the squamosals in *Thorius,* and the processes have apparently developed in response to pressures resulting from the shift. These processes have been encountered elsewhere only in a single large individual of *Oedipina complex*.

Opercular Plate

The opercular apparatus of salamanders has recently been reviewed by Monath (1965). On the basis of an incomplete study of plethodontids he stated that primitive, aquatic, semi-terrestrial, and terrestrial plethodontid genera retain a well-developed columella, but that columellar reduction has occurred independently in two lines (essentially the attached and free-tongued groups of von Wahlert, 1957). The major trend has been clear since Reed's (1920) study. Although I disagree with the phylogenetic speculations of Monath concerning plethodontids, the overall trend is clearly as Reed, Dunn (1941), and others in addition to Monath have suggested.

Desmognathus, Leurognathus, and *Phaeognathus* have large opercular plates which bear distinctive columellae on their anterolateral borders. The columellae are very short and stocky, and arise as broad-based, somewhat flattened processes.

Columellae of the remaining plethodontid genera, when present, are tubular rods of small diameter. Salamander columellae are primitively rod-like (Reed, 1920), and the situation in these genera is probably primitive in the family. Columellae are present and well developed in *Gyrinophilus, Pseudotriton, Stereochilus, Eurycea, Manculus, Typhlotriton, Typhlomolge, Haideotriton, Hemidactylium, Plethodon, Ensatina, Aneides,* and *Hydromantes*. Columellae of *Batrachoseps,* reported to be absent by Reed (1920), Dunn (1926), and Piatt (1935), and to be present by Hilton (1945 a) and Monath (1965), are present in all individuals examined. Columellae are well developed in *B. wrighti* and are only slightly reduced in the other species.

Neotropical genera are characterized by a trend toward columellar reduction and loss. Primitive *Chiropterotriton* have the best developed columellae, but in advanced species (*e.g., C. bromeliacia, C. xolocalcae, C. nasalis, C. abscondens*) columellae are lost. Very small columellae are present in *Lineatriton*. *Pseudoeurycea* has columellae that are usually vestigial and small. Vestigial, very short columellae are present in *Bolitoglossa dunni* and in one individual of *Parvimolge townsendi,* but are absent in all other species of both genera, and in all *Thorius* and *Oedipina*. When columellae are absent the columellar processes of the suspensoria extend to the opercula.

The opercula are essentially absent in some adult *Chiropterotriton multidentatus,* except for small amounts of tissue at the bases of the relatively well developed columellae.

Reed (1920) stated that *Typhlomolge* should not be included in the family Plethodontidae because the columellae contribute considerably more to the plate portions than in other members of the family. Similar, but less extreme conditions are encountered in *Haideotriton* and *Eurycea pterophila,* however, and appear to be related to the paedomorphic nature of these groups. The situation certainly does not warrant exclusion of the involved species from the Plethodontidae.

Mandible

The primitive salamander mandibular pattern is retained by the majority of plethodontid genera. Dentaries and prearticulars are of moderate to small size. Each mandible is curved primitively, so that the mandibular rami form broadly rounded arches. Meckelian grooves are open for much of the lengths of the dentaries, and at the anterior ends of the prearticulars.

Specialized mandibles are found in *Desmognathus, Leurognathus,* and *Phaeognathus.* In these genera the dentaries are large, massive structures that are particularly broad ventrally. The dentaries are straighter than in other genera, and the resultant mandibular arches are considerably more pointed than in more primitive genera. The meckelian grooves are completely, or almost completely closed, and the anterior extensions of the prearticulars are entirely enclosed within the O-shaped dentaries. These specializations are related to functional changes in the three genera. The organisms force their way beneath rocks and into crevices, and the rigid, relatively straight, strengthened mandibles are presumably of significance in such behavior.

The mandibular condition in *Desmognathus, Leurognathus,* and *Phaeognathus* is most closely approached by *Stereochilus,* in which the mandibular arches are relatively elongate and pointed, and the anterior portions of the meckelian grooves are closed.

The prearticulars in plethodontids are strongly inflected dorsomedially and shelves are small and directed medially in *Gyrinophilus* and *Pseudotriton.* In *Stereochilus, Eurycea, Manculus, Hemidactylium,* and *Typhlotriton* the shelves initially are inflected medially, then dorsomedially. Similar stiuations are encountered in *Desmognathus, Leurognathus,* and *Phaeognathus,* but the portions on which muscles insert are relatively larger than in other genera. The shelves are also directed dorsomedially in *Plethodon, Ensatina,* and *Aneides,* and the inflected portions are relatively very large in adult *A. ferreus, A. flavipunctatus* and *A. lugubris.* Prearticulars are very small in *Ensatina.* The relatively small prearticulars of *Hydromantes, Batrachoseps, Bolitoglossa, Oedipina, Pseudoeurycea, Chiropterotriton, Parvimolge, Lineatriton,* and *Thorius* are dorsomedially inflected.

Desmognathus, Leurognathus, and *Phaeognathus* have well developed, anterior, dorsal prearticular projections located just anterior to the prearticular shelves. The atlas-mandibular ligaments insert on the projections. Similar but considerably smaller projections are present in *Stereochilus,* some large *Eurycea bislineata,* and adult *Typhlotriton.* Slight indications of the processes are occasionally encountered in other genera.

Dentary bulk is relatively greatest in *Desmognathus, Leurognathus,* and *Phaeognathus,* and this bulk is approached, but not matched, by large, specialized species such as *Aneides lugubris.* The dentaries are relatively slender in most genera.

Raised, pointed, dentary processes are located in the coronoid region in *Typhlotriton,* and about match the prearticulars in height. Laterally inflected, flange-like processes are present in large *Plethodon* and *Aneides.* Other genera either have rather poorly developed or no dentary processes.

Very small coronoids that bear teeth occur on the inner margins of the dentaries in larval *Desmognathus, Leurognathus, Gyrinophilus, Pseudotriton, Stereochilus, Eurycea, Manculus, Typhlotriton,* and *Hemidactylium,* and in adults of the paedogenetic species. No indication of the element has been seen in embryos of species which undergo direct development.

Hyobranchial Skeleton

Larval structure

Desmognathus and *Leurognathus* have four larval epibranchials, but three are present in larvae of all other genera, and in the paedogenetic adults. *Bolitoglossa subpalmata* embryos, removed from egg capsules, have adult configurations with a single pair of epibranchials, and the same is true of hatchling *Plethodon* and *Batrachoseps.* Dent (1942) has reported three epibranchials in an embryo (unspecified size) of *Plethodon cinereus.*

Larval hyoids are found in adults of the paedogenetic species, and all have branchial plates. The branchial plates of *Typhlomolge* are notably elongated and proportionately longer than in other genera. The ceratobranchial arms are swept posteriorly and make considerably smaller angles with each other than in other genera.

Adult structure

Several important papers (Piatt, 1935; Tanner, 1952) have dealt with tongue morphology, including some aspects of the musculature. It is especially important that the attachment of the tongue to the anterior margin of the mouth be understood.

Genioglossal muscles primitively extend as well developed strap-like structures from the area of the mandibular symphysis dorsally into the tongue. They bind the anterior border of the tongue and aid in returning the extended tongue into the mouth. The primitive condition is encountered in *Desmognathus, Leurognathus, Phaeognathus, Plethodon* and *Aneides* (the muscles considered to be diagnostic of desmognathines by Tanner, 1952, are the genioglossals). The fibers proceed for a short distance medially from their origin on the dentaries, then swing abruptly dorsally and insert in the tongue. The genioglossals are modified and a little elongated in *Ensatina* and *Hemidactylium*. Each muscle originates somewhat posteriorly, along the medial margin of the dentary, and proceeds almost directly medially, then abruptly moves dorsally into the tongue. A bizarre arrangement is seen in *Batrachoseps,* in which the fibers originate near the articular end of the mandible and proceed anteriorly following the curve of the mandible. Near the anterior end of the mandible the fibers proceed medially, resembling the medially directed muscle in *Ensatina* and *Hemidactylium,* and finally move dorsally at the midline.

Anterior portions of the tongue are held tightly in the mouth by the stout genioglossals in *Desmognathus, Leurognathus, Phaeognathus, Plethodon,* and *Aneides.* In *Ensatina* and *Hemidactylium* movement is possible, and tongues may be propelled for some distance out of the mouth. The tongue of *Batrachoseps* may be protruded almost as far as in those genera which lack genioglossals: *Gyrinophilus, Pseudotriton, Stereochilus, Eurycea, Manculus, Typhlotriton, Hydromantes, Bolitoglossa, Oedipina, Pseudoeurycea, Chiropterotriton, Parvimolge, Lineatriton,* and *Thorius.* In *Stereochilus* and *Typhlotriton,* the tongues are attached anteriorly by fleshy, non-muscular tissue.

Ceratohyal

Anteriorly expanded ceratohyals are characteristic of most plethodontids, but the structures are attenuated anteriorly in *Hydromantes, Oedipina,* southern species of *Chiropterotriton* (*bromeliacia, abscondens,* see Rabb, 1958), *Lineatriton, Parvimolge richardi,* and *Thorius* (see Tanner, 1952). Attenuation occurs only in specialized groups, and is a specialized condition.

The attenuated ceratohyals of *Oedipina* are diagnostic of the genus (Tanner, 1952). The posterior cylindrical portions flatten slightly at about the level of the midpoint of the first basibranchial, and at that point small processes proceed anteromedially; the processes serve as the point of attachment of suprapeduncularis muscles. The ceratohyals extend well anterior to the processes as attenuated rods.

Tanner (1952) has indicated that the ceratohyals of *Bolitoglossa* are noticeably shorter than those of other neotropical genera, and that the elements do not proceed much beyond the origin of the relatively broad suprapeduncularis muscles. Shortened ceratohyals are also present in *Hydromantes,* and both *Bolitoglossa* and *Hydromantes* lack sublingual folds, structures related to the anterior elongation of the ceratohyals. Sublingual folds occur in all neotropical genera except *Bolitoglossa,* and in several midlatitude genera *(e.g., Pseudotriton),* but the folds appear to be artifacts of the structure of the ceratohyals and of the adetoglossal condition. There is no evidence to support Tanner's assurances that all folds are homologous structures.

Cornua

Paired cornua are associated with the anterior portions of the first basibranchials in all genera except *Hydromantes,* in which the tongue musculature normally associated with the cornua is firmly attached to the anterior basibranchial tip. The remainder of the genera may be grouped as follows:

1. Cornua distinctly separated from the first basibranchials, joined by connective tissue. *Desmognathus, Leurognathus, Phaeognathus, Gyrinophilus, Pseudotriton, Stereochilus, Eurycea, Manculus, Typhlotriton, Hemidactylium, Plethodon, Aneides, Ensatina.*
2. Cornua closely applied and broadly attached to the first basibranchials, often seemingly or actually continuous with the basibranchials. *Batrachoseps, Bolitoglossa, Oedipina, Pseudoeurycea, Chiropterotriton, Parvimolge, Lineatriton, Thorius.*

Cornual attachment is very clear for most of the genera. However, the cornua of *Typhlotriton* are relatively broad-based and superficially appear to be in direct continuity with the first basibranchial. Histological preparations reveal that the joint region contains densely packed cells similar to cartilage cells, but interstitial substance is absent in the joint region. The cartilages are not in direct continuity. Histological preparations of *Batrachoseps* and *Chiropterotriton* clearly show that the junction of the cornua and first basibranchial is an area containing cartilage cells and interstitial substance; there is no joint. The joint is sharp and clear in *Ensatina,* with the region between the cartilages consisting of densely packed fibroblasts and connective tissue fibers.

The genera of group 1 may be placed in subgroups. The narrow, elongate cornua of *Desmognathus, Leurognathus,* and *Phaeognathus* arise from narrow bases, and are about one-half or more of the total length of the first basibranchial. Those of *Gyrinophilus, Pseudotriton, Stereochilus,* and *Hemidactylium* are moderately broad-based structures one-fourth to one-half the length of the first basibranchial; in contrast to those of the other three genera the cornua of *Stereochilus* are expanded distally rather than pointed or cylindrical. The small, tapering, pointed cornua of *Eurycea, Manculus,* and *Typhlotriton* are less than one-half the length of the first basibranchials. Old adults of *Typhlotriton* have cornua with slight distal expansion. The large, distally expanded, wing-like cornua of *Plethodon, Ensatina,* and *Aneides* are one-third *(Ensatina)* or from two-fifths to three-fourths the length of the first basibranchials. Expanded distal portions are extremely thin. Proximal portions are cylindrical.

Batrachoseps has the longest cornua of the group 2 genera, and its long, thread-like cornua curve gracefully in 180° arcs with total lengths of from one-third to one-half the length of the first basibranchial. The cornua of *Bolitoglossa* strikingly resemble those of *Batrachoseps,* but are straighter and shorter (one-fifth to one-third times first basibranchial length). Cornua of the remaining genera are successively shorter and inconspicuous; each is equal to less than one-fifth of the first basibranchial length in *Pseudoeurycea, Chiropterotriton,* and *Oedipina,* and less than one-tenth in some *Chiropterotriton (e.g., bromeliacia, abscondens), Parvimolge, Lineatriton,* and *Thorius.*

Lingual cartilage

Piatt (1935) reported lingual cartilages to be present in *Gyrinophilus, Pseudotriton, Eurycea,* and *Manculus,* found "forerunners" in *Stereochilus* and *Typhlotriton,* but found no trace in other plethodontids. He considered lingual cartilages to be "paleotelic" features, homologous with the "Sehnenplatte" of *Salamandra,* but his work was biased by his assumption that plethodontids had been derived from salamandrids.

It is apparent that lingual cartilages are homologous with the anterior extensions of the first basibranchials of primitive salamanders, as suggested by Hilton (1947 a). Both serve as the sites of hyoglossal muscle insertion, and both occupy similar positions. They differ in that the lingual cartilages are squat (usually) rather than elongate, and separated from (usually) rather than continuous with the first basibranchials.

Plethodontids have long been grouped on the basis of tongue attachment. Uzzell (1961) introduced the useful terms deto- and adetoglossal to refer to presence and absence respectively of anterior tongue attachment, or to the attached and free-tongued conditions. Detoglossal genera are *Desmognathus, Leurognathus, Phaeognathus, Stereochilus, Typhlotriton, Hemidactylium, Plethodon, Aneides, Ensatina,* and *Batrachoseps,* but of these the genioglossal muscles have been lost in *Typhlotriton* and *Stereochilus,* and elongated from greater to lesser extents in *Batrachoseps, Ensatina,* and *Hemidactylium.* It is significant that anterior first basibranchial extensions are present as consistently well developed, distally knobbed structures only in genera in which the genioglossal muscles are short and strap-like (see Piatt, 1935), and in which essentially no movement of the anterior portions of the tongue out of the mouth is possible *(Desmognathus, Leurognathus, Phaeognathus, Plethodon, Aneides). Ensatina,* anatomically detoglossal but with a fairly protrusible tongue, has relatively smaller processes than the above genera, and the processes are pointed rather than distally expanded. Histological preparations show that the region just anterior to the cornual attachment in *Ensatina* is strongly depressed and contains densely arranged cartilage cells but notably small amounts of interstitial substance. This is in marked contrast with regions craniad and caudad where the cells are widely separated by large amounts of interstitial substance. This region is apparently flexible, and the anterior extension bends ventrally during tongue flipping. A joint apparently forms in the depressed region in some large individuals. Dissections reveal that portions anterior to the attachment of the cornua are occasionally separated from the first basibranchials in large *Ensatina,* and form small, triangular, cartilaginous structures on which insert hyoglossal muscle fibers. These structures must be considered lingual cartilages, and their appearance in *Ensatina* demonstrates the relationship of the anterior processes or first basibranchial extensions and the lingual cartilages. Both anterior extensions and lingual cartilages are absent in *Batrachoseps* and *Hemidactylium,* the other genera that have genioglossal muscles. I am unable to corroborate Hilton's (1959) observation that *Hemidactylium* has a lingual cartilage.

Stereochilus and *Typhlotriton* have true lingual cartilages despite Piatt's (1935) report that a

"Sehnenplatte" or membranous forerunner is present. In *Typhlotriton* lingual cartilage formation occurs rather late during ontogeny. In small adults the cartilages have a membranous appearance, as reported by Piatt. Microscopic sections of a tongue of an adult *Typhlotriton* (53.1 mm.) reveal that a well developed lingual cartilage is present and that it is attached to the anterior end of the first basibranchial at either lateral margin by dense aggregations of cartilage cells. On the midline only dense connective tissue fibers hold the vertically oriented cartilage to the horizontal basibranchial.

Well developed lingual cartilages are present in *Gyrinophilus, Pseudotriton, Eurycea,* and *Manculus.* In these genera the structures are irregular, squat, moderately broad elements that resemble those of *Stereochilus* and *Typhlotriton* rather than those of *Ensatina.*

The only remaining midlatitude genus, the truly adetoglossal *Hydromantes,* lacks both lingual cartilages and anterior basibranchial extensions.

Tanner (1952) corroborated Piatt's observation that lingual cartilages are absent in neotropical genera. Rabb (1955), however, reported lingual cartilages to be present in some individuals of a newly described species, *Chiropterotriton priscus,* and I have found the cartilages in some *Pseudoeurycea (bellii, cephalica),* some *Chiropterotriton (chiropterus, multidentatus),* and in *Parvimolge townsendi.* Small triangular structures similar to those of *Ensatina* are present in *Pseudoeurycea werleri,* and similarly shaped structures, but more definitely separated from the first basibranchials, are present in *Chiropterotriton multidentatus.* The cartilages of other species are rounded distally rather than pointed, and are short, squat structures. The cartilages are never as distinctly separated from the first basibranchials, nor as broad and flat, as those of *Gyrinophilus,* etc. The poorly defined, incompletely detached tissue found at the anterior ends of the first basibranchials in *Pseudoeurycea goebeli, P. leprosa, Chiropterotriton dimidiatus,* and *C. bromeliacia* may represent vestigial lingual cartilages.

It is apparent that lingual cartilages are homologous with the anterior first basibranchial extensions of anatomically and functionally detoglossal genera. Separation of anterior extensions and subsequent formation of lingual cartilages appears to be associated with acquisition of a degree of tongue freedom. It may be assumed that retention of anterior extensions is functionally undesirable in attainment of the adetoglossal condition, since well developed extensions are absent in all genera that have even a slight tendency toward the free-tongued condition. Lingual cartilages may be related to flipping the tongue pads, but they are lost in many accomplished tongue-flippers *(e.g., Bolitoglossa)* and are not functionally essential. Presence of lingual cartilages may represent a relatively advanced, functionally significant stage in the loss of the anterior first basibranchial extensions. Evidence is strong for parallel gain and subsequent parallel loss of lingual cartilages as part of an over-all morphological trend which is as follows:

1. Well developed anterior extensions of the first basibranchials present; no indications of lingual cartilages. *Desmognathus, Leurognathus, Phaeognathus, Plethodon, Aneides.*
2. Anterior basibranchial extensions small, pointed, flexible or partially detached; lingual cartilage-like structures thus formed. *Ensatina,* some *Pseudoeurycea.*
3. Completely detached lingual cartilages; first basibranchial extensions absent. *Gyrinophilus, Pseudotriton, Eurycea, Manculus, Stereochilus,* some *Chiropterotriton, Parvimolge townsendi, Typhlotriton,?* some *Hemidactylium.*
4. Poorly defined tissue present at first basibranchial tips which may represent lingual cartilage vestige or remnant; no anterior basibranchial extensions. Some *Typhlotriton,* some *Pseudoeurycea,* some *Chiropterotriton.*
5. Both anterior basibranchial extensions and lingual cartilages absent. *Hemidactylium, Hydromantes, Batrachoseps,* some *Pseudoeurycea,* some *Chiropterotriton, Lineatriton, Oedipina, Parvimolge richardi, Bolitoglossa, Thorius.*

The lingual cartilage of plethodontids is clearly not derived from the lingual process of the basibranchial of porolepiform fishes, as suggested by Jarvik (1963), but is a new element that appears for the first time in plethodontids and is clearly related to the evolution of tongue flipping. Piatt (1935) has discussed the homologies of the lingual cartilage. He considered it to be the homologue of the "Sehnenplatte" of *Salamandra.* The "Sehnenplatte" is a ligamentous plate which serves as the site of insertion of the hyoglossal and abdominohyoideal (anterior extension of rectus abdominis, also called rectus cervicis profundus) musculature. This ligamentous plate is present as a well developed structure in microscopic sections of the tongues of plethodontids dorsal to the first basibranchial in the posteroventral portion of the tongue pad. Both lingual cartilage and ligamentous plate are present in such forms as *Typhlotriton.* The hyoglossal musculature originates on the lingual cartilage and at least some of its posterior fibers insert on the plate. Clearly the cartilage and plate are functionally distinct, non-homologous structures. The presence of lingual cartilages in plethodontids in no way supports Piatt's theory of plethodontid origin from salamandrids. Since all evidence indicates that lingual cartilages occur only in plethodontids that have attained some degree of tongue freedom, Piatt was correct in stating that the lingual cartilage is not homologous with the otoglossal cartilages of ambystomatids, which serve as tongue pad supports.

First basibranchial

Plethodontid genera may be grouped on the basis of first basibranchial shape:

1. Major basibranchial expansion near midpoint. *Desmognathus, Leurognathus, Phaeognathus, Hydromantes.*
2. Major expansion slightly posterior to attachment of cornua. *Gyrinophilus, Pseudotriton, Stereochilus, Eurycea, Manculus, Typhlotriton, Hemidactylium, Plethodon, Ensatina, Aneides.*
3. No major expansion, but basibranchial broadest at anterior end. *Batrachoseps, Bolitoglossa, Oedipina, Pseudoeurycea, Chiropterotriton, Parvimolge, Lineatriton, Thorius.*

Hydromantes has cylindrical basibranchials that have thin, flattened, flange-like expansions on either side. The greatest width is equal to about 3.5 to 5 times the least diameter (width ratio) of each basibranchial. If the flanges are disregarded the first basibranchials resemble those of group 3. In the other genera of group 1 each first basibranchial is slightly flattened in the area of greatest expansion, but no flanges are present. Width ratios are from 1.5 to 3.

Thin lateral extensions arise from the anterior one-third of each basibranchial in *Eurycea, Manculus,* and *Typhlotriton.* Width ratios are from 5 to 6, the greatest in the family, and basibranchials are paddle-shaped. The basibranchials of *Pseudotriton* and *Gyrinophilus* are rather flattened, and have width ratios of 2.5 to 3. Width ratios are less than 2.5 in *Stereochilus, Hemidactylium, Plethodon, Ensatina,* and *Aneides,* but the expanded areas are much nearer the anterior ends in the first two. *Plethodon, Ensatina,* and *Aneides* differ from *Hemidactylium* in lacking sharply defined areas of expansion; *Stereochilus* is intermediate between the two conditions. The first basibranchials of *Stereochilus* and *Hemidactylium* resemble those of *Gyrinophilus* and *Pseudotriton* more closely than those of other genera, despite their relatively slight expansion.

The genera of group 3 have essentially continuous cornua which arise from the anterior ends of the basibranchials, and give the impression, more apparent than real, that the anterior ends are expanded. When present, expansion is gradual, not sharply defined.

Proportions of articulated elements

Plethodontid genera may be grouped according to the relative proportions of the articulated elements as follows:

1. Sequence of length from longest to shortest; ceratobranchial I-(ceratobranchial II, basibranchial I, or epibranchial). *Desmognathus, Leurognathus, Phaeognathus, Plethodon, Aneides.*
2. (Ceratobranchial I or epibranchial)-basibranchial I-ceratobranchial II. *Ensatina.*
3. Epibranchial-(ceratobranchial I or basibranchial I)-ceratobranchial II. *Manculus.*
4. Epibranchial-ceratobranchial I-(ceratobranchial II or basibranchial I). *Eurycea, Batrachoseps wrighti.*
5. Epibranchial-ceratobranchial I-ceratobranchial II-basibranchial I. *Gyrinophilus, Pseudotriton, Stereochilus, Typhlotriton, Hemidactylium.*
6. Epibranchial-basibranchial I-ceratobranchial I-ceratobranchial II. *Hydromantes,* most *Batrachoseps, Bolitoglossa, Oedipina, Pseudoeurycea* (one species, *P. bellii,* has ceratobranchial I and basibranchial I reversed), *Chiropterotriton, Parvimolge, Lineatriton, Thorius.*

The first ceratobranchials and the epibranchials are of nearly equal length in *Ensatina,* and the epibranchials are the longest elements in all of the remaining genera, except those of group 1. Epibranchial length is clearly associated with acquisition of tongue freedom; the longer the epibranchials (relatively), the farther the tongue can be extended from the mouth. Significantly, short epibranchials (at least shorter than the first ceratobranchials) are found only in the five genera (group 1, above) which have no osteological or myological modifications for even partially freeing the anterior tongue margins. The condition in which the first ceratobranchials are the longest elements and in which there is no tongue freedom is the condition in primitive families; it is clearly the primitive plethodontid condition.

The first are longer than the second ceratobranchials in all genera, and are longer than the first basibranchials in all but group 6. The first ceratobranchials are relatively shortest in *Hydromantes* (about one-half the length of the first basibranchials), and longest in *Stereochilus* (about one and two-thirds times first basibranchials).

The genera may be grouped according to second ceratobranchial length:

1. Second ceratobranchials less than 0.8 times first basibranchials. *Hydromantes,* most *Batrachoseps, Bolitoglossa, Oedipina, Pseudoeurycea, Chiropterotriton, Parvimolge, Lineatriton, Thorius.*
2. Second ceratobranchials more than 0.8 but less than 1.3 times first basibranchials. *Batrachoseps wrighti, Desmognathus, Leurognathus, Phaeognathus, Gyrinophilus, Pseudotriton, Eurycea, Manculus, Typhlotriton, Plethodon, Aneides, Ensatina.*
3. Second ceratobranchials more than 1.3 times first basibranchials. *Hemidactylium, Stereochilus.*

The relative dimensions of the first and second ceratobranchials may also be used to group the genera:

1. First ceratobranchials of significantly greater bulk than second ceratobranchials; minimal diameter of first equal to or greater than maximal diameter of second. *Desmognathus, Leurognathus, Phaeognathus, Gyrinophilus, Pseudotriton, Eurycea, Manculus, Stereochilus, Typhlotriton, Hemidactylium, Plethodon, Ensatina, Aneides.*
2. Second ceratobranchials of significantly greater bulk than first ceratobranchials; minimal diameter of second equal to or greater than maximal diameter of first. *Hydromantes, Batrachoseps, Bolitoglossa, Oedipina, Pseudoeurycea, Chiropterotriton, Parvimolge, Lineatriton, Thorius.*

First ceratobranchials that are stouter than second ceratobranchials are typical of primitive salamanders, and such a condition is primitive in plethodontids. All of the genera of the latter group (2) are functionally free-tongued (although *Batrachoseps* is anatomically detoglossal), and all have greatly elongated epibranchials. The subarcual rectus muscles envelop each epibranchial, and attach anteriorly to each ceratohyal. When these muscles are contracted, the epibranchials are moved forward. As a result the entire articulated hyobranchial skeleton, surrounding muscle, and connective tissue (*i.e.,* the tongue) are extended from the mouth. For efficiency in transmission of force it is functionally advantageous for the lines of force between articulated elements to be relatively straight. In all plethodontids the second ceratobranchials articulate directly with the posterior end of each first basibranchial, while the first ceratobranchials are attached by ligaments to the side of the basibranchial. Primitively the first ceratobranchials are the more dominant force transmission elements, and the dominance is maintained in most midlatitude plethodontids. In the eastern North American adetoglossals epibranchials are not greatly elongated, but the first ceratobranchials have acquired specialized braces of two types: (1) attachment behind the specialized first basibranchial anterior expansion *(Manculus, Eurycea),* (2) cartilaginous struts attached to the expanded ends of the ceratobranchials *(Gyrinophilus, Pseudotriton).* In *Hydromantes, Batrachoseps,* and the neotropical genera the primitively weak, relatively long, slightly sigmoid-shaped second ceratobranchials have become strongly shortened and straight, apparently as a result of selection pressures associated with attainment of the free-tongued condition and correlated lengthening of the epibranchials. In these genera the first ceratobranchials have been weakened and anteriorly bowed, and in some genera *(e.g., Thorius)* have lost their direct articulation with the basibranchial. As a result of these changes there is a direct, rather straight line of force transmission from each epibranchial through the short, stout ceratobranchial to the first basibranchial. The mechanics of tongue action have recently been discussed by Uzzell (1961), who cites the enlarged second ceratobranchials and their tendency to calcify in certain neotropical genera (see below) as evidence that pressure applied at the posterior ends of the epibranchials is probably transmitted to the first basibranchial through the second rather than first ceratobranchials.

As suggested above the length of the epibranchials is highly significant, and the genera may be grouped as follows:

1. Epibranchials less than 1.25 times first basibranchials. *Desmognathus, Leurognathus, Phaeognathus, Plethodon, Ensatina, Aneides.*
2. Epibranchials 1.5 to 2 times first basibranchials. *Gyrinophilus, Pseudotriton, Stereochilus, Eurycea, Manculus, Typhlotriton, Hemidactylium, Thorius.*
3. Epibranchials 2 to 3.5 times first basibranchials. *Hydromantes, Batrachoseps, Bolitoglossa, Oedipina, Pseudoeurycea, Chiropterotriton, Parvimolge, Lineatriton.*

Since the basibranchials in those genera which have anterior basibranchial extensions are proportionately longer than in those that lack the extensions, the epibranchials have also been compared with the first ceratobranchials:

1. Epibranchials less than or almost equal to length of first ceratobranchials. *Desmognathus, Leurognathus, Phaeognathus, Plethodon, Ensatina, Aneides.*
2. Epibranchials more than 1 but less than 1.7 times first ceratobranchials. *Gyrinophilus, Pseudotriton, Stereochilus, Eurycea, Manculus, Typhlotriton, Hemidactylium.*
3. Epibranchials 1.8 to 6 times first ceratobranchials. *Hydromantes, Batrachoseps, Bolitoglossa, Oedipina, Pseudoeurycea, Chiropterotriton, Parvimolge, Lineatriton, Thorius.*

The epibranchials of group 3 genera are remarkably long. The longest occur in *Hydromantes,* in which epibranchials may be 5.9 times the first ceratobranchials. Very long epibranchials are also found in *Chiropterotriton* (maximum, 4.6 times first ceratobranchials), *Oedipina* (4.0), *Parvimolge* (3.7), *Pseudoeurycea* (3.2), *Bolitoglossa* (2.9), *Batrachoseps* (2.6), and *Thorius* (2.7). The shortest adult epibranchials in group 3 are found in *Batrachoseps wrighti* (1.8). Of the group 1 and 2 genera only *Eurycea* has epibranchials that are more than 1.4 times the first ceratobranchials (1.33-1.67).

Second basibranchial

Presence or absence of second basibranchials in adults serves as a character to group plethodontid genera:

1. Second basibranchials present in adults. *Desmognathus, Leurognathus, Phaeognathus, Gyrinophilus, Pseudotriton, Stereochilus, Eurycea, Manculus, Typhlotriton, Hemidactylium, Haideotriton, Typhlomolge, Plethodon, Ensatina, Aneides.*
2. Second basibranchials absent in adults. *Hydromantes, Batrachoseps, Bolitoglossa, Oedipina, Pseudoeurycea, Chiropterotriton, Parvimolge, Lineatriton, Thorius.*

An extremely tiny second basibranchial, a small dot of ossified tissue, is present in the largest *Pseudoeurycea smithi* examined (73.2 mm.). Cope (1889) illustrated a second basibranchial in *Batrachoseps,* and Piatt (1935) reported a reduced second basibranchial, but Hilton (1947) and Uzzell (1961) say the structure is absent in their material. Second basibranchials are absent in seventy-seven *Batrachoseps* of five species examined by me. A very well developed but nonossified and noncalcified *inscriptio tendinis* is found in the longitudinal throat musculature of *Batrachoseps* in the same position as a second basibranchial, and less well developed structures are found in other genera of group 2. The element is ligamentous, not cartilaginous, and is considered a second basibranchial vestige by Tanner (1952).

The genera of group 1 may be further grouped on the basis of second basibranchial structure:

1. Width of second basibranchials in adults greater than length of first basibranchials. *Gyrinophilus, Pseudotriton, Eurycea, Manculus, Hemidactylium.*
2. Width of second basibranchials two-thirds to three-fourths times first basibranchials. *Stereochilus, Typhlotriton.*
3. Width of second basibranchials less than two-thirds times first basibranchials. *Desmognathus, Leurognathus, Phaeognathus, Plethodon, Ensatina, Aneides.*

Second basibranchials are very strongly triradiate with very long arms and long, medial, posteriorly extending processes in *Gyrinophilus, Pseudotriton, Eurycea, Manculus,* and *Typhlotriton.* The structures are distinctly triradiate, but have shorter lateral and posterior processes than the above genera in *Stereochilus, Typhlomolge,* and *Haideotriton.* In the latter genera, and in *Typhlotriton,* second basibranchials are somewhat cruciform with arms strongly swept posteriorly. Second basibranchials of remaining genera are usually bowed with arm-tips extended posterolaterally, and with no posteromedial projections. Small posteromedial enlargements may be present occasionally. Second basibranchials are notably reduced in size in *Phaeognathus* and some species of *Plethodon (e.g., dunni).*

Calcification

Calcifications of elements other than the second basibranchials occur in some genera. They are apparently not of universal occurrence in any single species or genus, and are more common in the larger members of a given population (Uzzell, 1961; Wake, 1963). The following list contains all observations of calcified elements known to me, and is a composite of my personal observations as well as those of Wiedersheim (1877), Piatt (1935), Hilton (1947a), and Uzzell (1961). Personal observations (*), unique observations (**):

1. Ceratohyals (calcification limited to region of posterior hook unless otherwise noted). Larval *Eurycea* (extensive, into expanded portions)**, *Eurycea***, *Typhlotriton***, *Hemidactylium***, *Batrachoseps***, *Oedipina* (extensive, at hook and into expanded portions)**.
2. First basibranchials (calcification usually limited to portions of central cores). *Desmognathus* (entire element)*, *Leurognathus***, *Manculus, Typhlotriton***, *Hemidactylium***, *Plethodon**, *Aneides***, *Lineatriton**, *Thorius***.
3. Cornua of first basibranchials. *Desmognathus***, *Leurognathus* (extreme proximal portions only)**.
4. First ceratobranchials (central portions). *Leurognathus* (proximal portions only)**, *Manculus, Hemidactylium***, *Parvimolge townsendi**, *Lineatriton**.
5. Second ceratobranchials (central portions or complete). *Leurognathus***, *Manculus, Hemidactylium***, *Parvimolge townsendi**, *Lineatriton**.
6. Epibranchials. Larval *Gyrinophilus**, larval *Eurycea**, larval *Stereochilus***, *Batrachoseps* (extreme distal tips)**, *Parvimolge townsendi* (proximal portions), *Lineatriton* (proximal portions).

Uzzell (1961) has recently reported sequence of calcification of hyobranchial elements in *Parvimolge* and *Lineatriton,* and has postulated close relationship on the basis of sequence similarities, as Rabb (1955) had earlier suggested. Calcification sequences reported by Uzzell are: (1) *Lineatriton,* second ceratobranchials-epibranchials-first basibranchials, (2) *Parvimolge townsendi,* second ceratobranchials-epibranchials, (3) *Manculus,* first basibranchials-second ceratobranchials-first ceratobranchials. In simple distribution *Leurognathus* and *Hemidactylium* resemble the condition reported in *Manculus* (all may have calcified first ceratobranchials, none have calcified epibranchials) more closely than that reported in *Parvimolge* and *Lineatriton* (both may have calcified epibranchials, none have calcified first ceratobranchials). Uzzell (1961) reports that the second ceratobranchials calcify before the first in *Manculus;* in at least some *Leurognathus* the opposite occurs.

Synthesis of hyobranchial characters

A synthesis of all of the above information concerning hyobranchial skeletal structure results in the following generic groupings (see Figs. 10 and 11):

1. *Desmognathus, Leurognathus, Phaeognathus.*
2. *Plethodon, Ensatina, Aneides.*
3. *Gyrinophilus, Pseudotriton, Stereochilus, Eurycea, Manculus, Typhlotriton, Haideotriton, Typhlomolge, Hemidactylium.*
4. *Hydromantes, Batrachoseps, Bolitoglossa, Oedipina, Pseudoeurycea, Chiropterotriton, Parvimolge, Lineatriton, Thorius.*

These groups correspond exactly with my proposed tribal grouping (see under systematic summary). At least one genus in each of the four groups has genioglossal muscles and is thus technically detoglossal (see Uzzell, 1961). Assuming the above groups to be natural, adetoglossy has arisen in parallel in groups 3 and 4 and may be evolving in group 2 (through *Ensatina*). Piatt (1935) also concluded that free tongues had arisen in parallel in groups roughly corresponding to my groups 3 and 4. He based his conclusions on the premise that the lingual cartilage, a supposed paleotelic character, was not present in *Hydromantes* and the neotropical genera. Tanner (1952) has discussed the illogic of this argument, and it has been shown (see above) that Piatt's data were incorrect. Nevertheless there is some congruence between Piatt's generic groupings, based on generalities concerning hyobranchial skeleton and four muscles, and mine.

Dentition

Each plethodontid tooth is composed of a crown and a pedicel (Parsons and Williams, 1962). In those genera with generally strengthened jaw closing adaptations *(Desmognathus, Leurognathus, Phaeognathus, Aneides)* the pedicels are particularly well developed. A remarkable situation is found in *Phaeognathus* in which the crowns are extremely shortened, very stocky, and blunted. The pedicels are very large and greatly strengthened, and are almost double the length of the crowns. Species with moderately to weakly developed skulls have relatively small, fragile pedicels.

All larval teeth are unicuspid, and during metamorphosis there is a gradual replacement with bicuspid crowns. Adult teeth are considerably variable as to shape and size, and both sexual and ontogenetic variation occur.

Maxillary, dentary, and vomerine teeth are normally bicuspid with large lingual cusps and small, crescentic labial cusps, but some exceptions occur (some *Aneides,* adult male *Hydromantes, Eurycea*).

Small individuals of all plethodontid species except *Aneides lugubris* have bicuspid premaxillary

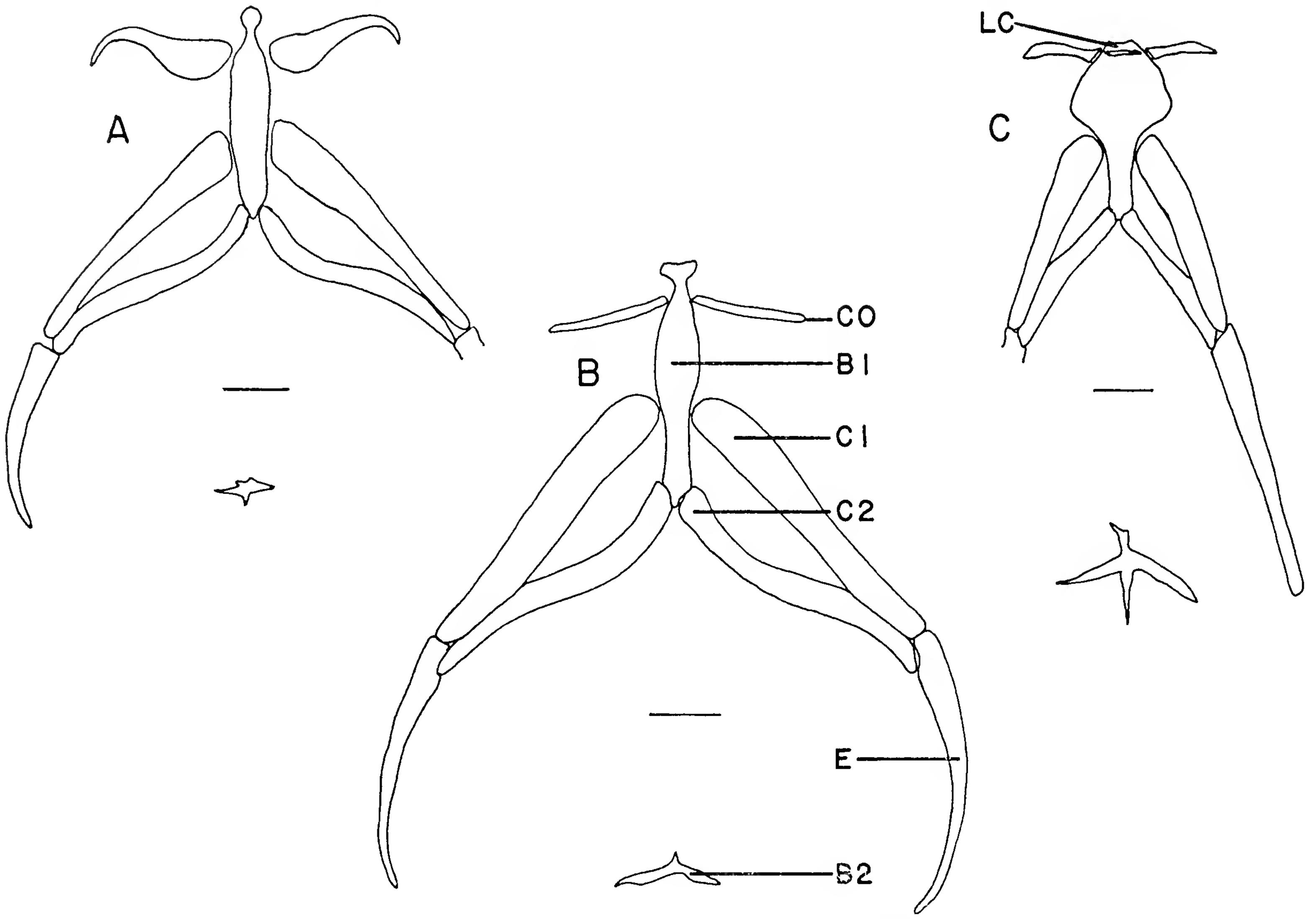


Figure 10. Hyobranchial apparatus. Ceratohyals removed. A. *Plethodon yonahlossee,* B. *Desmognathus quadramaculatus,* C. *Typhlotriton spelaeus.* Abbreviations: B1, first basibranchial; B2, second basibranchial; CO, cornua of first basibranchial, C1, first ceratobranchial; C2, second ceratobranchial; E, epibranchial; LC, lingual cartilage. Line equals one mm.

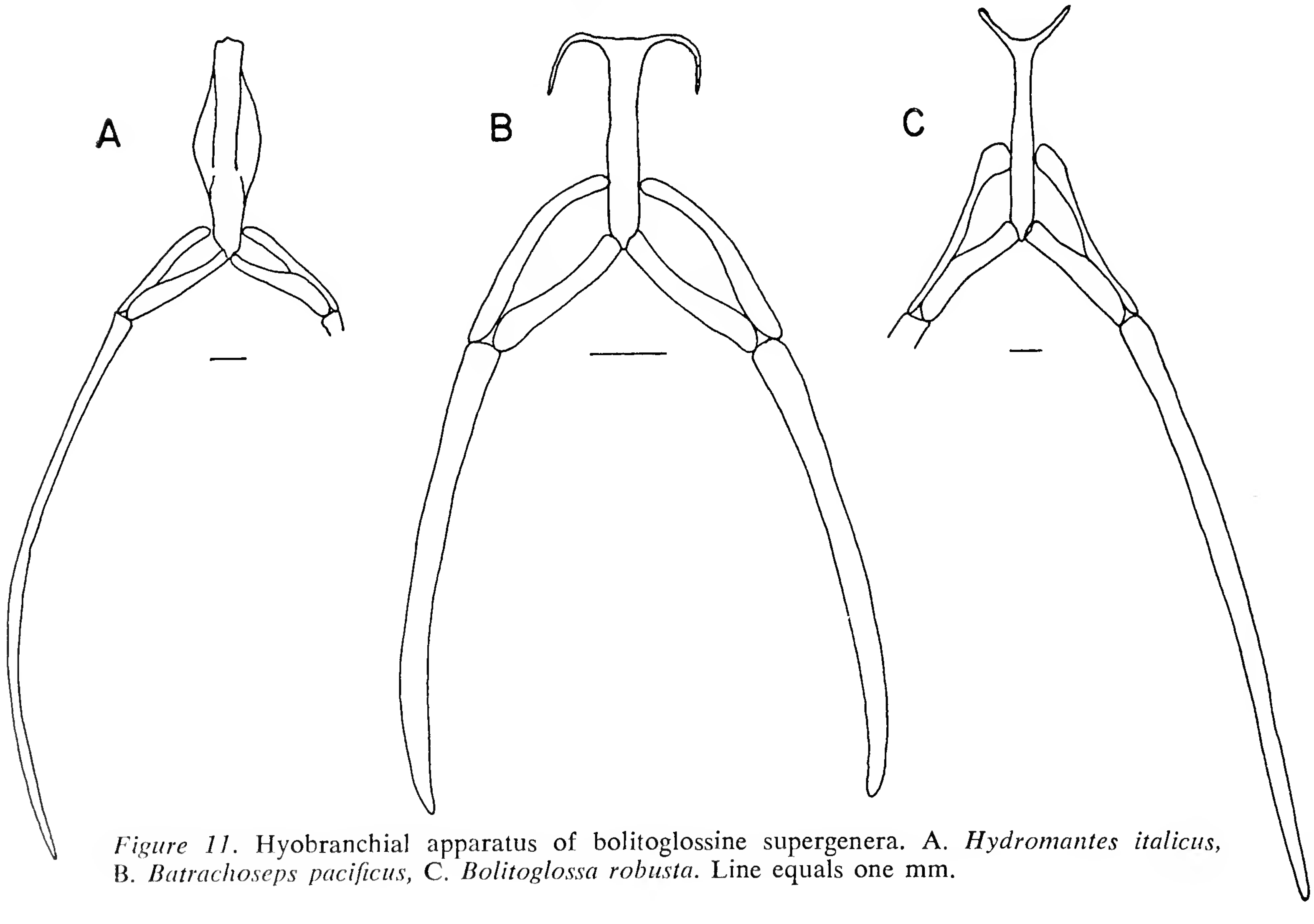


Figure 11. Hyobranchial apparatus of bolitoglossine supergenera. A. *Hydromantes italicus,* B. *Batrachoseps pacificus,* C. *Bolitoglossa robusta.* Line equals one mm.

teeth, and bicuspid teeth occur in adults of most species. Males of the more primitive genera *(Gyrinophilus, Pseudotriton, Stereochilus, Typhlotriton)* have premaxillary teeth that are only slightly modified, but the teeth are elongated and directed anteroventrally in adult males of at least some species of *Desmognathus, Leurognathus, Eurycea, Manculus, Hemidactylium, Plethodon, Aneides, Hydromantes, Batrachoseps, Bolitoglossa, Oedipina, Pseudoeurycea, Chiropterotriton, Lineatriton, Parvimolge,* and *Thorius.* The elongated teeth may be unicuspid and spine-like, or the labial cusps may be greatly elongated and either projected anteroventrally, or ventrally hooked (see also Noble, 1927 a). Hooked premaxillary teeth are common in male *Plethodon, Pseudoeurycea, Chiropterotriton,* and *Bolitoglossa.* Sexual dimorphism is more pronounced in advanced than in primitive genera, and elongated premaxillary teeth have unquestionably appeared more than once. There is no evidence that the character has disappeared and reappeared in the family, the views of Dunn (1927) and Noble (1927 a) to the contrary notwithstanding.

Maxillary teeth are greatly reduced in number or absent in some *Bolitoglossa (chica, colonnea, occidentalis, rufescens),* some *Oedipina (elongatus, alfaroi),* and most *Thorius.* It has been stated (Taylor, 1944; Smith and Taylor, 1948) that *Thorius* lacks maxillary teeth, but they occur in some numbers in several populations (see Gehlbach, 1959). Reduction in number of maxillary teeth also occurs in *Aneides,* especially in members of the *lugubris* species group (Wake, 1963). In general, it may be stated that reduction in maxillary dentition is a specialization encountered in highly specialized and advanced groups. Reduction in number coupled with hypertrophy in individual tooth size is also a specialized condition.

Vertebral Column

Regional differentation

A single cervical vertebra, the atlas, occurs in all salamanders. Trunk vertebrae in salamanders vary from 12 to over 60, and from 13 to 24 in plethodontids. A single sacral vertebra is typical of all salamanders, except sirenids. From 2 to 3 caudosacral vertebrae are present in plethodontids, but caudal vertebrae are extremely variable, and are subject to interspecific, individual, ontogenetic, and sexual variation in number.

Significant variation is encountered in the numbers of trunk vertebrae of plethodontids. Range and modal numbers of trunk vertebrae are presented in Table 1. The table is based primarily on my observations. Ranges of variation of trunk

TABLE 1. Variation in number of trunk and caudosacral vertebrae.

GENUS	TRUNK VERTEBRAE RANGE	TRUNK VERTEBRAE MODE	CAUDOSACRAL VERTEBRAE
Desmognathus	15	15	2
Leurognathus	15	15	2
Phaeognathus	21-23	22	2
Gyrinophilus	18-20	19	3
Pseudotriton	17-18	18	3
Stereochilus	18-20	19	3
Eurycea	14-21	15	3
Manculus	17-18	18	3
Typhlotriton	17-20	18	3
Typhlomolge	13-14	14	3
Haideotriton	14	14	3
Hemidactylium	15	15	3
Plethodon	14-24	17	3
Ensatina	14-15	14	3
Aneides	15-18	16	3
Hydromantes	13-14	14	3
Batrachoseps	16-21	20	2-3
Bolitoglossa	14	14	2
Oedipina	18-22	20	2
Pseudoeurycea	14	14	2
Chiropterotriton	14	14	2
Parvimolge	14	14	2
Lineatriton	14	14	2
Thorius	14	14	2

vertebrae doubtless will be extended for some genera, and I have relied on the literature for certain genera (*Phaeognathus* data from Brandon, 1965; *Typhlotriton* and *Gyrinophilus* from Brandon, 1966; *Plethodon* from Highton, 1962). A modal number of 14 is found in ten genera, four have modes of 15, one has 16, one has 17, three have 18, two have 19, two have 20, and one has 22. The genera thus cluster about the lower and higher extremes. A brief survey of the numbers of trunk vertebrae in relatively primitive families is instructive: *Salamandra* 14-15, *Salamandrina* 13, *Pachytriton* 12, *Chioglossa* 13, *Euproctus* 13, *Pleurodeles* 15, *Notophthalmus* 13, *Ambystoma* 14-16, *Rhyacotriton* 16-17, *Dicamptodon* 14-15, *Hynobius* 15-16, *Batrachuperus* 17, *Onychodactylus* 17. A tendency for low or relatively low numbers of trunk vertebrae in primitive groups is obvious. Numbers on the order of 13 to 17 are probably closer to the primitive plethodontid number than those from 18 to 24 range. Thus the relative constancy of the low vertebral number of most neotropical genera appears to be a primitive character in the otherwise specialized and advanced group.

Elongation, whether associated with increases in numbers of vertebrae or not, and attenuation have arisen in parallel a number of times in plethodontid evolution. Trunk elongation has appeared independently at least seven different times: (1) *Phaeognathus*, (2) *Gyrinophilus-Stereochilus*, (3) *Eurycea-Manculus*, (4) *Plethodon*, (5) *Batrachoseps*, (6) *Oedipina*, (7) *Lineatriton*. Attenuation has appeared at least as many times, and is found to some extent in *Phaeognathus, Stereochilus, Eurycea, Manculus, Typhlotriton, Plethodon, Aneides, Batrachoseps, Bolitoglossa, Lineatriton,* and *Oedipina*. Attenuation correlated with over-all size diminution is apparent in *Batrachoseps, Manculus, Chiropterotriton, Parvimolge,* and *Thorius*.

The elongation achieved in each major group of plethodontids usually involves both trunk and tail, and in most instances the numbers of trunk vertebrae increase. Several exceptions occur. In *Eurycea longicauda* and *E. lucifuga* generalized low numbers of body vertebrae are maintained, and the trunks are relatively non-elongated, but the numbers of caudal vertebrae are increased. In *Lineatriton* attenuation and elongation results in part from vertebral elongation. Elongation of *Oedipina* is accompanied by increases in the vertebral numbers of all species. The primitive *Batrachoseps wrighti* has relatively low numbers of trunk vertebrae (16-17), while the highly specialized species *(B. attenuatus, B. pacificus)* have high numbers (19-20). In two genera, *Eurycea* and *Plethodon*, great intrageneric variation is encountered; generalized species have low numbers of trunk vertebrae (*e.g., E. bislineata, E. longicauda, E. lucifuga,* 15-16; *P. vandykei* 15-16), but advanced, elongated species are also found (*E. multiplicata, E. tynerensis* 20-21; *P. cinereus, P. richmondi* 18-24). Elongation in some groups is correlated with increase in the numbers of trunk and caudal vertebrae *(Oedipina, Batrachoseps, Phaeognathus),* but only numbers of trunk vertebrae are noticeably increased in *Gyrinophilus* and *Stereochilus,* and tails are relatively short.

Most plethodontid genera have three caudosacral vertebrae, but two distinct generic groups have two: (1) *Desmognathus, Leurognathus, Phaeognathus,* (2) *Pseudoeurycea, Chiropterotriton, Lineatriton, Parvimolge, Thorius, Bolitoglossa, Oedipina* (*i.e.,* the neotropical genera). *Batrachoseps* is the only genus that shows variation in numbers of caudosacral vertebrae. *B. wrighti* and an undescribed species may have either two or three, but all other species have only two. Despite this fact, basal tail breakage is more common between caudal vertebrae one and two than in front of caudal one, and one is easily misled as to the number of caudosacral vertebrae. Most primitive salamanders have three or four caudosacrals, but *Cryptobranchus,* some species of *Ambystoma, Chioglossa,* and probably other genera, have only two. Three seems to be the standard number in most hynobiids, salamandrids, and ambystomatids, and is probably the primitive plethodontid number. Reduction in caudosacral numbers must have evolved in parallel in the family.

Accurate information concerning numbers of caudal vertebrae is difficult to obtain because of the common occurrence of autotomy or breakage of the tail and the regeneration of true vertebrae. In general most adult plethodontids have between 25 and 50 caudal vertebrae, but more than 50 are found in at least five genera: *Eurycea (lucifuga, longicauda), Manculus, Batrachoseps, Lineatriton,* and *Oedipina. Batrachoseps* and *Oedipina* commonly have more than 60, and *Oedipina,* with the longest tails in the family, often has more than 75 and may have 100 *(O. longissima).* Very short tails are present in *Hydromantes* and *Parvimolge;* maximum numbers of caudals in both are less than 25. Tail breakage is commonly encountered in all genera except *Hydromantes* and in some species of *Aneides (aeneus, ferreus, lugubris),* in which tails are used in locomotion. Tails are very stout proximally in *Desmognathus, Leurognathus, Phaeognathus, Gyrinophilus, Pseudotriton, Stereo-*

chilus, and in large species of other genera *(Eurycea, Aneides, Plethodon),* and breakage is usually limited to distal portions. Tails separate from the trunks at basal constrictions located just posterior to the last caudosacral vertebrae in *Hemidactylium, Ensatina, Bolitoglossa, Oedipina, Pseudoeurycea, Chiropterotriton, Parvimolge, Lineatriton,* and *Thorius,* but breakage can occur distally as well. In other genera breakage can occur at almost any point along the tail.

Cervical vertebra

Atlases of two very different types occur in the plethodontid genera. Vertebrae similar to those of primitive salamander families occur in the majority of the genera, but highly specialized elements are present in *Desmognathus, Leurognathus,* and *Phaeognathus.*

Primitive atlases have well developed, anteriorly directed, odontoid processes that bear large, laterally oriented facets that articulate with the inner walls of the foramen magnum. Anterior margins of the process are slightly concave, and the processes are deeply concave dorsoventrally. Paired enlarged condylar articulating facets which meet the occipital condyles are borne on stout anterolateral processes. The facets are almost flattened to slightly concave. Conical centra arise from the midpoints of the vertebrae and proceed posteriorly and just slightly ventrally. Neural arch pedicels arise on either side of the centra, meet dorsomedially, and form characteristic bony bosses where the mandibular adductor muscles attach. *Hydromantes, Bolitoglossa, Oedipina, Pseudoeurycea, Chiropterotriton, Parvimolge,* and *Lineatriton* have weakly fused pedicels, with little or no dorsal boss formation. The pedicels fuse without forming bosses in *Manculus, Batrachoseps (attenuatus, pacificus),* and *Thorius,* but some low ridges which serve as muscle attachments may be present. Median, anteriorly placed, raised nodes or nodule-like processes form in *Aneides, Plethodon, Eurycea, Typhlotriton, Typhlomolge, Haideotriton, Batrachoseps (wrighti), Pseudoeurycea (unguidentis, smithi), Chiropterotriton (nasalis),* and *Bolitoglossa (adspersa, cerroensis, dunni).* The nodules are crater-like in most, and especially in *Haideotriton* and *Typhlomolge.* Well developed, raised bosses are present in *Gyrinophilus, Pseudotriton, Hemidactylium, Ensatina,* and some *Aneides.* Well developed, nodule-like bosses are present on the posterior portions of the neural arches in *Stereochilus,* and are associated with well developed, vertical crests.

Highly specialized atlases are found in *Desmognathus, Leurognathus,* and *Phaeognathus.* Tension exerted by highly developed atlantal-mandibular ligaments (Fig. 9), holds the mandibles relatively rigid, and forces within the ligaments have been sufficiently great to result in the development of prearticular projections and marked posterior elevation of the atlas. The pedicels are fused in these genera, and very large, broad, dorsal bosses are present. The bosses are relatively low anteriorly, but rise steadily posteriorly. Precipitous drops occur posteriorly, and high, broad, bony cliffs are formed. The ligaments attach to posteriorly located, transverse ridges on top of the bosses. Because the mandibles are relatively fixed, the crania must be raised to open the mouths of members of these genera; such a situation is not encountered in other salamanders. Occipital condyles of *Desmognathus, Leurognathus,* and *Phaeognathus* are very convex, and articulate with enlarged, very concave, atlantal condylar facets. In addition the odontoid processes are very short. Ventral portions of the processes are greatly reduced, and the anterior margins are markedly concave and eroded. The lateral articular facets of the processes, which primitively articulate with the walls of the foramen magnum, are very small and fail to enter the foramen; rather they articulate with the inner, ventral portions of the condylar stalks. Because of these modifications, the cranio-atlantal joint is considerably more flexible in these genera than in other plethodontids.

The atlases of *Desmognathus, Leurognathus,* and *Phaeognathus* are raised above the level of the trunk vertebrae, and the centra are thus directed posteroventrally. The angle is so severe in *Desmognathus* that the dorsal, posterior surfaces of the centra are on about the same level as the odontoid processes. In preserved individuals elevation of the atlases over the trunk vertebrae is increased, apparently as a result of shortening of the mandibular-atlantal ligaments, and the result is the characteristic "pose" of the genera noted by many authors. The atlases of other plethodontids are not obviously raised.

Trunk vertebrae

Problems relating to vertebral structure and evolution are being studied currently by the author. Much of the information presented here must be considered preliminary, and no new information will be presented at this time concerning several aspects of vertebral morphology. In particular questions relating to the fate of the notochordal canal, the ontogeny of the intervertebral articulations, evolution of the vertebral centrum, and mechanism of tail autotomy are deferred to a later date. Reference is made to my earlier statements concerning these points (Wake, 1963).

Centrum structure

Central dimensions vary considerably in plethodontids, and are correlated to a large extent with elongation and relative thickness of trunk musculature. Posterior central diameter of adult, mid-trunk vertebrae is from about 2 to 2.8 times the central length (centrum ratio) in *Desmognathus*, *Leurognathus* and *Phaeognathus*. The smallest ratio is found in the elongated *Phaeognathus* in which the centra are relatively short and stout.

Typhlomolge and *Haideotriton* are short bodied, relatively weakly muscularized, aquatic genera for which the water's buoyancy provides the major body support, and in both the vertebral centra are small. Central ratios in both are about 3, and reflect the small size of the posterior portions of the centra rather than increased central length. Related genera (*Gyrinophilus, Pseudotriton, Stereochilus, Eurycea, Manculus, Typhlotriton* and *Hemidactylium*) have central ratios of from 2.2 to 2.5, and have neither very stout nor very elongated centra.

Relatively stout vertebral centra are present in *Ensatina* (centrum ratio 2.5) and *Aneides* (centrum ratio 1.8 to 2.4). *Plethodon* may be divided into two groups: (1) an eastern group with relatively stout centra and ratios of 2.5 to 2.8 (*cinereus, dorsalis, glutinosus, jordani, neomexicanus, ouachitae, richmondi, wehrlei, welleri*), (2) a western group with slenderer centra and ratios of 2.9 to 3.2 (*dunni, elongatus, larselli, vandykei, vehiculum*). I am unable to recognize the three major types of vertebrae in *Plethodon* proposed by Highton (1962).

Hydromantes vertebrae have ratios of 3 to 3.9, and the centra are somewhat elongated. Central diameter is relatively small. The slender, elongated species of *Batrachoseps* have small, semi-elongated centra with ratios of 3 to 3.5. The neotropical genera also have rather small centra. *Pseudoeurycea* and *Chiropterotriton* have relatively the largest centra and the lowest central ratios (2.5 to about 3). Centra are somewhat slenderer and more elongated in *Bolitoglossa* (ratios 2.8 to 3.5). Very slender, elongated centra with high ratios are found in the remaining genera (*Parvimolge* about 3, *Thorius* 3.4 to 3.7, *Oedipina* 3.0 to 3.5, *Lineatriton* 4.5). *Lineatriton* is an exceptionally elongated form that has maintained a primitive low number of trunk vertebrae. Elongation has involved pronounced elongation of the vertebral centra, and thus of the vertebrae.

All vertebrae of *Leurognathus* have ventromedial hypapophyses which are better developed than in any other genus. Hypapophysial keels are well developed on the anterior vertebrae of *Desmognathus*, but poorly developed posteriorly. Hypapophyses are best developed in large species (*D. quadramaculatus, D. monticola*), poorly developed in the small species (*D. aeneus, D. wrighti*). The best developed hypapophyses in the above genera are anteriorly placed, knob-like processes with small, posteriorly oriented keels, and small, posteriorly placed low keels. The keels may be continuous on anterior vertebrae in *Leurognathus*. The hypapophyses of *Phaeognathus* differ sharply from those of *Desmognathus* and *Leurognathus*. Well developed, uninterrupted keels extend virtually the full length of the centra on about the first seven vertebrae, and progressively lower keels, or low ridges, are present on the more posterior vertebrae. Anterior knobs, so conspicuous in the other genera, are poorly developed and obvious only anteriorly.

Remaining plethodontids lack well developed hypapophyses, but remnants occur in *Pseudotriton, Stereochilus, Eurycea* and very large *Typhlotriton*. Slight ridges are present on the posterior portions of the sixth vertebral centrum of *Pseudotriton*, and somewhat larger ridges are present on the posterior portions of centra three through six in *Stereochilus*. Small, keel-like projections are present on the posterior margins of centra four or five, or both, in *Eurycea bislineata*, and on centrum five in *E. aquatica*, but none occur in other species. Old *Typhlotriton* have a tiny vestige on centrum five.

Long, well developed, very stout, paired basapophyses are present on the posterior central margins in *Desmognathus* and *Leurognathus*, and the processes are only slightly less well developed in *Phaeognathus*. Basapophyses are well developed in many *Eurycea*, moderately developed in *Typhlotriton*, present on a few anterior vertebrae, but variously developed posteriorly in *Pseudotriton, Manculus*, and *Typhlomolge*, small and variously developed in *Hemidactylium* and *Stereochilus*, and virtually absent in *Haideotriton* and *Gyrinophilus*. *Ensatina* lacks basapophyses, and the processes are absent or only slightly indicated in *Plethodon* and *Aneides;* freely projecting processes are never present. The processes are absent in *Batrachoseps* and *Hydromantes*, and are irregularly distributed in the neotropical genera. Basapophyses are absent in *Oedipina, Pseudoeurycea, Parvimolge, Lineatriton*, and *Thorius*. Some *Chiropterotriton* (some individuals of *chiropterus, priscus, dimidiatus*) have variously developed and irregularly distributed, small processes. A number of presumably advanced members of the genus *Bolitoglossa* (*lignicolor*, *platydactyla, flaviventris, striatula, mexicana, salvinii)* have large, well developed, projecting basapophyses. Other *Bolitoglossa (borburata, cerroensis, occidentalis, rufescens, subpalmata)* have occasional small processes, and the remaining species have none.

Neural arch structure

Neural crests, primitively present in plethodontids, are subject to intergeneric, serial, and ontogenetic variation. A detailed discussion will be presented at a later date.

Hyperapophyses are moderately to well developed on the trunk vertebrae of all plethodontids, and two conditions are encountered: (1) hyperapophyses arise united and remain united on all, or almost all, trunk vertebrae, (2) hyperapophyses arise united or separated; if united, only on the anterior vertebrae, and separated posteriorly. Many kinds of variation are encountered, but *Leurognathus, Phaeognathus, Gyrinophilus, Pseudotriton ruber, Eurycea multiplicata, Ensatina, Hydromantes italicus, H. brunus,* and *H. genei* have condition 1. The remainder fall in group 2, except for peculiar conditions encountered in some species of *Desmognathus (monticola, quadramaculatus)* and in *Pseudotriton montanus* in which the hyperapophyses are divided on a few anterior vertebrae, but united on most vertebrae. In addition the hyperapophyses of *Typhlomolge* and *Haideotriton* are united for most of their lengths, but are separated at their tips. Hyperapophyses tend to be united in hynobiid salamanders, and united on most vertebrae in ambystomatids. In ambystomatids a tendency for division and elongation is apparent on the posterior vertebrae. It is apparent that united processes are more primitive than separated ones in salamanders in general, and probably in plethodontids as well. The genera of plethodontids in group 1 are relatively primitive, based on other characters.

Desmognathus, Leurognathus, and *Phaeognathus* differ from all other plethodontids in the possession of pterygapophyses on all or some trunk vertebrae (Fig. 9). The posterior margins of the neural arches extend posterolaterally above and beyond the postzygapophyses, and form wing-like or spine-like processes. The processes are always largest and longest on the first vertebrae, and gradually become reduced in size posteriorly. All trunk vertebrae of large *D. auriculatus* bear pterygapophyses, but the processes become progressively reduced in size posteriorly. Pterygapophyses are present on about the first seven vertebrae in *D. monticola,* with at least rudiments on all trunk vertebrae. In most *Desmognathus* pterygapophyses are well developed on the first three to five vertebrae, and are apparent to vertebrae eight to eleven. The processes are well developed only on the first one or two vertebrae of *D. quadramaculatus,* and are not apparent past the sixth vertebrae. No pterygapophyses are present in *D. wrighti.* Well developed processes that extend as spinous projections beyond the zygapophyses are present on the first four vertebrae of *Phaeognathus,* but the elements are reduced posteriorly and are not apparent past the ninth vertebra. Moderately developed pterygapophyses are present on the first vertebrae in *Leurognathus,* but they are very reduced by the fourth and only slightly indicated on more posterior vertebrae. The functional significance of pterygapophyses appears to lie in providing additional attachment sites for dorsal spinal muscles, which raise the skulls of the three genera to open their mouths.

Transverse processes

Diapophyses and parapophyses are long and well developed in *Desmognathus, Leurognathus,* and *Phaeognathus,* and extend far beyond the lateral zygapophysial margins. The posterolaterally directed processes are relatively straight. The centra of mid-trunk vertebrae are 0.7 to 0.9 times the distance across the parapophysial tips (centrum-parapophysial ratio). The parapophyses and diapophyses are entirely free, or are joined proximally only, in *Desmognathus* and *Leurognathus,* but are joined by thin bony webbing for their entire lengths in *Phaeognathus.* Parapophyses are directly below or just slightly anterior to the diapophyses. Alar expansions are usually present on the anterior margins of the parapophyses, especially on anterior and mid-trunk vertebrae. Alar processes are particularly well developed with distinct anterior projections in *D. monticola, D. quadramaculatus, Leurognathus,* and *Phaeognathus.* Well developed dorsal processes are present on the diapophyses and parapophyses of *D. monticola,* and slightly smaller processes are evident in *D. quadramaculatus* and *Leurognathus.* The processes correspond with raised processes on both rib heads.

Centrum-parapophysial ratios are about 0.8 to 0.85 in *Pseudotriton, Gyrinophilus,* and *Stereochilus,* about 1 in *Typhlomolge* and *Hemidactylium,* and 1 to 1.4 in *Eurycea, Manculus, Typhlotriton,* and *Haideotriton.* Parapophyses and diapophyses are moderately long and extend beyond the zygapophyses in *Gyrinophilus, Pseudotriton, Stereochilus, Typhlomolge,* and *Hemidactylium,* but are very shortened and do not extend (diapophyses) beyond the zygapophyses in *Eurycea,* *Manculus, Typhlotriton,* and *Haideotriton.* The diapophyses and parapophyses are fused proximally but free distally in *Pseudotriton, Gyrinophilus,* and *Stereochilus,* and are free for their entire lengths in *Eurycea, Manculus, Typhlotriton, Typhlomolge, Haideotriton,* and *Hemidactylium.* Parapophyses are slightly anterior to the diapophyses in *Gyrinophilus, Pseudotriton, Stereochilus,* and *Hemidactylium,* but are greatly in advance of the diapophyses in *Eurycea, Manculus, Typhlotriton, Typhlomolge,* and *Haideotriton.* In *Gyrinophilus* and allies the posterior margins of the parapophyses are located posterior to the anterior margins of the diapophyses. In *Eurycea* and allies the diapophyses are borne near the midpoints of centra, as in other plethodontids, but the parapophyses arise from the anterior one-third of the centra and are entirely in advance of the diapophyses. The advanced position of the parapophyses and the very short transverse processes of *Eurycea* and allied genera are unique characters among the plethodontids.

Centrum-parapophysial ratios of *Plethodon* and *Aneides* are from 0.85 to 1.2, and those of *Ensatina* are about 0.8. Diapophyses and parapophyses are moderately long and extend well beyond the zygapophyses. Transverse processes are separated completely in *Ensatina,* most *Plethodon,* and some individuals of *Aneides;* joined proximally but separated distally in some *Plethodon (wehrlei, cinereus)* and *Aneides (aeneus, ferreus);* and joined almost to their tips in some *Plethodon (elongatus, neomexicanus, richmondi)* and *Aneides (flavipunctatus, hardii, lugubris).* Parapophyses are either directly below or just slightly anterior to the diapophyses at their origins. Transverse processes are generally rather straight, and extend laterally with slight posterior angles (less than 30°) from the perpendicular with the vertebral axis. Alar expansions are generally absent, but relatively broad, shelf-like structures extend from the centra to points near the tips of the parapophyses both anteriorly and posteriorly in *A. lugubris,* and, to a lesser extent, in *A. flavipunctatus.*

Centrum-parapophysial ratios are 0.8 to 0.9 in *Hydromantes,* and the transverse processes are long, extending well beyond the zygapophyses. The transverse processes are initially straight, but may bend posteriorly past the midpoints of the centra. The processes are almost entirely separated in *H. platycephalus* and *H. shastae,* but may be joined for about one-half their lengths in *H. brunus.* The transverse processes of the European *Hydromantes (italicus, genei)* are joined proximally or are entirely separated on the first two vertebrae, joined to their tips on the third vertebra, and completely fused to form cylindrical processes with single distal articular facets on succeeding vertebrae. Apparently the parapophyses contribute most to the single processes, and the diapophyses are lost.

Centrum-parapophysial ratios are from 0.85 to 1.2 in *Batrachoseps,* and the transverse processes are long, extending beyond the zygapophyses. The processes are initially straight, but bend posteriorly just past their midpoints in a manner similar to *Hydromantes.* Transverse processes are separated for most of their lengths, but are joined for short distances proximally. As in *Hydromantes* the parapophyses are almost directly below the diapophyses. Alar expansion in *Batrachoseps* and *Hydromantes* is virtually nonexistent.

Centrum-parapophysial ratios are from 0.85 to 1.25 in *Bolitoglossa, Oedipina, Pseudoeurycea,* and *Chiropterotriton,* slightly more than 1 in *Parvimolge* and *Thorius,* and about 1.3 in *Lineatriton.* The *Lineatriton* ratio reflects elongated centra rather than shortened transverse processes. Transverse processes of all neotropical genera extend slightly to well beyond the zygapophyses. Transverse processes are completely separated or joined proximally only in *Chiropterotriton, Parvimolge, Thorius,* most *Pseudoeurycea,* and many *Bolitoglossa.* The processes are joined for most of their lengths in some *Pseudoeurycea (altamontana, smithi)* and many *Bolitoglossa (colonnea, dunni, engelhardti, marmorea, morio, orestes, platydactyla, rostrata, savagei, subpalmata).* The processes are initially separated in *Lineatriton,* but are completely joined past the third vertebra, and the diapophyses are lost by the fourth or fifth vertebrae; single processes are present on succeeding vertebrae. A similar situation is encountered in *Oedipina* in which single processes are present by the third or fourth vertebrae. *Lineatriton* and *Oedipina* resemble the European species of *Hydromantes* in this regard, and the character is not found elsewhere in the family. The parapophyses are borne almost directly below, or slightly in advance of, the diapophyses in most neotropical species. The parapophyses of some groups (some *Chiropterotriton* and especially *Parvimolge*) may be distinctly anterior to the origin of the diapophyses. Transverse processes are usually initially straight, but are slightly to distinctly bent posteriorly past their midpoints. The processes extend primarily laterally, but are slightly to moderately swept posteriorly in most genera, and are very strongly swept posteriorly in *Lineatriton* and *Oedipina.* Exceptions are *O. complex* and *O. parvipes* in which the processes are almost perpendicular to the vertebral axis. Slight anterior alar expansions are present on the parapophyses of several *Chiropterotriton (abscondens, multidentatus, nasalis)*. Very large alar expansions that form moderately broad shelves are present in front of the parapophyses in *Lineatriton*, and much smaller expansions are present posteriorly. Alar expansions are evident on the anterior margins of the parapophyses of several *Oedipina (inusitata, complex, bonitaensis, pacificensis, longissima)*, and may be drawn into anteriorly directed, pointed processes. Alar expansions are usually present but poorly developed in other *Oedipina*, and are poorly developed or absent in other neotropical genera than those discussed (see Tanner, 1950, for illustrations).

Caudal vertebrae

Tails of plethodontid salamanders are of three general types:

1. Very stout proximally, tapering distally. *Desmognathus, Leurognathus, Phaeognathus, Gyrinophilus, Stereochilus, Typhlomolge, Haideotriton.*
2. Relatively slender proximally, tapering somewhat distally. *Eurycea, Manculus, Typhlotriton, Plethodon, Aneides, Hydromantes.*
3. Constricted proximally, expanding beyond constriction, but tapering toward distal tips. *Hemidactylium, Ensatina, Bolitoglossa, Oedipina, Pseudoeurycea, Chiropterotriton, Parvimolge, Lineatriton, Thorius.*

Batrachoseps has slight indications of tail constriction, and rather bridges the gap between types 2 and 3. Some *Eurycea (e.g., E. longicauda)* bridge types 1 and 2.

First caudal vertebrae of *Ensatina* and *Hemidactylium*, and to a lesser extent, the neotropical genera, are highly specialized structures of importance in tail autotomy (see also Wake, 1963.) Detailed discussion is deferred to a later date.

Midcentrally located transverse processes are borne on virtually all caudal vertebrae of *Desmognathus, Leurognathus*, and *Phaeognathus*, and the processes are relatively stout, particularly in *Leurognathus*.

Transverse processes at midcentrum are moderately developed and present to about the tenth to eleventh caudal vertebrae of *Gyrinophilus, Pseudotriton, Manculus*, and *Typhlomolge*, to about the sixteenth of *Stereochilus*, and almost to the end of the tails of *Eurycea* and *Typhlotriton*. Small *Manculus* and *Eurycea*, and all *Haideotriton*, lack caudal transverse processes.

Hemidactylium has transverse processes on about the first nineteen vertebrae, and all but the first are midcentral.

Ensatina has rather poorly developed processes past the first vertebrae, and none occur past the tenth or eleventh vertebrae; all but the first few are located midcentrally. Transverse processes are somewhat better developed in *Plethodon*, and virtually all are midcentral. Midcentral processes are moderately developed and present on most caudal vertebrae of *Aneides*.

Cylindrical, midcentral transverse processes are present on most caudal vertebrae of *Hydromantes*. *Batrachoseps* has rather complex, broad-based, strutted processes on most caudal vertebrae in intermediate positions; some processes are at the anterior ends of the centra, while others are slightly posterior but ahead of midcentrum. *Bolitoglossa, Oedipina, Pseudoeurycea, Chiropterotriton, Parvimolge, Lineatriton*, and *Thorius* all have transverse processes on virtually all caudal vertebrae; the processes are located at the anterior ends of the centra and are swept moderately to strongly anteriorly.

Unusual neural crests are found in *Oedipina*; usually only the first one or two caudal vertebrae (but as many as ten) have single medial crests. Commencing on about the second vertebra the crests divide and form double, parallel crests on either side of the midline. The crests are broadest basally and angle toward one another dorsally. Double caudal crests are constant, unique characters of *Oedipina*.

Ribs

Ribs vary considerably in length in the family, and also vary serially within individuals. Mid-trunk ribs are from 0.6 to 0.75 times the transparapophysial distance (rib-parapophysial ratio) in *Desmognathus* and *Leurognathus*, but are relatively short in *Phaeognathus* (0.4). Ratios are from 0.65 to 0.8 in *Gyrinophilus, Pseudotriton, Stereochilus*, and *Hemidactylium*, about 0.9 in *Typhlomolge*, about 1 to 1.2 in *Manculus, Typhlotriton*, and *Haideotriton*, and from a little over 1 to about 1.5 in *Eurycea*. *Ensatina* has relatively short ribs (0.6), but ribs are longer in *Plethodon* (0.67 to about 1) and longer still in *Aneides* (0.85 to 1.25). *Hydromantes* and *Batrachoseps* have moderately short ribs with ratios of about 0.6 to 0.75. A distinct trend toward rib shortening is encountered in the neotropical genera. The trend is best exemplified by the genus *Chiropterotriton* in which relatively primitive species have moderately long ribs (*priscus*, ratio 1), but more specialized species have short ribs (*abscondens*, ratio 0.35-0.4). Rib-parapophysial ratios are about 0.75 to 0.8 in *Thorius*, 0.4 to 0.75 in *Pseudoeurycea* (lowest figure in *altamontana*, highest in *werleri*), 0.4 to 0.67 in *Bolitoglossa*, (lowest figure in *adspersa*, highest in *engelhardti*), 0.9 in *Parvimolge townsendi*, and 0.5 in P. *richardi*. Ribs are especially shortened in *Oedipina* (0.2-0.3) and *Lineatriton* (0.2-0.25). Members of the latter two genera are elongate, attenuate forms, and the shortened and reduced ribs are probably related to the change in habitus.

Rib heads are of moderate length and are well separated in most genera. The heads are greatly separated and rather long in *Eurycea, Manculus, Typhlotriton, Typhlomolge*, and *Haideotriton*. Rib heads are rather short in *Batrachoseps*. Fusion of the rib heads occurs in *Aneides lugubris, Hydromantes brunus, Phaeognathus*, some *Batrachoseps attenuatus, Pseudoeurycea altamontana, Bolitoglossa orestes*, and *B. subpalmata*. Usually the last one or two ribs of all species are unicipital. In *Hydromantes genei, H. italicus*, and in all species of *Oedipina* only the first three or four pairs of ribs are bicipital, and the remainder are unicipital. All but the first four or five pairs of ribs are unicipital in *Lineatriton*.

Limb Elements

Primitively plethodontid limb bones have cartilaginous heads, but calcifications occur in all *Thorius, Lineatriton, Parvimolge*, and some individuals of *Oedipina*. Apparently these calcifications are strengthening compensations for paedomorphic weakening.

Relative limb length is highly variable, and description is made more complex by allometric growth and ontogenetic, sexual, geographic, interspecific, and intergeneric variation. Certain of the attenuate genera *(Phaeognathus, Stereochilus, Manculus, Batrachoseps, Oedipina, Lineatriton, Parvimolge, Thorius)* have obviously shortened limb elements. Long limbs tend to be the end result of trends toward increased scansorial activity in several forms *(Eurycea lucifuga, Aneides lugubris, A. aeneus, A. ferreus)*. Moderately long limbs are present in *Ensatina, Hydromantes*, and primitive species of *Plethodon* and *Bolitoglossa*. Hind limbs are much longer and stouter than the fore limbs in *Desmognathus, Leurognathus*, and *Phaeognathus*. Fore limbs are a little shorter than the hind limbs in other genera, but the limbs are of about equal length in *Ensatina*. Femurs are always longer than humeri except in *Ensatina* where the situation is reversed. Limb length apparently increases as the species of *Eurycea* become increasingly troglobitic (see Mitchell and Reddell, 1965). The relatively longest limbs in the family are encountered in the extremely specialized troglobite, *Typhlomolge*. The elongated limbs of troglobitic species may be adaptations which enable the salamanders to walk about quiet cave pools with their bodies elevated above the bottom debris.

Distinct, well developed tibial spurs are present in most genera. The spurs are truncate and reduced in *Typhlotriton*, and are small and very slender in *Typhlomolge* and *Haideotriton*. *Ensatina* lacks tibial spurs, but well defined dorsal ridges are present. Very small tibial spurs, borne on the midsections of the bones and falling far short of the proximal ends, are found in *Hydromantes*. The spurs are present in most species of *Batrachoseps*, but are absent in most populations of *B. attenuatus*. A trend toward spur reduction is apparent in neotropical genera, reduced spurs being present in *Lineatriton, Parvimolge townsendi*, most *Pseudoeurycea, Chiropterotriton*, and *Thorius*, and in some *Bolitoglossa (dunni, engelhardti, helmrichi, rufescens)*. Spurs are absent in all *Oedipina*, most *Bolitoglossa*, some *Chiropterotriton (bromeliacia, nasalis, xolocalcae)*, and some individuals of various species of *Thorius* and *Pseudoeurycea*.

Mesopodial Elements

Primitively eight carpals and nine tarsals are present *(Desmognathus, Leurognathus, Phaeognathus, Gyrinophilus, Pseudotriton, Stereochilus, Eurycea, Typhlotriton, Haideotriton, Typhlomolge, Plethodon, Ensatina, Hydromantes, Pseudoeurycea)*. All have primitive carpi with ulnars and centrals separated except *Hydromantes* and *Pseudoeurycea* in which the elements are in contact. All of the above genera have primitive tarsi with fourth distal tarsals much larger than the fifth, which are the only tarsals that do not touch the centrals.

Aneides differs from the above genera in that the ulnars articulate extensively with the centrals, and the fifth distals are the largest tarsals and articulate broadly with the centrals. The intermedia and ulnars are fused in all carpi of *A. hardii*, and seven carpal elements are present.

The remaining genera have reduced numbers of carpals, tarsals, or both, in some or all species. *Batrachoseps, Manculus*, and *Hemidactylium* have lost their fifth toes, and have also lost the fifth distal tarsals. *Manculus, Hemidactylium, Batrachoseps wrighti*, and some populations of *B. pacificus* have eight carpals, but other *Batrachoseps* have seven, the result of fusion of ulnars and intermedia.

Tarsal patterns similar to those in *Aneides* are encountered in several *Chiropterotriton (abscondens, arboreus, chiropterus, dimidiatus, multidentatus, priscus),* but in two advanced species *(xolocalcae, bromeliacia)* the primitive plethodontid pattern is found. Another advanced species, *C. nasalis,* has seven carpals and eight tarsals as a result of radial-intermedial and fourth and fifth tarsal fusions. *C. abscondens* may have seven or eight mesopodial elements as the result of ulnar-intermedial or third and fourth carpal, and fourth and fifth tarsal fusions. All ankles of three individuals have seven tarsals; wrists usually have seven carpals, but one wrist each of two individuals has eight.

The tarsal patterns unique to *Aneides* and the primitive species of *Chiropterotriton* apparently have functional and evolutionary significance. In the primitive plethodontid tarsus the lines of force from the first, second, third, and fourth digits are directed through the first three distal tarsal elements to the large centrals. Lines of force from the fifth digits are directed through the relatively small fourth distal elements (distal tarsal 5) to the fibulars. The relative weakness of this arrangement is illustrated by parallel loss of the fifth distal tarsals and digits in three genera. The arrangement in *Aneides* and *Chiropterotriton* is one in which all lines of force are relatively straight, and all are directed to a single pivotal point in each tarsus, the centrale (see illustrations in Wake, 1963). Since the lines of force emanate from single points, they may be swung or rotated about these points. Relatively greater spread across the outer digital tips than in the primitive arrangement is thus possible; the increased spread has obvious advantages for organisms with climbing propensities. Both *Aneides* and *Chiropterotriton* contain species that are adept climbers. Apparently their mesopodial arrangement is a prospective adaptation that has significant adaptive value in arboreal and scansorial but not terrestrial organisms.

Parvimolge townsendi has six or seven carpal elements as a result of ulnar-intermedial and possible fourth distal carpal-central fusions. Distal tarsals 4 and 5 have fused, and eight tarsal elements are present.

A peculiar and unique situation is encountered in *Lineatriton.* Eight tarsal elements are present and distal tarsal 5 has fused with the fourth or has been lost; metatarsal 5 extends into the area seemingly vacated by the tarsal. Eight carpals are present.

Ulnar-intermedial and fourth distal carpal-central fusions result in six carpals in *Thorius.* Distal tarsals 4 and 5, the intermedia and fibulars, and distal tarsals 4 and 5 and the centrals may fuse, and six to eight tarsals result. Intraspecific variation is present in *Thorius,* and individuals may vary by one element from one side to the other.

Eight tarsal elements are present in most *Bolitoglossa* as a result of fusion of distal tarsals 4 and 5. A tendency for elimination of the third distal carpals from their articulation with the centrals, and subsequent reduction of carpal size, is apparent within the genus, especially in the group of species associated with *B. dunni* and *B. engelhardti.* Distal carpals 1 and 2 meet distal carpals 4 and distal carpals 3 are effectively walled-off from articulation with the centrals. The trend culminates in *B. occidentalis* and *B. rufescens* in which distal carpals 3 and 4 fuse to form single, strengthened, more efficient elements, and seven carpals result. A similar situation is encountered in the tarsi of *B. occidentalis* and *B. rufescens,* in which distal tarsals 3, 4, and 5 fuse, and seven tarsal elements are present. This condition is also encountered in one of three *B. platydactyla* examined.

The most extreme mesopodial specializations occur in *Oedipina.* The limbs, hands and feet are greatly reduced in size, and are considerably less functional than in primitive members of the family. From five to seven carpal and from five to eight tarsal elements are present as the result of the following fusions (arranged in probable fusion sequence): ulnar-intermedial, distal carpal 4-central, distal carpals 1, 2, and 3; distal tarsals 4 and 5 (fused in all species), distal tarsals 4, 5, and central, fibular-intermedial. Species of *Oedipina* vary as follows in the number of mesopodial fusions: *bonitaensis* 6 carpals, 7 tarsals; *complex* 6, 6; *cyclocauda, uniformis* 7, 7-8; *gracilis* 5, 5-7; *inusitata* 6, 6; *longissima* 6, 7; *pacificensis* 6, 7; *poelzi* 7-8, 7-8; *syndactyla* 6, 6; *sp. nov.* 7, 7-8.

In *Oedipina* in which the third distal tarsals are not fused with some other elements, they are very small and resemble the condition in *Thorius.* Further similarities of the two genera are the reduction in size of distal carpals and tarsals 1 and 3, and shifts of the articulation of the first metacarpals and metatarsals from distal elements to centrals 1. The latter condition is also found in some specialized *Chiropterotriton (e.g., abscondens).*

Mesopodial calcifications of probably functional and phylogenetic significance occur in certain plethodontids. Cope (1869) stated that *Thorius* has ossified mesopodial elements, and differs in this character from other plethodontids. Rabb (1955) reported calcified mesopodials in *Parvi-*

molge townsendi. Uzzell (1961) found mesopodial calcifications in only twelve of thirty-four adult *Thorius,* thirteen of seventeen *Parvimolge townsendi,* and three of thirteen *Lineatriton.* He found eight tarsals calcified in twelve ankles of seven individuals of *Thorius,* with lesser numbers in other species. Uzzell suggested the following calcification sequences: (1) carpus. intermedium-ulnare; radiale, centrale 1, or carpals 1 and 2; carpal 3; (2) tarsus. outer-most tarsal (either tarsals 4-5, or tarsals 4-5-centrale); intermedium; fibulare, or centrale; tibiale, or tarsals 1-2; tarsal 3, or centrale 1. Uzzell used slightly different terminology and calls centrals 1 of the carpi and tarsi the first carpals and tarsals, respectively.

Sequence of calcification in *Parvimolge* and *Lineatriton* was not determinable, but Uzzell reported six elements with as many as eight centers of calcification in *Parvimolge* carpi, and eight tarsal elements with as many as six calcifications. *Lineatriton* was reported to have from one to five carpal and from one to three tarsal calcifications.

Uzzell (1961) suggested that fusion of the intermedia and ulnars, and close approximation of the intermedia and fibulars reflect concentration of locomotor forces. In both wrists and ankles the outer or postaxial mesopodials fuse before the inner or preaxial elements, and it is likely that these are the elements of greatest importance in force transmission. Mesopodial fusions are far more common in the preaxial than in the postaxial portions of the carpi and tarsi throughout the family. However, fusions (*e.g.,* distal elements 1 and 2) are present in the preaxial portions of all plethodontids, and using Uzzell's reasoning for postaxial regions, the preaxial area might be the most significant primitively with the postaxial portion gaining importance secondarily.

Rabb (1955) interpreted several characters of *Parvimolge townsendi* to be the result of paedomorphosis, and Uzzell (1961) suggested that calcified mesopodials may compensate for the paedomorphic and presumably weak condition of the adult feet of *Lineatriton, Parvimolge,* and *Thorius.* Uzzell also suggested that calcified mesopodials of *Parvimolge* and *Lineatriton* reflect possible close relationship, but thought the conditions in *Thorius* might be due to parallelism.

The only material available to me of *Parvimolge townsendi* has been that used by Uzzell. I am unable to add to his data. Some, all, or none of the carpals and tarsals of *Thorius* may be calcified. The maximum numbers of calcifications observed by me in *Parvimolge* are five carpals (ulnare-intermedium, centrale, centrale 1, distal carpal 4, radiale) and seven tarsals (fibulare, intermedium, centrale, centrale 1, distal tarsals 1-2, 3, 4-5). I have not seen calcified mesopodials in *Lineatriton.*

Calcifications occur in several additional genera. Mesopodial calcifications observed include: fibulars of one *Desmognathus quadramaculatus;* fibulars and tarsal intermedia of two *Desmognathus ocoee* (three ankles); carpal and tarsal intermedia and fibulars of a single *Leurognathus;* tarsal intermedia, fibulars, distal tarsals 5, one radiale, and one distal tarsal 1-2 of one *Eurycea bislineata;* tarsal intermedia and fibulars of one *Typhlotriton;* tarsal and carpal intermedia, ulnars, fibulars, tarsal centrals 1, distal carpals 1-2, 3, 4, and distal tarsals 1-2, 3, 4, 5 of a single *Ensatina;* distal carpals 1-2 of a single *Plethodon neomexicanus;* distal carpals 1-2 and one distal tarsal 1-2 of a single *Pseudoeurycea unguidentis;* one ulnare, fibulars, one tibiale, distal carpals 4, one distal tarsal 1-2, and distal tarsals 4-5 of one *Chiropterotriton abscondens;* and ulnar-intermedia, fibular-intermedia, tibials, carpal centrals, centrals 1, radials, distal carpals, 1-2, distal tarsals 4-5, and one distal tarsal 1-2 of a single *Oedipina sp. nov.*

It is apparent that mesopodial calcifications have appeared independently in several evolutionary lines, but calcification is certainly more common in *Parvimolge townsendi* and *Thorius,* and probably in *Lineatriton,* than in the other plethodontid genera. Postaxial calcifications predominate, but preaxial calcifications appear first in some individuals. The most serious objections to Uzzell's (1961) suggestions concerning the functional significance of mesopodial fusions and calcifications are the preaxial distal elements 1 and 2 fusions universal in the family, and the tendency for loss of the fifth toes and fifth distal tarsals in the postaxial regions in several evolutionary lines.

Digits

Primitive plethodontids have four fingers and five toes, and the primitive phalangeal fomulae are 1-2-3-2 for each hand and 1-2-3-3-2 for each foot. Such formulae are characteristic of all *Desmognathus, Leurognathus, Phaeognathus, Gyrinophilus, Pseudotriton, Stereochilus, Eurycea, Typhlotriton, Haideotriton, Typhlomolge, Ensatina, Aneides, Hydromantes, Pseudoeurycea, Chiropterotriton,* and *Parvimolge. Hemidactylium, Manculus,* and *Batrachoseps* have lost the fifth toes and one phalanx from each fourth toe; the foot formula is 1-2-3-2 (rarely 0-2-3-2 in *B. attenuatus*). Single phalanges have been lost from the fifth toes of most individuals of two species of *Plethodon (larselli, neomexicanus)* and the formula is 1-2-3-3-1; all other *Plethodon* have the primitive formula. Some *Lineatriton* have the primitive formula, but reductions may occur to 1-2-3-1 in the hand and 1-2-3-2-1 in the foot. *Thorius* may have the primitive formulae, but intra- and interspecific variation occurs and formulae variations are: hand (0-1)-2-3-(1-2), foot (0-1)-2-3-(2-3)-(1-2). Most species of *Bolitoglossa* retain the primitive formulae, but *B. occidentalis* has lost one phalanx from each fourth toe (foot 1-2-3-2-2), and formulae variations in *B. rufescens* are: hand (0-1)-(1-2)-(2-3)-(1-2), foot 1-(1-2)-(2-3)-(2-3)-(1-2). Extensive phalangeal reduction occurs in *Oedipina,* in which only certain *O. poelzi* and *O. sp. nov.* retain the primitive formulae; formulae variations are: hand (0-1)-(1-2)-(2-3)-(1-2), foot (0-1)-2-(2-3)-(2-3)-(1-2). The commonest reductions occur in digits one, four, and five of the feet, and digits one and three of the hands.

A tendency for reduction of phalangeal elements and loss of digits in the postaxial portions of the hands and feet is evident. Reduction is most commonly encountered in attenuate, short-limbed species. Uzzell (1961) has suggested that the postaxial portions of the carpi and tarsi are the areas of greatest transmission of forces from the lower limbs to the digits, but postaxial phalangeal and digital reductions suggest that other areas may be as important.

SYSTEMATIC SUMMARY

Family Plethodontidae

Definition: adults lungless with nasolabial grooves, no bony pterygoids, no lacrimals, otic and occipital elements fused, columellae fused with opercula or absent, vomers with anterior laterally oriented tooth series and posterior multiple series borne below parasphenoids, no angulars; larvae present or absent, if present with three or four epibranchials, fused premaxillae, teeth on premaxillae, vomers, palatopterygoids, dentaries, and coronoids.

Range: eastern and western North America with some species in central regions; Middle America from Tamaulipas and Nuevo Léon in northeastern Mexico and Nayarit in western Mexico to eastern Brazil and central Bolivia; the Maritime Alpes of southeastern France, the Piedmont of Italy, and the island of Sardinia.

Content: two subfamilies, twenty-three genera, about one hundred eighty-four species.

Subfamily Desmognathinae

Definition: plethodontid salamanders having four rather than three larval epibranchials, a unique mouth opening mechanism by means of which the mandibles are held relatively rigid and the skulls proper are raised, extensive skeletal and muscular modifications related to functional changes in mouth opening mechanics, and pterygapophyses and well developed hypapophysial keels on anterior trunk vertebrae.

Characterization: (1) skulls rigid, depressed, streamlined, composed of dense, heavy bones, (2) larvae lack protruding gill rami, (3) larval skulls composed of ossified premaxillae, frontals, parietals, occipito-otics, opercula, vomers, palatopterygoids, parasphenoids, quadrates, squamosals, dentaries, prearticulars, and coronoids, (4) four larval epibranchials, (5) larval vomers in broad median contact, (6) larval palatopterygoids well separated from quadrates, (7) unicuspid larval teeth, bicuspid adult teeth, (8) single larval and adult premaxilla, (9) premaxillae very broad and depressed, internasal fontanelles small or closed over, (10) frontal processes of premaxillae stout and broad, arise broadly from toothed portions, (11) maxillae long, extend beyond eyeballs, small to large posteromedially oriented jugal processes present, (12) maxillary facial lobes very large, articulate extensively with frontals, (13) palatal shelves of premaxillae and maxillae very broad, (14) septomaxillae present, but reduced, (15) nasals small, articulate firmly with maxillae and premaxillae, (16) prefrontals absent, (17) vomerine preorbital processes toothless, (18) anterior vomerine teeth present or absent, (19) anterior vomerine teeth discontinuous, (20) posterior vomerine teeth borne in dense, separated patches, (21) anterior portions of frontals very large, expanded, occupy prefrontal and antorbital regions, (22) frontals flat dorsally with sharp angular ridges along orbital borders, bones uncovered by musculature, (23) deep parietal-otic troughs extend as bony processes into orbits, (24) well developed crests border posterolateral margins of parietal-otic troughs, (25) large posterolateral parasphenoid processes, (26) parasphenoids relatively short, abut against posterior margins of vomers in simple articulations, (27) quadrates very large, articulate with parasphenoids and occipito-otics, cartilaginous portions of suspensoria relatively small, (28) orbitosphenoids large, well developed, quadrangular, (29) squamosals large, solidly anchored to skulls, (30) occipital condyles stalked, (31) columellae short, stocky, rather flattened, (32) dentition well developed, (33) meckelian grooves essentially closed, dentaries O-shaped anteriorly, (34) detoglossal; genioglossal muscles present, (35) cornua elongate, attaching to first basibranchials behind anterior extensions of latter, (36) lingual cartilages absent, (37) well developed first basibranchial anterior extensions, (38) no marked anterior first basibranchial expansion, (39) first ceratobranchials longest of articulated hyobranchial elements, (40) first ceratobranchials considerably larger than second, (41) epibranchials less than 1.25 times first basibranchials, and shorter than first ceratobranchials, (42) second ceratobranchials short, less than two-thirds length of first basibranchials, (43) atlases large and stout, bear very large, markedly concave, condylar articular facets, (44) odontoid processes of atlases very small, (45) posterior margins of atlases very large, broad, markedly raised, (46) fifteen or twenty-one to twenty-three trunk vertebrae, (47) two caudosacral vertebrae, (48) larval vertebrae structurally amphicoelous, intervertebral cartilages become calcified in adults and resemble classical opisthocoelous condition, (49) hypapophysial keels well developed on at least the first few trunk vertebrae, or on all trunk vertebrae, (50) hyperapophyses well developed, tend to be united, but may be divided on anterior vertebrae, (51) well developed, stout basapophyses on posterior central margins, (52) pterygapophyses present on some anterior trunk vertebrae, (53) parapophyses and diapophyses long, separated or fused, (54) centra shorter than distance across tips of parapophyses, (55) ribs usually absent on last trunk vertebrae, (56) ribs less than 0.75 times distance across parapophyses, (57) tails stout proximally, no basal constriction, (58) well developed tibial spurs, (59) hind limbs much larger than fore limbs, (60) fingers and toes long and slender with distinctive tendon arrangements and fleshy palms, (61) eight carpals and nine tarsals, (62) distal tarsals 5 do not articulate with central tarsals, (63) four fingers and five toes, (64) phalangeal formulae 1-2-3-2, 1-2-3-3-2, (65) adults aquatic to terrestrial, (66) aquatic larvae in most, but trends toward direct terrestrial development, (67) pigmented, lobed testes in old males, (68) small gularis muscles present posterior and external to very large quadrato-pectoralis muscles.

Content: three genera—*Desmognathus, Leurognathus, Phaeognathus.*

Desmognathus Baird, 1850

Definition: desmognathine salamanders with fifteen trunk vertebrae; small maxillary jugal processes; internal nares open medially; vomerine preorbital processes well separated from vomers proper, and not extending laterally beyond vomer bodies; an internasal fontanelle; vomers and premaxillae joined by septum-like processes which form fontanelle borders; hypapophysial keels well developed on anterior trunk vertebrae, not present or only slightly indicated on posterior vertebrae; neural crests present only on first two or three trunk vertebrae; parapophyses and diapophyses separated for most of lengths; ribs more than one-half the distance across parapophyses; stout, stocky habitus; limbs moderately long; aquatic larvae, or direct development.

Range: eastern North America, particularly in Appalachian Mountain region.

Content: *aeneus* Brown and Bishop, 1947; *auriculatus* (Holbrook, 1838); *fuscus* (Rafinesque, 1820); *monticola* Dunn, 1916; *ochrophaeus* Cope, 1859; *ocoee* Nicholls, 1949; *quadramaculatus* (Holbrook, 1840); *wrighti* King, 1936.

Leurognathus Moore, 1899

Definition: desmognathine salamanders with fifteen trunk vertebrae; small maxillary jugal processes; internal nares open laterally near lateral margins of vomers; vomerine preorbital processes slightly separated from vomers proper, extend laterally beyond vomer bodies; only in young an internasal fontanelle which becomes progressively closed during ontogeny; skulls strongly depressed, premaxillae and vomers in close proximity with no septum-like connecting processes; hypapophysial keels strongly developed on all trunk vertebrae, particularly anteriorly; neural crests present only on first two or three trunk vertebrae; parapophyses and diapophyses separated for most of lengths; ribs more than one-half the distance across the parapophyses; stout, stocky habitus; limbs moderately long; aquatic larvae and adults.

Range: southern Appalachian Mountains of eastern United States.

Content: *marmoratus* Moore, 1899.

Phaeognathus Highton, 1961

Definition: desmognathine salamanders with twenty-one to twenty-three trunk vertebrae; very large, expanded maxillary jugal processes that extend almost to quadrates; internal nares open medially; vomerine preorbital processes well separated from vomers proper, extend laterally beyond vomer bodies; an internasal fontanelle; vomers and premaxillae joined by septum-like processes which form fontanelle borders; anterior cranial elements sculptured; hypapophysial keels present on all trunk vertebrae, best developed anteriorly; neural crests present on all trunk vertebrae; parapophyses and diapophyses joined for virtually entire lengths; ribs less than one-half the distance across the parapophyses; stout but elongated habitus with extremely long trunks and long, attenuated tails; limbs and digits markedly shortened; life history unknown, but adults are terrestrial burrowers.

Range: known only from the pine woods of the Coastal Plain in south-central Alabama.

Content: *hubrichti* Highton, 1961.

Subfamily Plethodontinae

Definition: plethodontid salamanders having less than four larval or embryonic epibranchials, normal salamander mouth opening mechanisms in which the skulls proper remain relatively rigid and the mandibles are lowered, and trunk vertebrae which lack pterygapophyses and well developed hypapophyses.

Characterization: (1) skulls variable in shape and rigidness, usually relatively broad, moderately high, and not strongly constructed; distinct tendencies in many groups for skull reduction and weakening, (2) larvae with protruding gill rami, (3) larval skulls comprised of ossified premaxillae, frontals, parietals, occipito-otics, opercula, vomers, palatopterygoids, parasphenoids, quadrates, squamosals, dentaries, prearticulars, and coronoids, (4) three larval epibranchials, (5) larval vomers in narrow anteromedial contact, well separated posteriorly, (6) larval palatopterygoids with long, posteriorly oriented processes that approach or articulate with the quadrates, (7) unicuspid larval teeth, bicuspid or specialized unicuspid adult teeth, (8) a single larval premaxilla, adults with single or paired elements, (9) premaxillae highly variable in shape, broad to narrow with a tendency for depression; internasal fontanelles usually large, tend to close during ontogeny of a few species, (10) premaxillary frontal processes highly variable, usually arise narrowly from toothed portions, (11) maxillae of variable lengths but usually fall short of posterior eyeball margins, no jugal processes, (12) maxillary facial lobes moderate to small, frontal-maxilla articulation normally absent, (13) palatal shelves moderately broad in some species, narrow in most, very small in some, (14) septomaxillae primitively large, tend to be reduced or lost in one generic group, (15) nasals small to large, articulations highly variable from genus to genus, but articulation with maxillae usually neither firm nor extensive, (16) prefrontals primitively present, lost in a few genera, (17) vomerine preorbital processes present in most, absent or reduced in a few; teeth may or may not extend onto processes, but do so primitively, (18) anterior vomerine teeth present, (19) anterior and posterior vomerine teeth continuous in primitive members of one group, discontinuous in adults of all others, (20) posterior vomerine teeth borne sparsely or densely on narrow to broad, continuous or discontinuous posterior vomerine projections, (21) anterior portions of frontals moderately large and expanded, do not occupy antorbital regions and rarely occupy prefrontal regions, (22) frontals moderately rounded with no angular orbital ridges, frontals slightly to extensively covered by adductor mandibulae anterior musculature, (23) no parietal-otic troughs, but many have posterior parietal depressions, (24) well developed squamosal-otic and parietal-otic crests in some genera, others have various types of otic crests, or no crests, (25) posterolateral parasphenoid processes moderate to small, or absent, (26) parasphenoids relatively long, broadly overlap vomers, (27) quadrates moderate to small, do not articulate with either occipito-otics or parasphenoids, cartilaginous portions of suspensoria moderately large, (28) orbitosphenoids large, moderate, or small, posteriorly constricted in some genera, (29) squamosals large to small, anchorage to skulls variable, (30) occipital condyles sessile, (31) columellae present except in some neotropical genera, usually moderately long and cylindrical, (32) dentition poorly to well developed, (33) meckelian grooves open, dentaries C-shaped anteriorly, (34) detoglossal or adetoglossal; genioglossal muscles present or absent, (35) cornua broad and long to short and attenuate, attaching to or continuous with first basibranchials, (36) lingual cartilages present or absent, (37) anterior first basibranchial extensions present only in some groups which lack lingual cartilages, (38) first basibranchials anteriorly expanded or not, (39) first ceratobranchials or epibranchials longest of articulated hyobranchial elements, (40) first ceratobranchials larger than second in most genera, smaller in one generic group, (41) epibranchials more than 1.5 times first basibranchials; epibranchials shorter than first ceratobranchials in two genera, but longer in others, (42) second basibranchials present or absent, width more or less than first basibranchial length, (43) moderate-sized atlases bear large condylar articular facets that are relatively flat to slightly concave, (44) large atlantal odontoid processes, (45) posterior atlantal margins relatively unmodified, (46) thirteen to twenty-four trunk vertebrae, (47) two or three caudosacral vertebrae, (48) vertebrae mostly amphicoelous, but parallel tendencies toward a secondary opisthococly, (49) hypapophysial keels usually absent, rudiments present on one or two vertebrae in a few species, (50) hyperapophyses usually well developed and divided, but united in some species, (51) basapophyses present or absent, when present poorly to moderately developed, (52) no pterygapophyses, (53) parapophyses and diapophyses short to long, separated or united; diapophyses absent on posterior trunk vertebrae of three genera, (54) centra shorter or longer than distance across tips of parapophyses, (55) ribs present on last trunk vertebrae in some, absent in other genera, (56) ribs from 0.2 to 1.5 times distance across parapophyses, (57) tails stout to slender proximally, basal tail constriction present or absent, (58) tibial spurs present or absent, (59) hind limbs only slightly larger than fore limbs, (60) fingers and toes highly variable in shape, no fleshy palm pads; digits long and slender with pointed to expanded tips in most, or short and stout, or joined, or united by webbing, (61) five to eight carpals, five to nine tarsals, (62) distal tarsals five do not articulate with central tarsals except in two genera, (63) four fingers and five toes, except for three genera which have four toes, (64) primitive phalangeal formulae 1-2-3-2; 1-2-3-3-2; various reductions occur with extreme reduction possible 0-1-2-2, 0-1-2-2-1 in forms with five toes, (65) adults aquatic, terrestrial, subterranean, or arboreal, (66) aquatic larvae in one group, direct terrestrial development in most species, (67) testes pigmented or unpigmented, lobed testes occur in some groups, (68) quadrato-pectoralis and gularis, or only gularis muscles.

Content: three tribes, twenty genera—*Gyrinophilus, Pseudotriton, Stereochilus, Eurycea, Typhlotriton, Typhlomolge, Haideotriton, Hemidactylium, Plethodon, Aneides, Ensatina, Hydromantes, Batrachoseps, Bolitoglossa, Oedipina, Pseudoeurycea, Chiropterotriton, Parvimolge, Lineatriton, Thorius.*

Tribe 1. Hemidactyliini

Definition: plethodontine salamanders differing from all others by having aquatic larvae; differing from the Plethodontini in lacking anterior first basibranchial extensions, and from the Bolitoglossini by having large, ossified second basibranchials, and larger first than second ceratobranchials.

Characterization: (1) premaxillae fused or separate, (2) internasal fontanelles primarily enclosed by premaxillary frontal processes, or fontanelles secondarily closed, (3) maxillary facial lobes almost entirely anterior to midpoints of toothed portions, (4) septomaxillae and prefrontals present and well developed, (5) vomerine tooth series sharply arched anteriorly, continuous or not with posterior vomerine teeth, (6) vomers proper extend posterolaterally beyond anterior tooth series, (7) anterior portions of parasphenoids strongly expanded, (8) parietals depressed posteriorly, with distinct lateral aspects; no posterolateral parietal spurs, (9) otic crests, when present, double, involving parietals and squamosals; crests process-like, (10) columellae present and well developed, (11) detoglossal or adetoglossal; genioglossal muscles present or absent, (12) cornua distinctly separated from first basibranchials, (13) no anterior first basibranchial extensions, (14) first basibranchials moderately to greatly expanded anteriorly, (15) first ceratobranchials of significantly greater diameter and bulk than second ceratobranchials, (16) epibranchials longest of articulated hyobranchial elements; 1.5 to 2 times the first basibranchials, longer than but less than 1.7 times the first ceratobranchials, (17) second basibranchials with widths greater than two-thirds first basibranchial lengths, (18) thirteen to twenty-one trunk vertebrae, (19) three caudosacral vertebrae, (20) transverse processes may or may not extend beyond zygapophyses, (21) diapophyses and parapophyses present on all but last one or two vertebrae, ribs all bicipital, (22) ribs 0.6 to 1.5 times distance across parapophyses, (23) tibial spurs well developed, (24) aquatic larvae with three epibranchials, some paedogenetic species remain aquatic, adults of other species aquatic to semiterrestrial.

Range: eastern North America with some species in central North America north of Mexico.

Content: eight genera—*Gyrinophilus, Pseudotriton, Stereochilus, Eurycea, Typhlotriton, Typhlomolge, Haideotriton, Hemidactylium.*

Gyrinophilus Cope, 1869

Definition: adults paedogenetic or fully transformed, eyes well developed and functional; premaxillae separate, fused in paedogenetic species; parietal-otic and squamosal-otic crests; well developed orbitosphenoids; anterior and posterior vomerine teeth continuous; adetoglossal with lingual cartilages and no genioglossal muscles; eighteen to twenty trunk vertebrae; tranverse processes of trunk vertebrae extend beyond zygapophyses; no basal tail constriction; four fingers and five toes.

Range: eastern North America from southern Maine and Quebec, and Ohio, to northern Alabama and Georgia.

Content: *danielsi* (Blatchley, 1901), *palleucus* McCrady, 1954; *porphyriticus* (Green, 1827).

Pseudotriton Tschudi, 1838

Definition: adults fully transformed; eyes well developed and functional; premaxillae fused; parietal-otic and squamosal-otic crests; well developed orbitosphenoids; anterior and posterior vomerine teeth continuous; adetoglossal with lingual cartilages and no genioglossal muscles; seventeen or eighteen trunk vertebrae; transverse processes of trunk vertebrae extend beyond zygapophyses; no basal tail constriction; four fingers and five toes.

Range: eastern North America from New York and Ohio to Florida and Louisiana.

Content: *montanus* Baird, 1849; *ruber* (Sonnini, 1802).

Stereochilus Cope, 1869

Definition: adults fully transformed; eyes well developed and functional; premaxillae fused; parietal-otic and squamosal-otic crests; well developed orbitosphenoids; anterior and posterior vomerine teeth continuous; detoglossal with lingual cartilages and no genioglossal muscles; eighteen to twenty trunk vertebrae; transverse processes of trunk vertebrae extend beyond zygapophyses; no basal tail constriction; four fingers and five toes.

Range: Atlantic Coastal Plain from Virginia to Georgia.

Content: *marginatus* (Hallowell, 1857).

Eurycea Rafinesque, 1822

Definition: adults paedogenetic or fully transformed; eyes well developed and functional; premaxillae fused; parietal-otic and squamosal-otic crests, or no crests; well developed orbitosphenoids; anterior and posterior vomerine teeth discontinuous; adetoglossal with lingual cartilages and no genioglossal muscles; fifteen to twenty-one trunk vertebrae; transverse processes of trunk vertebrae do not extend beyond zygapophyses; no basal tail constriction; four fingers and four or five toes.

Range: eastern North America from Quebec and New Brunswick to Florida, Oklahoma, and Texas.

Content: *aquatica* Rose and Bush, 1963; *bislineata* (Green, 1818); *latitans* Smith and Potter, 1946; *longicauda* (Green, 1818); *lucifuga* Rafinesque, 1822; *multiplicata* (Cope, 1869); *nana* Bishop, 1941; *neotenes* Bishop and Wright, 1937; *pterophila* Burger, Smith and Potter, 1950; *quadridigitata* (Holbrook, 1842); *troglodytes* Baker, 1957; *tynerensis* Moore and Hughes, 1939.

Typhlotriton Stejneger, 1892

Definition: adults essentially fully transformed, but eyes poorly developed and nonfunctional; premaxillae fused or separate; no otic crests; orbitosphenoids with very small optic fenestrae; anterior and posterior vomerine teeth continuous; detoglossal with lingual cartilages and no genioglossal muscles; seventeen to twenty trunk vertebrae; transverse processes of trunk vertebrae do not extend beyond the zygapophyses; no basal tail constriction; four fingers and five toes.

Range: Interior Highlands of Missouri, Arkansas, Kansas, and Oklahoma.

Content: *spelaeus* Stejneger, 1892.

Typhlomolge Stejneger, 1896

Definition: adults blind, gilled, paedogenetic; premaxillae fused; no otic crests; no orbitosphenoids; no posterior vomerine teeth; larval attached tongues; thirteen or fourteen trunk vertebrae; transverse processes of trunk vertebrae extend beyond zygapophyses; no basal tail constriction; four fingers and five toes.

Range: Balcones Escarpment region of south-central Texas.

Content: *rathbuni* Stejneger, 1896; *tridentifera* (Mitchell and Reddell, 1965).

Haideotriton Carr, 1939

Definition: adults blind, gilled, paedogenetic; premaxillae fused; no otic crests; no orbitosphenoids; no posterior vomerine teeth; larval attached tongues; fourteen trunk vertebrae; transverse processes of trunk vertebrae do not extend beyond zygapophyses; no basal tail constriction; four fingers and five toes.

Range: southern Georgia and north-central Florida.

Content: *wallacei* Carr, 1939.

Hemidactylium Tschudi, 1838

Definition: adults fully transformed, eyes well developed and functional; premaxillae separate; no otic crests; orbitosphenoids well developed; anterior and posterior vomerine teeth discontinuous; detoglossal with genioglossal muscles and no lingual cartilages; fifteen trunk vertebrae; transverse processes of trunk vertebrae extend beyond zygapophyses; basal tail constriction; four fingers and four toes.

Range: eastern North America from Nova Scotia and Ontario to Arkansas, Louisiana, and Florida.

Content: *scutatum* (Schlegel, 1838).

Tribe 2. Plethodontini

Definition: plethodontine salamanders which lack aquatic larvae; differing in addition from the Hemidactyliini by having anterior first basibranchial extensions, and from the Bolitoglossini by having large, ossified second basibranchials and larger first than second ceratobranchials.

Characterization: (1) premaxillae fused or separate, (2) internasal fontanelles primarily enclosed by premaxillary frontal processes, secondarily closed by osseous ornamentation in one species, (3) maxillary facial lobes arise from central one-third of toothed portions, (4) septomaxillae and prefrontals well developed, (5) vomerine tooth series gently curved anteriorly, not continuous with posterior vomerine teeth, (6) vomerine tooth series marks posterolateral extent of vomers proper, (7) anterior portions of parasphenoids not expanded, (8) parietals slightly or not depressed posteriorly, no lateral aspects or parietal spurs, (9) otic crests, when present, single involving otics only or otics and squamosals; crests long and continuous, (10) columellae well developed, (11) detoglossal, short genioglossal muscles present, (12) cornua distinctly separated from first basibranchials, (13) anterior first basibranchial extensions well developed, (14) first basibranchials moderately expanded just anterior to midpoints, (15) first ceratobranchials of significantly greater diameter and bulk than second ceratobranchials, (16) first ceratobranchials longest of articulated hyobranchial elements in most, but epibranchials equal first ceratobranchials in one species; epibranchials less than 1.25 times first basibranchials, and shorter than or same length as first ceratobranchials, (17) second basibranchials with widths less than two-thirds first basibranchial lengths, (18) fourteen to twenty-four trunk vertebrae, (19) three caudosacral vertebrae, (20) transverse processes extend well beyond zygapophyses, (21) diapophyses and parapophyses present on all but last one or two vertebrae, ribs all bicipital, (22) ribs 0.6 to 1.25 times distance across parapophyses, (23) tibial spurs well developed, or absent, (24) direct terrestrial development with no aquatic larval stage, adults terrestrial to arboreal.

Range: eastern and western North America with species in the Rocky Mountains, the Interior Highlands, and Texas.

Content: three genera—*Plethodon, Ensatina, Aneides.*

Plethodon Tschudi, 1838

Definition: adults differ from *Aneides* in having two premaxillae, and from *Ensatina* in having tibial spurs and lacking basal tail constriction.

Range: eastern North America to the Interior Highlands and Texas, but particularly in the Appalachian region; western North America, primarily west of the Cascade-Sierra Nevada divide, but with populations in the Rocky Mountains of Idaho-Montana, New Mexico, and ? Utah.

Content: *caddoensis* Pope and Pope, 1951; *cinereus* (Green, 1818); *dorsalis* Cope, 1889; *dunni* Bishop, 1934; *elongatus* Van Denburgh, 1916; *glutinosus* (Green, 1818); *jordani* Blatchley, 1901; *larselli* Burns, 1953; *longicrus* Adler and Dennis, 1962; *neomexicanus* Stebbins and Riemer, 1950; *ouachitae* Dunn and Heintze, 1933; *richmondi* Netting and Mittleman, 1938; *stormi,* Highton and Brame, 1965; *vandykei* Van Denburgh, 1906; *vehiculum* (Cooper, 1860); *wehrlei* Fowler and Dunn, 1917; *welleri* Walker, 1931; *yonahlossee* Dunn, 1917.

Ensatina Gray, 1850

Definition: adults differ from *Aneides* and *Plethodon* in having basally constricted tails with highly specialized first caudal vertebrae, and in lacking tibial spurs.

Range: far western United States from southern British Columbia to extreme southern California, west of the Cascade-Sierra Nevada divide.

Content: *eschscholtzii* Gray, 1850.

Aneides Baird, 1849

Definition: adults differ from *Plethodon* and *Ensatina* in having single premaxillae and specialized tarsi in which all elements articulate with the centrals.

Range: Applachian region of eastern North America, mountainous regions of south-central New Mexico, and far western North America west of the Cascade-Sierra Nevada divide from Vancouver Island and Oregon to California and northern Baja California.

Content: *aeneus* (Cope and Packard, 1881); *ferreus* Cope, 1869; *flavipunctatus* (Strauch, 1870); *hardii* (Taylor, 1941); *lugubris* (Hallowell, 1849).

Tribe 3. Bolitoglossini

Definition: Plethodontine salamanders which differ from the Hemidactyliini and Plethodontini by lacking second basibranchials and having larger second than first ceratobranchials; differing in addition from the Hemidactyliini by lacking aquatic larvae, and from the Plethodontini by having epibranchials that are much longer than the first ceratobranchials.

Characterization: (1) premaxillae fused or separate, (2) anterior margins only of internasal fontanelles formed by premaxillary frontal processes, (3) maxillary facial lobes almost completely anterior to midpoints of toothed portions, (4) septomaxillae and prefrontals present or absent, trends for reduction and loss of both, (5) vomerine tooth series gently curved anteriorly, not continuous with posterior vomerine teeth, (6) anterior vomerine tooth series marks posterolateral extent of vomers proper, (7) anterior portions of parasphenoids slightly or not expanded, (8) parietals slightly or not depressed posteriorly; no lateral aspects, but usually with well developed posterolateral parietal spurs, (9) no otic crests, (10) columellae present in some, but definite trend for reduction and loss, (11) adetoglossal, no genioglossal muscles; modified detoglossal with extremely specialized, elongate genioglossal muscles in one genus, (12) cornua present or absent, when present apparently continuous with first basibranchials, (13) no anterior first basibranchial extensions, (14) first basibranchials slightly or not at all expanded anteriorly, (15) second ceratobranchials shorter, but of significantly greater diameter and bulk than first ceratobranchials, (16) epibranchials longest of articulated hyobranchial elements; 2 to 3.4 times the first basibranchials; 1.8 to 6 times the first ceratobranchials, (17) no second basibranchials, (18) fourteen to twenty-two trunk vertebrae, (19) two or three caudosacral vertebrae, (20) transverse processes extend beyond zygapophyses, (21) diapophyses and parapophyses present on most trunk vertebrae of most genera, but diapophyses lost on most trunk vertebrae of several genera; ribs bicipital or unicipital, (22) ribs 0.2 to 1 times distance across parapophyses, (23) tibial spurs relatively small or absent, (24) direct terrestrial development with no aquatic larval stage, adults terrestrial to arboreal.

Range: far western North America west of the Cascade-Sierra Nevada divide from ?Alaska and Oregon to northern Baja California, Mexico; the total neotropical (Mexico to Brazil and Bolivia) and European (Italy, France, Sardinia) range of the family.

Content: three supergenera, nine genera—*Hydromantes, Batrachoseps, Bolitoglossa, Oedipina, Pseudoeurycea, Chiropterotriton, Parvimolge, Lineatriton, Thorius.*

Supergenus *Hydromantes*

Definition: plethodontine salamanders with separated premaxillae; no prefrontals; no posterolateral parietal spurs; well developed columellae; adetoglossal, with no genioglossal muscles; no cornua; no omohyoideus muscles; fourteen trunk vertebrae; three caudosacral vertebrae; no basal tail constriction; five toes; and unilobed testes.

Content: one genus—*Hydromantes.*

Hydromantes Gistel, 1848

Definition: see above.

Range: three species in California at from low to high elevations in the Cascade and Sierra Nevada regions; two species in Europe from north-central and western Italy to extreme southwestern France, and on the island of Sardinia.

Content: *brunus* Gorman, 1954; *genei* (Schlegel, 1838); *italicus* Dunn, 1923; *platycephalus* (Camp, 1916); *shastae* Gorman and Camp, 1953.

Supergenus *Batrachoseps*

Definition: plethodontine salamanders with fused or separated premaxillae; extremely reduced or no prefrontals; posterolateral parietal spurs; somewhat reduced columellae; highly modified detoglossal tongues with extremely elongated and slender genioglossal muscles; relatively long slender cornua; omohyoideus muscles; sixteen to twenty-one trunk vertebrae; two or three caudosacral vertebrae; slight basal tail constriction; four toes; and multilobed testes.

Content: one genus—*Batrachoseps.*

Batrachoseps Bonaparte, 1839

Definition: see above.

Range: western Oregon and California, and extreme northwestern Baja California; ? southeastern Alaska and ? Jalisco, Mexico.

Content: *attenuatus* (Eschscholtz, 1833); *pacificus* (Cope, 1865); *wrighti* (Bishop, 1937).

Supergenus *Bolitoglossa*

Definition: plethodontine salamanders with fused premaxillae; well developed, reduced, or no prefrontals; posterolateral parietal spurs; columellae reduced or absent; adetoglossal, with no genioglossal muscles; slender, sinuous, relatively short cornua; no omohyoideus muscles; fourteen or eighteen to twenty-two trunk vertebrae; two caudosacral vertebrae; slight to marked basal tail constriction; five toes; and multilobed testes.

Content: seven neotropical genera—*Bolitoglossa, Oedipina, Pesudoeurycea, Chiropterotriton, Parvimolge, Lineatriton, Thorius.*

Bolitoglossa Duméril, Bibron, and Duméril, 1854

Definition: salamanders with prefrontals present or absent; no posteriorly directed, rod-like squamosal processes; columellae extremely reduced or absent; no sublingual folds; fourteen trunk vertebrae; most ribs bicipital; distal tarsals 4 and 5 fused.

Range: northeastern Mexico to eastern Brazil and central Bolivia.

Content: *adspersa* (Peters, 1863); *altamazonica* (Cope, 1874); *alvaradoi* Taylor, 1954; *arborescandens* Taylor, 1954; *biseriata* Tanner, 1962; *bor-*

burata Trapido, 1942; *brevipes* Bumzahem and Smith, 1955; *capitana* Brame and Wake, 1963; *chica* Brame and Wake, 1963; *cerroensis* Taylor, 1952; *colonnea* (Dunn, 1924); *cuchamatana* (Stuart, 1943); *dofleini* (Werner, 1903); *dunni* (Schmidt, 1933); *engelhardti* (Schmidt, 1936); *epimela* Wake and Brame, 1963; *flavimembris* (Schmidt, 1936); *flaviventris* (Schmidt, 1936); *franklini* (Schmidt, 1936); *helmrichi* (Schmidt, 1936); *hypacra* (Brame and Wake, 1962); *lignicolor* (Peters, 1873); *lincolni* (Stuart, 1943); *macrinii* (Lafrentz, 1930); *marmorea* (Tanner and Brame, 1961); *mexicana* Duméril, Bibron, and Duméril, 1854; *morio* (Cope, 1869); *nicefori* Brame and Wake, 1963; *nigrescens* (Taylor, 1949); *nigroflavescens* Taylor, 1941; *occidentalis* Taylor, 1941; *omniumsanctorum* (Stuart, 1952); *orestes* Brame and Wake, 1962; *palmata* (Werner, 1897); *pandi* Brame and Wake, 1963; *peruviana* (Boulenger, 1883); *phalarosoma* Wake and Brame, 1962; *platydactyla* (Gray, 1831); *riletti* Holman, 1964; *robusta* (Cope, 1894); *rostrata* (Brocchi, 1883); *rufescens* (Cope, 1869); *salvinii* (Gray, 1869); *savagei* Brame and Wake, 1963; *schizodactyla* Wake and Brame, 1966; *schmidti* (Dunn, 1924); *sima* (Vaillant, 1911); *sooyorum* Vial, 1963; *striatula* (Noble, 1918); *subpalmata* (Boulenger, 1896); *vallecula* Brame and Wake, 1963; *veracrucis* Taylor, 1951; *yucatana* (Peters, 1882).

Oedipina Keferstein, 1868

Definition: salamanders with no prefrontals; no posteriorly directed, rod-like squamosal processes; no columellae; sublingual folds; eighteen to twenty-two trunk vertebrae; most ribs unicipital; distal tarsals 4 and 5 fused.

Range: southern Mexico through Central America and western Colombia to north-central Ecuador.

Content: *alfaroi* Dunn, 1921; *bonitaensis* Taylor, 1952; *collaris* (Stejneger, 1907); *complex* (Dunn, 1924); *cyclocauda* Taylor, 1952; *elongata* (Schmidt, 1936); *gracilis* Taylor, 1952; *ignea* Stuart, 1952; *inusitata* Taylor, 1952; *longissima* Taylor, 1952; *pacificensis* Taylor, 1952; *parvipes* (Peters, 1879); *poelzi* Brame, 1963; *syndactyla* Taylor, 1948; *taylori* Stuart, 1952; *uniformis* Keferstein, 1868.

Pseudoeurycea Taylor, 1944

Definition: salamanders with prefrontals; no posteriorly directed, rod-like squamosal processes; columellae greatly reduced; sublingual folds; fourteen trunk vertebrae; most ribs bicipital; distal tarsals 4 and 5 separated, 4 larger than 5, and 5 does not articulate with the centrale.

Range: Nuevo Leon and Tamaulipas in northeastern and Nayarit in western Mexico to Guatemala.

Content: *altamontana* (Taylor, 1938); *bellii* (Gray, 1849); *brunnata* Bumzahem and Smith, 1955; *cephalica* (Cope, 1865); *expectata* Stuart, 1954; *firscheini* Shannon and Werler, 1955; *gadovii* (Dunn, 1926); *galeanae* (Taylor, 1941); *gigantea* (Taylor, 1938); *goebeli* (Schmidt, 1936); *leprosa* (Cope, 1869); *melanomolge* (Taylor, 1941); *nigromaculata* (Taylor, 1941); *rex* (Dunn, 1921); *robertsi* (Taylor, 1938); *scandens* Walker, 1955; *smithi* (Taylor, 1938); *sulcata* (Brocchi, 1883); *unguidentis* (Taylor, 1941); *werleri* Darling and Smith, 1954.

Chiropterotriton Taylor, 1944

Definition: salamanders with prefrontals present or absent; no posteriorly directed, rod-like squamosal processes; columellae present, reduced, or absent; sublingual folds; fourteen trunk vertebrae; most ribs bicipital; distal tarsals 4 and 5 separated or fused, when separated 5 usually larger than 4 and articulates with centrale, or, if 4 larger than 5, prefrontals are absent.

Range: southern Nuevo Leon and southwestern Tamaulipas through eastern and east-central Mexico to Guatemala, El Salvador, Honduras, and Costa Rica.

Content: *abscondens* Taylor, 1948; *arboreus* (Taylor, 1941); *barbouri* (Schmidt, 1936); *bromeliacia* (Schmidt, 1936); *chiropterus* (Cope, 1863); *chondrostega* (Taylor, 1941); *dimidiatus* (Taylor, 1939); *lavae* (Taylor, 1942); *magnipes* Rabb, 1965; *megarhinus* Rabb, 1960; *mosauri* (Woodall, 1941); *multidentatus* (Taylor, 1938); *nasalis* (Dunn, 1924); *picadoi* (Stejneger, 1911); *priscus* Rabb, 1956; *xolocalcae* (Taylor, 1941).

Lineatriton Tanner, 1950

Definition: salamanders with prefrontals; no posteriorly directed, rod-like squamosal processes; columellae reduced; sublingual folds; fourteen trunk vertebrae; most ribs unicipital; no distal tarsal 5.

Range: central Veracruz, Mexico.

Content: *lineola* (Cope, 1865).

Thorius Cope, 1869

Definition: salamanders with prefrontals extremely reduced or absent; posteriorly directed, rod-like squamosal processes; no columellae; sublingual folds; fourteen trunk vertebrae; most ribs bicipital; distal tarsals 4 and 5 fused.

Range: southern Veracruz and Puebla to Guerrero and Oaxaca, Mexico, north of the Isthmus of Tehuantepec.

Content: *dubitus* Taylor, 1941; *macdougalli* Taylor, 1949; *maxillabrochus* Gehlbach, 1959; *minutissimus* Taylor, 1949; *narisovalis* Taylor, 1939; *pennatulus* Cope, 1869; *pulmonaris* Taylor, 1939; *schmidti* Gehlbach, 1959; *troglodytes* Taylor, 1941.

Parvimolge Taylor, 1941

This genus, recognized by recent authors, is a poorly defined and apparently unnatural assemblage of three distinct species, and diagnosis is not possible. The species may prove to be members of the genera *Chiropterotriton* and *Pseudoeurycea*, but at least one, *P. townsendi*, appears sufficiently distinct to warrant a separate genus. The two species which have been examined *(P. richardi, P. townsendi)* have small prefrontals; no posteriorly directed, rod-like squamosal processes; extremely reduced or no columellae; sublingual folds present; fourteen trunk vertebrae; and bicipital ribs. Distal tarsals 4 and 5 are fused in *P. townsendi*.

Range: central and southern Veracruz, Mexico, and north-central Costa Rica.

Content: *praecellens* Rabb, 1955; *richardi* Taylor, 1949; *townsendi* (Dunn, 1922).

EVOLUTIONARY RELATIONSHIPS AND TRENDS

Relationships

Major Familial Divisions

The family Plethodontidae, as proposed by Gray (1850), included species now included in the families Hynobiidae and Ambystomatidae as well as the following four groups: *Plethodon; Desmognathus* and *Hemidactylium; Batrachoseps, Spelerpes* (which included species now placed in *Eurycea, Manculus, Pseudotriton, Gyrinophilus,* and *Pseudoeurycea*), *Geotriton (=Hydromantes),* and *Oedipus (=Bolitoglossa); Ensatina.* Hallowell (1856) used family endings for three groups included in Gray's single family: (1) Plethodontidae—*Plethodon, Aneides, Desmognathus,* (2) Bolitoglossidae—*Pseudotriton, Spelerpes, Batrachoseps, Geotriton,* (3) Hemidactylidae—*Hemidactylium.* The groups were not precisely defined and never became established in the literature.

Cope (1859) recognized two groups on the basis of tongue attachment; those with free tongues (including *Batrachoseps*) were called Spelerpeae, those with attached tongues, Plethodontae. In 1866 Cope revised his views and recognized two families of present day plethodontids. A single genus, *Desmognathus,* was placed in the Desmognathidae, and the other genera in the Plethodontidae. Cope (1869) erected the family Thoriidae for the genus *Thorius.* Cope (1859, 1866, 1869) was the first to present osteological information of any significance and to characterize and discuss relationships of salamander families. Desmognathids were said to differ from plethodontids in having stalked rather than sessile occipital condyles, opisthocoelous rather than amphicoelous vertebrae, and a frontal process extending into the superpalatal vacuity. Thoriids were said to have opisthocoelous vertebrae and ossified carpals and tarsals. Cope thought thoriids combined the characters of the Desmognathidae, Plethodontidae, and Ambystomatidae.

Boulenger (1882) reduced the three families of Cope to two subfamilies (thoriids included in Desmognathinae) of the Salamandridae, but Cope (1889) rejected this work. Cope later modified his views (1894 a) and placed *Thorius* in the Desmognathidae. As a result of his discovery of *Haptoglossa,* an elongate Costa Rican genus with an attached tongue and opisthocoelous vertebrae, Cope (1894 b) recognized a subfamily Thoriinae within the family Desmognathidae. The subfamily included *Haptoglossa, Thorius,* and *Typhlotriton* (described as a desmognathid by Stejneger, 1892). The unique type of *Haptoglossa* is lost and the status of the genus remains enigmatic (see also Taylor, 1944).

The family Typhlomolgidae was erected for the single genus *Typhlomolge* by Stejneger and Barbour (1917), despite Emerson's (1905) study which showed it to be closely related to *Eurycea.* The family received no support and Fowler and Dunn (1917) simply stated "*Typhlomolge* is a permanent larva of some plethodont."

On the basis of his studies of vertebral articulations, Moore (1900) suggested that desmognathids be included in the family Plethodontidae. He was followed by most subsequent workers (Stejneger and Barbour, 1917; Fowler and Dunn, 1917; Dunn, 1917 and 1926; Noble, 1931; Herre, 1935; Piatt, 1935; Schmidt, 1953; Conant, 1958). Dunn's (1926) classical work, which has long been the standard authoritative reference on plethodontids, recognized no formal groupings below the family level.

Recently there has been an attempt to revive the family Desmognathidae. Smith and Taylor (1948) recognized two families of lungless salamanders, and two subfamilies (Thoriinae and Plethodontinae) of plethodontids. The Thoriinae included only *Thorius.* Soler (1950) presented evidence of the distinctiveness of *Desmognathus* and *Leurognathus*, and argued for recognition of a family Desmognathidae. In a rather uncritical review based on the literature, von Wahlert (1957) recognized a superorder Plethodontoidea (suggested by Laurent, 1947) with two families, Desmognathidae and Plethodontidae. Two subfamilies of plethodontids were recognized: Plethodontinae (*Aneides, Batrachoseps, Ensatina, Hemidactylium, Plethodon, Stereochilus*) and Thoriinae (remaining nondesmognathine plethodontids). Recent authors (Tecge, 1956; Conant, 1958; Highton, 1961; Martof, 1962; Wake, 1963; Estes, 1964 and 1965; Monath, 1965) have not recognized a family Desmognathidae.

Plethodontid salamanders fall into two major assemblages that I consider to be of subfamilial rank. The subfamily Plethodontinae contains twenty of the twenty-three genera, and is the more generalized and progressive group. The more specialized subfamily Desmognathinae is comprised of three genera. It is difficult to discuss the subfamilies in terms of one being more primitive or advanced than the other. Primitive members of both groups have aquatic larvae, but desmognathine larvae have four epibranchials and plethodontines have three. In some respects (*e.g.*, palatal elements, gill rami) plethodontine larvae are the more generalized, but several plethodontine larvae have secondary specializations (elongate snout and reduced eyes of *Gyrinophilus*, pond specialization of *Hemidactylium, Manculus* and *Stereochilus*). Some plethodontines retain the primitive premaxillary metamorphic pattern, but others do not nor do the modern desmognathines. Primitive characters found in primitive plethodontines but not in desmognathines include presence of nasolacrimal ducts, large septomaxillae, well developed prefrontals, toothed vomerine preorbital processes, continuous anterior and posterior vomerine tooth series, amphicoelous vertebrae, cartilaginous antorbitals, convex frontals, and open meckelian grooves. Other primitive characters (tibial spurs, mesopodial numbers and configuration) are shared by desmognathines and primitive plethodontines. Desmognathines have many unique morphological specializations, but subfamily-wide plethodontine specializations are not apparent. The desmognathines probably diverged from a pre-plethodontine stock at an early date (Mesozoic). Desmognathines have become highly specialized, but have retained a number of primitive characters. The Plethodontinae is a considerably more generalized and diverse group than the Desmognathinae, yet some plethodontine genera can be considered more advanced than any desmognathine genus (see below). The plethodontine genera are probably morphologically more similar to the ancestral common stock than are the desmognathines, and the Plethodontinae must be considered the most primitive subfamily (see Fig. 12).

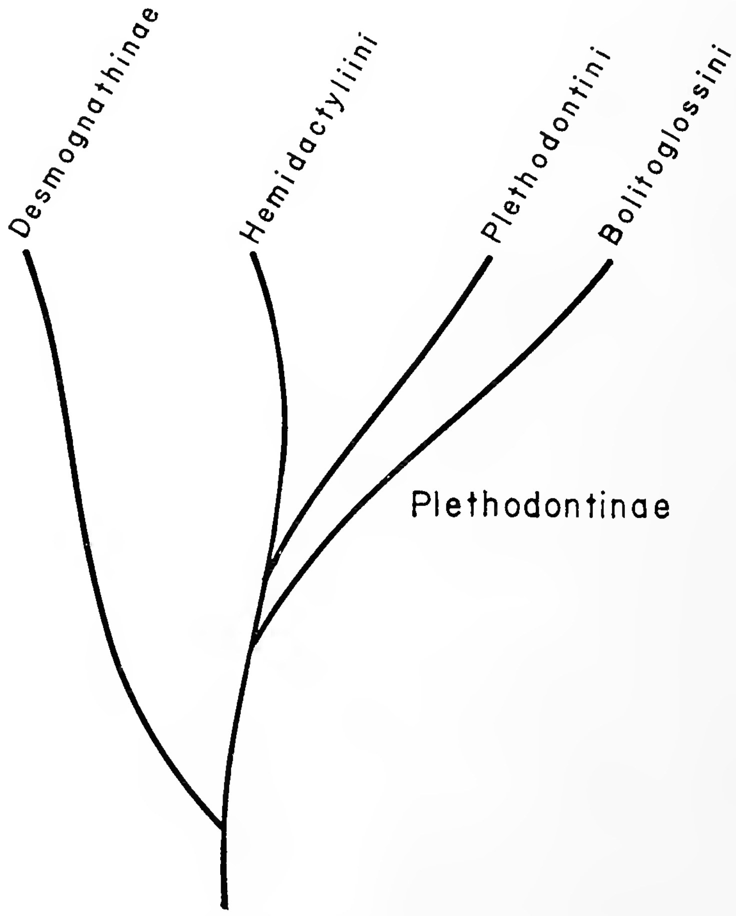


Figure 12. Diagrammatic representation of the relationships of the major groups of plethodontid salamanders.

Functional specializations of four types in the desmognathines have led to drastic skeletal modifications. These modifications sharply distinguish desmognathine from plethodontine genera, and include: (1) streamlining, a response to selective forces operative in the primitive, swift mountain brook environments, (2) skull strengthening, a response to selective forces correlated with use of heads as wedges, (3) new mouth opening mechanisms, the result of selective forces in the primitive environment and related to peculiarities in use of the heads, (4) vertebral and limb modifications, the results of locomotor specializations.

Streamlining is a common occurrence in vertebrates which inhabit aquatic environments, and especially those that occur in swift streams. Certainly the remarkable desmognathine skull flattening is the most important of the streamlining modifications. Flattening imparts an elongate wedge-shape to the skulls, a factor of particular advantage to these organisms which not only inhabit rapidly flowing brooks, but also hide under rocks and in rock crevices by forcing their way head first (Dunn, 1926; Martof, 1962). The anterior cranial elements of desmognathines are relatively dense, thickened, closely articulated bones, and the dorsal surfaces of the skulls are solid and relatively smooth. The frontals and anterior margins of the parietals are also flat and smooth. Head muscles that primitively originate on the dorsal surfaces of the frontals and parietals have shifted their origins lateroventrally, and arise from the lateral margins of the bones, below the ridge-like dorsolateral margins, and from the orbitosphenoids. Reduction or absence of vomerine vaulting is also directly associated with the streamlining and skull depression.

Other features associated with streamlining include well developed eyes which are neither prominent nor strongly protuberant, fore limbs considerably smaller than hind limbs, and very smooth transitions from relatively small heads to cylindrical trunks and stout tails.

Skulls of plethodontines remain relatively rigid in reference to the vertebral column, and the mandibles are lowered to open the mouths. In contrast the mandibles of desmognathines are held relatively rigid and the skulls proper are raised somewhat during mouth opening. The mandibles are far from immobile in Desmognathines (see Noble, 1931), but are much more so than in plethodontines. It has been suggested (Dunn, 1926; Conant, 1958) that the relative immobility of the lower jaws stiffens the anterior portions of the bodies so the salamanders can more readily force their way under objects. Functional modifications of the jaw musculature immobilize the mandibles. Slips of the adductor mandibulae musculature (adductor mandibulae externus) extend from the prearticulars to the atlas in all plethodontids, but desmognathines differ from plethodontines in that the slips contain stout, relatively inflexible ligaments that limit the ventral movement of the mandibles relative to the trunk.

Desmognathines have stalked occipital condyles that effectively move the skull away from the atlas and provide room for swinging the skull up and down to open and close the mouth. Further modifications facilitating skull movement on the vertebral column are the drastic reduction in size of the odontoid process and movement out of the foramen magnum. In addition the occipital condylar articular facets are strongly convex and are received by enlarged, strongly concave atlantal cotyles.

Muscular modifications have evolved to enable skull elevation. The depressor mandibulae muscles lower the mandibles of plethodontines, but are of relatively minor importance in desmognathines; apparently the anterior dorsal spinal muscles have assumed the primary desmognathine mouth opening function. The dorsal spinal muscles are exceptionally well developed in desmognathines and extend onto the skull to insert on raised otic crests, behind the parietal-otic troughs, and on the parietals in front of the troughs. The muscles originate on the dorsal surfaces of the anterior trunk vertebrae. Unique, moderately to well developed vertebral pterygapophyses provide additional area for dorsal spinal muscle origin.

Despite the fact that the adductor mandibulae musculature contains ligaments, it plays a role in lowering the desmognathine skull onto the mandibles. Additional musculature also is brought into play. The quadrato-pectoralis musculature is remarkably well developed in desmognathines, extending as stout bands from the quadrate region to the gular fold (see Piatt, 1935); contraction of the quadrato-pectoralis muscles pulls the skull down while contraction of the adductor mandibulae muscles raises the mandibles. The two sets of muscles effectively close the mouth.

When the skull swings dorsally on the atlas, the mandibles are also raised. Mandibular elevation ceases, however, as the depressor mandibulae muscles contract and facilitate mouth opening by restricting dorsal mandibular motion. The skull swings dorsally and movement of the quadrates on the articulars occurs. Since the atlas is a relatively solid fulcrum and vertical motion of the mandibles is restricted, skull movement propels the mandibles forward. Movements of the quadrates on the articulars perhaps has served as a selective force that has led to strengthened quadrates. Desmognathine quadrates are enlarged and firmly articulated with the parasphenoids and occipito-otics, and anchored by strong jugal ligaments to the maxillae. The great tensions in the ligament are evidenced by the formation of moderate to very large maxillary jugal processes in the desmognathines. The squamosals are stout and articulate firmly with the quadrates and occipito-otics. The results of the above modifications are that the desmognathine quadrates are solidly anchored to the brain case, and the posterior portions of the skull are as strong and rigid as the anterior portions.

Primitive desmognathines are aquatic organisms living in swift streams. A number of morphological specializations are related to stream locomotion. Among these are the heavily muscularized trunks and stout, compressed tails. Development of opisthocoely facilitates increased intervertebral movement, the result of increased trunk and tail flexure.

Desmognathine trunk vertebrae are also characterized by the presence of hypapophysial keels and basapophyses. Auffenberg (1961) and Estes (1964) suggest that such processes relate to the development of muscles aiding lateral undulation and to swimming efficiency.

A final feature associated with aquatic habits and the particular behavior of desmognathines is the hypertrophy of the hind limbs, which are much larger than the fore limbs. The large hind limbs apparently play important roles in the locomotion of desmognathines, particularly in aiding the salamanders to force their way under and between objects.

There is no question as to the distinctiveness of the Desmognathinae, but if the differences which separate desmognathines and plethodontines are carefully examined, it is apparent that most result from adaptation to a particular habitat. Thus streamlining, skull strengthening, mouth opening modifications, vertebral modifications, and limb modifications are all directly related to way of life of the salamanders, and are specialized adaptations to the environment in which they occur.

Desmognathines and plethodontines are closely related, and it is likely that they have had some common ancestor. The differences between the groups are sharp, but when analyzed carefully, are shown to be the results of relatively minor specializations in the Desmognathines. So many characteristics are held in common by the plethodontines and desmognathines that recognition of a family Desmognathidae as proposed by Cope (1869) and recently advocated by Smith and Taylor (1948) and Soler (1950) appears unwarranted.

Relationships of the Desmognathine Genera

Desmognathus and *Leurognathus* are the best known of the three desmognathine genera, and similarities and differences of the two have been discussed to some extent by Moore (1899), Dunn (1926), and Martof (1962). The genera are basically similar, and differences are primarily the result of the peculiar selective pressures within the strictly aquatic environment to which *Leurognathus* has adapted. *Leurognathus* has a more flattened skull and a sharper, more pointed snout than *Desmognathus*. Internal nares are reduced to small, laterally placed slits, and the internasal fontanelles of large *Leurognathus* are completely closed. The fontanelles primitively contain glands that furnish lubricant utilized while swallowing by salamanders in terrestrial or semiterrestrial situations; *Leurognathus* has become so completely aquatic that such lubrication is unnecessary, and selection has favored dorsal and ventral fontanelle closure as parts of trends toward skull strengthening. *Leurognathus* is unique in having very long vomerine preorbital processes that extend beyond the vomerine bodies to articulate firmly with the maxillary palatal shelves. *Leurognathus* differs further in having better developed hypapophysial keels on more vertebrae, and fused hyperapophyses on all trunk vertebrae.

One specialization found in *Desmognathus* but not in *Leurognathus* is the presence of large, calcified plaques within the mouths under the eyes (the "crushing plates" of Noble, 1931). The large, irregularly-shaped plaques are found in at least three species *(D. quadramaculatus, D. monticola, D. ochrophaeus)*, and are apparently unique features of the genus.

Since Moore's (1899) description of *Leurognathus* the status of the genus has not been seriously questioned. Osteological data indicate that *Leurognathus* probably arose as a specialized branch of a *Desmognathus* ancestral stock that may have been very similar to modern *D. quadramaculatus* (see also Dunn, 1926). It is more difficult to separate *D. quadramaculatus* from *L. marmoratus* than from other *Desmognathus*. One might question the advisability of generic recognition of a single species so obviously closely related to a larger, rather diverse genus. I agree with Martof (1962) that recognition is justifiable because *Leurognathus* has entered upon a new way of life, one not followed by any species of *Desmognathus*, and is morphologically distinct from all *Desmognathus*. *Leurognathus* is the most aquatic of any of the metamorphosed plethodontids and is restricted to aquatic situations (Martof, 1962). The distinctive morphology, ecology, and life history of the species, *L. marmoratus*, warrant separation from *Desmognathus* and placement in a distinct genus.

Highton (1961) announced the discovery of a remarkable new genus and species, *Phaeognathus hubrichti*, a very large, elongate, terrestrial burrower. Valentine (1963 b, 1963 c) and Brandon (1965) have recently provided some information that supports Highton's suggestion that *Phaeognathus* is a desmognathine, and I have corroborated many of their observations; additional support has been presented above. *Phaeognathus* differs sharply and strikingly from *Desmognathus* and *Leurognathus* in many characters. *Desmognathus* and *Leurognathus* are rather stout, short-bodied forms with fifteen trunk vertebrae, but the slender, elongate *Phaeognathus* has twenty-one to twenty-three; limbs and digits of *Phaeognathus* are greatly shortened in comparison with the other genera. *Phaeognathus* is a terrestrial burrower, a habit not encountered elsewhere in the Desmognathinae, and several characters are apparently related to burrowing. The skull is rather bullet-shaped and only slightly flattened. The head is small relative to body size. Skin covering the snout is co-ossified to the anterior cranial elements, which are sculptured and eroded. Particularly striking are the large, spatulate, maxillary jugal processes which extend almost to the quadrates. Size of the processes testifies to the extreme tension in the jugal ligaments, and to the over-all strength of the skulls.

The mandibular adductor series of muscles of desmognathines consist of two major bundles, the adductor mandibulae anterior and the adductor mandibulae externus (terminology of Edgeworth, 1935). The former extend from the medial margins of the prearticulars to the lateral walls of the braincase, particularly the dorsal portions of the orbitosphenoids and the ventrally directed lateral lips of the frontals. The adductor mandibulae externus are the muscles called temporalis by various authors (*e.g.*, Soler, 1950) and extend from the atlases to the prearticulars. *Phaeognathus* has larger adductor mandibulae anterior and smaller adductor mandibulae externus muscles than *Desmognathus* and *Leurognathus*. Unique, lateral, frontoparietal ridges of *Phaeognathus* serve as points of attachment for the enlarged adductor mandibulae anterior musculature. In addition the dorsal spinal musculature is better developed in *Phaeognathus* than in other desmognathines, and the points of insertion of most of the musculature are the sites of the raised terminal projections of the prominent fronto-parietal ridges. As a result of the relatively large amounts of musculature which insert on the parietals anterior to the parietal-otic troughs, the parietals are less flattened and the two parietal regions are less distinguishable in *Phaeognathus* than in *Desmognathus* or *Leurognathus*.

The quadrato-pectoralis and especially the gularis muscles are considerably less developed in *Phaeognathus* than in the other desmognathine genera. The gularis muscles are barely perceptible and are of little functional importance, and the quadrato-pectoralis muscles are relatively slender. It is obvious that skull raising specializations are less well developed in *Phaeognathus* than in *Desmognathus* or *Leurognathus*. The strong development of the dorsal spinal musculature could as well be a burrowing as a mouth opening adaptation.

Phaeognathus differs further from the other desmognathines in characters of the vertebrae and vomers (see above). The characters have no obvious connection with ancestral conditions and may be related to new types of locomotion and feeding.

There is no question concerning the distinctiveness of *Phaeognathus*. Apparently it is a relatively advanced, specialized genus derived from a *Desmognathus-Leurognathus* ancestral stock at a relatively early date.

Of the three desmognathines *Desmognathus* is the most generalized and primitive. *Leurognathus* is closely related to *Desmognathus* and has entered a new adaptive subzone—the aquatic environment. *Phaeognathus* is more closely related to *Desmogthus* than to *Leurognathus,* and was probably derived from the common ancestral stock at an earlier date than was *Leurognathus* (see Fig. 13). *Phaeognathus* has entered a new adaptive zone—the terrestrial environment—in an opposite evolutionary direction from that of *Leurognathus*. *Desmognathus* has primitive species which occupy the primitive semiaquatic niche (see below), but the genus is undergoing an adaptive radiation and includes species which have successfully entered terrestrial niches. *Desmognathus* is the most successful and evolutionarily the most plastic of the three genera.

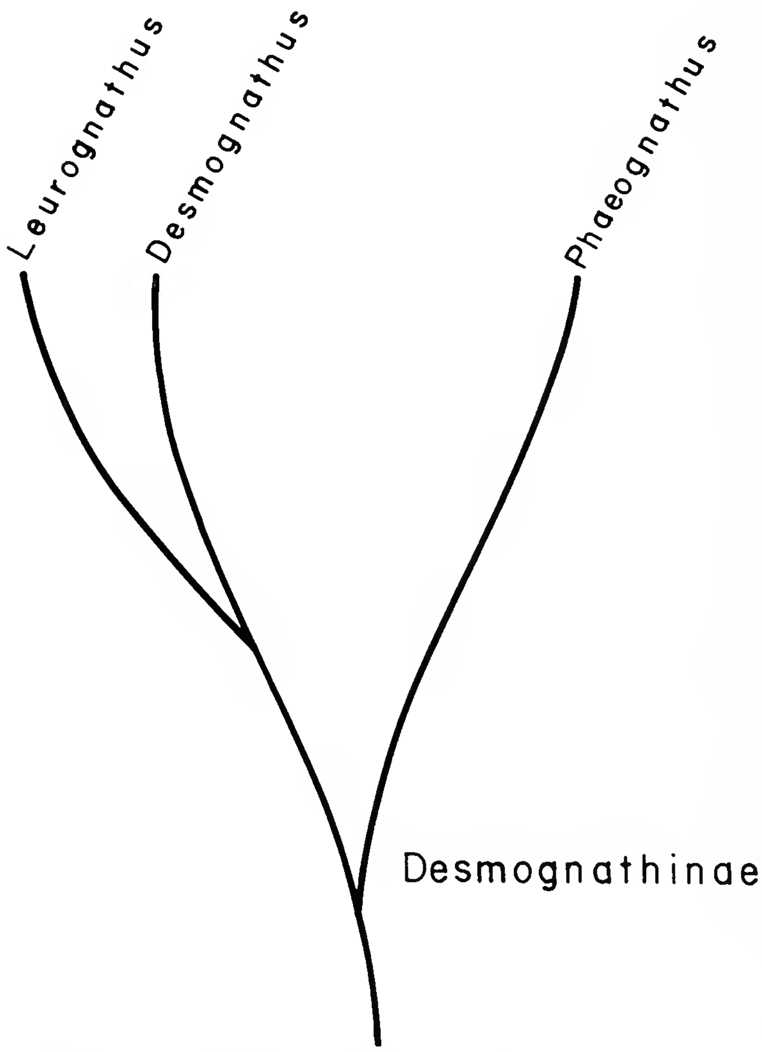


Figure 13. Diagrammatic representation of relationships within the subfamily Desmognathinae.

Relationships of the Plethodontine Genera

Tribal relationships

By far the largest number of species and genera of lungless salamanders are included within the subfamily Plethodontinae. These species may be placed conveniently in three natural subgroups or tribes on the basis of structural similarities. The generic assemblages are sufficiently distinct to indicate continuity of descent within each tribe, but not to warrant subfamilial recognition. Certain genera are somewhat intermediate between two tribes, and no tribe is as distinct a group as the subfamily Desmognathinae.

The groupings proposed here differ from those of other authors, and some historical information is necessary as an introduction to the following discussion. Dunn's (1926) comprehensive work recognized two major groups of non-desmognathine genera, the attached tongued *Plethodon* group *(Plethodon, Ensatina, Aneides, Hemidactylium, Batrachoseps)* and the free tongued *Eurycea* group *(Eurycea, Manculus, Gyrinophilus, Pseudotriton, Hydromantes, Oedipus)* with *Typhlotriton, Typhlomolge,* and *Stereochilus* intermediate. Most subsequent authors have followed Dunn. Noble (1925, 1927 a, 1927 b, 1931) suggested that there might be a relationship between *Hydromantes* and *Plethodon.* Herre (1935) saw an *Oedipus-Hydromantes* group arising from a *Plethodon* stock and derived the desmognathines from a *Pseudotriton*-like ancestor, but otherwise followed Dunn. Piatt (1935) recognized *Stereochilus (Stereochilus, Typhlotriton, Typhlomolge)* and *Gyrinophilus (Gyrinophilus, Pseudotriton, Eurycea, Manculus)* groups in one assemblage, and *Plethodon (Plethodon, Aneides, Ensatina, Hemidactylium)* and *Oedipus (Oedipus, Hydromantes, Batrachoseps)* groups in another. Piatt's arrangement was unique in that he proposed parallel evolution of free tongues. He stated "*Hydromantes* and *Oedipus* have no close affinities to the *Gyrinophilus* group but arose from early *Plethodon* stock by means of a form like *Batrachoseps.*" Piatt's arguments were not particularly convincing and he has not been followed by subsequent workers. Tanner (1952) recognized two groups of free tongued genera which he thought were derived from a common free tongued ancestor. His groups were: (1) *Gyrinophilus, Pseudotriton, Eurycea, Manculus* and (2) *Hydromantes, Bolitoglossa, Magnadigita, Pseudoeurycea, Chiropterotriton, Oedipina, Parvimolge, Lineatriton, Thorius.* Tanner suggested that the relationships of *Batrachoseps* were with *Plethodon* and rejected Piatt's proposal. Von Wahlert (1957) recognized two subfamilies (Plethodontinae: *Aneides, Batrachoseps, Ensatina, Hemidactylium, Plethodon, Stereochilus;* Thoriinae: *Bolitoglossa, Chiropterotriton, Eurycea, Gyrinophilus, Hydromantes, Lineatriton, Magnadigita, Manculus, Oedipina, Parvimolge, Pseudotriton, Pseudoeurycea, Thorius, Typhlotriton, ?Eladinea, ?Haideotriton, ?Typhlomolge*). His treatment of *Stereochilus* was novel and without explanation. The only recent authors to recognize a subfamily Thoriinae have been Smith and Taylor (1948) and they clearly included only *Thorius.* The family group name Bolitoglossidae (Hallowell, 1856) has clear priority over Thoriidae (Cope, 1869) as used by von Wahlert (his Thoriinae). This was recognized by Monath (1965) who follows von Wahlert but refers to members of the latter's subfamily Thoriinae as "bolitoglossines." Brame (1960) has also referred to this group as the bolitoglossine genera.

The tribe Hemidactyliini is restricted in distribution to eastern North America and contains eight genera: *Gyrinophilus, Pseudotriton, Stereochilus, Eurycea, Typhlotriton, Typhlomolge, Haideotriton,* and *Hemidactylium.* The tribe Plethodontini has a discontinuous distribution in eastern, central, and western North America, and contains three genera: *Plethodon, Aneides,* and *Ensatina.* Members of the tribe Plethodontini are called plethodonines in this paper. The tribe Bolitoglossini occurs in western North America, Mexico, Central and South America, and Europe, and contains nine genera: *Hydromantes, Batrachoseps, Bolitoglossa, Oedipina, Pseudoeurycea, Chiropterotriton, Parvimolge, Lineatriton,* and *Thorius.* The bolitoglossine group has the most genera, the most species, the most diversity, and the most specialization of the assemblages of the Plethodontinae.

All members of the Hemidactyliini have aquatic larvae, but all members of the other two tribes have direct terrestrial development. This is a character of major importance and one of the main reasons for considering the Hemidactyliini the most primitive of the three tribes. The hemidactyliine genera are aquatic to semiterrestrial as adults, while the other tribes are strictly terrestrial or arboreal.

Hemidactyliine genera have larger and stronger second basibranchials than other plethodontids, and the character is apparently related to aquatic life. The bony second basibranchials are associated with the hyobranchial musculature, forming transverse septa in the rectus cervicis of adults. The second basibranchials presumably play a role in strengthening this musculature, which is of great importance in gill movements of larvae, and flotation and submergence mechanisms of adults. Second basibranchials are present in plethodonines, but are relatively smaller than in hemidactyliines; the elements are absent in all bolitoglossines.

Several additional characters associated with hyobranchial structure are among the most diagnostic of the tribes (see above under hyobranchial skeleton).

Several skull characters separate the tribes. Significant anterior parasphenoid expansion occurs only in the hemidactyliine genera. The anterior vomerine tooth rows mark the posterior margins of the vomers proper in plethodonines and bolitoglossines, but bony vomerine growth extends posterior to the tooth series, below the parasphenoids, in hemidactyliines. Anterior and posterior vomerine tooth series are continuous only in four hemidactyliine genera. Maxillary facial lobes arise from the central one-third of the maxillae in plethodonines, but the lobes are entirely anterior to the mid-points in the other tribes. The parietals of plethodonines and bolitoglossines are relatively flat, but those of hemidactyliines have distinct lateral aspects.

Ribs tend to be shorter, and vertebral centra longer and slenderer in bolitoglossines than in the other two tribes.

A number of specialized characters occur in at least some species in two or more tribes, and most or all are the result of parallel evolution. These include proximal tail constriction (Hemidactyliini, Plethodontini, Bolitoglossini), loss of fifth toes, (H,B), raised atlantal bosses (H,P), elongation, and increased numbers of trunk and tail vertebrae (H,P,B), otic crests (H,P), fused premaxillae (H,P,B), loss of vomerine preorbital processes (H,P,B), attainment of significant tongue freedom and ability to protrude tongues for significant distances from the mouths (H,P,B), loss of genioglossal muscles (H,B), reduction and loss of tibial spurs (P,B), and tendencies toward opisthocoely (H,P,B).

The Bolitoglossini is obviously the most specialized and advanced of the three tribes. Specialized and advanced conditions found only in some to all bolitoglossine genera include unicipital ribs and loss of the diapophyses on most trunk vertebrae, loss of prefrontals, loss of septomaxillae, loss of columellae, loss of maxillary teeth, loss of omohyoideus muscles, fusion of premaxillary frontal processes, extensive mesopodial fusions, second basibranchial loss, and presence of parietal spurs. Some bolitoglossines have reduced numbers of chromosomes (Kezer, *in litt.*). The above characters are found in several to many bolitoglossine genera. Generalized and presumably primitive features of the bolitoglossines included paired premaxillae in primitive species, and low and invariable numbers of trunk vertebrae in most genera.

The Hemidactyliini and Plethodontini include relatively primitive genera, and are rather generalized groups in comparison with the Bolitoglossini. Primitive features found in some or all hemidactyliines include aquatic larvae, primitive nasolacrimal duct pathways, retention of genioglossal muscles, retention of all primitive plethodontid cranial elements, relatively long maxillae, continuous anterior and posterior vomerine tooth series, and separated premaxillae.

Certain hemidactyliines have specialized conditions which include loss of the fifth toes, presence of basal tail constriction, great first basibranchial expansion, genioglossal muscle loss (most genera), attainment of true adetoglossy, separation of the anterior and posterior vomerine tooth series, shortened transverse processes, presence of hypapophysial rudiments, presence of well developed basapophyses, attainment of paedogenesis, and premaxillary fusion.

Plethodonines are primitive in having detoglossy and genioglossal muscles in all species. In addition they have all the primitive cranial elements, and two of the three genera have paired premaxillae. Specializations found in all species include separation of anterior and posterior vomerine tooth series, advanced nasolacrimal duct routes, and direct terrestrial development. Certain species have other specializations including loss of tibial spurs and of vomerine preorbital processes, strengthened skull elements, fused premaxillae, specialized maxillae, specialized arrangements of mesopodial elements, and hypertrophy of quadratopectoralis musculature.

All available evidence indicates that the hemidactyliine line is the most primitive and generalized of the three. A major consideration is the retention of an aquatic larval stage in all members of the tribe. Plethodonines have a more primitive tongue structure with retention of anterior attachments, strong genioglossal muscles, and relatively short epibranchials; however, one hemidactyliine genus, *Hemidactylium,* also retains both anterior attachment and genioglossal muscles. Features in which plethodonines are apparently more primitive than hemidactyliines are primarily those related to tongue structure, and in most other characters hemidactyliines are definitely more primitive.

The plethodonine line is closer to the hemidactyliine line than is the bolitoglossine line (see (Fig. 12). The primary feature relating hemidactyliines and bolitoglossines is the attainment of true adetoglossy, but evidence has been presented which indicates that parallelism likely has occurred.

The above evidence indicates that hemidactyliines are probably closer to the ancestral plethodontid stock than any desmognathine, plethodonine, or bolitoglossine. Desmognathines were probably the earliest derivatives of the stock, followed by bolitoglossines and finally by plethodonines. Within the Plethodontinae the tribe Hemidactyliini is apparently the central, primitive group, the Plethodontini is somewhat more advanced, and the Bolitoglossini is the most specialized and advanced of the tribes (see Fig. 12).

Relationships of the hemidactyliines

Generic groupings

Three distinct generic assemblages of hemidactyliine salamanders are apparent: (1) *Gyrinophilus, Pseudotriton, Stereochilus,* (2) *Eurycea, Typhlotriton, Haideotriton, Typhlomolge,* (3) *Hemidactylium* (see Fig. 14).

Gyrinophilus, Pseudotriton, and *Stereochilus* are relatively primitive, rather closely related groups, but all represent unquestionably distinct evolutionary lines worthy of generic recognition. The genera share a number of characters, including: (1) similar anterior cranial elements, in a broad sense, (2) broad palatal shelves, (3) parietal-otic and squamosal-otic crests (shared with some *Eurycea*), (4) continuous anterior and posterior vomerine tooth series (shared with *Typhlotriton* and some *Eurycea*), (5) broadly similar hyobranchial structure, (6) lingual cartilages (shared with *Eurycea*), (7) no genioglossal muscles (shared with *Eurycea* and *Typhlotriton*), (8) moderate first basibranchial expansion (shared with *Hemidactylium*), (9) moderate-sized cornua, (10) high modal numbers of vertebrae (shared with *Typhlotriton*), (11) proximally fused diapophyses and parapophyses, (12) long transverse processes (shared with *Hemidactylium*), (13) diapophysial origins just slightly in advance of parapophysial origins (shared with *Hemidactylium*), (14) short ribs (shared with *Hemidactylium*), (15) stout, relatively short vertebral centra, (16) long frontals.

Pseudotriton and *Gyrinophilus* resemble each other more closely than either resembles *Stereochilus*. In addition to the above characters they share enlarged adductor mandibulae anterior muscles, which insert on top of the frontals and virtually cover the interorbital regions. This mus-

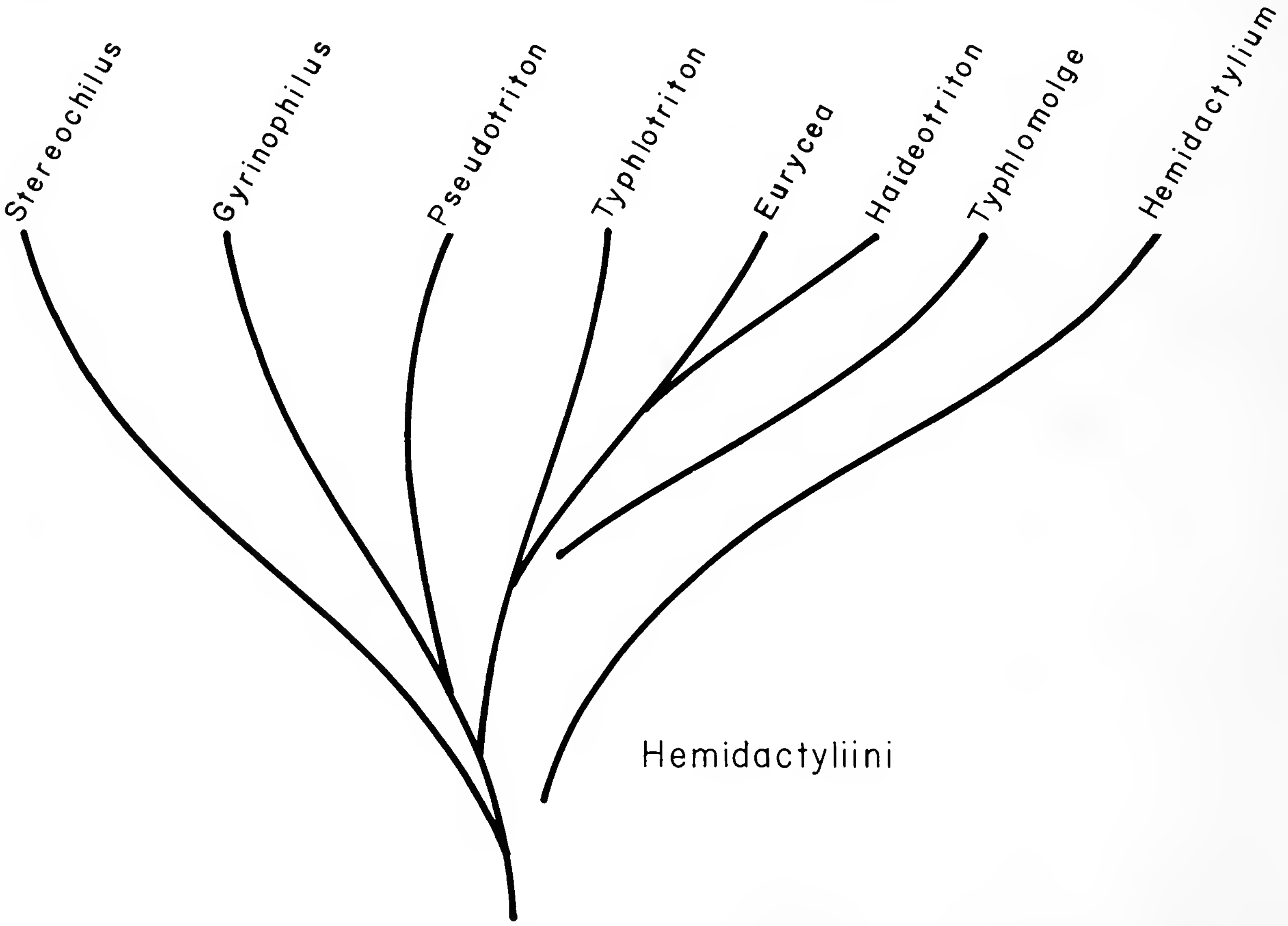


Figure 14. Diagrammatic representation of the relationships of the hemidactyliine genera.

culature covers only the posterolateral frontal extremities in other hemidactyliines. Second basibranchial width is greater than first basibranchial length in the two genera, but lesser in *Stereochilus*. Both *Gyrinophilus* and *Pseudotriton* have large, adetoglossal tongues, but *Stereochilus* has a relatively small tongue with a membranous anterior attachment.

Grobman (1959) placed *Gyrinophilus* in the synonymy of *Pseudotriton* on morphological grounds, but Martof and Rose (1962) disagreed and reported that the two genera differ in skull bone density (*Gyrinophilus* light, *Pseudotriton* heavy) snout length (*G.* long, *P.* short), frontal and toothed portions of premaxillae fused (*P.*) or not (*G.*), and nasals elongate and contacting maxillae (*G.*), or broad and separated from maxillae (*P.*). My observations corroborate their statements in large part, but the nasals are in contact with the maxillae in some *Pseudotriton*. Other significant differences include presence of ventromedial quadrate projections, nasolacrimal duct impressions on the anterodorsal prefrontal surfaces, and broad and extensive overlap of the premaxillary frontal processes by the nasals in *Pseudotriton* but not in *Gyrinophilus*.

Stereochilus resembles *Pseudotriton* in having fused premaxillary toothed and frontal processes, and hypapophysial remnants on some trunk vertebrae. Moderate maxilla-nasal articulation and no nasolacrimal duct impressions relate *Stereochilus* to *Gyrinophilus*. Numerous characters separate *Stereochilus* from both genera. The snouts and heads are greatly compressed laterally, and this compression is reflected in the extensive fusion of the premaxillary frontal processes anterior as well as posterior to the fontanelles, ontogenetic closure of the internasal fontanelles, and medial juncture of the vomerine tooth series below the anterior portions of the parasphenoids.

Despite its specializations *Stereochilus* is a relatively primitive form, not far removed in most features from an idealized familial ancestral stock. One of the most primitive characters of *Stereochilus* is the presence in adults of a distinct, well developed lateral line system on the heads. The system is better developed than in any other plethodontid genus (see Hilton, 1947 b; 1950). *Stereochilus* diverged from the ancestral plethodontid stock at a somewhat later date than the stock which gave rise to the desmognathines, but it may have been one of the earliest hemidactyliine derivatives.

Gyrinophilus, Stereochilus, and *Pseudotriton* form the most primitive generic group in the family. The larvae of *Gyrinophilus* are somewhat specialized (elongate snout, reduced eyes) and adults are adetoglossal with elongated anterior cranial elements, but in most other features the genus is generalized; it may well be the most primitive plethodontid, as suggested by Dunn (1926).

The *Eurycea-Typhlotriton-Haideotriton-Typhlomolge* line appears to have been derived from a *Gyrinophilus-Pseudotriton* ancestral stock. *Typhlotriton* is more primitive than *Eurycea,* and paired premaxillae, relatively long snouts, nasal-maxilla articulation, and absence of nasolacrimal duct impressions ally it with *Gyrinophilus*. *Typhlotriton* differs from other members of its line, and resembles *Gyrinophilus, Pseudotriton,* and *Stereochilus* in having continuous vomerine tooth series.

Eurycea resembles *Pseudotriton* more closely than *Gyrinophilus*. *Eurycea* and *Pseudotriton* share several important characters, including fused premaxillae, relatively short snouts, marked nasolacrimal duct impressions, and hypapophysial vertebral remnants. Lingual cartilages and parietal-otic and squamosal-otic crests, all present in *Gyrinophilus, Pseudotriton,* and *Stereochilus,* are present in *Eurycea* but absent in *Typhlotriton*.

Typhlotriton and *Eurycea* are closely related, as is evident from the number of common characters, including: (1) similar hyobranchial structure, despite presence of membranous anterior attachments in *Typhlotriton,* (2) greatly expanded first basibranchials, (3) short cornua, (4) well developed sublingual glands of unknown function which are poorly developed or absent in other genera, (5) extremely short transverse processes, (6) complete parapophysial and diapophysial separation, (7) parapophysial origin greatly in advance of diapophysial origin, (8) ribs longer than distance across parapophyses, (9) elongate centra, (10) well developed basapophyses.

Apparently *Typhlotriton* is related to the *Gyrinophilus-Pseudotriton-Stereochilus* assemblage, but it is closer to *Eurycea*. Many similarities between *Typhlotriton* and *Eurycea* suggest probable descent from an ancestral stock related to that from which *Gyrinophilus* and *Pseudotriton* were derived. Separation of *Typhlotriton* and *Eurycea* from the more primitive genera is based primarily on the striking hyobranchial and vertebral differences.

Hemidactylium is a member of the Hemidactyliini but its relationships to other hemidactyliine genera are not clear. The outstanding primitive characters are retention of separated premaxillae, detoglossy, and genioglossal muscles. *Hemidactylium* has low numbers of trunk vertebrae, and is the only non-paedogenetic hemidactyliine that does not have a tendency for opisthocoely. It resembles *Gyrinophilus* and allies in vertebral and hyobranchial characters, but resembles *Eurycea* in having separated anterior and posterior vomerine tooth series. The nasolacrimal ducts follow routes similar to those in *Eurycea*, and their paths are impressed on the prefrontals. Specialized features of *Hemidactylium* include loss of the fifth toes and fifth distal tarsals, and presence of basally constricted tails with concomitant vertebral modifications.

Hemidactylium has a puzzling mosaic of primitive and advanced characters indicating specialization of a relatively primitive stock. It is closer to the plethodonine line than is any other hemidactyliine. *Hemidactylium* may be a specialized derivative of a primitive stock ancestral to all hemidactyliines. Despite the statements of Dunn (1926), Noble (1931), Piatt (1935), and others to the effect that *Hemidactylium* is a derivative or close relative of *Plethodon,* there can be little question concerning its closer relationship to the hemidactyliine line. Bishop (1941) intimated that *Hemidactylium* was more distantly removed from *Plethodon* than had formerly been suggested, but he did not mention possible relationship to other genera. The aquatic larval stage of *Hemidactylium* is clearly a primary, primitive character of great importance, not a derived feature as suggested by Noble (1927 a).

The tribe Hemidactyliini presents a mosaic pattern of primitive and advanced characters. It is obvious that many ancestral and intermediate groups are no longer extant, and that parallel loss has occurred in regard to several characters.

Status of the genus *Manculus*

The genus *Manculus,* with a single species, *M. quadridigitatus,* has been recognized as forming a distinct group by most authors since 1869, when the genus was proposed by Cope. The sole exception was Dunn (1923), who suggested that the single species be placed in the genus *Eurycea.* Dunn (1926) reiterated his position, stating, "I cannot think the genus *Manculus* worthy of recognition. The sole difference from *Eurycea* is the absence of the fifth toe." Dunn's suggestion was not followed and Noble (1927a) was soon recognizing *Manculus;* the genus has been recognized by all subsequent authors.

No one has questioned the close affinity of *Manculus* and *Eurycea.* Noble (1931) frankly stated, "*Manculus* is a dwarf form of *Eurycea*. . . It differs chiefly in the loss of the fifth (outer) toe."

Manculus differs from *Eurycea* in lacking fifth distal tarsals and toes, in being smaller, in having smaller anterior cranial elements, in having pond rather than stream larvae, and in being restricted to lowland habitats. The many striking similarities far outweigh the differences, however, and include similar hyobranchial structure, similar vertebrae, and similarly shaped and arranged cranial elements. Cranial similarities include presence of relatively short frontals and very distinct posterolateral frontal processes. Both *Eurycea* and *Manculus* lack well developed vomerine preorbital processes, but other hemidactyliines have the structures well developed. The posterior maxillary tips are relatively short and sinuous in both, and as a result, the subocular grooves intersect the lips below the eyes at the posterior maxillary tips. A connecting groove is present in many genera, but actual continuation of the subocular groove to the lip occurs elsewhere only in *Thorius.*

Unquestionably *Manculus* is distinct from all other *Eurycea,* but when differences are weighed against similarities, it is apparent that *Manculus* is simply a specialized offshoot of the *Eurycea* line. No purpose is served by isolating the single species in a separate genus. Other genera which have lost fifth toes (*Hemidactylium, Batrachoseps*) warrant generic recognition on the basis of marked differences from other groups in numerous characters. It is recommended that the species *quadridigitatus* be placed in the genus *Eurycea,* and that *Manculus* be considered a subjective junior synonym of *Eurycea.*

Status of the genera *Haideotriton* and *Typhlomolge*

Following completion of this paper a new paedogenetic and troglobitic species, *Eurycea tridentifera,* was described (Mitchell and Reddell, 1965). The authors considered the new species to be intermediate between *Typhlomolge* and *Eurycea* and suggested that the former be placed in the synonymy of the latter. Through the kindness of James P. Bogart I have recently had an opportunity to examine three specimens of *E. tridentifera* and one of *E. troglodytes.* Information concerning these species is limited to this portion of the paper. My investigations, discussed below, indicate that the genus *Typhlomolge* is distinct from *Eurycea* and contains two species (*tridentifera* and *rathbuni*).

Paedogenetic plethodontids occur in four general regions: 1) northern Alabama and southeastern Tennessee *(Gyrinophilus palleucus),* 2) southwestern Georgia and north-central Florida *(Haideotriton wallacei),* 3) eastern Oklahoma *(Eurycea tynerensis),* and 4) central and west-central Texas, along the Balcones Escarpment and on the Edwards Plateau (*Typhlomolge rathbuni, T. tridentifera; Eurycea latitans, E. nana, E. neotenes, E. pterophila, E. troglodytes*). Evolution of paedogenesis has apparently occurred independently in each of these areas. *G. palleucus* is clearly assignable to *Gyrinophilus,* and is not a close relative of other paedogenes. *Haideotriton* shows as many similarities to larvae of such forms as *E. bislineata* and *E. longicauda* as to the Texan paedogenes. *E. tynerensis* seems to be more closely related to *E. multiplicata* of the Interior Highlands than to the Texas *Eurycea.* The Texas *Eurycea* form a quite distinct group and there is no clear evidence of close relationship to any single species of transformed *Eurycea.*

The three epigeal species, *E. nana, E. neotenes,* and *E. pterophila,* are the least specialized of the Texan species and resemble generalized plethodontid larvae. Mitchell and Reddell (1965) have correctly stated that specializations related to subterranean life become increasingly pronounced in the order *E. latitans, E. troglodytes, T. tridentifera,* and *T. rathbuni.* Specializations include such features as eye degeneration, skin depigmentation, limb attenuation and elongation, snout depression, truncation and elongation, and reduction in number of trunk vertebrae. Mitchell and Reddell agreed with Baker (1957) that each species has evolved independently of the others since the original colonization of the subterranean habitat by the ancestral stock, and that present similarities of the species are likely due to convergent evolution.

Unquestionably *Typhlomolge rathbuni* is the most highly specialized and distinctive species of the Texan group. The species is much larger, has longer limbs, more extremely specialized head and snout, more reduced eyes, and is more depigmented than any of the other species. In addition its distinctive skull is greatly flattened and broadened. The toothed portion of the premaxilla is much broader and the frontal processes are broader and more depressed than in any of the other species. The palatopterygoids are very widely separated and are longer and more spatulate than in the other species. There are no orbitosphenoids. The parietals bear distinct crests, and the otic capsules are disproportionately large. Transverse processes are relatively long and extend beyond the lateral margins of the zygapophyses. There are only 13 or 14 trunk vertebrae.

The paedogenetic species of *Eurycea* (*tridentifera* excluded) all differ from *T. rathbuni* and resemble nonpaedogenetic species of *Eurycea* in having more than 14 trunk vertebrae, diapophyses which extend no farther than the zygapophysial margins, and well developed orbitosphenoid bones. In addition all differ from *T. rathbuni* and resemble larval *Eurycea* in general skull dimensions and in the relative development of skull elements. All have very well developed columellae, thus resembling *Typhlomolge* rather than *Eurycea.* Mitchell and Reddell (1965), citing Burger, Smith and Potter (1956) and Baker (1957), state that the second basibranchial (posterior basibranchium) is continuous with the hyobranchial apparatus proper in *T. tridentifera* and *T. rathbuni* and separated from it in the other species; the elements are also continuous in my *E. nana, E. pterophila* and *E. troglodytes.*

T. tridentifera resembles the paedogenetic Texan *Eurycea* in general proportions of the anterior cranial elements, but in few other characters. Most of the skeletal similarities are in features common to all plethodontine larvae. The otic capsules are large and resemble those of *T. rathbuni.* Like *T. rathbuni,* the orbitosphenoids are absent, the diapophyses are long and extend beyond the lateral margins of the zygapophyses, the numbers of trunk vertebrae are reduced (14 in two specimens, 13 in one), and the adpressed limbs overlap. Small alar processes are present on the anterior margins of the parapophyses as in *T. rathbuni.* Such processes are not found in other paedogenetic *Eurycea.* Basapophyses are absent; the processes are very well developed in *E. pterophila,* and are present and usually well developed in the other *Eurycea.* Basapophyses are very poorly developed in *T. rathbuni.* Several unique features occur in *tridentifera.* The columellae are longer than in any other plethodontid and have a distinct bow (the columellae are also very long in *T. rathbuni*). In addition the columella may have a dorsolateral spur near the opercular-columellar junction. The columellar process of the suspensorium is ossified (or heavily calcified), a unique condition among plethodontids. There are only eight tarsals in the single tarsus available, a result of the fusion of distal tarsals four and five. Eye reduction reaches an extreme in *T. rathbuni* and *Haideotriton wallacei,* in which lenses are absent. Lenses are absent in about half the *tridentifera* known (Mitchell and Reddell, 1965), but are present in other Texan paedogenes. *T. tridentifera* is much smaller than *T. rathbuni,* has more pigmentation, lacks parietal crests, and has a less extremely specialized snout (although snout flattening is more extreme than in any *Eurycea*).

Larvae of non-paedogenetic plethodontids are all basically very similar with only minor subfamilial differences. Interpretation of the characters of paedogenetic species has been partially discussed by Dundee (1962) who emphasized problems of definitions of higher categories. Interpretation is especially difficult in the case of the Texan paedogenes, between which greater differences are found than occur between the larvae of distantly related genera. The fact that morphoclines exist in regard to several characters with one of the less specialized *Eurycea* paedogenes on one end and *T. rathbuni* invariably on the other is not necessarily evidence that all have had a common ancestor or that these are chronoclines. No information concerning selection pressures in the various environments is available, but it is known that the surrounding terrain is inhospitable to transformed hemidactyliines. In order to survive in the area any hemidactyliine would have been forced to remain in the larval habitat or to enter the permanent waters of springs and underground caverns. The Texan paedogenes are a diverse lot and need not have a common ancestor. It seems inadvisable to refer *T. rathbuni* to *Eurycea* until more information concerning many aspects of the biology of all the species involved becomes available.

Mitchell and Reddell (1965) suggest that *T. tridentifera* is intermediate between *T. rathbuni* and the known paedogenetic Texan *Eurycea*. It is obvious from the above discussion that *tridentifera* is, in regard to most characters, much more similar to *T. rathbuni* than to any other species. Because the diversity within the Texan paedogene group is so great and because the vertebral and orbitosphenoid characters enable the group to be conveniently divided, I choose to recognize the genus *Typhlomolge* and refer to it the species *rathbuni* and *tridentifera*. The species *E. troglodytes* is the nearest to an intermediate but it is closely related to other *Eurycea* and is intermediate only in being largely depigmented, in having reduced eyes, and in having relatively elongate, attenuated limbs.

In some ways the genus *Haideotriton* is more similar to the larvae of non-paedogenetic *Eurycea* than are either *T. rathbuni* or *T. tridentifera*. The vertebrae of *Haideotriton*, like *Eurycea*, have short diapophyses and lack parapophysial alar processes. Limbs are not nearly as long as in *Typhlomolge*. *H. wallacei* resembles *Typhlomolge* in having poorly developed basapophyses, 14 trunk vertebrae, lensless eyes, in lacking orbitosphenoid bones, and in being greatly depigmented. The snout of *H. wallacei* is more truncate and the otic capsules are smaller than in *Typhlomolge*. The skull is relatively much larger, both longer and broader, than any *Eurycea*. The toothed portions of the premaxillae are much larger than those of any *Eurycea* or than *T. tridentifera* and approach those of *T. rathbuni* in size. The vomers are very broad and "L" shaped, and the palatopterygoids are large and spatulate; both elements resemble those of *T. rathbuni*. The skull presents an almost rectangular appearance, unique in the family, because of the greatly expanded snout and relatively small otic capsules.

Dundee (1957) reported some success in artificially inducing transformation in *T. rathbuni*, but the species metamorphosed to a lesser extent than paedogenetic *Eurycea*. Atrophy of labial folds, gills, and fins was noted. The gill slits remained open. Maxillae, maxillary teeth, and a small unpaired anterior ossification (septomaxilla or nasal?) appeared. One of the specimens of *T. tridentifera* examined was kept alive by James P. Bogart for five months and was treated with thyroxin as well as with pituitary implants. The gills are greatly reduced and only the anterior slit remains open. Some changes are apparent in the labial region. Skull shape is virtually identical to that of smaller, untreated individuals despite the appearance of an elongate *pars dentalis* of the maxilla and a series of maxillary teeth. Small, paired nasals (?) are also present. Coronoids are present despite the fact that they are normally among the first of the larval elements to disappear during metamorphosis. The margins of the palatopterygoids are eroded. Apparently *T. tridentifera* transforms under the influence of metamorphosing agents to about the same degree as *T. rathbuni*, and to a much lesser degree than paedogenetic *Eurycea* (*E. nana, E. neotenes, E. tynerensis;* Dundee, 1962).

In contrast to the paedogenetic species of *Gyrinophilus* and *Eurycea, Haideotriton wallacei* undergoes only a few minor integumentary changes, loses only a single bone (coronoid) and gains no new bony elements when treated with metamorphosing agents (Dundee, 1962). Dundee concludes that *Haideotriton*, like *Typhlomolge* and *Necturus*, appears to be genetically resistant to thyroid secretions. He states further that *H. wallacei* is the most resistant to thyroxin of all plethodontids investigated. *Haideotriton* is clearly a close relative of *Eurycea*. Because the genus is biologically distinct from all others and because there is no evidence that it evolved from a direct ancestor either of *Typhlomolge* or of the paedogenetic *Eurycea*, the genus *Haideotriton* is maintained.

Mitchell and Reddell (1965) have correctly noted the lack of information concerning evolutionary rates and selection pressures in subterranean habitats. Until such information becomes available it is not advisable to assume that all the subterranean plethodontids of the Edwards Plateau entered the underground environments approximately at the same time. It is more likely that those with the more extreme adaptations entered the environments first. Perhaps the ancestral *Typhlomolge* stock entered the subterranean habitats at a relatively early date, and the *Eurycea* somewhat later. Anatomical evidence indicates that both genera evolved from the same general evolving ancestral stock but that *Typhlomolge* was derived from a pre-*Eurycea* ancestor and the other Texan paedogenes from a *Eurycea* or very *Eurycea*-like ancestor. *Haideotriton* seems not to be closely related to *Typhlomolge*. It probably originated from a *Eurycea*-like stock in the Southeast.

Comments concerning *Typhlomolge* found elsewhere in this paper are based on study of *T. rathbuni* and do not necessarily refer to *T. tridentifera*.

Relationships of the plethodonines

Ensatina, Plethodon, and *Aneides* are a compact group of closely related genera which form the tribe Plethodontini. I have discussed their relationships recently (Wake, 1960; 1963), and only a review is presented here.

The plethodonine genera appear to have been derived from a relatively primitive, common ancestral stock. *Plethodon* is the central and most generalized genus, and the other two are specialized offshoots. *Ensatina* is a primitive genus, and was probably derived from a *Plethodon-Aneides* ancestral stock. It is more closely related to *Plethodon* than to *Aneides*. *Aneides* resembles *Plethodon* much more closely than it does *Ensatina*. Characters which relate *Aneides* to *Ensatina* are those characteristic of the tribe and are shared by *Plethodon* as well. *Aneides* is the most specialized and advanced of the genera, and is closely related to *Plethodon*. My ideas concerning plethodonine relationships are illustrated in Figure 15.

Primitive features of *Ensatina* include paired premaxillae (shared with *Plethodon*), very high numbers of maxillary, dentary, and vomerine teeth, very long vomerine preorbital processes, low numbers of trunk vertebrae, poorly developed otic crests, and relatively large otic capsules. Specializations found in *Ensatina* include basally constricted tails, shortened first caudal vertebrae, elongated limb elements, especially fore limbs, acquisition of considerable tongue freedom, rather elongated genioglossal muscles, and possibly primordial lingual cartilages. *Ensatina* differs further from *Aneides* and *Plethodon* in details of hyobranchial construction (shorter cornua, larger epibranchials and second basibranchials, small and unexpanded anterior first basibranchial extensions) and in vertebral characters (fused hyperapophyses, lack of caudal transverse processes, shorter ribs).

Plethodon and *Ensatina* resemble each other and differ from *Aneides* in sharing such generalized characters as paired premaxillae, unmodified maxillae, relatively weak prefrontal-maxilla articulations, relatively unmodified dentition, and primitive tarsal and carpal configurations. *Plethodon* has lower numbers of maxillary, dentary, and vomerine teeth than *Ensatina,* and has a great amount of vertebral number variation. *Plethodon* is a generalized group, and only a few specializations occur, including elongation of certain species *(cinereus, elongatus, neomexicanus, richmondi),* unusual otic crests *(elongatus),* and reduction in fifth toe phalangeal number *(larselli, neomexicanus).*

Aneides is so similar to *Plethodon* that it is tempting to postulate direct origin from *Plethodon.* Primitive species of *Aneides* (especially female *hardii*) differ from *Plethodon* only in having fused premaxillae and modified tarsal configurations. Almost all of the many specializations which occur in the advanced species of *Aneides* are either feeding or climbing adaptations. Advanced species of *Aneides* differ sharply from *Plethodon* because of these specializations, which include reduction in number but increase in size of all teeth, sabre-like, enlarged, unicuspid maxillary and dentary teeth, enlarged otic crests that serve as points of origin of enlarged cephalo-hyo-mandibulare musculature, specialized interlocking maxilla-prefrontal articulations, loss of the vomerine preorbital processes, greatly elongated limbs, bifurcated and decurved terminal phalanges, greatly enlarged, edentulous posterior maxillae with cleaver-like cutting edges, hypertrophied quadrato-pectoralis musculature and prehensile tails.

Despite the multitude of differences separating advanced species of *Aneides* from *Plethodon,* the presence of such primitive species as *A. hardii* clearly reveals close relationship of the two genera and suggests origin from either a common ancestral stock or of origin of *Aneides* from *Plethodon.*

Relationships of the bolitoglossines

Bolitoglossine salamanders form three groups sufficiently distinct to warrant recognition of supergenera. These groups are the supergenus *Hydromantes* with a single genus, the supergenus *Batrachoseps* with a single genus, and the supergenus *Bolitoglossa* with seven genera (*Bolitoglossa, Oedi-*

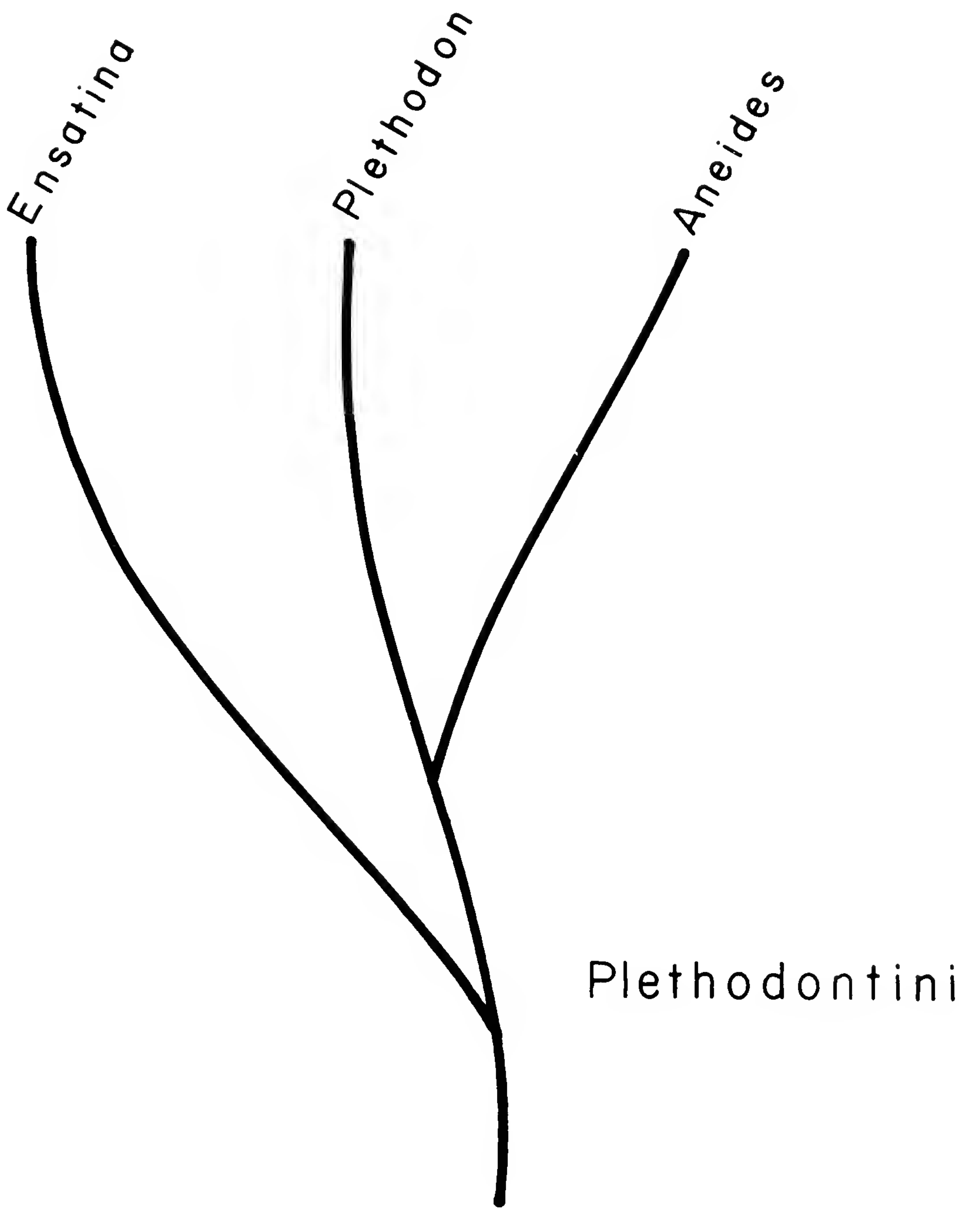


Figure 15. Diagrammatic representation of the relationships of the plethodonine genera.

pina, Pseudoeurycea, Chiropterotriton, Parvimolge, Lineatriton, Thorius).

The supergenera *Bolitoglossa* and *Batrachoseps* share several important characters that are absent in *Hydromantes,* including fused premaxillae (with fused frontal processes in some species of each group), similar basibranchial cornua, posterolateral parietal spurs, columellar reduction, and multilobed testes. James Kezer has told me (*in litt.*) that *Batrachoseps* and the supergenus *Bolitoglossa* (he has not examined *Parvimolge*) have haploid chromosome numbers of thirteen, while *Hydromantes* and all other plethodontids examined have fourteen.

One species of *Batrachoseps* (*B. wrighti*) has paired premaxillae in adults and is similar in that respect to *Hydromantes,* but the evolutionary trend in *Batrachoseps* is in the direction of premaxillary fusion, as in the supergenus *Bolitoglossa. Hydromantes* and *Batrachoseps* resemble one another, and differ from supergenus *Bolitoglossa,* in having three rather than two caudosacral vertebrae and in the universal presence of septomaxillae. However, two caudosacral vertebrae occur in at least some individuals of all species of *Batrachoseps,* and in all members of three species.

Hydromantes is very similar to certain members of the supergenus *Bolitoglossa* (*e.g., Bolitoglossa*) in habitus and external morphology. In addition *Hydromantes* and the neotropical genera resemble each other, and differ from *Batrachoseps,* in having truly free tongues with no genioglossal muscles, low numbers of trunk vertebrae, tendencies for unicipital ribs and loss of diapophyses, loss of omohyoideus muscles, and five rather than four toes.

Batrachoseps and *Hydromantes* are relatively primitive, and retain such primitive features as three caudosacral vertebrae (some individuals) and paired premaxillae *(B. wrighti). Batrachoseps* is highly specialized, however, and is elongated with increased numbers of trunk vertebrae, multilobed testes, tendencies for fusion of the premaxillary toothed and frontal processes, loss of prefrontals, reduced frontals and parietals, well developed parietal spurs, and no fifth toes and fifth distal tarsals. It retains cornua, genioglossal muscles, and modified detoglossy, all relatively primitive features, but *Hydromantes* has lost both cornua and genioglossal muscles and has adetoglossy. *Hydromantes* is the most generalized of the three supergenera, retaining such primitive characters as unilobed testes, relatively large and separated premaxillae with relatively attenuated frontal processes, large columellae, and spurless parietals.

Bolitoglossa is the most advanced of the three supergenera, and advanced characters found in at least several genera include septomaxillary, maxillary tooth, and columellar loss, tendencies toward opisthocoely, acquisition of basapophyses, distinct tail constrictions, phalangeal modifications, and mesopodial fusions and reductions. Advanced characters shared with one or the other of the bolitoglossine supergenera include bilobed testes, reduced numbers of chromosomes, tendencies for unicipital ribs, fused premaxillae, and adetoglossy.

Hydromantes is apparently closer to the bolitoglossine ancestral stock than are either of the other two supergenera. Both *Hydromantes* and *Batrachoseps* are more closely related to the advanced *Bolitoglossa* than to each other, but *Batrachoseps* may be closer to *Bolitoglossa* than is *Hydromantes* (see Fig. 16).

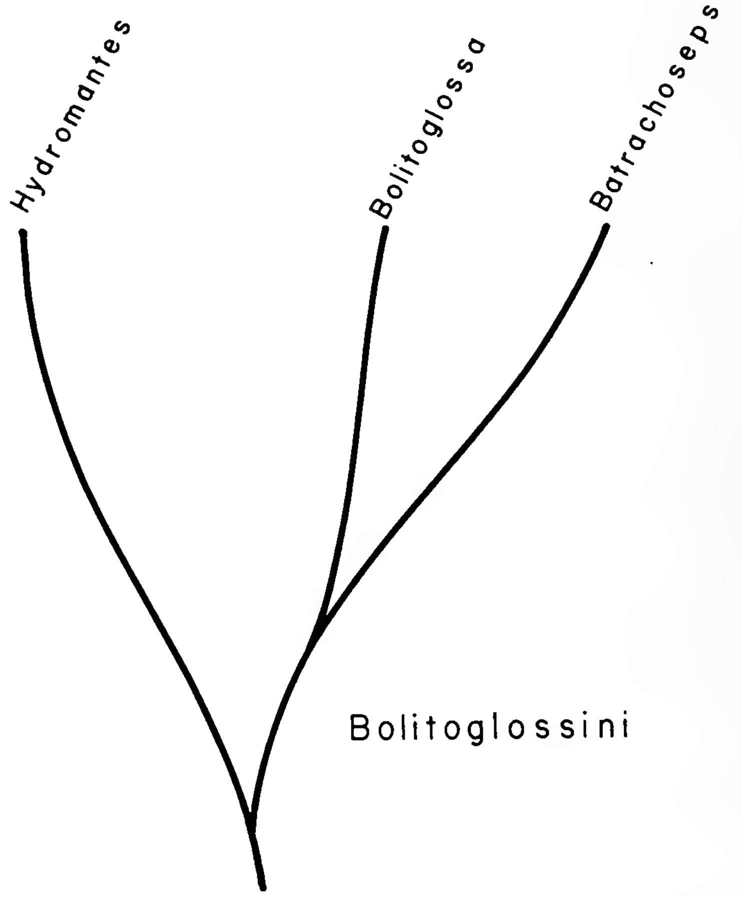


Figure 16. Diagrammatic representation of the relationships of the bolitoglossine supergenera.

Tanner (1952) presented a diagrammatic family tree of the free-tongued plethodontids, and discussed relationships of these genera. His study was based on throat musculature and hyobranchial cartilage structure, and he assumed that the free-tongued genera formed a natural group. Tanner suggested than an ancestral stock had given rise to two diverging generic groups, one containing *Gyrinophilus, Pseudotriton, Eurycea,* and *Manculus,* and the other containing *Hydromantes* and the neotropical genera. *Hydromantes* was considered to be close to *Bolitoglossa* and *Magnadigita,* but the other neotropical genera were placed in a separate line. Within the latter group three divergent evolutionary lines were recognized: (1) *Thorius,* (2) *Oedipina,* (3) *Parvimolge, Pseudoeurycea, Chiropterotriton, Lineatriton.* Tanner stated that he considered association of *Batrachoseps* with *Hydomantes* and the supergenus *Bolitoglossa,* as had been proposed by Piatt (1935), to be entirely unwarranted.

Although I strongly disagree with Tanner's conclusions concerning relationships of the neotropical genera to other plethodontids, our views of relationships within the neotropical group are similar, with one notable exception in the case of *Thorius.*

Salamanders of the supergenus *Bolitoglossa* present a bewildering mosaic of characters and an extremely complex evolutionary pattern. Three major generic groups may be recognized: (1) the *Bolitoglossa* group with one genus and about fifty species, (2) the *Oedipina* group with one genus and about sixteen species, (3) the *Thorius* group with five genera *(Thorius, Pseudoeurycea, Chiropterotriton, Parvimolge, Lineatriton)* and about forty-six species.

Bolitoglossa differs from the other genera of the supergenus *Bolitoglossa* in lacking sublingual folds. The folds are advanced characters and are related to the elongation of the ceratohyals into the anterior portions of the mouths. Within the Bolitoglossini, *Bolitoglossa, Hydromantes,* and *Batrachoseps* are the only genera that lack the folds.

Wake and Brame (1963a, 1963b) and Brame and Wake (1963) have presented evidence that the genera *Magnadigita* and *Bolitoglossa* in the sense of Taylor (1944) are not recognizable and have assigned all species to *Bolitoglossa.* It has been possible to examine skeletons of only about half of the species but all sections of the genus are represented. A number of osteological characters that vary interspecifically have been discovered, but none coincide with the old generic division based on amount of webbing (complete in *Bolitoglossa,* less extensive in *Magnadigita*). Detailed discussion of osteology and evolution of *Bolitoglossa* is deferred to a later date, but it is clear that a mosaic distribution of characters occurs. Species groups which bridge the old genera are recognizable, but only on internal characters; none warrants generic rank.

Oedipina differs from all other genera of the supergenus *Bolitoglossa* in having eighteen to twenty-two rather than fourteen trunk vertebrae. The marked elongation of the trunks and tails are specializations related to the evolution of specialized behavior and ecology of *Oedipina.*

Oedipina and *Bolitoglossa* are offshoots in different directions from the ancestral stock that gave rise to the relatively generalized members of the *Thorius* group. *Bolitoglossa* is the more primitive of the two, and both contain highly specialized species. Specialized characters of *Bolitoglossa* include loss of the septomaxillae and columellae by most species, and the prefrontals and tibial spurs by many, presence of basapophyses in many species, vomerine reduction in many species, tendencies for increased amounts of hand and foot webbing, and presence of mesopodial fusions. *Oedipina* has a number of specialized and advanced characters, including high vertebral numbers, many unicipital ribs, no septomaxillae (most species), prefrontals, columellae, or tibial spurs, the most specialized and advanced premaxillae in the family, and extensive mesopodial fusions and phalangeal losses.

The *Thorius* group of genera differs from *Bolitoglossa* and *Oedipina* in that distinct tendencies for intervertebral cartilage calcification are evident and transitional stages between amphicoely and opisthocoely occur. Included in the *Thorius* group are the most generalized and primitive species of the supergenus *Bolitoglossa,* but other species are among the most highly specialized and advanced in the family. Primitive *Chiropterotriton* retain such generalized and primitive features as septomaxillae, prefrontals, lingual cartilages, well developed columellae, vomerine preorbital processes, unfused premaxillary frontal processes, tibial spurs, nine tarsals, and eight carpals; but primitive species have advanced tarsal arrangements. The most advanced *Chiropterotriton* may lack septomaxillae, prefrontals, columellae, lingual cartilages, vomerine preorbital processes, and tibial spurs, and may have fused premaxillary frontal processes, seven carpals, and eight tarsals in a primitive configuration. All members of the genus retain bicipital ribs. Advanced species have strongly opisthocoelous vertebrae.

Primitive *Pseudoeurycea* have prefrontals, lingual cartilages, reduced columellae, vomerine preorbital processes, unfused premaxillary frontal processes, tibial spurs, eight carpals, nine tarsals, primitive tarsal arrangements, and bicipital ribs. These features are common to most species. Septomaxillae are absent in most species. No *Pseudoeurycea* have truly opisthocoelous vertebrae, but some intervertebral cartilage calcification occurs.

Pseudoeurycea and *Chiropterotriton* are very closely related, and can be separated consistently only on the basis of tarsal structure. Primitive and most advanced species of *Chiropterotriton* have specialized tarsi in which the fifth distal tarsals are larger than the fourth and articulate with the centrale. All *Pseudoeurycea* retain primitive tarsi in which the fourth distal tarsals are larger than the fifth, and articulation of the fourth tarsals with the fibulars eliminates the fifth tarsals from articulation with the centrals. Some advanced species of *Chiropterotriton (xolocalcae, bromeliacia)* have the primitive configuration encountered in *Pseudoeurycea* but they can be distinguished from all *Pseudoeurycea* because they lack prefrontals. Primitive *Chiropterotriton* can usually be distinguished from *Pseudoeurycea* by having septomaxillae, but advanced species lack septomaxillae and some species of *Pseudoeurycea* may have the structures. Tanner (1952) found differences in the details of hyobranchial structure between the genera, but I cannot corroborate his observations. Despite the fact that primitive members of *Chiropterotriton* and *Pseudoeurycea* are very similar, it is apparent that two groups are represented and the two genera are retained.

Tanner (1952) considered *Pseudoeurycea* to be the most primitive of the neotropical plethodontids. *Pseudoeurycea* and *Chiropterotriton* share several primitive and generalized characters, but each retains primitive characters reduced or lost in the other. As a genus *Chiropterotriton* has radiated and specialized to a greater extent than has *Pseudoeurycea,* but primitive members of both genera are almost equally primitive. If the total species complements are considered, the largely ground-dwelling, morphologically relatively uniform *Pseudoeurycea* must be considered more primitive than the largely arboreal, morphologically diverse *Chiropterotriton.* Primitive members of the two genera are very closely related and have diverged only slightly from common ancestral stocks.

The three remaining genera of the *Thorius* group apparently diverged from a pre-*Pseudoeurycea-Chiropterotriton* stock and have become highly specialized. *Parvimolge* and *Lineatriton* are probably closer to each other than either is to any other genus, but the two are also relatively closely related to both *Pseudoeurycea* and *Chiropterotriton.*

The single species of *Lineatriton* is an elongate form that has unicipital ribs, elongated vertebrae with only parapophyses on most vertebrae, and noticeably shortened limb elements. Septomaxillae have been lost. The genus is somewhat closer to *Pseudoeurycea* than to *Chiropterotriton,* but it is distinct from both. Resemblance to *Oedipina* is probably the result of parallel evolution.

The genus *Parvimolge* is probably an unnatural assemblage. Adequate material has been unavailable, and final assignment of the three species remains uncertain. I have not examined skeletal material of *P. praecellens* (known only from the unique type). *P. townsendi* has been considered to be very closely related to *Pseudoeurycea* by Tanner (1952) on the basis of similarities in throat musculature, and Uzzell (1961) has suggested that the species is closely related to *Lineatriton* because of similarities in hyoid and mesopodial calcification patterns. *P. townsendi* resembles *Chiropterotriton* in having septomaxillae and primitive species of both *Chiropterotriton* and *Pseudoeurycea* in having such generalized features as columellae (reduced), bicipital ribs, prefrontals, vomerine preorbital processes, and tibial spurs. The species differs from both genera in being dwarfed, in having distinctively shaped hands and feet (see Taylor, 1944), in having distinctive, large, dorsal glands, and in having the fourth and fifth distal tarsals fused. The species differs further from most *Pseudoeurycea* in having septomaxillae, and from all members of that genus in having eight rather than nine tarsals.

The species *richardi* was placed in *Parvimolge* by Taylor (1949), presumably on the basis of hand and foot shape. Rabb (1955) described *P. praecellens,* including it in *Parvimolge* because it shared several features with *P. townsendi,* including similar feet, coloration, conspicuous dorsal glands, and tail shape. Dorsal glands are absent in *richardi,* and Rabb suggested that absence of the glands, differences in foot structure, and enormous range disjunction (*richardi* in Costa Rica, *praecellens* and *townsendi* in Veracruz, Mexico) imply that *richardi* is not congeneric with *praecellens* and *townsendi.*

Septomaxillae, reduced columellae, lingual cartilages, and mesopodial and hyobranchial calcifications all occur in *P. townsendi,* but not in *P. richardi.* Nothing is known concerning the mesopodial pattern in *richardi,* but there is no reason why *richardi* cannot be placed in *Chiropterotriton* despite some differences in external foot morphology. It is true that the characters lacking in *richardi* but present in *townsendi* are those often lost in southern species of *Chiropterotriton.* This fact might support the suggestion that *richardi* is a member of *Chiropterotriton,* but it is also possible that the same losses have occurred in parallel in *Parvimolge.* Until more information concerning the species presently assigned to *Parvimolge* becomes available the problem is insoluble, and *richardi* is tentatively retained in the genus.

Thorius probably represents the earliest divergent stock of the line that leads to *Pseudoeurycea* and *Chiropterotriton* (Fig. 17). Dwarfing is severe in the genus, and the cranial elements are greatly reduced in size and modified in appearance. The genus is further characterized by such specializations as loss of columellae and vomerine preorbital processes, variable loss of septomaxillae, high frequency of mesopodial calcifications, fusion of distal tarsals 4 and 5, intervertebral cartilage calcification, and presence of posteriorly directed squamosal processes. Primitive characters retained by the genus include bicipital ribs, fourteen trunk vertebrae, and tibial spurs. Highly modified prefrontals are usually present. This mosaic pattern of generalized and specialized characters indicates that modern *Thorius* is the specialized end point of a line derived from a stock ancestral to other genera of the *Thorius* group. Calcification and ossification of such elements as the ends of long limb bones, intervertebral cartilages, and mesopodials may be interpreted as compensations for paedomorphic influence that has led to general skeletal dwarfing and reduction (see below, Paedomorphosis). Calcified mesopodials have been considered diagnostic of the genus since the time of Cope (1869), but the character lacks reliability. The largest *Thorius* that I have examined (28.2 mm.) has uncalcified mesopodials (see also Uzzell, 1961). There is no justification in removing *Thorius* from other neotropical genera and placing it in its own subfamily, the Thoriinae, as Cope (1893), and more recently Smith and Taylor (1948), have suggested. I also consider the genus less distinct from other neotropical genera than did Tanner (1952), and think that *Thorius* is closer to *Pseudoeurycea, Chiropterotriton, Parvimolge,* and *Lineatriton* than are either *Oedipina* or *Bolitoglossa.*

To briefly summarize, the tribe Bolitoglossini contains three distinct lines. The ancestral stock has given rise to the relatively unspecialized *Hydromantes.* Two main specialized branches have resulted in the related supergenera *Batrachoseps* and *Bolitoglossa* (see Fig. 16). Within the supergenus *Bolitoglossa* there has been a further divergence, with the *Thorius* group of genera closest to the ancestral stock. Within the *Thorius* group *Pseudoeurycea* and *Chiropterotriton* are the most primitive genera, and *Thorius* is the most specialized and advanced. *Thorius* probably represents the first divergence from the group ancestral stock, and *Lineatriton* and *Parvimolge* have diverged somewhat more recently. *Bolitoglossa* and *Oedipina* represent offshoots in different evolutionary directions from the ancestral stock of the

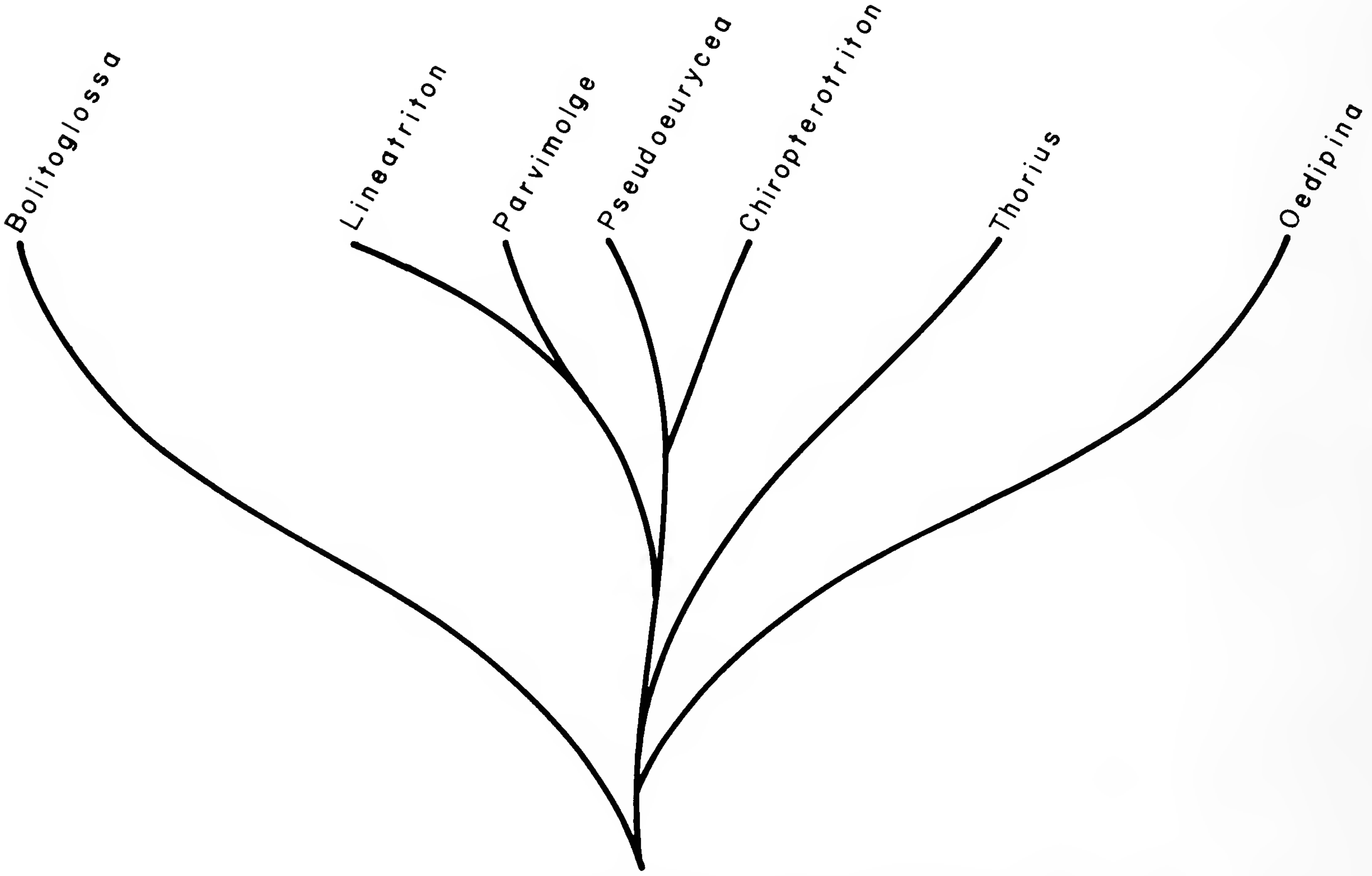


Figure 17. Diagrammatic representation of relationships within the supergenus *Bolitoglossa.*

Thorius generic group. *Oedipina* is the most specialized and advanced plethodontid genus.

Trends

Ecology and Life History

The ancestral adaptive zone

Simpson (1953: 199) states that at any instant in time environments and organisms of a given taxonomic level define a field or type of adaptation characteristic of the group. These adaptive types can be visualized if represented on paper as bands or zones that form sorts of grids (Fig. 18). Zone breadth is a reflection of general adaptation; the broader the zone, the more generally adapted are the organisms. Such zones involve abstraction and oversimplification but are useful in explaining evolutionary patterns and pathways. Simpson emphasizes that such a zone is not geographic, physical, or even environmental in character, but "an adaptive zone, representing a characteristic reaction and mutual relationship between environment and organism, a way of life and not a place where life is lived." I conceive of an adaptive zone as the sum total ecological niche relationships of a group of organisms with the same base level of general adaptation. Thus modern reptiles can be said to occupy a terrestrial adaptive zone in a broad sense, because of the general adaptational level associated with amniotic egg evolution. Birds, close reptilian relatives, have entered a new aerial adaptive zone as a result of a base level of general adaption (in the broadest sense) associated with the evolution of feathered flight. In order to establish the ancestral adaptive zone of plethodontid salamanders it is essential to briefly consider the relationships of the family to other salamander families, and the nature of the ancestral plethodontid stock.

Plethodontid origins

Cope (1866, 1867, 1869, 1889) considered plethodontids to be closely related to and possibly derived from ambystomatid salamanders. Stejneger (1907) placed the families Ambystomatidae (including hynobiids), Salamandridae, and Plethodontidae (including desmognathines) in a superfamily Salamandroidea, a group first proposed by Sarasin and Sarasin (1887-1890) for all salamanders except amphiumids. Dunn (1922) completed the transition from Cope's ambystomatid theory by stating "it is probable that some primitive salamandrid . . . gave rise to the much degenerate Plethodontidae." His statement was based on a study of the otic apparatus, and on the work of Wilder (1920) which demonstrated that plethodontid parasphenoid teeth were ontogenetically derived from the anterior vomerine teeth. The vomerine arrangement of plethodontids, Dunn argued, could most easily have been derived from the posteriorly directed vomerine tooth series typical of salamandrids. In 1926 Dunn included six families (Proteidae, Ambystomatidae, Pleurodelidae, Salamandridae, Plethodontidae, Amphiumidae) in the suborder Salamandroidea. He declared that "the Plethodontidae can be most easily derived from the Salamandridae." Dunn's ideas have been wholly accepted by most recent workers (*e.g.*, Noble, 1931; Piatt, 1935; Herre, 1935; Tanner, 1952; Auffenberg, 1961). Noble (1931) added one modification — the ambystomatids were placed in a separate suborder, the Ambystomatoidea. Since that time salamandrids and plethodontids have continued to be associated in the same suborder, and ambystomatids have been placed in a separate suborder (Goin and Goin, 1962).

Laurent (1947) thought the vomerine tooth patterns observed in salamandrids and plethodontids represented separate evolutionary derivations, and he suggested that both conditions could have evolved from an ambystomatid type. He also cited similarities in the vertebrae of plethodontids and ambystomatids (primitively amphicoelous versus opisthocoelous in salamandrids), presence of septomaxillae and costal folds in both families (absent in salamandrids), and absence of paraoccipital processes and fronto-squamosal arches in both (both present in primitive salamandrids). Laurent concluded that the suborder Salamandroidea of recent workers was an artificial assemblage, and suggested that the Plethodontidae be housed in a third suborder, the Plethodontoidea. Laurent's Ambystomatoidea includes only the Ambystomatidae, the Plethodontoidea includes only the Plethodontidae, and the Salamandroidea includes the Salamandridae, Amphiumidae, Proteidae, and Sirenidae. As an alternative Laurent suggests inclusion of all of the above families in a single suborder, the Salamandroidea.

Teege (1956) found that plethodontid vertebrae were more similar to those of ambystomatids than to salamandrids. She was unable to find supporting data for Dunn's theory. Larsen (1963) found little to support salamandrid origin of plethodontids based on his study of cranial morphology, and suggested that plethodontids and ambystomatids were rather closely related. Both groups were thought to have arisen from a prohynobiid ancestor. Recently Monath (1965) has shown that the opercular apparatus in plethodontids is basically quite distinct from that of salamandrids. He has suggested that plethodontids were not derived from salamandrids, but from a primitive salamander stock.

During the course of this study I have had occasion to investigate salamandrid, hynobiid, and ambystomatid anatomy. In addition to data presented by Laurent, Teege, Larsen and Monath, I have noted similarities in the throat musculature of salamandrids and hynobiids, and in plethodontids, ambystomatids, and hynobiids. Ambystomatids and plethodontids also resemble one another, and differ from salamandrids, in hyoid and mesopodial structure. Larval and adult palatal and vomerine structure of plethodontids is much more similar to that observed in hynobiids and ambystomatids than that in salamandrids.

I recognize four suborders in the order Caudata. The suborder Cryptobranchoidea includes the families Cryptobranchidae and Hynobiidae. Members differ from the other suborders in having external fertilization and in retaining distinct angulars in the lower jaws. The suborder Sirenoidea includes only the family Sirenidae, a group recently raised to ordinal level as the Order Trachystomata by Goin and Goin (1962). Sirenids differ from other salamanders in lacking hind limbs and in the peculiar structure of their vertebrae (see Goin and Auffenberg, 1958), but resemble salamanders in cranial morphology, particularly of the palatal elements, and in hyoid morphology. I agree with Estes (1965) in considering ordinal status unwarranted. The suborder Ambystomatoidea includes the families Ambystomatidae and Plethodontidae, and differs from the remaining suborder, the Salamandroidea (Salamandridae, Proteidae, Necturidae, and questionably Amphiumidae), in that primitive ambystomatoid genera have vomerine preorbital processes which bear laterally oriented series of teeth, and have septomaxillae.

My hypothesis of the present state of salamander evolution is that the modern and progressive suborders Ambystomatoidea and Salamandroidea represent separate evolutionary lines that have diverged independently from an ancestral stock similar to modern hynobiids. Ambystomatoids dominate the New World, and salamandroids dominate the Old World, but representatives of both occur in both regions.

The foregoing account has been necessary because most previous theories concerning plethodontid ancestry have assumed origin from salamandrid stocks. Despite their apparent error in establishing plethodontid ancestry, the most acceptable theory concerning the ancestral adaptive zone (their ancestral home) was advanced by Dunn (1917), Wilder and Dunn (1920), and Dunn (1926). All plethodontids are lungless and lack ypsiloid processes on the pelvis. These losses are presumed to be rheotropic adaptations. The reasoning is that lungs are hydrostatic organs and disadvantageous for stream bottom dwellers. Ypsiloid processes aid in emptying the lungs, and are of little value in lungless forms. Wilder and Dunn (1920) reviewed literature reports and showed that lunglessness or greatly reduced lungs are associated with mountain brook environments in European salamandrid genera *(Euproctus, Salamandrina, Chioglossa)*. The list of nonplethodontid lungless forms should also include the ambystomatid genus *Rhyacotriton* of northwestern North America, and the Asian hynobiid genus *Onychodactylus;* both are mountain brook forms. Because the entire family Plethodontidae is lungless, Wilder and Dunn reasoned that the species have had a common lungless ancestor, and that this ancestor likely inhabited mountain brook environments. The southern Appalachian region (Appalachia) contains the greatest diversity of plethodontids, including all of the mountain brook genera and the most primitive members of the family. Appalachia is a very ancient upland, and presumably this relatively stable area has been the region of origin, the primary distribution center, and the dominant area of survival of the family Plethodontidae.

The ancestral adaptive zone can be characterized as a way of life in semiaquatic, montane, warm temperate niches such as probably existed in late Mesozoic times in what is now eastern North America.

Evolution within the adaptive zone

The Desmognathinae and the Hemidactyliini have remained primarily within the ancestral adaptive zone, but the Bolitoglossini and Plethodontini both have occupied new terrestrial adaptive zones. In addition there are tendencies in desmognathine and hemidactyliine genera toward splitting the old zone into subzones and toward moving out of the zone (see Fig. 18).

Within the genus *Desmognathus* the most important trend obviously is the one leading in the direction of increased terrestriality (see below), but primitive species have remained in the ancestral adaptive zone. *Phaeognathus* is probably a terrestrial species that has left the old adaptive zone. *Leurognathus* has remained in the ancestral zone, but selection has resulted in special adaptation and in restriction to a specialized segment of the ancestral environment — the mountain stream bottoms. Martof (1962) has recently considered in some detail the ecology of *Leurognathus*. He states that the genus is restricted to cool mountain streams and that only during times of droughts do *Leurognathus* and *D. quadramaculatus* (the most aquatic *Desmognathus*) utilize a common habitat. *Leurognathus* should not be fitted into the predominant adaptive sequence toward terrestrialism; the evolutionary trend in the genus has been from semiaquatic to strictly aquatic existence.

The tribe Hemidactyliini has remained closer to the ancestral adaptive zone than any other group of plethodontids. Evolution within the group has been characterized by movements out of the ancestral mountain brook environment into closely adjacent environments and by restriction to specialized aquatic environments. *Gyrinophilus* and *Pseudotriton* have remained very close to the ancestral environment and occur in spring and stream habitats. A single species, *Gyrinophilus palleucus*, is a paedogenetic form in subterranean waters in Tennessee and Alabama.

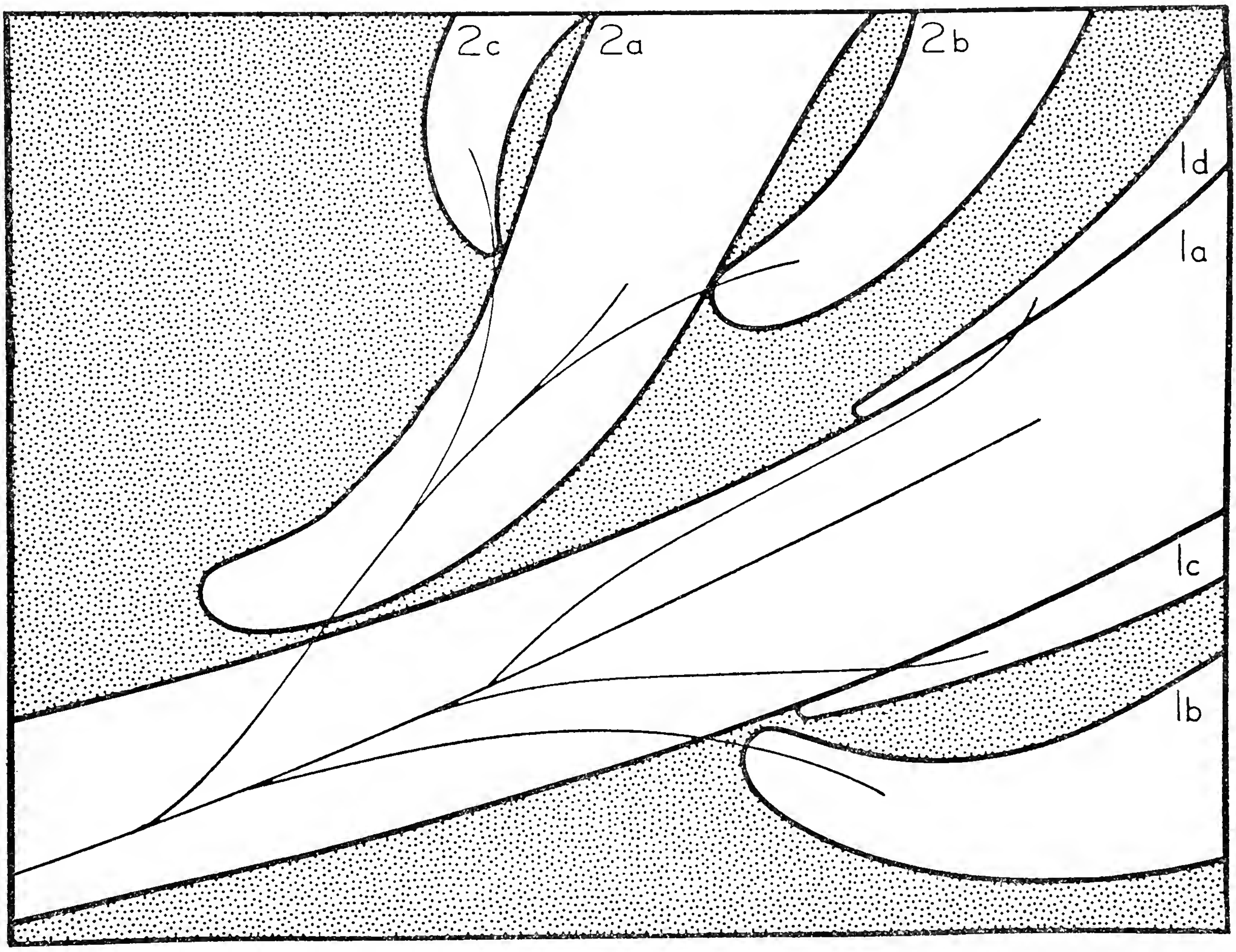


Figure 18. Adaptive zones and subzones in the family Plethodontidae. 1a, semiaquatic zone; 1b, paedogenetic subzone; 1c, aquatic subzone; 1d, swamp-bog subzone; 2a, terrestrial zone; 2b, arboreal subzone; 2c, semifossorial subzone.

Eurycea has become somewhat diversified. Primitive species such as *E. aquatica, E. bislineata,* and *E. multiplicata* inhabit brooksides and springs, situations that resemble the ancestral habitat. *E. longicauda* inhabits streams and springs, but also the twilight zone of caves, and *E. lucifuga* is essentially limited to the twilight zones of limestone caves (Hutchison, 1958). Several species of *Eurycea* are paedogenetic and have adapted to specialized aquatic situations. *E. tynerensis, E. nana, E. neotenes,* and *E. pterophila* inhabit springheads and cold swift streams. *E. latitans* occurs in cave waters, and *E. troglodytes* occurs in the waters of a large solution cave on the Edwards plateau of Texas (Baker, 1957; 1961). These species occur only at the periphery of the generic range. Specialization into restricted portions of the ancestral habitat or into specialized adjacent habitats has allowed survival in areas beyond the general generic range.

Typhlomolge, Haideotriton, and *Typhlotriton* are all close relatives of *Eurycea.* All are found in areas peripheral to Appalachia in specialized aquatic habitats. All are unpigmented, blind, and subterranean and have apparently survived in rather unfavorable climatic regions following climatic change by adapting to specialized, relatively very stable, underground habitats.

E. quadridigitata is more terrestrial than other *Eurycea,* and is found in low swampy areas, trickles from springs, and sphagnum bogs (Bishop, 1943; Carr, 1940). *Hemidactylium, Stereochilus,* and *E. quadridigitata* have entered pond and swamp habitats, and this movement is associated with occupancy of new adaptive subzones (Fig. 18). Apparently three separate and parallel evolutionary lines are represented. All breed in ponds and swamps in relatively quiet waters. The larvae resemble each other and differ from all other plethodontids, including sympatric species, in possessing relatively high dorsal fins that extend onto the trunks of the animals (Bishop, 1941; Goin, 1951; Schwartz and Etheridge, 1954). Goin compared the rudimentary hind limbs of hatchlings of *Hemidactylium* with those of *E. quadridigitata* and noted that both have toeless lobes at early stages. Both have four toes as adults, and that fact may be related to the slow rate of development of the hind limbs in larval stages. Hind limbs of *Stereochilus* larvae apparently are better developed than the others. Movement out of the stream and into pond environments has been accompanied by acquisition of pond-type larvae. Significantly all have ranges that are peripheral to those of the primitive hemidactyliine genera which have stream-type larvae. *E. quadridigitata* is semiaquatic, *Stereochilus* is aquatic, and *Hemidactylium* is terrestrial in the adult stage.

Occupation of new adaptive zones and subzones

Simpson (1953) has discussed the biological basis of evolutionary or radiative movements into new adaptive zones, and the acquisition of new ways of life. In order for populations to enter new adaptive zones there are, according to Simpson, three essentials. The populations must have *physical access* to the new zones. They must also have the necessary preadaptations which will be of significant adaptive value in the new way of life, that is they must have *evolutionary access.* Finally, competitive encounters in the new zones must be at a minimum so that the populations have *ecological access* to the zones. Only when populations have all types of access can occupation of new adaptive zones begin.

Evolutionary trends within the subfamily Desmognathinae are particularly instructive in elucidating how occupation of new adaptive zones may have occurred. Although primitive desmognathines remain in the primitive adaptive zone, a significant diversification has occurred within the subfamily. Occupation of a new aquatic adaptive subzone by *Leurognathus* has been discussed above. A terrestrial trend is evident in *Desmognathus.* Organ (1961 a) recently completed a significant analysis of the ecology of five species of *Desmognathus* which occur in a variety of habitats on Whitetop Mountain, Virginia. The most aquatic and generalized is *D. quadramaculatus,* a species that inhabits streams and stream banks. *D. monticola* represents the next evolutionary stage and is found on stream banks and in seepage areas, habitats more terrestrial than those of *quadramaculatus. D. fuscus* is slightly more terrestrial than *monticola,* and *D. ochrophaeus* is unquestionably more terrestrial than *fuscus. D. wrighti* is the terminal and most terrestrial species within the series; it is primarily a forest floor form with only breeding females and hibernating individuals ever found in aquatic sites. The species arranged in order of increasing terrestriality are *quadramaculatus-monticola-fuscus-ochrophaeus-wrighti.* Arranged in order of decreasing larval period, the species are *quadramaculatus-fuscus-monticola-ochrophaeus-wrighti; wrighti* has direct terrestrial development with no free-living larvae. Organ presented survivorship curves which show that male survivorship increases in the series *quadramaculatus - monticola - fuscus-ochrophaeus-wrighti,* a trend identical to the aquatic-terrestrial series. Female survivorship in *quadramaculatus* and *monticola* is about equal to that of males of the same species, but mortality of mature females of *fuscus, ochrophaeus,* and *wrighti* is considerably higher than that of males of the species at the same ages. Organ has shown that brooding females of *ochrophaeus* and *wrighti* return to aquatic sites, and, as a group, have higher mortality rates than those parts of the populations that remain terrestrial during the brooding season. In addition the more terrestrial the species, the higher is the proportion of mature males to mature females in the populations; this is another indication of the higher mortality of mature brooding females in aquatic nesting sites. Plethodontid evolution has been characterized by parallel invasion and occupation of terrestrial adaptive zones (see below). As a result of Organ's study it is now known that survivorship is increased in terrestrial habitats within a series of related species and within populations of a single species. Selection favors terrestrial over less terrestrial individuals within the populations. It is likely that the populations involved in crossing the adaptive threshold between the semi-aquatic and terrestrial zones (probably in early Tertiary) were under strong environmental selection pressures, and that the populations evolved sequentially at very rapid, progressive rates.

Although the trend in *Desmognathus* is toward increased terrestriality, the genus has not entered a new adaptive zone. One species, *D. wrighti,* has abandoned the aquatic larval stage and is essentially terrestrial, but it is a highly specialized form that is unlikely to give rise to an adaptive radiation. Even if the species has the necessary evolutionary plasticity, it is doubtful that successful occupation of the new adaptive zone will be possible, for the terrestrial niches in Appalachia are already largely occupied by species of *Plethodon* and *Aneides* and ecological access is not available.

Available information indicates that *Phaeognathus* is a terrestrial species (Valentine, 1963 b; 1963 c; Brandon, 1965). Characters that suggest terrestriality include terrestrial adult habitat, co-ossified skin on anterior cranial elements and elongation as a result of the addition of trunk vertebrae (both adaptions related to terrestrial burrowing), and large, yolky oviducal eggs resembling those of terrestrial plethodontines. *Phaeognathus* apparently represents an invasion of the terrestrial adaptive zone by a specialized, dead-end group.

All genera of the tribes Plethodontini and Bolitoglossini have achieved true terrestriality. All lack free living larvae, and have directly developing embryos that are retained within the egg membranes; eggs are laid on land. The two assemblages are distinct morphologically, and terrestriality in the groups may have evolved in parallel. Movement to land is truly movement into a new adaptive zone and adoption of a new way of life for salamanders. Terrestriality has resulted in a significant elevation of the base level of general adaptation, which has been followed in parallel lines by significant evolutionary diversifications and adaptive radiations.

The terrestrial environment borders the ancestral mountain brook habitat, the presumed home of plethodonine and bolitoglossine progenitors, and physical access to the new adaptive zone was no great problem. At the time the adaptive shift was proceeding (Cretaceous or early Tertiary periods) the ancestral environment was probably crowded with salamanders and competition was keen. By contrast the terrestrial environment adjoining was relatively unpopulated by potential competitors so that the pioneers had ecological access to the new zone. Today plethodontids have a wide variety of larval types ranging from permanent larvae *(Typhlomolge)* and species with long larval stages *(Desmognathus quadramaculatus, Gyrinophilus)* to species with brief larval stages *(Desmognathus aeneus, Hemidactylium).* The larvae may be stream or pond types. The variety of larvae in modern forms and the presence of distinct terrestrial trends in a single, primitively aquatic genus *(Desmognathus)* are indications of the evolutionary plasticity of plethodontid developmental processes. This plasticity might be considered the prospective adaptation which provided evolutionary access to the new terrestrial adaptive zone.

Diversification usually follows occupation of new adaptive zones with the extent of subsequent adaptive diversity roughly proportional to the distinctiveness of the new adaptive type and extent and diversity of the new territory (Simpson, 1953). The diversification is related to the number of new adaptive subzones to which the evolving populations have access. In the case of the Plethodontini and Bolitoglossini diversification has been, relative to other salamander groups, very great.

Within the Bolitoglossini terrestriality has been achieved and movement into several adaptive subzones has been initiated. The tribe as a whole has a high base level of general adaptation, but most genera are very specially adapted to specific environments.

Hydromantes is associated with a rather restricted habitat in limestone areas. The species occur on the surface under rocks and other debris, but individuals also inhabit caverns. Survival of this relatively ancient group has been related to association with relatively stable microenvironments.

Distinct evolutionary trends in the direction of trunk and tail elongation and general skeletal reduction are found in *Batrachoseps.* The most primitive species *(B. wrighti)* has relatively low numbers of trunk vertebrae, moderately long tails, and relatively long limbs, but the advanced species have many trunk vertebrae, very long tails, and very small limbs. All have lost fifth toes and fifth distal tarsals. These specializations indicate that *Batrachoseps* has undergone an evolutionary modification of both locomotor morphology and behavior, and these changes are apparently associated with occupancy of a new environment. Storer (1925) stated that *Batrachoseps* uses the excavations made by earthworms and insects, and interpreted elongation of the body, increase in the number of trunk vertebrae, reduction in size of limbs and feet, and tail elongation as specializations for subterranean life. From personal acquaintance with *Batracho-*

seps in the field it is apparent to me that the southern California species spend considerably more time in subterranean refuges than they do on the surface and that morphological specializations are directly correlated with behavioral and ecological specializations. The genus is in the process of invading a new semi-fossorial or fossorial adaptive subzone. Many plethodontids have genetically fixed numbers of vertebrae. Apparently variability in the numbers of trunk vertebrae and attenuate habitus have given *Batrachoseps* evolutionary access to the new adaptive subzone.

The supergenus *Bolitoglossa* is unique in being the only tropical group of salamanders. Within the neotropics the group has undergone a considerable and significant radiation. The supergenus comprises seven tropical genera and over 100 species—almost two-thirds of the plethodontid species. Plethodontids probably arose in what is now the Nearctic region, and the primary dispersal center has been northern; but a second center of dispersal is today the southern and eastern borders of the Mexican Plateau, and it is inappropriate to speak of the family Plethodontidae as a Holarctic or Nearctic group.

Most tropical plethodontids occur at high elevations in relatively cool habitats, and only two genera *(Bolitoglossa, Oedipina)* have successfully invaded the tropical lowlands (*Lineatriton* and *Parvimolge* may also occur in tropical lowlands but both have very limited distributions).

Neotropical species occupy a variety of terrestrial niches. *Lineatriton* and *Oedipina* are greatly elongated with reduced limbs and feet and extremely long tails. Not much information is available concerning the habits of the two, but apparently both are subterranean to some extent and utilize burrows of earthworms, mammals, etc. (Dunn, 1928). Other genera *(Pseudoeurycea, Thorius)* are more or less surface litter forms found under rocks and logs and under the loose bark of fallen trees. Some *Chiropterotriton* are terrestrial and occur in mossy areas on banks and cliffs.

Species of the genera *Bolitoglossa, Chiropterotriton, Pseudoeurycea,* and *Parvimolge* are moving into a new adaptive subzone—the arboreal subzone. *Chiropterotriton* is a genus of primarily highland, climbing species. The group has an adaptation which has apparently given it evolutionary access to the new subzone; this feature is the articulation of all distal tarsals with the centrals (see above, mesopodial elements). The mesopodial pattern is apparently of significance in facilitating climbing by allowing greater digital spread.

Primitive species of *Bolitoglossa* occur at moderate to high elevations from southern Mexico to northwestern Colombia, and have little to moderate hand and foot webbing. Most primitive species are ground-dwellers living under rocks and surface debris in primarily unforested highlands. Some extend to moderate elevations and may occur in bromeliads as well as on the ground *(e.g., B. subpalmata).* Throughout its range *Bolitoglossa* has invaded the tropical lowlands and expanded its peripheral range. Invasions of lowlands have invariably been accompanied by increased webbing, flattening of the hands and feet, and increased arboreality. Fully webbed hands and feet provide more surface area and are of great significance in forms such as *Bolitoglossa,* which depend on surface tension to support their weight while walking and climbing on smooth, moist leaf surfaces. Genetic potential for variation in hand and foot morphology and subsequent molding by selection are the most important factors providing evolutionary access to the lowland arboreal subzone. The problem of ecological access is particularly acute in tropical lowlands. The "salamander niches" of higher latitudes and elevations are filled —primarily by frogs and possibly by snakes and lizards. Ecological access has been available, however, in arboreal habitats, the route taken by *Bolitoglossa,* and in semi-fossorial habitats, the route followed by *Oedipina.*

The final group, tribe Plethodontini, probably left the semiaquatic adaptive zone at a later date than the Bolitoglossini, and as a group is more generally and less specially adapted. Species of *Aneides* and *Plethodon* still occur in Appalachia, but the bolitoglossines all occupy ranges far from the ancestral center. Two of the three plethodonine genera, *Plethodon* and *Ensatina,* are primarily ground-dwellers and are most frequently encountered under rocks, logs, and other surface litter, or out wandering about on the forest floor. Most or all species of the two genera spend considerable amounts of time below the surface. *Ensatina* is a rather stout-bodied form which uses burrows of larger organisms such as rodents as a means of getting below the surface (Stebbins, 1954). Species of *Plethodon* are more elongate than *Ensatina.* Slender attenuate forms such as *P. cinereus, P. richmondi,* and *P. elongatus* have reduced limbs and feet and are able to enter burrows of relatively small size. Some of the larger, longer-legged species are capable of some scansorial locomotion; I have encountered *P. jordani* at distances one to three feet above ground on tree trunks. Other large species such as *P. yonahlossee* inhabit burrows of relatively large diameter. One species, *P. dunni,* has secondarily returned to a semiaquatic habitat in the Pacific Northwest and is commonly encountered in rocky, moss-covered seepage areas. The primary habitat of both *Plethodon* and *Ensatina,* however, is at the surface of the ground away from running water.

The genus *Aneides* is an excellent example of a group entering a new adaptive subzone, the arboreal way of life. The most primitive species, *A. hardii,* is a *Plethodon*-like form that lives in, under, and on fallen logs. Three other species *(A. aeneus, A. ferreus, A. lugubris)* are arboreal to a large degree and have numbers of specializations related to arboreal life (depressed body, long limbs and digits, bifurcated terminal phalanges, prehensile tail). A detailed analysis of evolutionary patterns and trends in *Aneides* has been prepared and will be published elsewhere.

A final species, *A. flavipunctatus,* is a short-legged salamander with a cylindrical body. It is often encountered in very moist situations such as brooksides (Myers and Maslin, 1948). It is similar to *Plethodon dunni* in this regard and has a much greater affinity for wet habitats than other *Aneides.* Return to semiaquatic habitats (but with retention of the terrestrial "way of life") has occurred only in the Pacific Coast species of *Plethodon* and *Aneides,* since such ecological niches are occupied by *Desmognathus, Eurycea,* etc., in the East.

Paedomorphosis

Paedomorphic influence and plethodontid evolution

Paedomorphosis is a term used to denominate several morphological modes or patterns of evolution. Paedomorphosis involves characters that are present or make their appearance in the young stage of an ancestral group and which in the ontogeny of a descendent appear: (1) in the young and adult stage, producing a substitution of a new adult condition for the old, resulting in progressive deviation in the ontogeny of the descendent from that of the ancestor; or (2) in the adult, by a relative retardation of the development of the bodily structures as compared with the reproductive organs (DeBeer, 1958). Paedomorphosis is and has been of extreme importance in the evolution of plethodontid salamanders, and the general principle involved may be restated as the mode by which larval and youthful characters in the ancestor can influence adult characters in the descendent (Garstang, 1922; De Beer, 1958).

Conditions of two distinct types have resulted from paedomorphic influence in plethodontids. The first is paedogenesis in which sexual maturity is accelerated and all members of the species retain larval morphology (except reproductive system) throughout life. Paedogenesis is genetically fixed, leads to specialization and degeneration, and is of little significance as far as future phylogenetic progress is concerned. De Beer (1958) used the term neoteny to describe the permanent larval condition of salamanders, but he fails to distinguish between environmentally induced and genetically fixed conditions. The later (called permanent neoteny) perfectly fits his description of paedogenesis. The other major condition which results from paedomorphosis is a phenomenon called arrested development or differential metamorphosis. Differential metamorphosis is a term that describes the paedomorphic pattern in which metamorphic processes are extended over a considerable period of time, with some elements (bones in the present case) completing metamorphosis early, others very late, and some not at all. This condition is more characteristic of terrestrial than aquatic groups of plethodontids and has been of great importance in providing an escape from specialization in the ancestral adaptive zone and access to new adaptive zones.

Paedogenesis occurs only in the following species, all members of the tribe Hemidactyliini: *Gyrinophilus palleucus* (three distinct, allopatric races), *Eurycea latitans, E. nana, E. neotenes, E. pterophila, E. troglodytes, E. tynerensis, Typhlomolge rathbuni, T. tridentifera,* and *Haideotriton wallacei.* Based on the morphological evidence presented above, paedogenesis has probably evolved in parallel at least four, and possibly more times. All paedogenetic species are highly specialized, and their distribution is somewhat to greatly peripheral to the main tribal range. Paedogenesis may have arisen initially in response to selection pressures operative in marginal habitats during arid periods. Most paedogenetic species occupy subterranean waters exclusively or to a considerable degree. Certainly aquatic larvae of ancestral populations had physical access to such environments, and the very fact that ancestral populations had aquatic larvae provided evolutionary access to the new aquatic or subterranean adaptive subzone. Subterranean waters are notably free of competitors, and the invaders also had ecological access.

Differential metamorphosis has not been a major feature of the evolution of the desmognathines. Perhaps shortening of the larval periods and speeding of the metamorphic processes in advanced *Desmognathus* are related to paedomorphosis. Small adult size and resemblance in osteological structure to young stages of primitive species characterize *D. aeneus* and *D. wrighti*. Examples are retention of anterior vomerine teeth in adults, relatively slight sexual dimorphism, and relatively thin, light cranial elements. These features are a result of paedomorphic influence, and sexual maturity is achieved at a morphological stage roughly equivalent to a juvenile stage of such species as *D. quadramaculatus*. Both species have distinct terrestrial tendencies.

Apart from the paedogenetic effect, paedomorphosis has had some influence in the Hemidactyliini. *Hemidactylium* and *Eurycea quadridigitata* have only four toes. The larvae of both differ from those of other plethodontids in that the hind limbs develop slowly and are represented in hatchlings by undifferentiated lobes. Failure of the fifth toes to develop may be the result of differential initial growth rates and delayed limb development. Paedomorphosis may also be responsible for the relatively weak cranial elements and tenuous cranial articulations of such species as *E. quadridigitata* and *E. multiplicata*, diminutive size of *E. quadridigitata,* retention of a lateral line system on the head of adult *Stereochilus,* relatively small eyes of *Stereochilus,* and relatively poorly developed eyes, eyelids, and nasolacrimal glands of *Typhlotriton*.

Bolitoglossines have been influenced by paedomorphosis to a greater degree than any other terrestrial plethodontid group. *Hydromantes* has retained the primitive metamorphic pattern in regards to premaxillary structure, but paedomorphosis may be responsible for the failure of prefrontals to develop, the relatively weak skull articulations, and for the high numbers of unicipital ribs in the European species.

Batrachoseps has been profoundly influenced by paedomorphosis, and differential metamorphosis is apparent in the modern species. Premaxillae are fused in the young of all species and in the adults of all except *B. wrighti*. Premaxillary metamorphosis is thus delayed relatively long in *wrighti,* and is never achieved in the other species. A further example of differential metamorphosis is the appearance in very large *wrighti* of tiny prefrontal bones, which are absent in other species. Other paedomorphic effects evident in members of the genus include weak development of frontals and parietals, incomplete cranial roof formation, incomplete development of vomers with no preorbital processes, absence of second basibranchials, weak limb and foot development, and absence of fifth toes. Prefrontals and vomerine preorbital processes are among the last elements to develop during primitive plethodontid metamorphosis.

Neotropical salamanders (supergenus *Bolitoglossa*) have been affected by paedomorphosis more than any other plethodontid group with the exception of the paedogenetic species. Examples of paedomorphic influence include fusion of premaxillae and absence of second basibranchials in all genera. Examples found in individual genera follow.

Bolitoglossa: failure of prefrontals to develop, or irregular prefrontal development in a number of advanced species belonging to different species groups *(rufescens, occidentalis; savagei, adspersa, orestes; cerroensis, robusta; colonnea);* failure of septomaxillae to develop in most species; partially to fully webbed feet (a condition encountered in young or embryonic stages of other genera).

Oedipina: failure of prefrontals and septomaxillae to develop; weak development of limbs and feet, with reduced phalanges and variable numbers of mesopodial fusions; high percentage of unicipital ribs; extremely small premaxillae; weak skull articulations.

Pseudoeurycea: failure of septomaxillae to appear in all but a few species, which have irregular degrees of development.

Lineatriton: failure of septomaxillae to become well developed; diminutive size; reduced limbs and feet.

Thorius: variously developed septomaxillae; all cranial elements greatly reduced in size; diminutive size; reduced limbs and feet; enlarged nostrils of some species.

Two genera, *Chiropterotriton* and *Parvimolge,* deserve special comment. Primitive *Chiropterotriton* are but slightly affected by paedomorphosis, but an evolutionary gradient related to paedomorphosis exists in the genus on a roughly north to south axis (see also Rabb, 1960). The northern species usually have prefrontals, septomaxillae, tibial spurs, and vomerine preorbital processes, but the elements are absent in some of the southern species. In addition southern species demonstrate features considered by Rabb (1960) and me to be strengthening compensations in certain elements to paedomorphic weakening in others. These compensations include calcification of normally cartilaginous structures such as mesopodial elements, heads of limb bones, and intervertebral cartilages, fusion of premaxillary frontal processes, and mesopodial fusions. These compensations are also encountered in varying degrees in *Batrachoseps, Lineatriton, Parvimolge, Oedipina,* and *Thorius*. Table 2 is a representation of the distribution of paedomorphic characters and compensations to paedomorphosis in some species of *Chiropterotriton*. It is apparent that the southern, more advanced species have more paedomorphic characters than the more primitive northern species. The first four species *(priscus, chiropterus, multidentatus, dimidiatus)* occur north of the Isthmus of Tehuantepec; the remainder occur south of the Isthmus. *C. dimidiatus* and *C. multidentatus* occur sympatrically at some localities, otherwise the chart is arranged on a geographical north-south axis. Some of the data in the table are at variance with information presented by Rabb (1960), but the important point is that evolutionary specialization and advance in *Chiropterotriton* is associated with a geographic trend and with trends in the direction of increased paedomorphosis.

Parvimolge townsendi of Veracruz, Mexico, is strongly affected by paedomorphosis (diminutive size, reduced limbs and feet, mesopodial fusions, calcified mesopodials, calcified intervertebral cartilages, reduced septomaxillae and columellae). It resembles *P. richardi* of Costa Rica in some characters (see above) but differs in others. The two species probably represent different evolutionary lines, one of which *(townsendi)* may have arisen from a *Pseudoeurycea-Chiropterotriton* ancestor, the other from a *Chiropterotriton* stock. If placed in Table 2, *richardi* would have three paedomorphically related characters (no septomaxillae, no columellae, calcified intervertebral cartilages), somewhat fewer than other southern *Chiropterotriton*. It is also possible that evolution is following similar patterns in *Chiropterotriton* and *Parvimolge,* and *richardi* may be an advanced member of the latter. Further speculation must await information concerning *P. praecellens* and the mesopodial structure of *richardi.*

As a group the tribe Plethodontini has been little affected by paedomorphosis.

The evolutionary significance of paedomorphosis

The major role played by paedomorphosis in plethodontid evolution is demonstrated by different adaptive trends that relate to the phylogeny of two distinct groups. Paedogenesis permits survival of several species of hemidactyliines in specialized and restricted habitats. These habitats are found primarily in regions that are not favorable for the survival of related, non-paedogenetic species. Extreme specialization within such unusual habitats and consequential loss of evolutionary plasticity (potentiality for future evolutionary progress) characterize the paedogenetic forms. Differential metamorphosis, a pattern most apparent in the bolitoglossine genera, is associated with occupancy of and survival in terrestrial habitats. The bolitoglossine genera are all highly specialized, but they have avoided overspecialization through paedomor-

TABLE 2. Paedomorphic characters and compensations in *Chiropterotriton.*

	Characters Species	Septomaxillae Fail to Develop	Prefrontals Fail to Develop	Vomerine Preorbital Processes Fail to Develop	Tibial Spurs Fail to Develop	Columellae Fail to Develop	Premaxillary Frontal Processes Fuse	Enlarged Nostrils	Mesopodial Fusions	Mesopodial Calcifications	Intervertebral Cartilage Calcification	Totals
NORTH	*priscus*											0
	chiropterus											0
	multidentatus											0
. . .	*dimidiatus*	X					X					2
. . .	*xolocalcae*	X	X		X	X						4
. . .	*bromeliacia*		X	X	X	X		X				5
SOUTH	*nasalis*	X		X	X	X	X	X	X			7
	abscondens	X	X			X	X		X	X	X	7

phosis. This appears to be associated with and, in fact, may be responsible for a great increase in evolutionary plasticity.

Paedogenetic plethodontids are degenerate species living in habitats that are secluded, difficult, or unfavorable from the standpoint of the major group, *viz.*, the primitive hemidactyliine genera. These habitats are invariably on the margins of the present generic or tribal ranges. Such a distribution suggests that the species are descended from remnants of species which inhabited the regions when conditions were more favorable for their survival than at present. They probably entered their present habitats in response to strong eliminative pressures in the environments of the adults of ancestral populations. Such elimination may have been random and nonselective with the organisms virtually defenseless against such severe climatic factors as drought or extremes of heat or cold. Permanent occupancy of the larval habitat or of physically adjacent and accessible habitats, such as subterranean water systems, was necessary for survival. Under conditions of nonselective elimination there is selection for survival of progeny through increased fertility, and, particularly in salamanders, acceleration of the life cycle with earlier reproductive maturity. Accordingly, individuals do not complete ontogeny earlier than individuals of related species, but certain systems (*e.g.* reproductive) mature while others do not. Most systems are characterized by larval morphology.

Selection probably favored neotenic individuals over those that transformed, with eventual genetic fixation of neoteny, *i.e.*, paedogenesis. The premature maturation of reproductive organs linked with degeneration or underdevelopment, or both, of other organs is typical of this type of selection and characterizes the paedogenetic plethodontids. Results of such selection in other organisms have been summarized by Schmalhausen (1949).

The second kind of paedomorphosis (differential metamorphosis) is associated with the evolutionary activity of the tribe Bolitoglossini. Terrestrial plethodontids lack aquatic larvae. Their metamorphic changes tend to be spread over a greater period of time and tend to be less extreme than in those species with larval stages that undergo complete transformation in a relatively short period of time. In terrestrial plethodonines most metamorphic changes occur before hatching. It is by differential metamorphosis in the bolitoglossines that some of these changes (premaxillary separation, development of prefrontals, etc.) occur relatively late in life, or not at all. Differential metamorphosis has activated the variational potential of bolitoglossines and has led to the great differentiation of the group.

Differential metamorphosis is most obvious in peripheral and marginal habitats where either selection is very strong or entrance into a foreign environment was difficult for the ancestral stock. The genus *Batrachoseps* provides an example of the significance of these paedomorphic effects. *B. wrighti,* an inhabitant of environments similar to those occupied by primitive plethodontids, is influenced but slightly by paedomorphosis. The other species, all with peripheral or marginal distributions, are strongly affected by paedomorphosis. Selection in the latter species probably favored populations or individuals in which reproductive maturity occurs at an early developmental stage. A similar example has been discussed earlier in regard to the southward spread of the genus *Chiropterotriton* in the Neotropics.

Metamorphosis and ontogenetic anatomical changes require energy expenditure beyond maintenance levels. Thus, an additional factor in the evolution of paedomorphosis is the selection in marginal habitats of individuals that could reproduce at relatively early overall developmental stages. Paedomorphic individuals expend relatively less energy in order to contribute to the gene pools than non-paedomorphs. Therefore the paedomorphs could reproduce at higher rates than non-paedomorphs, and the populations would evolve in the direction of the former. Biotic selective pressures are strong in the bolitoglossines, particularly in such densely populated habitats as the tropical lowlands. These pressures have contributed to a substantial increase in the significance of paedomorphosis in bolitoglossines, relative to more primitive plethodontids.

Evolutionary stagnation has resulted from paedomorphosis in the paedogenetic hemidactyliines. In contrast, paedomorphosis in the bolitoglossines has increased evolutionary plasticity and has exerted a profound directing influence in their phylogeny. Bolitoglossines may have been the first plethodontid group to abandon the aquatic larval stage and to become truly terrestrial. Ancestors of this group were probably the first terrestrial plethodontids to extend their ranges out of Appalachia. Bolitoglossines must have begun specializing very early, so that they were no longer capable of effectively competing with the relatively generally adapted and vigorous plethodonines when the latter invaded terrestrial habitats. Elimination of bolitoglossines in Appalachia resulted. Bolitoglossines in the West were forced to continue trends toward increased specialization as a means of avoiding competition. Only a fragment of a presumed early radiation survived, and these were the ancestors of the modern supergenera. Only one group, the tropical salamanders of the supergenus *Bolitoglossa,* has been successful, and all of its species are moderately to profoundly affected by paedomorphosis. The tropical environment is foreign to salamanders, and the association of paedomorphosis with the tropical salamander radiation suggests that it provided a means of evolutionary escape from overspecialization for ancestral stocks. The highly adaptive tropical radiation has resulted in the evolution of several genera and over 100 species of salamanders. Paedomorphosis seems to have been a means of releasing the evolutionary potential of the group.

At the present time plethodontid evolutionary activity seems to be most intense in the wet tropical lowlands, a densely populated environment. Invasion and radiation in such an environment by salamanders, which, except for this single group, are otherwise restricted to northern temperate environments is highly significant. The vigor with which the radiation has proceeded and the high degree of species differentiation attest to the evolutionary plasticity of the group. The fact that all of the more advanced species of the various genera are increasingly affected by paedomorphosis demonstrates its dynamic, progressive influence in the group. The active role of paedomorphosis has been the dominant feature in the evolution and adaptive radiation of the tropical salamanders.

Although little factual supportive evidence has been provided, paedomorphosis has been considered by Garstang, DeBeer, Rensch, Schmalhausen, and other biologists to be an important evolutionary process. Few attempts have been made to reinterpret the early work on paedomorphosis in the light of modern genetic and evolutionary theory. As a result paedomorphosis is often assigned only a minor role in theories of the evolution of higher levels of organization, and receives only passing mention in major treatises on evolution (*e.g.* Simpson, 1953; Mayr, 1962). Recently additional facts have been made available. Manwell (1963) cites the almost identical nature of biochemical and physiological properties of the hemoglobins of adult brook lampreys *(Entosphenus lamottei)* and ammocoete larvae of other species as evidence of paedomorphosis in the former. Several kinds of morphological evidence of paedomorphosis are described in the present paper. These and other data indicate that a reinvestigation of the general biological significance of paedomorphosis and other ontogenetic phenomena (DeBeer, 1958; Rensch, 1959) might have fruitful results.

Paedomorphosis may result from a relatively simple genetic mechanism. There is some suggestion that control or regulatory genes, in some ways analogous to the operator genes of microorganisms, exist in vertebrates, and these may influence the activity of numerous structural genes or gene complexes (Ingram, 1961; Manwell, 1963). Cooper (1965) has demonstrated that cartilage inducing activity in embryonic stages of vertebrates is a stage-specific phenomenon, with no single "inducer" having a dominant role. Presumably there is an intricate pattern of gene activation and inactivation. Regulator genes, or their equivalent, may play very important integrating roles in these developmental patterns. It is possible, however, that polygenic systems, operative at early stages of development, rather than single genes, are involved (see Waddington, 1956). Modification of these mechanisms could have very widespread effects, leading to differential metamorphosis and other evolutionary phenomena. Selection for favorable combinations of such genes or gene complexes could result in the fixation of new morphological arrangements. Favorable new arrangements, once introduced in populations, might play key roles in initiating major new evolutionary trends, especially if they provide access to a new habitat or a new adaptive zone.

Genetic fixation of paedomorphic characters is closely associated with the evolution of compensatory adaptations. Selection for developmental arrythmia or partial developmental failure would not be successful without concomitant compensatory changes in the genetic background of the population as a result of counter selection. Examples are evident in some neotropical salamanders. In members of the paedomorphic genus, *Thorius,* diminutive size and weak bony and muscular development are compensated for and strengthened by calcifications of normally uncalcified cartilaginous structures such as the ends of long bones, the mesopodial elements, and the intervertebral cartilages.

Accumulating evidence indicates that paedomorphosis is of extreme importance in providing new opportunities to populations of organisms. Paedomorphosis might initiate and even direct major evolutionary and phylogenetic trends, and provide a mechanism of rejuvenation for overspecialized or slowly evolving groups. Evolutionary break throughs which result may be involved in the adoption of new ways of life and may form the basis for subsequent adaptive radiations. Paedomorphosis clearly is a major feature of plethodontid evolution and phylogeny, and investigations of the significance of the phenomenon in other groups of organisms are suggested.

BIOGEOGRAPHY AND PHYLOGENY

The Fossil Record

The only undoubted plethodontid fossils are Pleistocene remains of *Plethodon glutinosus* of essentially modern structure from the Wisconsin and Illinoian ages of Florida (Holman, 1958; 1959 a; 1959 b). Peabody (1959) reported trackways of several salamanders, including *Batrachoseps,* from the Lower Pliocene of Tuolomne County in the Sierra Nevada of California. The *Batrachoseps* trackway was referred to *B. pacificus* on the basis of large size and body and limb dimensions, but it fits equally well an undescribed species which occurs near the fossil locality. These are the only New World Cenozoic plethodontid records.

Herre and Lunau (1950) described a new genus and species of fossil salamander, *Dehmiella schindwolfi,* from the Lower Miocene (Burdigalium) of southern Germany, and Herre (1950) described a new genus and species, *Geyeriella mertensi,* from the Paleocene of Germany. Both are known only from vertebrae and are said to resemble plethodontids because of the presence of well developed basapophyses. Such processes are well developed in desmognathines and some plethodontines, but not in salamandrids. Ambystomatids and hynobiids have either differently shaped processes at the front ends of the centra, or none at all. *Dehmiella* was considered to be a plethodontid, but *Geyeriella* was thought to be a forerunner of the plethodontids.

Auffenberg (1961) suggested that *Geyeriella* may represent a side line of the main evolutionary sequence leading to the Plethodontidae and that *Dehmiella* represents the first "true plethodontid." He assumed a close salamandrid-plethodontid relationship, and this assumption obviously influenced his judgment. Estes (1964) stated that *Dehmiella* is probably a plethodontid, but that the status of *Geyeriella* is uncertain.

I have not examined the material upon which the genera *Geyeriella* and *Dehmiella* are based, but it is doubtful that either is a plethodontid. The character upon which the genera are based (basapophyses) is an adaptive feature that has arisen a number of times within the Plethodontidae. It is apparent from the descriptions and illustrations that both fossil genera differed in a number of structural features from modern plethodontids. *Geyeriella* differed in the extreme posterior placement and great length of the transverse processes, and in the relative neural arch length. It apparently had opisthocoelous vertebrae. *Dehmiella* had stout neural crests that were considerably higher than the posterior neural arch margins, a condition not encountered in plethodontids. Transverse processes were much straighter than in most plethodontids and were almost perpendicular to the central axis. The vertebrae of *Dehmiella* were apparently somewhat broader than those of any modern plethodontid, but were amphicoelous. Certainly the vertebrae of the two genera bear little resemblance to those of *Hydromantes,* the only modern European plethodontid, or to other plethodontids. Experience has shown that parallelism is common in salamander evolution, and basapophyses, found only in a few plethodontids, are not sufficient reason for assignment of fossil forms to the family Plethodontidae.

Certain Mesozoic species may be plethodontids or close relatives. Auffenberg (1961) described a new genus and species, *Opisthotriton kayi,* from vertebrae collected from the Lance Formation, Upper Cretaceous, of eastern Wyoming. *Opisthotriton* was tentatively assigned to the Salamandridae on the basis of very long maxillae and opisthocoelous vertebrae. Hypapophysial keels and basapophyses led Auffenberg to consider the genus to be close to plethodontids.

Estes (1964) examined much more material of *Opisthotriton* than was available to Auffenberg. He showed that material (a maxilla) on which proposed salamandrid relationship was based is referable to *Scapherpeton,* a fossil cryptobranchid. Estes considered the vertebrae of *Opisthotriton* to be definitely opisthocoelous. On the basis of vertebral characters, including presence of pterygapophyses, *Opisthotriton* is questionably referred to the subfamily Desmognathinae.

Opisthotriton differed from all modern plethodontids in lacking internasal fontanelles, and had hour glass-shaped palatopterygoids unlike those of any plethodontid. It further differed from desmognathines in having two premaxillae and open meckelian grooves, but both are primitive characters that might be expected in an ancestral group. Transverse processes were considerably longer than those of any modern plethodontid, but otherwise the figures of the vertebrae are similar to those of modern desmognathines. The maxillae are strikingly different from those of all plethodontids. Estes thinks *Opisthotriton* was a larval or semilarval form.

Estes (1964) described a new salamander genus and species, *Prodesmodon copei,* from the Upper Cretaceous of Eastern Wyoming. The genus is also known from the early Cretaceous of Texas (Hecht, 1963). The species was considered by Estes to be a desmognathine on the basis of disarticulated bony elements. Important characters of the genus include: opisthocoelous vertebrae with strongly protruding condyles, strongly developed hypapophyses, pterygapophyses, and basapophyses; large, concave, atlantal condylar articulating facets; small odontoid processes; alar processes; paired premaxillae; no internasal fontanelles; closed meckelian grooves; sculptured anterior cranial elements; sinuous tooth bearing dentary margins; small maxillary facial lobes; interlocking mandibular symphyses; non-pedicellated teeth; no ribs. This is a mosaic of primitive and advanced characters unlike any pattern found in modern plethodontids. Lack of ribs and internasal fontanelles, and presence of non-pedicellated teeth and interlocking mandibular symphyses distinguish *Prodesmodon* from all plethodontid genera. Most of the characters suggest a relationship to desmognathines, but modern desmognathines have a single premaxilla and large maxillary facial lobes. Paired premaxillae are to be expected in primitive desmognathines, however, and on the basis of the information presented by Estes, *Prodesmodon* apparently is a specialized (no ribs, vertebral specializations) offshoot of a primitive desmognathine stock.

Research on fossil salamanders is actively being pursued by Estes, and further comments are deferred until results are made available.

Historical Backgrounds and the Primary Dichotomy

Origin of plethodontid salamanders in what is now called the Appalachian Highland physiographic province (Atwood, 1940), or Appalachia, was first discussed by Wilder and Dunn (1920), and the proposal was expanded and detailed by Dunn (1926). Since that time the theory has gained wide acceptance. Three of the four major groups of plethodontids occur in Appalachia, including all of the primitive genera. Wilder and Dunn (1920) and Dunn (1926) developed the thesis that mountain brooks were the ancestral plethodontid habitats; mountain brook plethodontids occur only in Appalachia. Evolution of the family requires an area that has been relatively stable geologically and climatically for a very long time, at least since mid-Mesozoic; Appalachia is such a region. Thornbury (1954) states that mountain building affected Appalachia as early as the Ordovician and continued intermittently throughout the Paleozoic. The Appalachian revolution at the close of the Paleozoic was apparently the culmination of mountain building trends. Erosion, sedimentation, and peneplanation have since modified the landscape, but Appalachia has provided a relatively stable environment for the development of the biota since the end of Permian (Graham, 1964).

It was stated in rather unequivocal terms by Dunn (1926) that plethodontids have been derived from a salamandrid stock in the general present-day Appalachian region during late Eocene to Miocene. Evidence has been presented above to show that the plethodontid-salamandrid relationship is not close, and that it is highly unlikely that the two groups have had a common ancestor. The report of highly specialized desmognathine salamanders in early Cretaceous (Estes, 1964, 1965; Hecht, 1963) suggests that family characteristics of the Plethodontidae were established during Mesozoic. The probability that the specialized *Prodesmodon* occupied swampy environments beyond the western periphery of Appalachia in Cretaceous indicates that plethodontids had then been in existence for some time, and suggests that if plethodontids did arise in what is present-day Appalachia, they may have originated in mid-Mesozoic or earlier.

Based on morphological similarities, plethodontids may have arisen from an ambystomatid or pre-ambystomatid ancestral stock, which in turn was probably the New World derivative of the ancestors of the Old World Hynobiidae. The family Ambystomatidae is an endemic North American family which is more primitive than the family Plethodontidae. Modern ambystomatids apparently have less evolutionary plasticity than plethodontids, but the family has undergone a moderate diversification. Significantly, one genus, *Rhyacotriton*, occupies mountain brook habitats in northwestern North America, and it is virtually lungless. It is postulated that a similarly adapted population, but one with great genetic and evolutionary plasticity and a higher base level of general adaptation, successfully occupied the mountain brooks of Appalachia during Mesozoic times and gave rise to the plethodontid radiation.

Because the fossil record is scanty and incomplete it is impossible to date the primary dichotomy of the Plethodontidae. Divergence of the desmognathine line from the more generalized stock that gave rise to the present plethodontines must have taken place in Mesozoic. Certain characters (*e.g.*, separated premaxillae) of *Prodesmodon* indicate that it was relatively close to the ancestral stock. The closed meckelian grooves, opisthocoelous vertebrae, and shape of cranial elements indicate that the primary plethodontid dichotomy had already occurred, and that the Cretaceous *Prodesmodon* was a specialized desmognathine offshoot which had left the ancestral habitat.

Tertiary events are responsible for the subfamilial evolutionary patterns seen in the plethodontids. Because the fossil record is scanty, paleobotanical and paleoclimatic data must be used to infer the past history of the Plethodontidae.

The evolution of flowering plants has been reviewed by Axelrod (1960) who states that close relationship between modern plants and fossils of the later Oligocene makes it possible to reconstruct the habitats and climates under which Tertiary floras lived, to outline the belts of Tertiary vegetation, and to explain the evolution of modern patterns of plant distributions. Three broad, worldwide belts of distinctive vegetation were present in early Tertiary: the Arcto-Tertiary Geoflora in the North, the Antarcto-Tertiary Geoflora in the South, and the very broad Tropical-Tertiary Geoflora in between. Many modifications occurred during Tertiary, but the modern floristic patterns can be derived from these three belts. Plants are the dominant members of biotic communities, which in turn are evolutionarily conservative units. Information about modern plant-animal associations allows one to make hypotheses concerning past events.

Tertiary events resulted in numerous reorganizations of the early Tertiary pattern. The tropical vegetational belt gave rise in the New World to the Neotropical-Tertiary Geoflora which is ancestral to modern neotropical forest formations. A major geoflora, the Madro-Tertiary, developed *in situ* in southwestern North America in early Tertiary in response to increasing cooling and aridity which forced the old communities out. This geoflora was derived primarily from Neotropical-Tertiary floral elements. The Madro-Tertiary Geoflora expanded steadily in the increasingly arid Southwest from late Eocene throughout Tertiary, and has given rise to the modern semiarid woodland, chaparral, thorn forest, arid scrub, desert grassland, and desert vegetation of southwestern North America. Of considerable interest to the present study are the modern forest derivatives of the Arcto-Tertiary Geoflora. The more important of these in North America are the Eastern Deciduous, Hemlock-Hardwood, Boreal, Rocky Mountain, Pacific, and Southeast Evergreen Forests. In addition disjunct elements of the Geoflora survive today interspersed with Neotropical-Tertiary derivatives in the highlands of Mexico, Guatemala, and other Central American countries (Braun, 1950; Martin and Harrell, 1957; Axelrod, 1960). Plethodontid salamanders are today primarily members of communities dominated by Arcto-Tertiary Geofloral derivatives. Salamanders and Arcto-Tertiary derivatives are both relatively ancient groups. Their association is probably ancient and the communities may have evolved rather slowly throughout Tertiary. Savage (1960) has suggested that correlation of geologic and geofloral history forms a firm basis for development of concepts concerning historical bigeography of animal groups; this approach is followed in the present work.

Historical elements of the North American herpetofaunas have been discussed by Savage (1960). Of particular interest is the concept of an Old Northern Herpetofaunal Element first proposed by Dunn (1931) and further developed by Savage. The Old Northern Element as defined by Savage consists of descendents of temperate circumpolar groups found in the far northern continental areas in early Tertiary but forced southward as the tropical limits were restricted by long-term Tertiary climatic trends. Savage emphasized the historical association of the Old Northern Element with the Arcto-Tertiary Geoflora, and his analysis aptly fits the family Plethodontidae. Savage further subdivides the Old Northern Element into four historical zoogeographical complexes. These complexes and the plethodontid genera I consider to be members of each are:

1. Eastern American Complex. *Desmognathus, Leurognathus, Gyrinophilus, Pseudotriton, Stereochilus, Eurycea, Typhlotriton, Typhlomolge, Hemidactylium.*
2. Western American Complex. *Hydromantes, Batrachoseps, Ensatina.*
3. Central American Complex. *Bolitoglossa, Oedipina, Pseudoeurycea, Chiropterotriton, Lineatriton, Parvimolge, Thorius.*
4. Southeastern American Complex. *Phaeognathus, Haideotriton.*

Species groups of *Aneides* and *Plethodon* are members of both 1 and 2. In the following sections the probable history of these genera is reviewed.

The Desmognathines

Desmognathines have remained close to the plethodontid source region. Some species of *Desmognathus* today occupy what might well be the primitive habitat. A moderate diversification has occurred in the subfamily, however, and some groups have left Appalachia (Fig. 19).

Prodesmodon represents the earliest known divergence from the generalized desmognathine stock. It left the ancestral habitat and familial source region, became morphologically specialized, and occupied a peripheral swampy habitat by early Cretaceous; divergence must have occurred at a relatively very early date.

Phaeognathus may represent a somewhat later, but still very early divergence (Fig. 13). Ancestors of *Phaeognathus* left Appalachia, became terrestrial, and occupied the Coastal Plain at the periphery of Appalachia. The Coastal Plain slowly emerged from the sea starting in early Tertiary and has been in existence since Eocene (see also Graham, 1964). Today *Phaeognathus* appears to be a Coastal Plain relict, a specialized survivor of a group that was probably more widespread during Tertiary than at present (see Valentine, 1963 a, for further speculations concerning the genus).

Another divergent desmognathine line is represented by *Leurognathus,* a southern Appalachian endemic. It has adapted to a specialized, strictly aquatic environment, and it is impossible to date its divergence. Adaptation to the new adaptive subzone has taken place very slowly and over a long period of time. The modern genus *Leurognathus* is probably the culmination of long Tertiary trends, and divergence from the ancestral stock has been more recent and less extreme than that of *Phaeognathus.*

Desmognathus has remained relatively close to the ancestral desmognathine stock, both morphologically and ecologically. The genus is centered in Appalachia, but has entered the Coastal Plain, the Interior Highlands, and adjacent areas. Movement into peripheral lowland areas by species such as *D. auriculatus* and *D. fuscus* has been accompanied by adaptation to slower moving waters than in the ancestral habitat, and invasion of the Interior Highlands has probably been via lowland routes. Several montane species *(D. ochrophaeus, D. aeneus, D. wrighti)* have become increasingly terrestrial. Major trends in *Desmognathus* are clearly in the direction of dwarfing and increased terrestriality. *Desmognathus* is ecologically the most diverse plethodontid genus, but it is remarkable uniform osteologically. Most of the osteological differences are related to size and development stage.

Evolution within the Desmognathinae and particularly within *Desmognathus* has proceeded *in situ* in southern Appalachia. The course of evolution within the subfamily has involved a successive occupation of distinct ecological niches in the same general environmental and geographic region (Dunn, 1917; 1926; Hairston, 1949; Organ, 1961 a). Radiation within the subfamily is a miniature of that in the family as a whole.

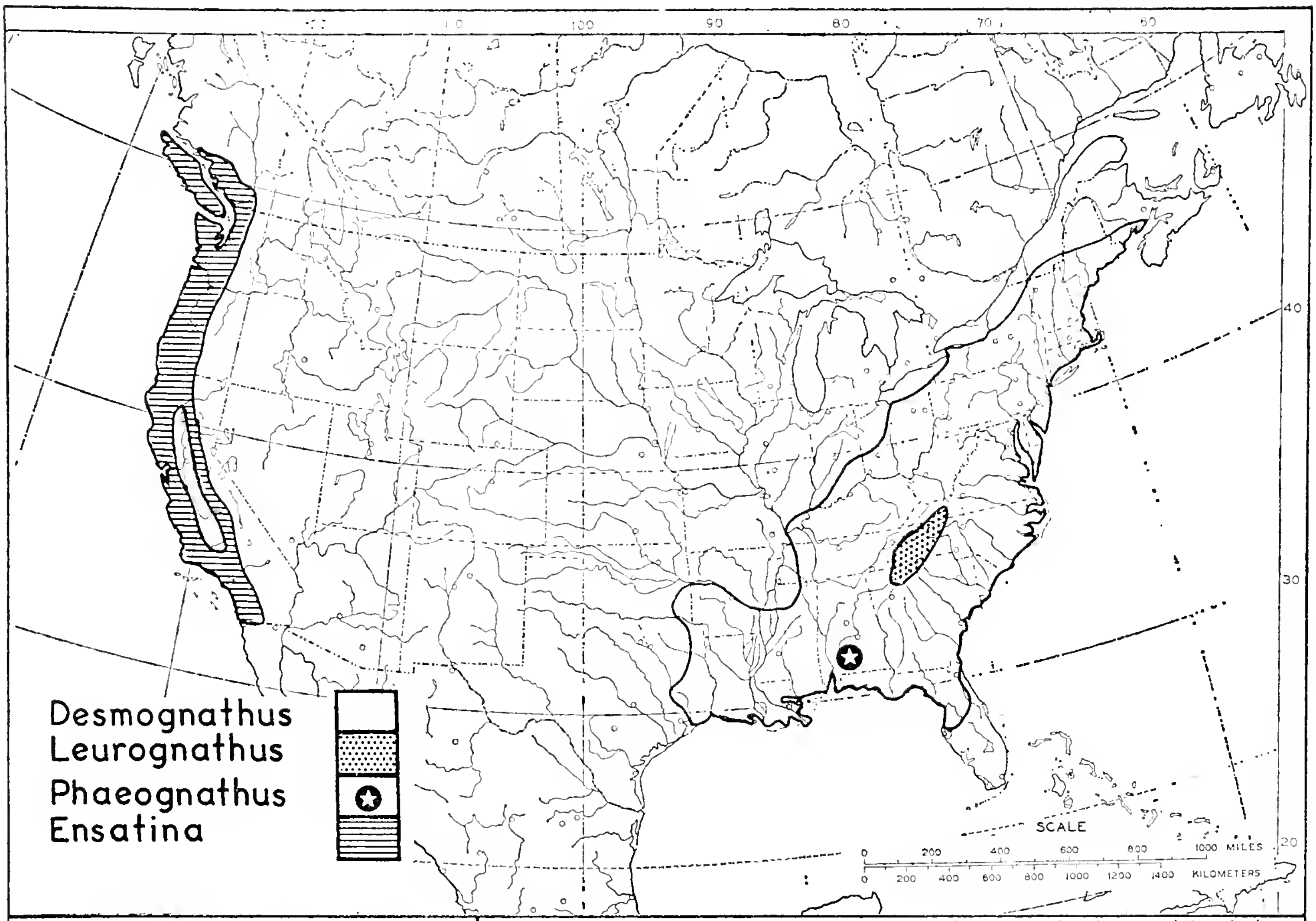
The Plethodontines

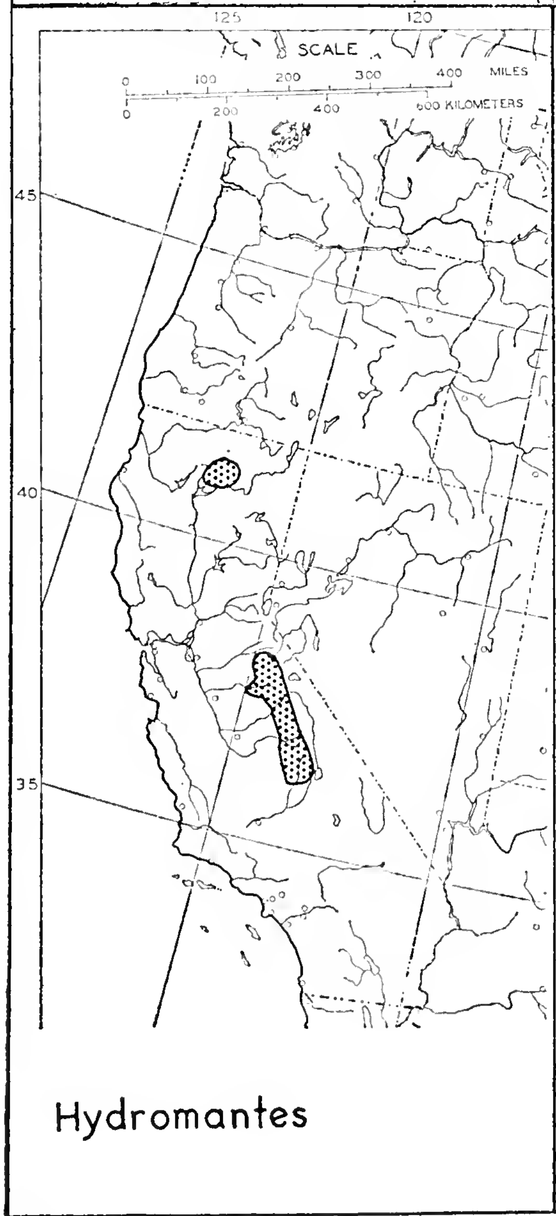
Tribal Origins

The plethodontines are more generalized morphologically than are the desmognathines and have remained closer to the ancestral plethodontid stock. The plethodontine stock gave rise relatively early to three major evolutionary lines (Fig. 12). The first probably diverged from the generalized stock at the beginning of Tertiary. The immediate factors in the divergence of this group, the forerunners of the Bolitoglossini, were the loss of aquatic larvae, acquisition of terrestrial habits, and occupation of terrestrial niches by generally adapted populations with genetic and evolutionary plasticity. Occupation of the new adaptive zone provided impetus for the subsequent diversification and adaptive radiation of the Bolitoglossini.

Several types of evidence support the theory of early origin of the bolitoglossines. The group today contains three distinct, specialized subgroups. It has differentiated to a greater degree than either of the other two tribes. The high degree of diversification suggests a long history, and morphological differences suggest an ancient separation from the ancestral stock. Bolitoglossines are distantly peripheral to the source and dispersal center of the family and are the only plethodontid group that no longer occurs either in Appalachia or its borderlands. It is the only group that has invaded Europe and the Tropics. Finally, a *Batrachoseps* trackway from the Mio-Pliocene border of California (Peabody, 1959) indicates that the genus was of essentially modern construction at that early date. The above facts suggest a very early origin of the Bolitoglossini and an early spread with subsequent displacement by other plethodontids.

The second evolutionary line, which has given rise to the Plethodontini, diverged from the generalized plethodontid stock at a later date than the bolitoglossine ancestors. This divergence also involved entrance into a new adaptive zone with concomitant loss of aquatic larvae and occupation of terrestrial niches by generally adapted populations. There are several reasons for thinking the plethodonine divergence followed rather than preceded the bolitoglossine evolution. Members of the group left Appalachia and reached the Rocky Mountains and the Pacific Coast, but the group as a whole is not as peripherally distributed as the bolitoglossines, and two of the three genera are still represented by Appalachian species. Modern plethodonines are more primitive morphologically than the bolitoglossines, but this fact may be due to the more generalized nature of the plethodonines and





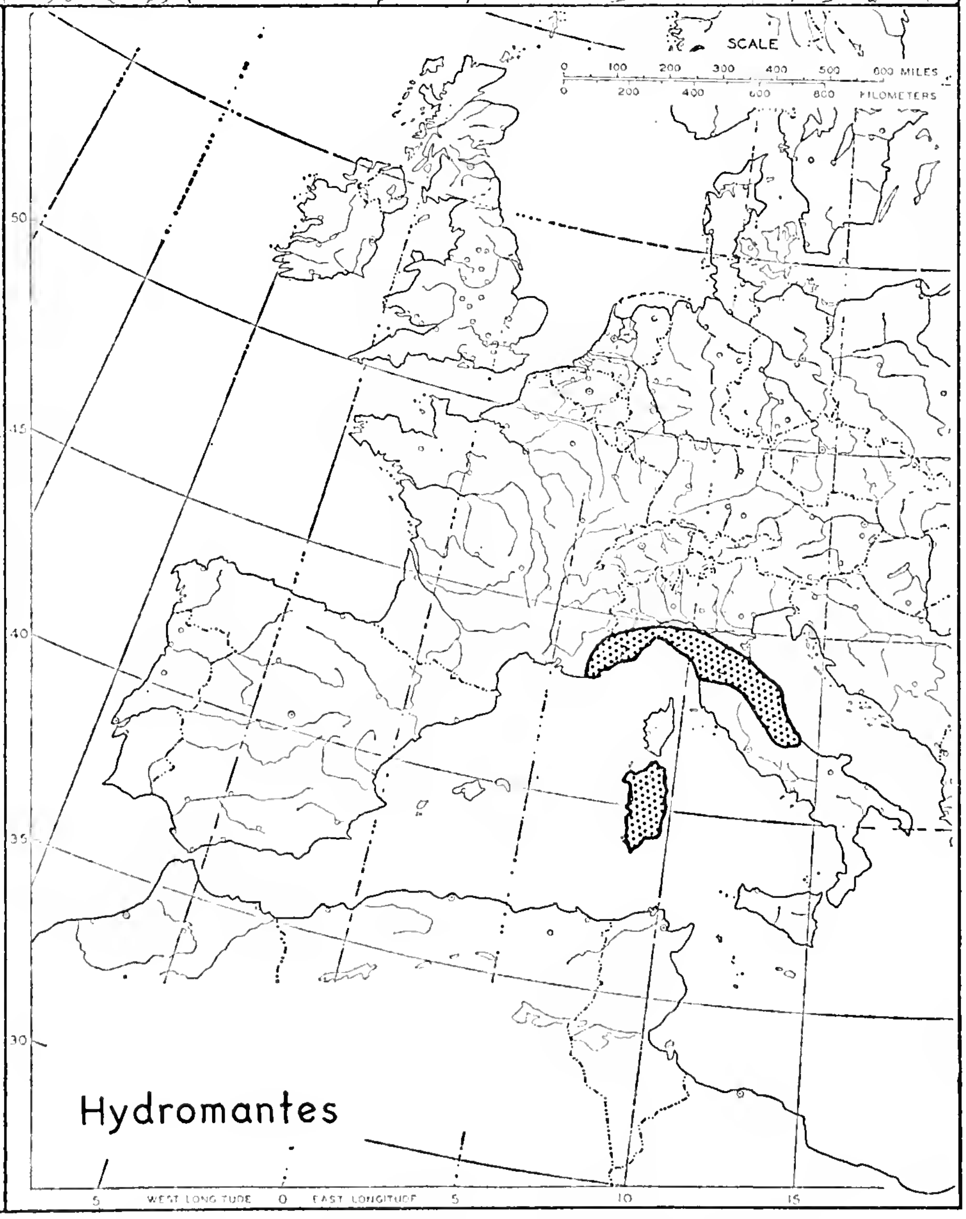


Figure 19. Distribution of *Desmognathus, Leurognathus, Phaeognathus,* and *Ensatina.*

Figure 20. Distribution of *Hydromantes* in California.

Figure 21. Distribution of *Hydromantes* in Europe.

their more recent association with the generalized plethodontine ancestral stock.

The final group, the Hemidactyliini, has remained primarily in Appalachia and its borderlands. It is closer morphologically to the ancestral stock than is any other plethodontid group. Evolution and differentiation has been centered in eastern United States.

History of the Hemidactyliines

The history of the hemidactyliine genera is closely tied to the Cenozoic history of the eastern United States. Only one genus, *Gyrinophilus,* is now limited in its distribution to the general Appalachian region, but two other genera, *Eurycea* and *Pseudotriton,* occur widely in Appalachia (Fig. 22, 24, 25). Appalachia is the center of dispersal of the tribe. Dispersal has been centrifugal in all directions from Appalachia.

Gyrinophilus is morphologically the most primitive hemidactyliine and it has remained close to the ancestral home. Today the generic range corresponds to the approximate limits of ancient Appalachia. *Gyrinophilus* is found in mountain brook habitats, but may occur in springs and woodland seepage areas.

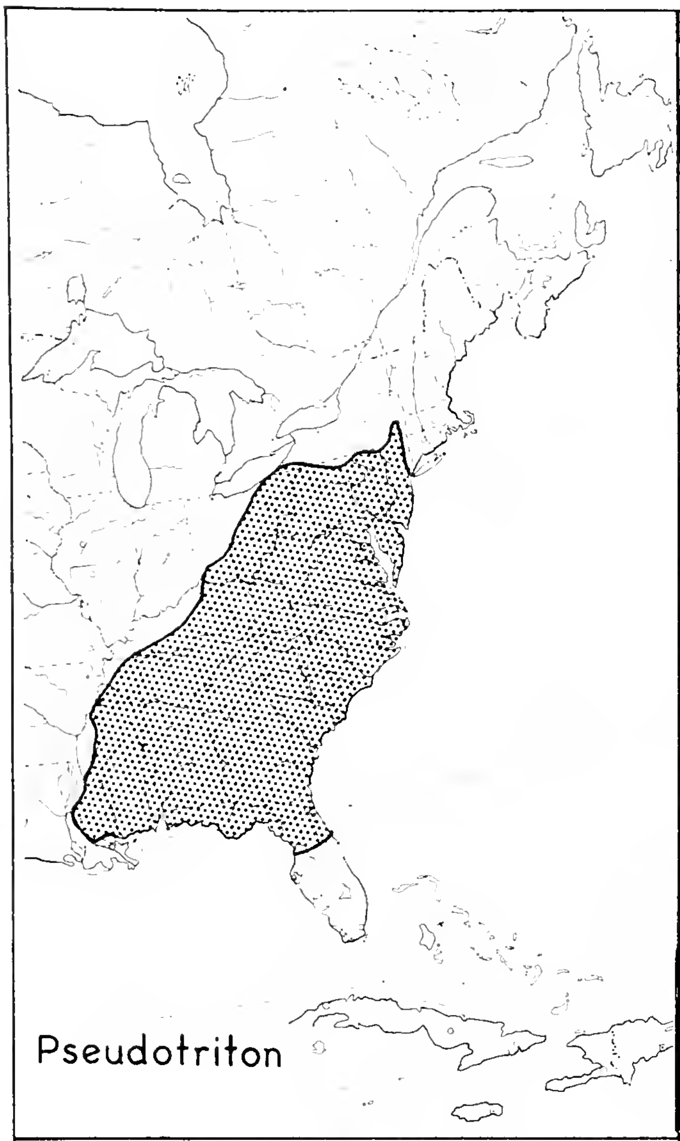
Paedogenetic populations that occur in caves in southeastern Tennessee and northern Alabama have been assigned to *Gyrinophilus (G. palleucus)* on the basis of their resemblances to larvae of *Gyrinophilus porphyriticus* and *G. danielsi.* The salamanders have been induced to metamorphose by Dent, Kirby-Smith, and Craig (1955), Dent and Kirby-Smith (1963), and Blair (1961). These authors state that *G. palleucus* will undergo complete metamorphosis in the laboratory, and that metamorphosed individuals closely resemble other species of *Gyrinophilus;* but Blair (1961) reports that the premaxillae remain fused, a larval feature. Further, the vomers retain larval configuration. It is apparent from X-ray photographs presented by Dent and Kirby-Smith (1963) that fused premaxillae and larval vomers are also retained in their supposedly completely metamorphosed specimens. In most characters *G. palleucus* does resemble other *Gyrinophilus,* but generic assignment remains tentative. It could also be a remnant of a primitive *Gyrinophilus*-like stock. The distribution of *G. palleucus* is that expected of a paedogenetic species — on the periphery of the range of its non-paedogenetic congeners.

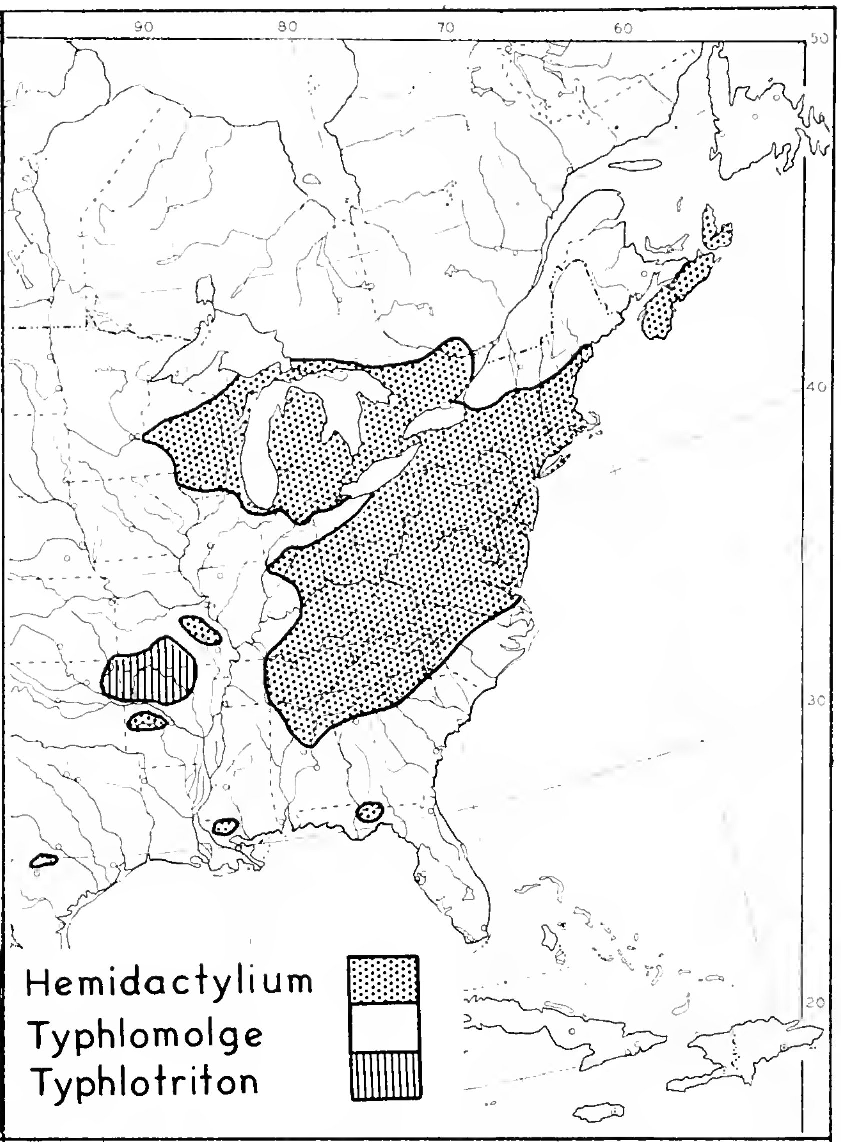
Stereochilus is the derivative of an early hemidactyliine stock that invaded and successfully adapted to the swampy environments of the Atlantic Coastal Plain. Numerous primitive features plus several specializations (*e.g.*, skull compression, habitat) suggest a relatively early divergence from the tribal stock. *Stereochilus* divergence and differentiation probably dates from the establishment of the Coastal Plain in early Tertiary.

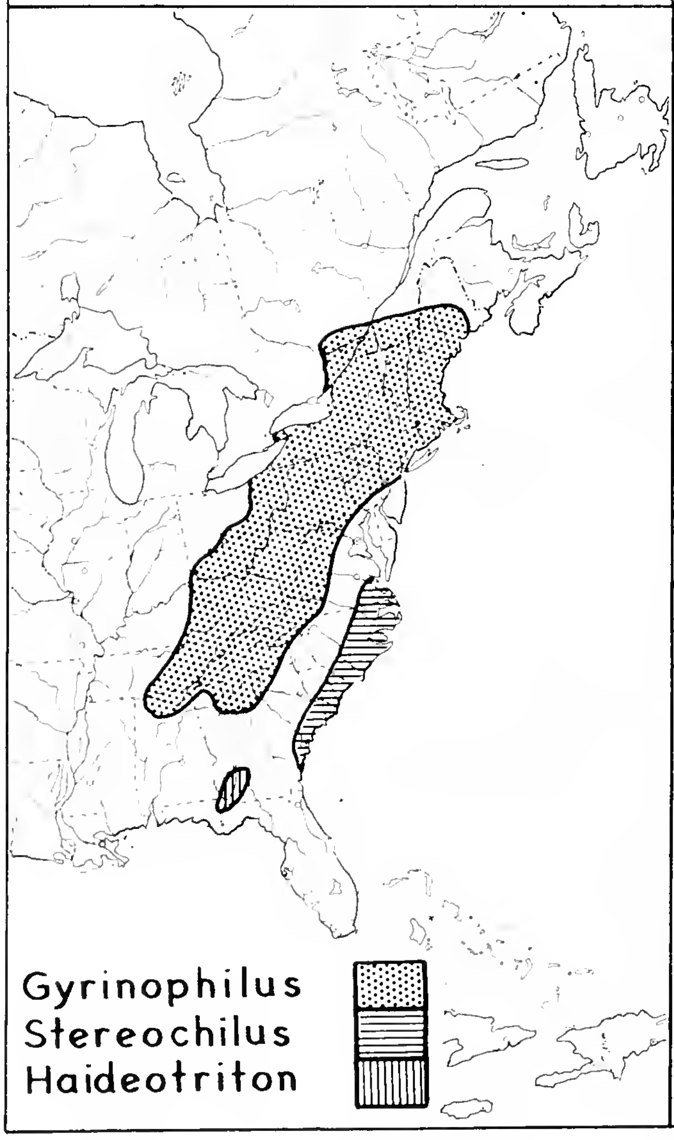
Atwood (1940) divides the Appalachian Highlands Physiographic Province into two parts: the northeastern division (New England-Acadian) and the southwestern division (Hudson Valley to central Alabama). *Gyrinophilus* is found throughout both divisions, but *Pseudotriton* is associated only with the latter. *Pseudotriton* has a more extensive, but more southerly range than *Gyrinophilus* (Fig. 22 and 24). Although *Pseudotriton* occurs in springs and seeps at high elevations and may be sympatric with *Gyrinophilus,* it can survive in the warm waters of low elevations. *Pseudotriton* has successfully invaded the Coastal Plain from Louisiana to the mouth of the Hudson River, and *P. montanus,* in particular, has adapted to very muddy, mucky areas. Thus in its ecology and distribution, as well as in its morphology, *Pseudotriton* demonstrates evolutionary advance over *Gyrinophilus.*

Eurycea ranges more widely than any of the above genera and has successfully invaded the Coastal Plain, the Interior Highlands, and the Balcones Escarpment-Edwards Plateau areas of Texas in addition to occupying the entire Appalachian Highland region (Fig. 25). Presumably the genus arose relatively early in Tertiary. *Eurycea* has undergone a moderate evolutionary diversification. The three widest ranging species, *E. longicauda, E. lucifuga,* and *E. bislineata,* are all found in the Appalachian Highlands, and *E. aquatica* is found on the southern borders of Appalachia in northern Alabama. Both *longicauda* and *bislineata* also occupy favorable microhabitats (seepages and swamps near springs and rivers) on the Coastal Plain but retain primitive stream larvae. *E. quadridigitata* has adapted (pond larvae) to the swamps of the Coastal Plain.

The ranges of *E. lucifuga* and *E. longicauda* extend from Appalachia through a narrow corridor across northwestern Kentucky and southern Illinois and Indiana to the Interior Highlands Physiographic Province (Atwood, 1940) in Missouri, Arkansas, eastern Oklahoma, and extreme southeastern Kansas. Two distinct species of *Eurycea (tynerensis* and *multiplicata)* and the genus *Typhlotriton,* a *Eurycea* relative, are confined to the Interior Highlands. Other plethodontines found in the Interior Highlands include the endemic species, *Plethodon ouachitae* and *P. caddoensis,* and *P. glutinosus* ranges southwest from Appalachia in a pattern sim-







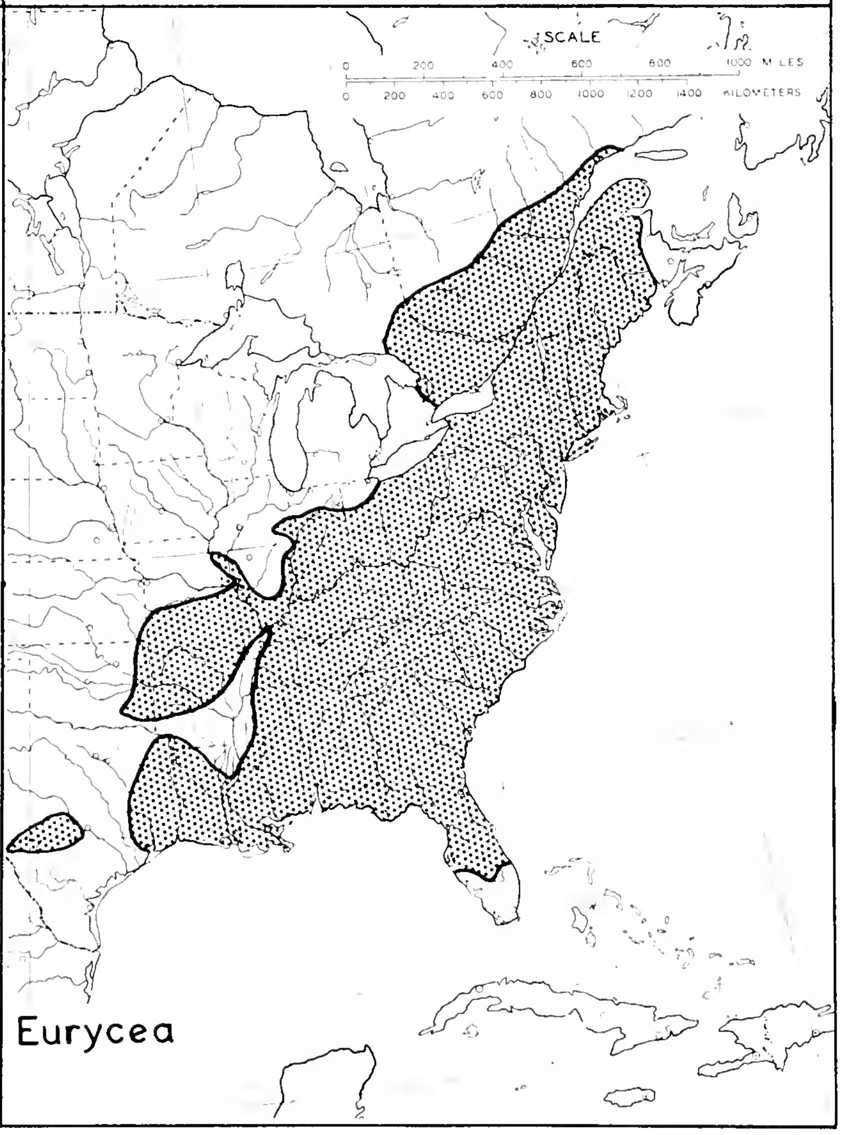


Figure 22. Distribution of *Pseudotriton.*

Figure 23. Distribution of *Hemidactylium, Typhlomolge,* and *Typhlotriton.*

Figure 24. Distribution of *Gyrinophilus, Stereochilus,* and *Haideotriton.*

Figure 25. Distribution of *Eurycea.*

ilar to that of *E. longicauda* and *E. lucifuga*. Disjunct western and southwestern populations of *P. cinereus, P. dorsalis,* and *Hemidactylium scutatum* also occur in the Interior Highlands.

Five species of paedogenetic *Eurycea (latitans, nana, neotenes, pterophila, troglodytes)* and the paedogenetic genus *Typhlomolge,* derived from a pre-*Eurycea* stock, are endemic to the Balcones Escarpment-Edwards Plateau region of central Texas. Disjunct populations of *P. glutinosus* also occur in the region. For biogeographic purposes the entire plethodontine fauna of the Interior Highlands and of Texas is discussed as a unit, although both hemidactyliine and plethodontine species are involved.

The problem of disjunct populations of Appalachian organisms in the Interior Highlands and on the Edwards Plateau has been discussed by numerous authors. The works of Braun (1950), Smith (1957), Dowling (1958), Blair (1958), and Conant (1960) are pertinent to this discussion. Dowling discussed the geology and paleoclimatology of the Interior Highlands, and stated that the region has been above sea level since Pennsylvanian times. Dating the time of isolation of the Interior Highlands is controversial and probably impossible with the data at hand, but most authors agree that it was a Cenozoic event; Atwood (1940) suggests mid-Tertiary as the time of isolation from eastern highlands.

The modern Interior Highlands Physiographic Province, as described by Atwood (1940), includes the St. Francois Mountains and Salem Plateau, the Ozark Plateau, and the Boston Mountains, all north of the Arkansas River Valley, and the Ouachita Mountains to the south of the valley. The province is bounded on the north and west by the Prairie Province, on the east by the Mississippi Lowland, and on the south by the Coastal Plain.

Braun (1950) has discussed the significance of disjuncts of Appalachian forest plants which occur in the Interior Highlands and canyons in the Edwards Plateau. She interprets these disjuncts as relicts of a former more widespread mesophytic forest (the East American Element of the Arcto-Tertiary Geoflora; Axelrod, 1960). Today the Interior Highlands are drier than Appalachia and Oak-Hickory communities dominate. Braun suggests that a mixed mesophytic forest was continuous across eastern North America and into the Mexican Highlands in Early Tertiary. Interior regions were drying in middle Tertiary and the mixed forest was forced to retreat northward and eastward. At this time the Oak-Hickory Association evolved in the Interior Highlands, and drier western and southwestern plants (derivatives of the Madro-Tertiary Geoflora; see below) invaded the Edwards Plateau. Mesophytic species of the mixed forest survive as relicts in only a few spots west of the Mississippi River. Humid corridors were reestablished during Pleistocene pluvials below the glacial borders. The primary corridor between the Appalachians and the Interior Highlands was through the Hill Section of the Western Mesophytic Forest Region of Braun (1950), which extends from the Knob region of western Kentucky through the Norman and Crawford uplands of southern Indiana, and the Ozark Hills of southern Illinois. This corridor has been especially important for plethodontine distribution.

Plethodontines in the Interior Highlands and the Edwards Plateau represent three levels of divergence from the ancient Appalachian populations. The earliest level includes the two endemic genera, *Typhlotriton* of the Interior Highlands and *Typhlomolge* of the Edwards Plateau borders. Ancestors of these genera may have entered the regions in early Tertiary when favorable climatic conditions prevailed and relatively uniform forest communities extended from Appalachia into Mexico and to the West Coast. They have survived drier surroundings than are generally considered suitable for survival of plethodontids by occupying subterranean aquatic habitats. Paedomorphosis has been the key to the success and survival of both genera. *Typhlomolge* is paedogenetic and is restricted to underground water systems. *Typhlotriton,* which is probably not closely related to *Typhlomolge,* occurs in surface creeks in the larval state, but the adults are restricted to caverns.

The second level of differentiation is represented by the endemic species of Appalachian genera which occur in the two regions. These include *Eurycea latitans, E. nana, E. neotenes, E. pterophila* and *E. troglodytes* of the Edwards Plateau, and *E. multiplicata, E. tynerensis, Plethodon ouachitae,* and *P. caddoensis* of the Interior Highlands. Six of the seven species of *Eurycea* are paedogenetic, and the seventh *(multiplicata)* is sometimes neotenic (Conant, 1958). *P. ouachitae* and *P. caddoensis* are much better adapted to dry conditions than *P. glutinosus* (Pope and Pope, 1951). Dowling (1958) has suggested that isolation and differentiation of the Interior Highland endemics dates from Miocene to Pliocene on the generic level and the late Pliocene to early Pleistocene on the specific level. Blair (1958) attempted to explain the distribution of the relict species of *Plethodon* and *Eurycea* on the basis of Pleistocene events. These times seem much too recent. *Typhlomolge* and *Typhlotri-*

ton probably were differentiated when Tertiary drying was beginning to drive plethodontids eastward. They survived in specialized microhabitats to which they became increasingly more highly adapted. The species of *Eurycea* are probably descendents of populations "trapped" in isolated favorable microhabitats as increasing Tertiary aridity forced the genus as a whole eastward. Paedomorphosis has been a universal means of survival for these endemics. They have survived by remaining for all (the paedogenetic species) or much *(multiplicata)* of their lives in waters that are surrounded by terrain largely or wholly unsuited for urodele terrestrial or semiterrestrial existence. In these niches they survived the late Pliocene and Pleistocene droughts.

Plethodon caddoensis and *P. ouachitae* have been considered to be members of the *yonahlossee* species group, the most primitive of the nine groups of *Plethodon* recognized by Highton (1962). The other members of the group, *P. longicrus* and *P. yonahlossee,* have limited ranges in the southern Appalachians. Highton suggests that the prototype of the group was once widely distributed in the eastern United States. The primitive nature of *P. caddoensis* and *P. ouachitae,* and the fact that they are adapted to live in relatively dry environments (Pope and Pope, 1951; Dowling, 1958) suggest a rather early divergence and an *in situ* adaptation to the increasing dryness of the Interior Highlands from mid-Tertiary to Recent.

The final level of differentiation is represented by populations of primarily Appalachian species that are subspecifically distinct from the main populations to the east. These include the Balcones Escarpment populations of *Plethodon glutinosus,* the Ouachita Mountain populations of *P. cinereus,* the Ozark Plateau populations of *P. dorsalis,* and the Interior Highland populations of *Eurycea longicauda.* Undifferentiated Interior Highland populations of *Eurycea lucifuga* and *Hemidactylium scutatum,* and Balcones Escarpment and Interior Highland populations of *P. glutinosus* also may be included with this group. Some of these populations are truly disjunct (Balcones Escarpment *P. glutinosus;* Interior Highland *P. cinereus, P. dorsalis,* and *H. scutatum*); ranges of the other species are continuous with those of more easterly populations. I agree with Dowling (1958), Smith (1957), and Blair (1958) that the distribution of this final group is the result of Pleistocene and Recent events. It is likely that invasion of the regions occurred from the east during pluvial periods, possibly with the differentiated populations entering relatively early, the undifferentiated entering later. The Interior Highland populations of *Hemidactylium* are relicts of a former more southerly distribution (see below).

The corridor by means of which Pleistocene invasion of the Interior Highlands occurred extends from the Appalachians through the hill sections of western Kentucky and southern Indiana, the Ozark Hills of southern Illinois, and the St. Francois Mountains and Salem Plateau of eastern and southeastern Missouri. The entire corridor region is occupied today by *Eurycea longicauda, E. lucifuga,* and *Plethodon glutinosus. Plethodon cinereus* extends south to the Ohio River and west to the Illinois border in Indiana and has populations on the Salem Plateau. *P. dorsalis* extends as far west as the Mississippi River, and *Hemidactylium* has a relict Salem Plateau population. To the north of the corridor region the distribution of plethodontids is limited by prairies, and to the south by the Coastal Plain. The corridor is most constricted in southern Illinois. There is a striking correlation between the northern limits of the ranges of several of the species, particularly *E. longicauda* and *E. lucifuga,* and the maximum southern extent of continental glaciation during the Kansan glacial period (the farthest southern glacial penetration) as mapped by Smith (1961) for the salamanders, and Flint and co-workers (1958) for the glaciers. Glaciated terrain does not provide suitable habitat for most plethodontids.

The highly specialized, paedogenetic *Haideotriton* occurs in limestone caverns and underground water systems of the Coastal Plain in southwestern Georgia and northern Florida and was probably derived from a *Eurycea*-like ancestral stock relatively early. Invasion of the coastal plain by *Haideotriton* ancestors may have occurred as early as Eocene.

The relationship of *Hemidactylium* to other hemidactyliine genera is not clear, but the combination of primitive and specialized characters indicates a relatively early origin from a hemidactyliine stock. *Hemidactylium* has departed from the primitive way of life and is rather terrestrial in habits; it breeds in sphagnum bogs and has pond larvae. *Hemidactylium* has followed favorable environments to the north and northwest and extends considerably farther to the northwest (western Wisconsin) than any other hemidactyliine (Fig. 23). Disjunct relict populations of the genus occur in sphagnum areas in the southern Appalachians, northern Florida, eastern Louisiana, the Ouachita Mountains of Arkansas, and the Salem Plateau of southeastern Missouri. It is apparent that *Hemidactylium* occupied more southerly regions during periods of Pleistocene glacial maxima than it does now, and that following the last glacial retreat it has spread rapidly into formerly glaciated regions (*e.g.*, Michigan). The relicts of lower latitudes are the remnants of populations that once occupied Pleistocene refugia (see Smith, 1957). Conant (1960) thinks the disjunctness of *Hemidactylium* in Missouri and Arkansas, of *Plethodon glutinosus* in Texas, and of other amphibians and reptiles may be attributed to climatic changes during the Xerothermic Interval following Climatic Optimum in post-Wisconsin times.

The First Terrestrial Encounter
—the History of the Bolitoglossines

Divergence of the bolitoglossine ancestral stock proceeded very rapidly following movement of the primitive bolitoglossine stock across the adaptive threshold between the aquatic and terrestrial adaptive zones. Establishment of the group probably occurred very early, possibly in late Cretaceous or early Tertiary. The group spread out from Appalachia into terrestrial communities dominated by elements of the Arcto-Tertiary Geoflora, which extended in a broad belt across Holarctica as a mixture of conifers and deciduous hardwoods. The Arcto-Tertiary Geoflora linked western Europe, the alpine belt, northeastern Asia, western North America, and eastern North America from early through middle Tertiary, and provided the continuous forest corridor that has presumably been essential for plethodontid dispersal.

Bolitoglossines probably reached the West Coast of North America some time in early Tertiary via terrestrial forest corridor routes. Subsequent divergence of the plethodonine terrestrial species may have brought plethodonines and bolitoglossines into competition, with resultant extinction of the less well adapted bolitoglossines in Appalachia and surrounding eastern North America. Absence of bolitoglossine species from the Great Plains and Rocky Mountains is almost certainly related to Tertiary drying and cooling, and inhospitable Quaternary climates.

Three distinct groups of bolitoglossines survive today, the supergenera *Hydromantes, Bolitoglossa,* and *Batrachoseps*. Of these *Hydromantes* is the most primitive and may be relatively little changed from the ancestral bolitoglossine stock (Fig. 16).

The present range of *Hydromantes* is a classic example of disjunct distribution and relict populations (Figs. 20 and 21). It is apparent that a once widespread, primitive, but rather specially adapted ancestral group was unable to adapt to the Tertiary climatic, physiographic, and biotic changes in its former habitat, and survived only in a few rather isolated, specialized habitats in widespread segments of its former range. Two species, *H. italicus* of Italy and France and *H. genei* of Sardinia, are the sole living European plethodontids. The route by which *Hydromantes* entered Europe, probably in early Tertiary, was the Bering Land Bridge between northeastern Asia and northwestern North America. Simpson (1947) and others think the bridge was above sea level for most of Tertiary, and was submerged only for considerable lengths of time in middle Eocene and middle to late Oligocene. It is likely that *Hydromantes* reached Europe as early as early Eocene through an Arcto-Tertiary Forest corridor on the Bering Land Bridge. Absence of *Hydromantes* from northwestern North America and northern Eurasia may be the result of extinction of most populations during unfavorable climatic periods of late Pliocene and Pleistocene. Modern species of *Hydromantes* are all limited to specialized and rather isolated limestone areas, and all species, both European and American, have relatively small ranges.

Several authors have proposed theories in conflict with that suggested above for *Hydromantes* dispersal. Dunn (1926) suggested *Hydromantes* reached Europe in late Miocene or Pliocene. Noble (1931) thought plethodontids reached Europe by way of Greenland "at a time when this northern region enjoyed a warmer climate." Schmidt (1946) suggested that the relation between west European and west North American faunas is based on a later Tertiary, Pleistocene, and Recent dispersal across the Bering Land Bridge.

The genus *Batrachoseps* is an ancient group of highly specialized salamanders. The most primitive and generalized species is *B. wrighti,* which occupies forests derived from the Arcto-Tertiary Geoflora in the Cascade Mountains in northern and central Oregon. The species is the only one restricted to the presumed ancestral environment. *B. attenuatus* ranges from southern Oregon to southern California, and occurs in a variety of habitats—in forests derived from the Arcto-Tertiary Geoflora to areas dominated by derivatives of the Madro-Tertiary Geoflora. *B. pacificus* of the lowlands of Southern California and northern Baja California is restricted to coastal plant communities derived from Madro-Tertiary elements. Two and possibly more undescribed species occupy disjunct, relict ranges in areas of Arcto-Tertiary derived plant communities in the Santa Lucia Mountains and southern Sierra Nevada of California, and the high Sierra San Pedro Martir of northern Baja

California. This distributional pattern (Fig. 26) suggests a once far-ranging group which has been restricted to relatively small areas in what are for plethodontid salamanders specialized environments. Evidence that the genus once had a more extensive range is based on two marginal records. The first is the collection of the types of *Batrachoseps caudatus* from southeastern Alaska (Cope, 1889). No further individuals of the species have been found, and subsequent authors (Dunn, 1926; Stebbins, 1951) have questioned the authenticity of the locality data. There has been little collecting in Alaska and there is little reason to question the record. The second is the collection of a single immature individual of *Batrachoseps* from the northern slope of the Nevado de Colima at about 7,000 feet elevation in the state of Jalisco, Mexico. The collector was Hans Gadow, a noted biologist, who discussed conditions of the collection in some detail in two separate publications (1905, 1908). He was aware of the significance of his discovery from the first. The specimen, in the British Museum, has been examined by Stebbins and Lowe (1949), Hendrickson (1954), Arden H. Brame, Jr. and me. All concur that it is a *Batrachoseps*. The Mexican record makes good biogeographic sense for a bolitoglossine genus, and I consider it to be authentic. It is possible that other populations of *Batrachoseps* occur as relicts in the Sierra Madre Occidental of Mexico. Failure of collectors to obtain additional material may be due to the relative lack of intensive collecting during the right seasons in the critical areas.

The entrance of the supergenus *Bolitoglossa* into Mexico has recently been discussed in some detail (Brame and Wake, 1963), and only a review will be presented here. It is proposed that a bolitoglossine stock ancestral to the supergenus *Bolitoglossa* was associated in early Tertiary with elements of the Arcto-Tertiary Geoflora at relatively high latitudes. Axelrod (1960) has stated that a mixing of elements of the Arcto-Tertiary and Madro-Tertiary Geofloras started in middle Cretaceous and formed what he calls a broad "ecotone." The "ecotone" extended southward along low mountains into Mexico during Cretaceous and early Eocene. Species of plants, or paired-species, which now occur disjunctly in Appalachia and the Mexican and Guatemalan highlands, probably entered the area at this time (see also Braun, 1950; Martin and Harrell, 1957); these plants are relicts of the old world-wide Arcto-Tertiary Geoflora, and similar species occur today in eastern Asia. Plethodontid salamanders may also have entered the "ecotone" along with their Arcto-Tertiary associates, both plant and animal. The entire assemblage shifted to the south, especially at high elevations, as the tropical border continued to move southward in Oligocene and Miocene in response to long range Tertiary cooling trends.

The Madro-Tertiary Geoflora was developing in the increasingly arid southwestern United States and northern Mexico from Eocene throughout Tertiary. Increased lowland aridity favored expansion of the Geoflora between the main portions of the Arcto-Tertiary belt to the north and the Arcto-Tertiary-Neotropical-Tertiary "ecotone" isolated in the highlands to the south. Presumably the long-range Tertiary climatic trends resulted in effective separation of the ancestral populations of the supergenus *Bolitoglossa* from other bolitoglossine populations to the north.

It is apparent that Appalachia is the primary dispersal center of plethodontid salamanders, but it is equally apparent that the moist borders of the Mexican Plateau have acted as a secondary center of evolution and dispersal. Seven genera and over one hundred species of bolitoglossine salamanders have been derived from the ancestral Tertiary populations. A number of species remain in the ancient "ecotonal" situation, but several lines have successfully adapted to other habitats where they are associated with derivatives of the Neotropical Tertiary Geoflora. Significantly the more structurally primitive and generalized species have remained in the highland "ecotone."

Three distinct lines of tropical bolitoglossine evolution are apparent (Fig. 17). Perhaps the earliest divergence from the ancestral stock was by *Bolitoglossa*. The genus is found in the Mexican Highlands but has also extended into the Central American and South American highlands as far south as Ecuador and Venezuela. Throughout its range various species have invaded and adapted to the lowland habitats where many species have become arboreal. Lowland species of *Bolitoglossa* range from Mexico through Central America to Bolivia and Brazil (Figs. 27 and 29). Invasion of the lowlands and acquisition of arboreal habits has apparently occurred in parallel several times in the genus. Highland species are usually both more primitive and more generalized than lowland species. With only a few exceptions *(e.g., rufescens, occidentalis)* the more northerly species of any habitat type are more primitive and generalized than their more southerly ecological equivalents. Stuart (1954) has suggested that *Magnadigita* (= primitive highland *Bolitoglossa*) is autochthonous in Central America, and has spread north and south from the Guatemalan Highlands. What may be the

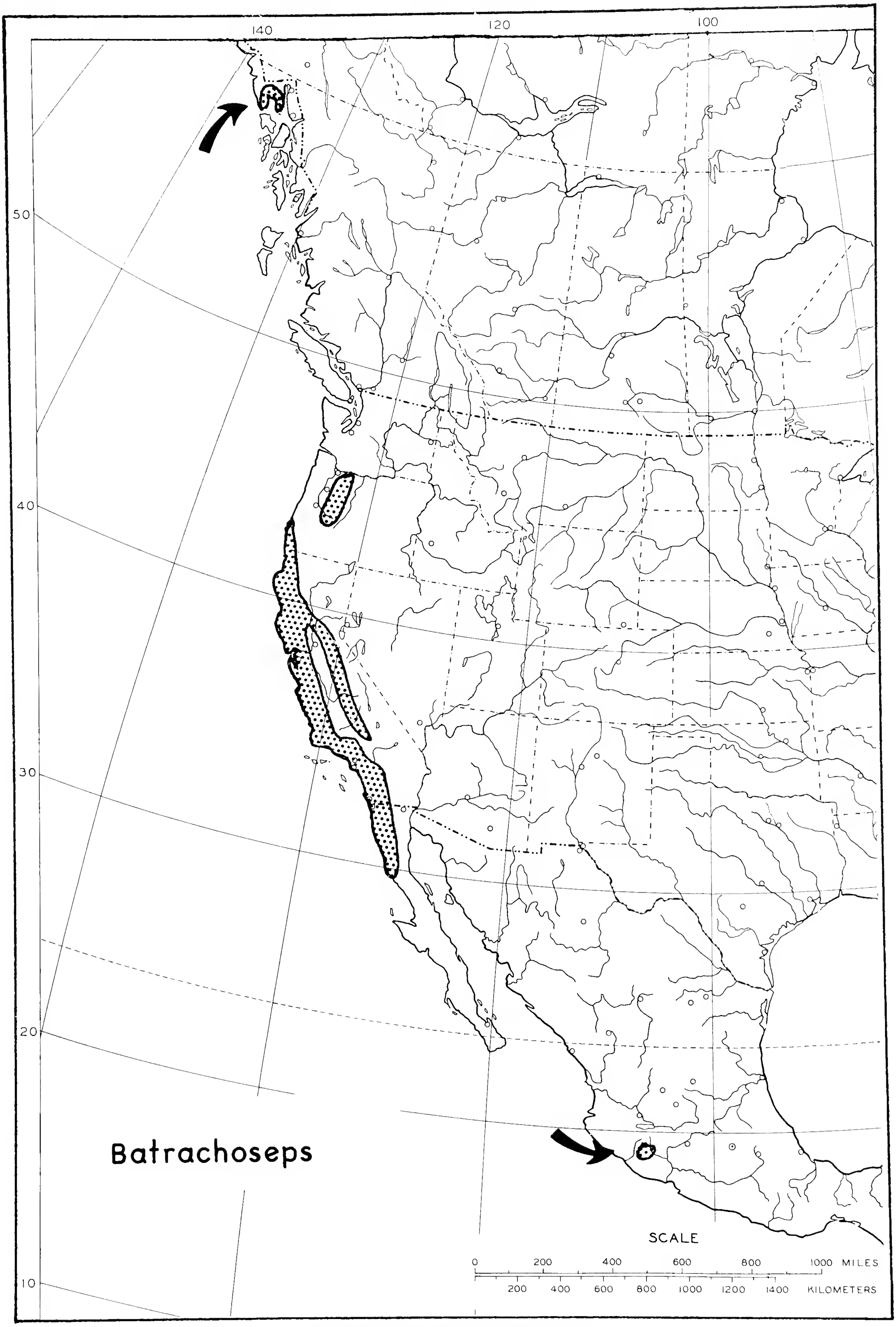
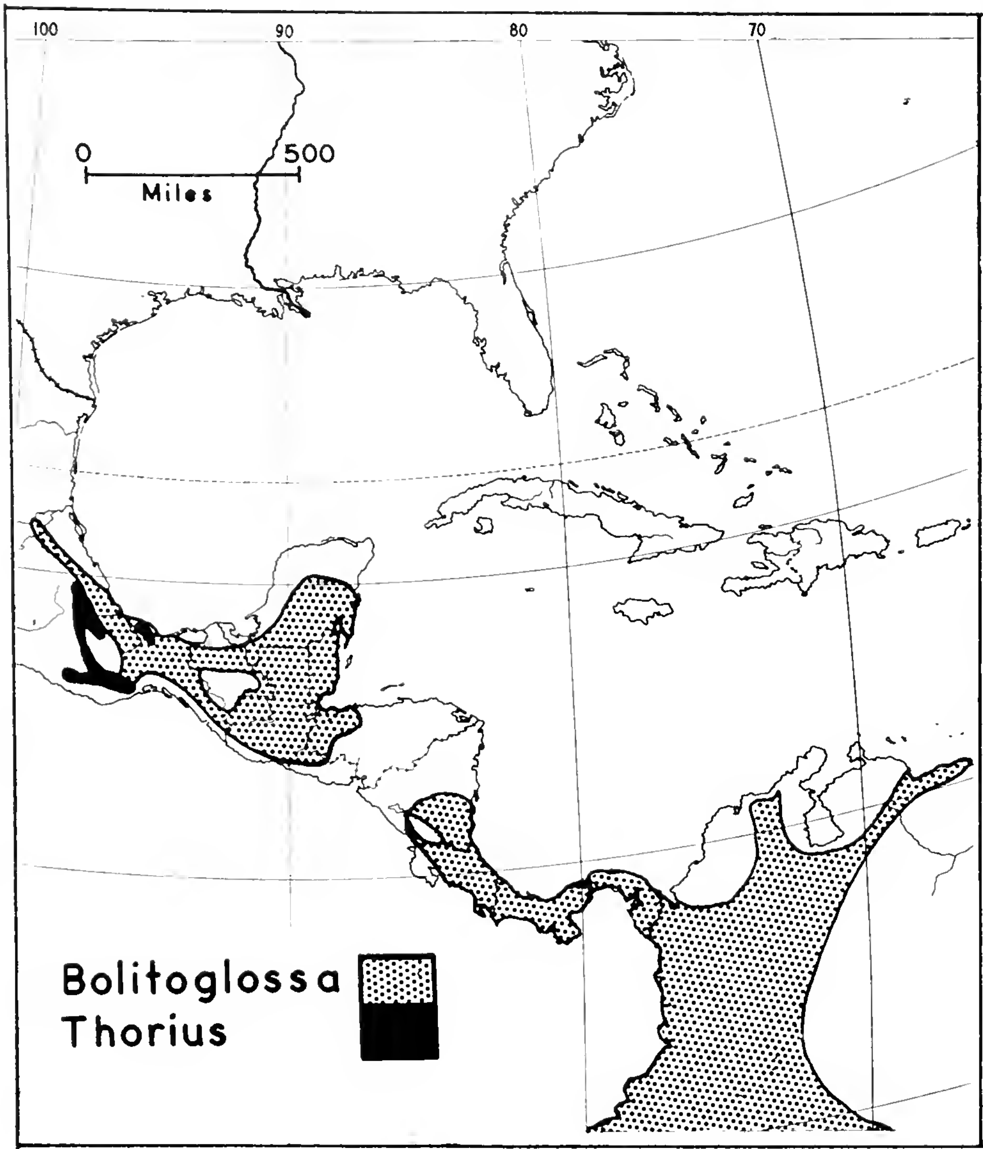
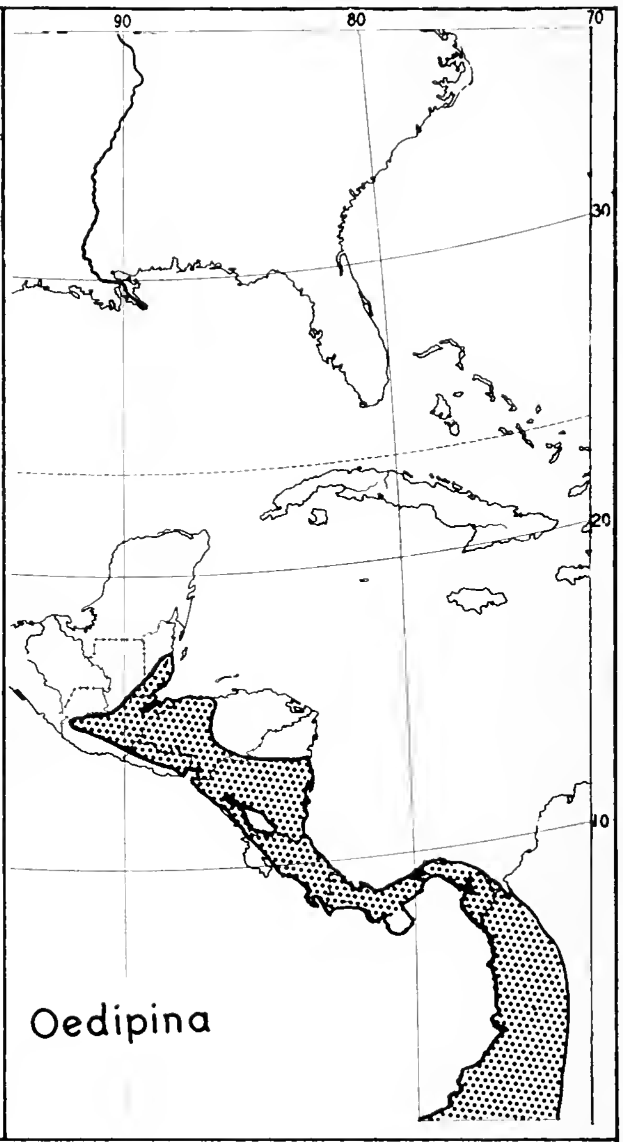


Figure 26. Distribution of *Batrachoseps.*





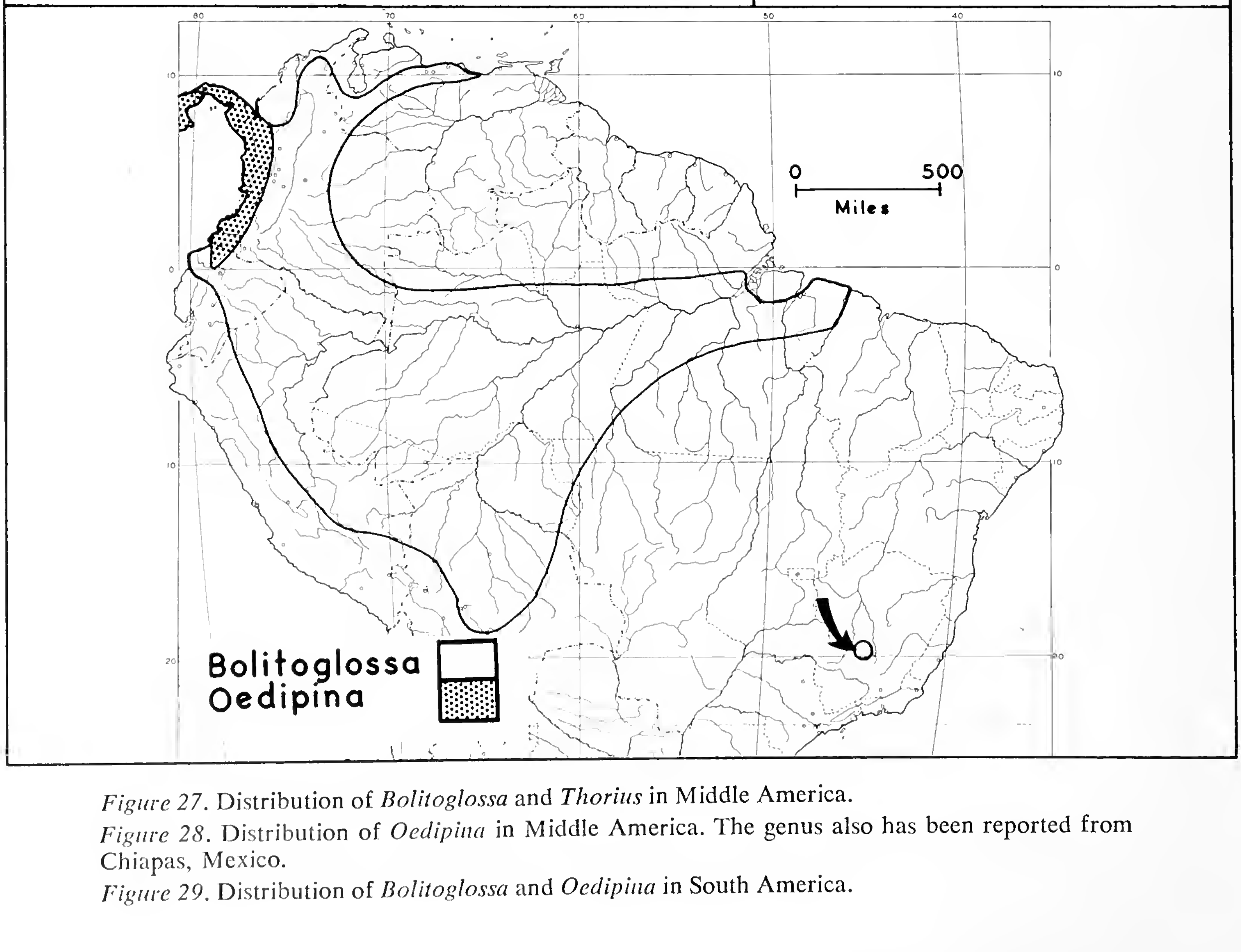


Figure 27. Distribution of *Bolitoglossa* and *Thorius* in Middle America.

Figure 28. Distribution of *Oedipina* in Middle America. The genus also has been reported from Chiapas, Mexico.

Figure 29. Distribution of *Bolitoglossa* and *Oedipina* in South America.

most primitive species is a Guatemalan highland form, *B. dunni,* which retains columellae, prefrontals, primitive vertebrae, long limbs, slightly webbed hands and feet, primitive numbers of carpals and tarsals, tibial spurs, and primitive vomers. The most specialized species appear to be *B. rufescens* of the northern lowlands and members of the South American *palmata* and *altamazonica* groups (Brame and Wake, 1963).

A second phylogenetic line contains the highly specialized, greatly elongated species of *Oedipina.* These bizarre organisms are attenuate forms with elongated trunks, reduced limbs, and extremely long tails (often over seventy-five per cent of total length). The high degree of specialization, adaptation to lowland environments, and penetration of South America all suggest early divergence from the common tropical bolitoglossine ancestral stock. Two major sections are evident. One contains relatively short-bodied forms with few or no maxillary teeth and relatively large, essentially fully webbed feet *(elongatus, parvipes, complex);* they are found over the entire range of the genus from Mexico, British Honduras, and Guatemala to north-central Ecuador. The other section includes relatively long-bodied species with many maxillary teeth and rather small, syndactylous feet (all other species) which range from Guatemala to western Panama. *Oedipina* is the only plethodontid genus found primarily in tropical lowlands and is the only tropical genus that does not occur in the highlands along or near the southern and eastern margins of the Mexican Plateau. Costa Rica is the present dispersal center and apparently has been the center of evolution of this, the most specialized and advanced plethodontid genus (Figs. 28 and 29).

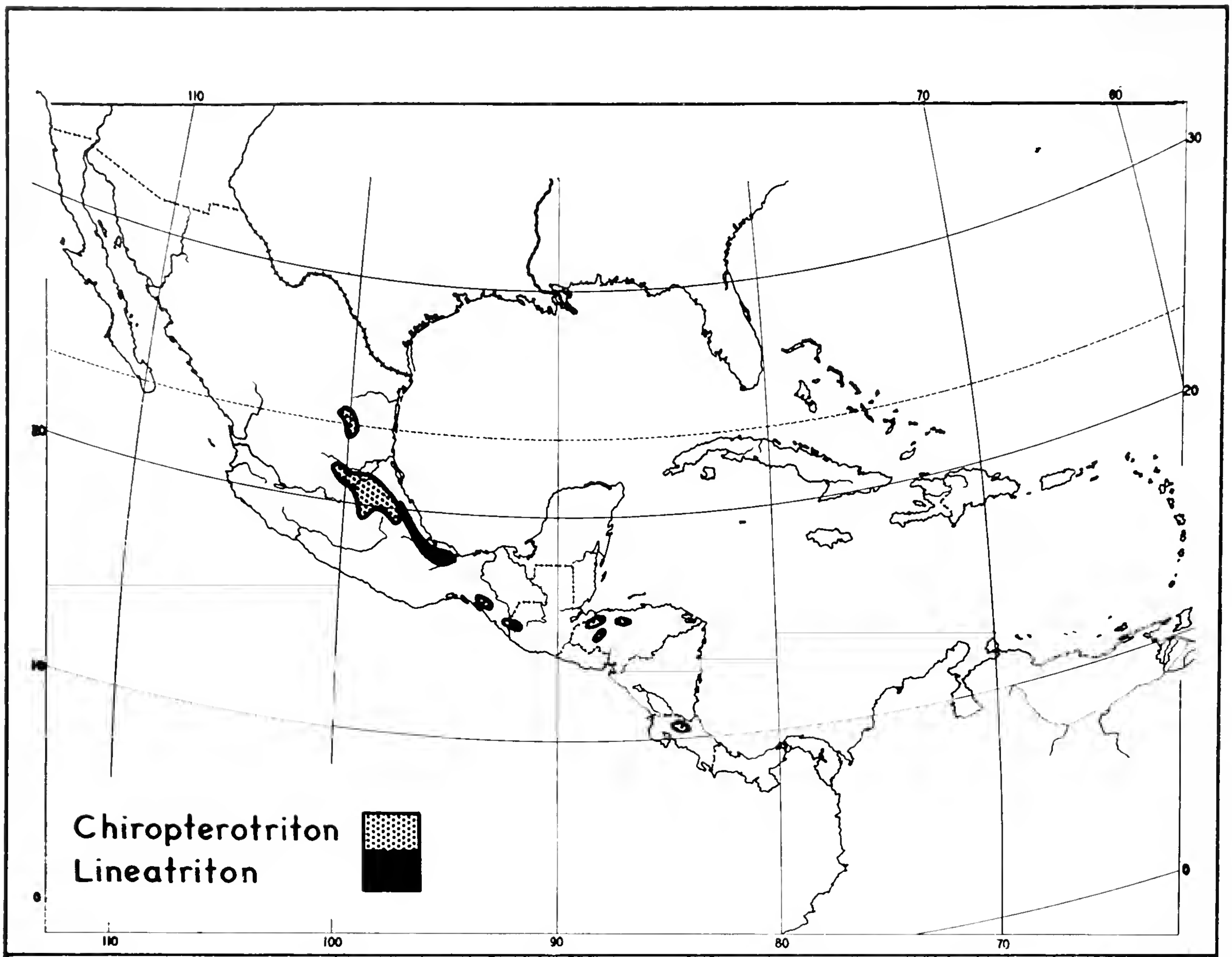
The third and final line includes those species now assigned to the genera *Pseudoeurycea, Chiropterotriton, Thorius, Parvimolge,* and *Lineatriton.* All are found in mountains in and around the southern margins of the Mexican Plateau (Figs. 27, 30, 31). *Thorius, Lineatriton,* and probably *Parvimolge* (depending on the assignment of the Costa Rican species, *richardi*) are limited to the area north of the Isthmus of Tehuantepec. The primitive species of both *Pseudoeurycea* and *Chiropterotriton* are also found north of the Isthmus. The mountainous southern and eastern margins of the Mexican Plateau have been the center of evolution of the group.

Pseudoeurycea and *Chiropterotriton* extend farther to the northeast than any other bolitoglossines, occurring in the mountains of southwestern Tamaulipas and southern Nuevo Leon. These northeastern populations are separated from the main populations to the south by dry gaps (*e.g.,* San Louis Potosian Gap). Martin (1958 a) refers these populations to a humid montane group of the Northeast Madrean Herpetofaunal Component. The salamanders of this component must be considered one of several in the Central American Complex of the Old Northern Herpetofaunal Element of Savage (1960). Martin (1958 a) suggests that the northeastern isolates reflect post-pluvial confinement of a habitat formerly widespread. Several species *(C. multidentatus, P. bellii, P. cephalica)* occur on both sides of the ecological barrier and the suggestion seems reasonable.

Both *Pseudoeurycea* and *Chiropterotriton* have crossed the Isthmus of Tehuantepec and entered the mountains of southern Mexico and Guatemala. *Chiropterotriton* extends even farther to the south into northeastern Costa Rica. The increasing specialization of the southern *Chiropterotriton* has been previously discussed. Stuart (1957) has suggested that *Pseudoeurycea* moved southward over the high plateaus of Chiapas and Guatemala after crossing the low, hot Isthmus of Tehuantepec in the Pleistocene. Stuart (1954) thinks that *Pseudoeurycea* is unquestionably a recent entrant into Nuclear Central America from Mexico, and the slight penetration of *Pseudoeurycea* into Central America supports this suggestion. Stuart (1954) also suggests that *Chiropterotriton* reached Guatemala by relatively low Pacific mountain-slope routes. In view of the great differentiation and greater southward penetration of *Chiropterotriton,* it is possible that the genus may have crossed the Isthmus of Tehuantepec at an earlier date than *Pseudoeurycea.*

Numerous biogeographic problems of considerable interest and importance to the local and regional distribution of the genera *Pseudoeurycea, Chiropterotriton, Bolitoglossa,* and *Oedipina* in Guatemala are discussed by Stuart (1935, 1943, 1948, 1950, 1951, 1954, 1957, 1958) and Schmidt (1936).

To summarize, the history of the neotropical plethodontids has involved mainly southward movements along the Central American axis. Major movements have probably been via highland routes. Two genera, *Bolitoglossa* and *Oedipina,* have been in Nuclear Central America for a long time and may have arisen there. Others *(Pseudoeurycea, Chiropterotriton, ?Parvimolge)* are probably more recent invaders. It seems likely that northward movements of *Bolitoglossa* and southward movements of *Pseudoeurycea* across the Isthmus of Tehuantepec by highland routes may have occurred during Pleistocene. Stuart (1954) has stated that geographic continuity existed during Pleistocene,



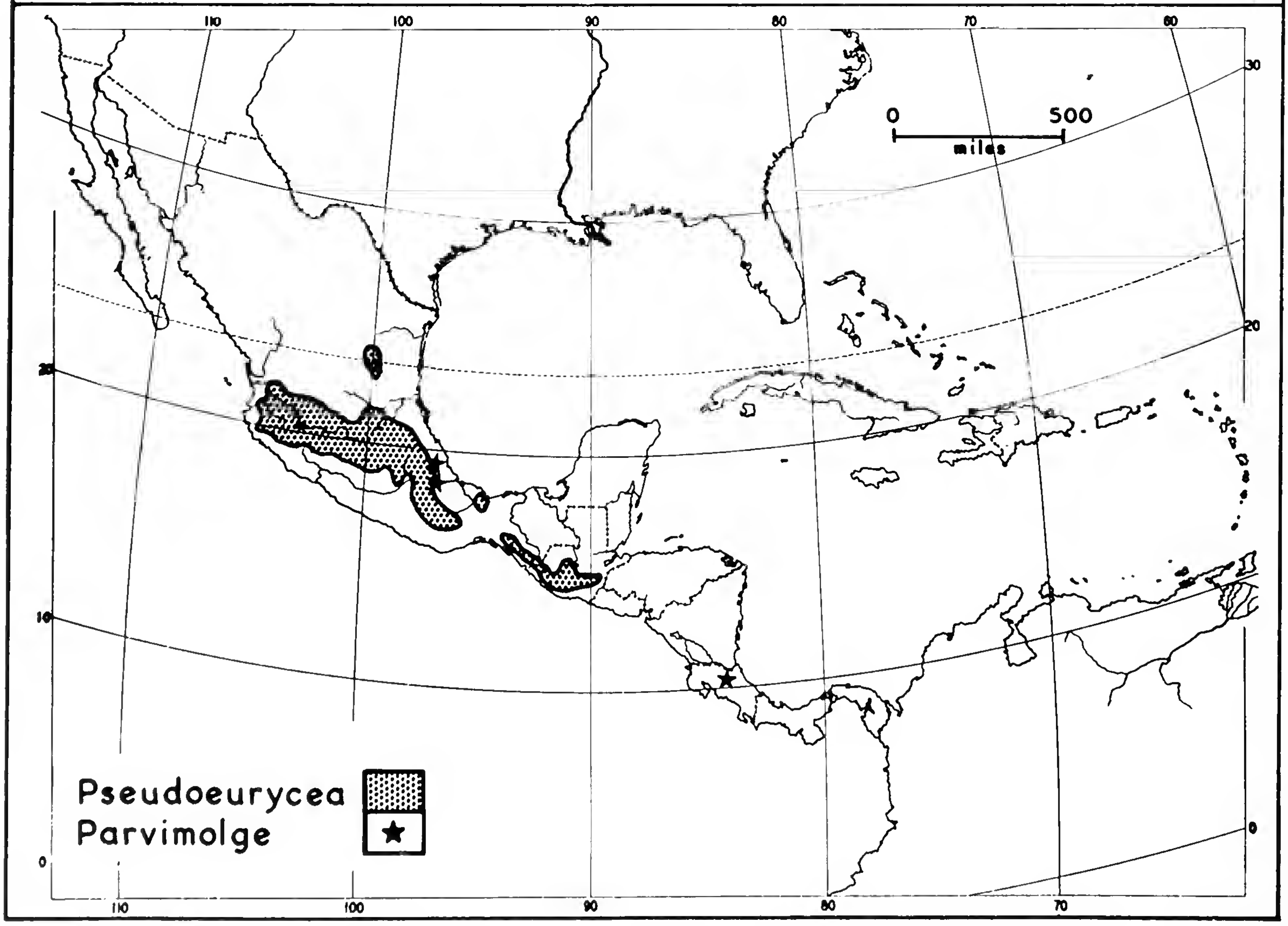


Figure 30. Distribution of *Chiropterotriton* and *Lineatriton*.

Figure 31. Distribution of *Pseudoeurycea* and *Parvimolge*.

when a temperature drop of about 5° C would have permitted the majority of highland species to move across Nuclear Central America. While the degree of southward distribution is dependent in part upon the time of entrance into Nuclear Central America, the vagility of the group must also be considered (Stuart, 1954). *Bolitoglossa* and *Oedipina* are clearly early derivatives of the ancestral stock, but the greater southward penetration of *Bolitoglossa* may be more a reflection of greater vagility than of greater antiquity.

The Second Terrestrial Encounter —the History of the Plethodonines

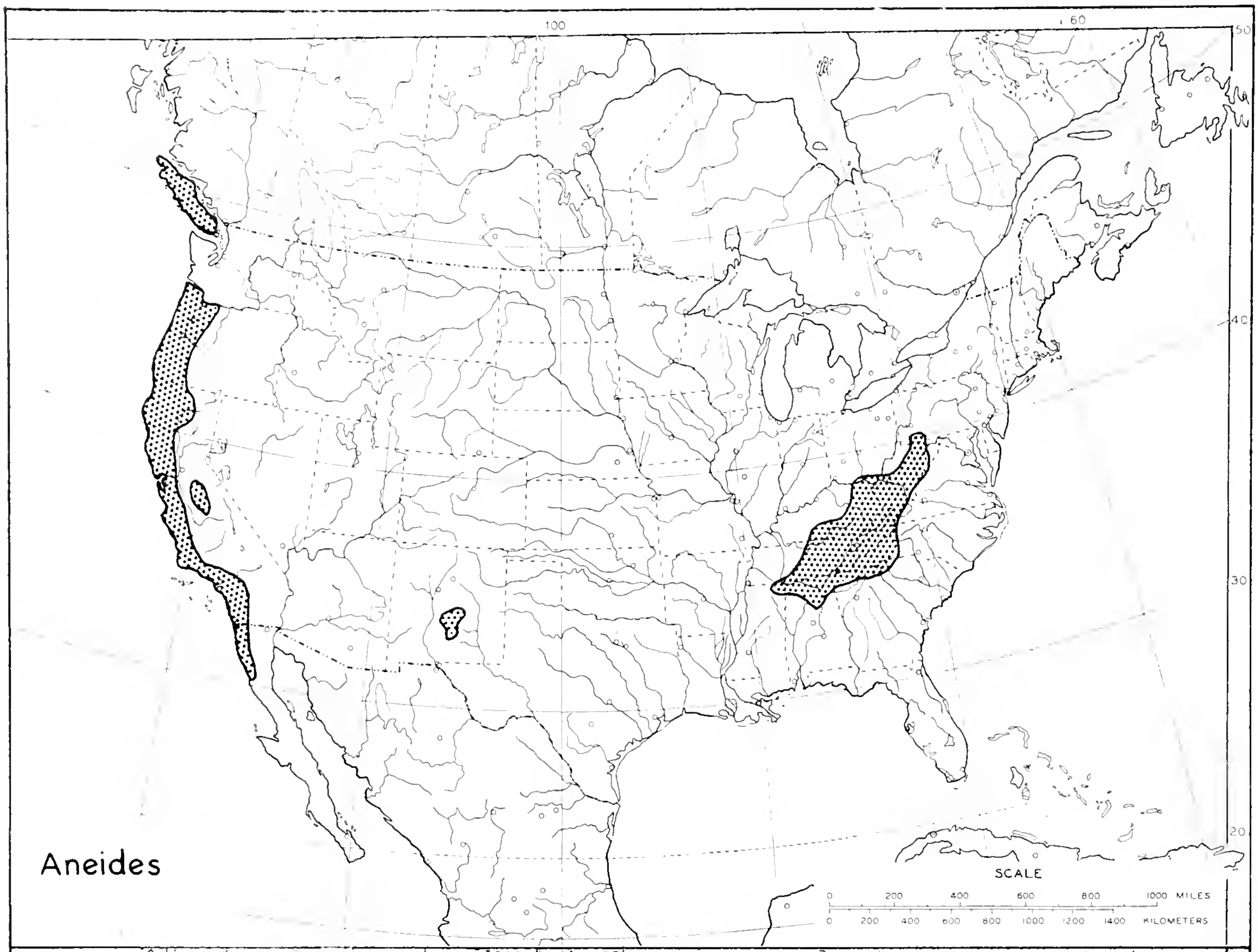
The second terrestrial group, the Plethodontini, is found today in eastern and western North America, with several Rocky Mountain isolates. The ancestral stock probably diverged from a primitive plethodontine group in what is now Appalachia later than the divergence of the bolitoglossine stock. Neither terrestrial group is ancestral to the other. Although bolitoglossines may have arisen earlier, both groups were probably well established by Oligocene.

There are three genera of plethodonines. *Aneides* has one species *(aeneus)* in southern Appalachia, one *(hardii)* in the high mountains of south-central New Mexico, and three *(ferreus, flavipunctatus, lugubris)* on the Pacific Coast (Fig. 32). *Plethodon* has eleven species in eastern North America of which six *(welleri, richmondi, wehrlei, jordani, longicrus, yonahlossee)* are primarily Appalachian species, two *(ouachitae, caddoensis)* are endemic to the Interior Highlands, two *(cinereus, dorsalis)* occur in both areas, and one *(glutinosus)* occurs in Appalachia, the Coastal Plain, the Interior Highlands, and the Edwards Plateau of Texas. Five species of *Plethodon (elongatus, dunni, larselli, stormi, vehiculum)* are restricted to the Pacific Coast of northwestern United States and southern British Columbia, one (*vandykei*) occurs in western Washington, northern Idaho, and northwestern Montana, and one *(neomexicanus)* occurs in the highlands of north-central New Mexico (Fig. 33). The single species of *Ensatina (eschscholtzii)* ranges from British Columbia to extreme southern California along the Pacific Coast and the slopes of the Cascade-Sierra Nevada system (Fig. 19).

Lowe (1950) suggested that the history of *Aneides* is related to the Cenozoic history of the Arcto-Tertiary Geoflora in North America. It is assumed by Lowe and by me that the present day association of *Aneides* with Arcto-Tertiary floral elements is an ancient one and that much can be learned about the history of *Aneides* by studying the history of the geoflora. All plethodonine genera are now members of communities in which floral elements derived from the Arcto-Tertiary Geoflora dominate or play important roles, so that Lowe's suggestions concerning *Aneides* are at least in part applicable to the tribe as a whole.

The history of the Arcto-Tertiary Geoflora in North America has been outlined in broad form by Chaney, Condit, and Axelrod (1944), Axelrod (1948, 1950, 1956, 1957, 1960), Braun (1950, 1955), and MacGinitie (1958). In early Tertiary the Tropical-Tertiary Geoflora formed a broad belt which in North America extended as far north as southeastern Alaska on the West Coast and possibly to Nova Scotia on the East Coast (Axelrod, 1960). Above the tropical border was the circumpolar Arcto-Tertiary Geoflora. Tertiary cooling and drying trends resulted in a southward shift of the tropical border and a concomitant southward shift of the Arcto-Tertiary Geoflora. A broad "ecotone" formed where the two major floral groups met. As a result of climatic changes during middle and late Tertiary a number of segregated elements evolved, two of which, the East American Element and the West American Element (Chaney, Condit, and Axelrod, 1944; Axelrod, 1960), are of primary importance to this discussion.

Ancestral plethodonines invaded and adapted to the terrestrial environment in the Arcto-Tertiary forests of Appalachia and began to move westward in the favorable habitats provided by the forests, probably sometime in early Tertiary. Secular cooling and drying trends reinforced by the rainshadow following the uplift of the Rocky Mountains disrupted the Arcto-Tertiary belt in central North America. Forests were replaced by savannah and possibly some grassland. It is difficult to date the disjunction, but Miocene is my best estimate. In an important discussion of late Tertiary biogeography of the Great Basin, Shotwell (1961) reviewed the distribution of fossil horses from late Miocene to the end of Tertiary. He records *Merychippus (Protohippus)* from as far north as northwestern Montana as early as the Barstovian faunas (late Miocene). This is an indication of savannah and possibly grassland habitats (see Shotwell, 1961; 1963, for correlations of fossil horse genera and habitats). He also indicates that central North America was covered by dry facies of Arcto-Tertiary vegetation during late Miocene; such a situation was probably unsuitable for continuous plethodontid occupation. *Pliohippus* is present in Clarendonian faunas (early Pliocene) in many areas of central United States, coinciding with the



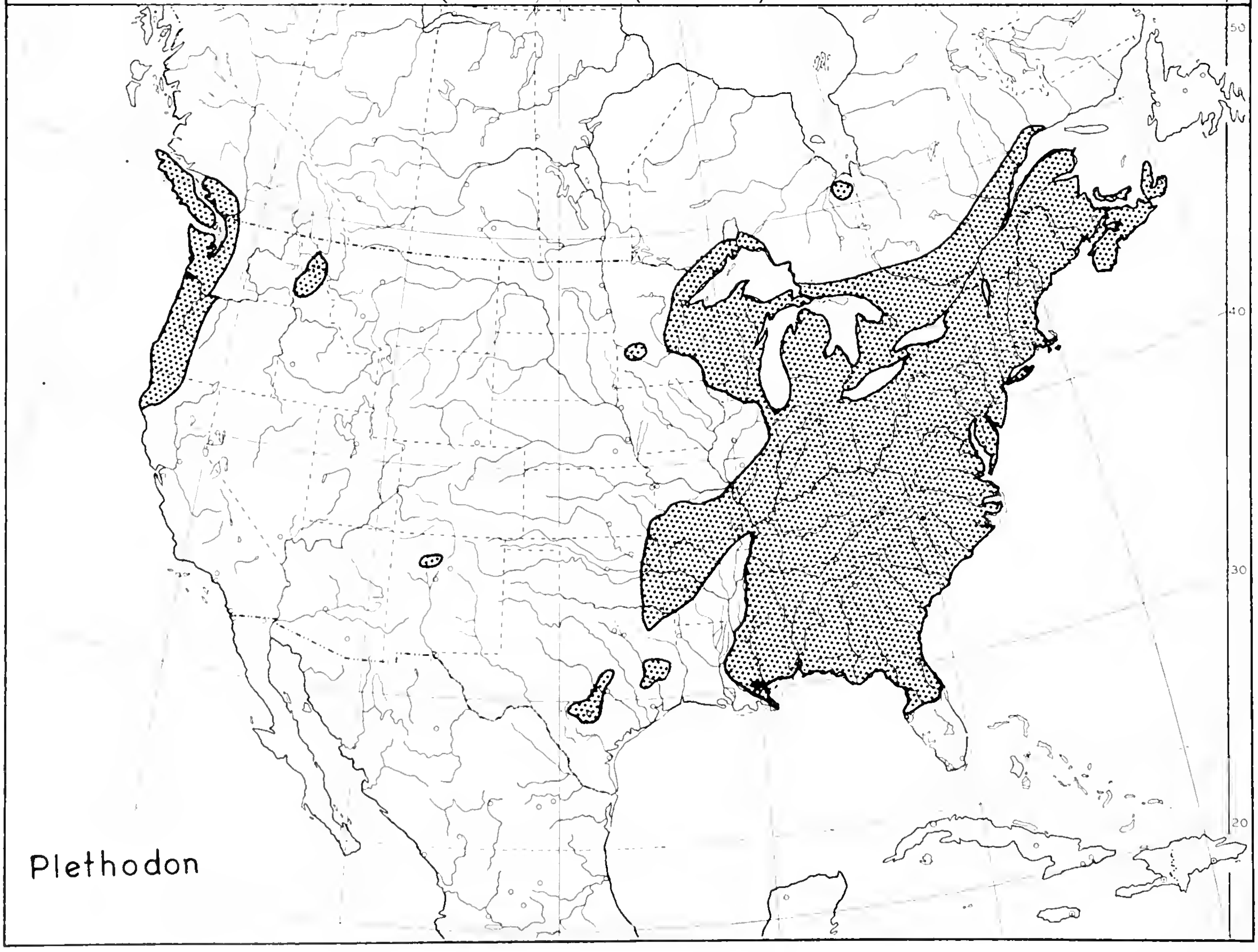


Figure 32. Distribution of *Aneides*.
Figure 33. Distribution of *Plethodon*.

expansion of open grassland (Shotwell, 1961). However, MacGinitie (1962) doubts that large grassland areas existed until Pleistocene or Recent times. MacGinitie has shown that what is now northern Nebraska was a savannah region in late Miocene with Neotropical-Tertiary relicts, pine-oak forest elements (Madro-Tertiary), and a swamp cypress component of the East American Element of the Arcto-Tertiary Geoflora. All such habitats are now unsuitable for plethodontid dispersal. Thus at some time from middle Miocene to early Pliocene the environment of central North America became inhospitable for plethodontids, and the species in the east and in the west were separated.

The theory proposed here for dating of the disjunction of the ranges of plethodonine genera is in conflict with that of Dunn (1926), who did not have the benefit of the important paleobotanical literature of the past thirty years. My theory is in fairly close agreement with that of Lowe (1950), which placed disjunction of *Aneides* in late Miocene with complete disjunction during early Pliocene.

Plethodonine genera were well established by the time of the disjunction. Two of the three genera *(Aneides, Plethodon)* occur on both sides of the grassland barrier, and forest corridors are not known to have existed across the barrier.

Dating of the disjunction of the ranges of *Plethodon* and *Aneides* provides some indirect evidence on the relative age of the genera. Divergence of *Aneides* from a *Plethodon*-like ancestral stock must have occurred at an early date. By the time of the range disjunctions both genera were widespread, perhaps with transcontinental distributions. Generic differentiation may date from Oligocene or early Miocene.

Aneides and *Ensatina* may have arisen independently from *Plethodon* in western North America. While the most primitive species of *Plethodon* are found in eastern North America (Highton, 1962), the most primitive *Aneides* (*hardii,* see Wake, 1963) is found in the west (New Mexico) and *Ensatina* is limited to the Pacific Coastal region. Four of the five *Aneides* are western species and the fifth (*aeneus* of Appalachia) is a morphologically specialized species that occupies a highly specialized arboreal-rock crevice habitat (Gordon, 1952; Wake, 1963).

Plethodonines were probably widespread in western United States in Miocene. Elimination of the group from most of the area east of the Cascade-Sierra Nevada divide and west of the Great Plains occurred subsequent to midcontinental disjunction. The researches of Axelrod (1957, 1958), Axelrod and Ting (1960, 1961), and Shotwell (1961, 1963) are particularly pertinent to this discussion. Development of the xeric Madro-Tertiary Geoflora in the interior southwestern United States began in early Tertiary. During Tertiary there was a general drying of western North America favoring expansion of the Madro-Tertiary elements at the expense of the Arcto-Tertiary elements. On the basis of geofloral distribution and the distribution of fossil horses, Shotwell (1961, 1963) has made the following suggestions concerning the history of the Great Basin in late Tertiary. In Barstovian times the mesic Arcto-Tertiary elements extended throughout the Great Basin but were mixed with drier Madro-Tertiary elements in the south. Shotwell states that by Clarendonian times the Madro-Tertiary Geoflora extended northward, and Arcto-Tertiary elements had largely been displaced from the central Great Basin except for moister local areas (high elevations, stream borders). *Pliohippus* has been found in Clarendonian deposits in much of the Great Basin. This fact indicates that savannah or grassland was present. Both habitats are unfavorable for plethodontids. By Hemphillian times (middle to late Pliocene) increasing cold stopped the northward extension of the Madro-Tertiary elements, but the present semiarid character of the Great Basin was already established. No woodland elements were present in Hemphillian times in the northern Great Basin (Shotwell, 1963).

Later Tertiary and Quaternary changes in the flora of the Great Basin were the result of secular drying and cooling reinforced by Pleistocene warping and faulting which raised the Sierran crest from five thousand to nine thousand feet (Axelrod, 1950; 1957; Axelrod and Ting, 1960; 1961). This uplift, according to Axelrod (1957), would have accounted for a ten to fifteen inch reduction in rainfall to the east. Increasing continentality of climate, rain shadow effect of the Sierran uplift, and severe cooling of Pleistocene glacial periods all contributed to the disappearance of plethodontids over most of the Rocky Mountain and interior range of the group. The distribution of the West Coast species was further severely limited by the major Sierra Nevada uplift of Pleistocene times (see Axelrod and Ting, 1961).

Three species of plethodonines occur today in the Rocky Mountains. *Plethodon vandykei* of coastal Washington has disjunct populations in northern Idaho and Montana. Several other amphibians are also found in both areas *(Ascaphus truei, Dicamptodon ensatus, Taricha granulosa)* and at least one lizard *(Gerrhonotus coeruleus)* is distributed continuously across intervening mountain ranges in southern British Columbia. Disjunct distribution of *P. vandykei* is probably the result of Pleistocene or Recent events.

P. neomexicanus and *A. hardii* of New Mexican highlands are apparently relicts of the mid-Tertiary Rocky Mountain fauna as suggested by Lowe (1950). Murray (1957) thinks final isolation may have occurred as late as late Pleistocene. Martin (1958 b) states that 4,000 to 4,500 foot altitudinal displacement of biotic zones occurred during full-glacial periods in the Southwest. It is possible that final southern displacement of the species may have occurred at that time. Survival of the two species is related to the fact that they have been able to adapt to favorable microhabitats in the relatively inhospitably cold Rocky Mountains.

Blair (1958) has suggested that *P. neomexicanus* may have arisen from populations that dispersed directly across Oklahoma in Wisconsin times, and that *A. hardii* may have been connected with the eastern population as recently as late Pleistocene. The New Mexican highland flora as a whole is clearly derived from the West American Element of the Arcto-Tertiary Geoflora. This indicates a western, not eastern origin for the salamanders as well (see Chaney *in* Chaney, Condit, and Axelrod, 1944). Both species are isolated at altitudes above 8,000 feet. They are well defined species, not closely related to any others. It is likely that they are displaced southern relicts of the ancient Rocky Mountain fauna, and their evolutionary history is not related strictly to Pleistocene events.

Pacific Coast species have undergone a moderate amount of diversification. *Ensatina eschscholtzii* is the most primitive in morphology, the most generally adapted in ecology, and the most widespread of the western plethodonines. Other species have more restricted ranges, and are generally more specialized (see Peabody and Savage, 1958, for detailed biogeographic analyses of western species).

To summarize, the plethodonines occurred all across the continent in early Tertiary. Middle and late Tertiary events are responsible for the present generic disjunctions. Plethodonines are more successful than other high latitude terrestrial genera and were apparently the victors in competitive encounters with the bolitoglossines in the east. Western plethodonines have also had notable success, and the bolitoglossine genera have survived the plethodonine invasion only by specializing. The failure of plethodonines to reach the tropics and the Old World is probably the result of relatively recent derivation from the plethodontine ancestral stock.

CONCLUSIONS AND SUMMARY

The large, diverse family Plethodontidae contains more than two-thirds of the living species of salamanders. The morphology, ecology, and behavior of the species have shown them to be the most progressive and advanced group within the order Caudata. The general adaptive level of the family is high, relative to other salamanders, and a successful radiation of specially adapted species has occurred. Because so many of the adaptive types have survived, the family has been ideal for the study of major features of evolution, especially the morphological bases for adoption of new ways of life and the ensuing adaptive radiations that typically characterize such events.

A functional and evolutionary morphological analysis has been employed to outline the evolutionary patterns of individual bony elements, functional anatomical units, and groups of organisms. This analysis has led to a new classification of the family and has formed the basis of theories concerning major features of evolution within the family.

The twenty-three genera and one hundred eighty-four species of plethodontids may be grouped in two subfamilies based on morphological evidence. The more specialized subfamily Desmognathinae is the smaller and has the more restricted geographic range. Its three genera (ten species) live in eastern North America, centered in the southern Appalachian mountains, an area presumed to be the ancestral home of the family. The larger and more generalized subfamily Plethodontinae includes twenty genera grouped in three tribes. The most primitive tribe, the Hemidactyliini (eight genera, twenty-four species) is concentrated in eastern North America. The tribe Plethodontini (three genera, twenty-four species) occurs in both eastern and western North America. The remaining nine genera are included in the most advanced tribe, the Bolitoglossini (one hundred twenty-six species), a group that ranges from western North America into the Neotropics, and has two species in Europe. It is the only plethodontid group that lacks representatives in eastern North America.

The two subfamilies of lungless salamanders differ markedly in the functional morphology of the head. In the Desmognathinae the lower jaw can be lowered only until a ligament extending from the mandible to the atlas vertebra becomes taut. The skull is then raised to open the mouth further. Morphological modifications directly and indirectly associated with this functional shift are great and the desmognathine salamanders differ considerably from the more generalized plethodontines. The three tribes of plethodontines differ mainly in anatomical details, such as hyobranchial configuration, form of cranial elements, and vertebral differences.

Each of the four major groups of plethodontids has undergone a secondary adaptive radiation. As a result structural and ecological parallelism are common phenomena in the family, and include the following examples. Tongues are primitively attached to the front of the mouth in salamanders, including the Desmognathinae and Plethodontini. In one genus each of the Hemidactyliini *(Hemidactylium)* and Bolitoglossini *(Batrachoseps)* tongues are attached, although in a modified form, to the anterior margins of the mouth. Parallel evolution of free tongues has occurred in these two tribes and free tongues are found in nearly all species of the groups. In addition there is a trend in the direction of tongue freedom in some Plethodontini *(Ensatina)*. Primitive members of the family have aquatic larvae and are aquatic to semiaquatic as adults. There are distinct parallel trends in the direction of terrestrialism with loss of aquatic larvae. All species of the Bolitoglossini and Plethodontini are terrestrial and there are definite tendencies in the direction of terrestrialism in certain species of the other groups as well *(Desmognathus aeneus* and *wrighti; Hemidactylium scutatum)*. Elongated trunks have evolved in parallel in each of the four groups and within genera of a single group. Basal tail constriction and associated specializations have arisen independently in the three tribes. The fifth toe has been lost in three separate genera. Many additional instances of parallelism have been cited. Parallelism is the rule rather than the exception in the evolution of the family.

One genus dominates each group in terms of numbers of species and size of geographic range *(Desmognathus, Eurycea, Plethodon, Bolitoglossa)*. Within each of these genera a tertiary level of adaptive radiation has occurred. Diversity of size, habitat, behavior, and coloration characterizes each of the genera.

Paedomorphosis has been a very important morphological mode of evolution in the family. Species of four genera of hemidactyliines are paedogenetic. This developmental phenomenon has permitted survival of specialized forms in permanently aquatic and underground habitats in regions unsuitable for their more generalized relatives. Paedogenetic species are so highly specialized that they are probably evolutionary dead-ends. By contrast the phenomenon of differential metamorphosis has given bolitoglossines access to new ways of life in tropical environments and has contributed to a relatively large scale adaptive radiation and evolutionary diversification.

The evolution of a great variety of special adaptive features has been associated with the adaptive radiation of the lungless salamanders. Many examples have been cited, among them new feeding mechanisms in desmognathines, skull strengthening adaptations in forms that force their way head first under rocks or make burrows (desmognathines) and in forms that have adopted new feeding techniques *(Aneides)*, limb shortening in burrowers of several genera, toe loss, basal tail constriction and adaptations for tail autotomy, specialized climbing adaptations in the limbs, hands and feet, eye reduction and loss in cave dwellers, size diminution, gigantism, and others. The radiation has been extensive and complex, with the adaptations appearing in parallel and multiple parallel lines found within the family and familial subgroups. The result is an evolutionary pattern that is characterized by the mosaic distribution of primitive and advanced, generalized and specialized characters on all taxonomic levels.

Knowledge of the late Mesozoic and Cenozoic history of the Northern Hemisphere, fossil history of the family, ecology and distribution of the living species, and evolutionary relationships within the family has formed the basis for a theoretical consideration of the phylogeny and biogeography of the family. Ancestors of the family were probably derived from a stock close to that which gave rise to ambystomatid salamanders. Appalachia is the present center of dispersal and earlier suggestions that this region is the source area are accepted. Divergence of the desmognathine line from the main line of plethodontid evolution occurred very early, probably by the beginning of Cretaceous times. Plethodontine tribal divergence probably dates from earliest Tertiary. The first plethodontine group to differentiate may have included the terrestrial ancestors of the modern bolitoglossines. The plethodonines are thought to have arisen after the bolitoglossines because they have a less extensive range, have undergone a less extensive adaptive radiation and diversification, and they have living representatives in eastern North America. Possibly competition with the more vigorous plethodonines led to elimination of the older and more specialized bolitoglossines from eastern North America. The Hemidactyliini represent the diversification of the ancestral stock. Some of the genera *(e.g., Hemidactylium)* diverged from the stock very early, perhaps as early as the ancestors of the other tribes. The group is thus less compact than the other two tribes.

There is evidence that the family remains evolutionarily active. Entrance into the tropics has given the salamanders access to new ways of life, and such genera as *Thorius, Oedipina,* and *Bolitoglossa* may be initiating new phylogenetic trends. Activity of these groups is attested by the facts that forty per cent of all living species of salamanders are found within a single supergenus that ranges from Mexico into South America, and more than twenty-five per cent of the species of plethodontid salamanders are members of the genus *Bolitoglossa.*

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