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**COMMENTS ON THE OSTEOLOGY AND PHYLOGENY  
OF AMBYSTOMATID SALAMANDERS**

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# COMMENTS ON THE OSTEOLOGY AND PHYLOGENY OF AMBYSTOMATID SALAMANDERS

J. A. THIEN<sup>1</sup>

**SYNOPSIS:** The family Ambystomatidae is a strictly Nearctic family, probably derived from the Asiatic Hynobiidae in the late Mesozoic or very early Tertiary. Osteological evidence indicates that the Pacific Coast forms *Dicamptodon* and *Rhyacotriton* were derived very early, and independently, from the proto-ambystomatid stock. These forms are so distinct from each other and from the remainder of the family that recognition of three separate subfamilies is proposed. These are the Dicamptodontinae, including *Dicamptodon* and, presumably, the fossil genus *Ambystomichnus*; the Rhyacotritoninae, including only the genus *Rhyacotriton*; and the Ambystomatinae, including all other forms.

Two well-defined genera are recognized in the subfamily Ambystomatinae. One of these, *Rhyacostredon*, contains only four species. The other, *Ambystoma*, is in turn divided into three subgenera, *Ambystoma*, *Bathysiredon*, and *Linguae-lapsus*. Four imperfectly delineated species groups are recognizable in the subgenus *Ambystoma*—the *mexicanum* group (which includes the fossil species *kansense*), the *tigrinum* group, the *opacum* group, and the *maculatum* group.

It is postulated that *Dicamptodon* and *Rhyacotriton* developed from a branch of the original proto-ambystomatid stock that established itself in the western part of the continent very early in the history of the family, while the primary center of dispersal for the remainder of the family was in the northeast. Establishment of this eastern group probably preceded the Miocene, with the various species groups being developed not later than the early Pliocene, and many of the extant species by or in the early Pleistocene.

## INTRODUCTION

The family Ambystomatidae<sup>2</sup> is a strictly Nearctic group of salamanders, ranging geographically from southern Alaska and extreme

<sup>1</sup> The author is at present a Research Associate in the University of Florida School of Medicine, under an Atomic Energy Commission contract. He has been particularly interested in the paleontological history of living amphibian and reptile groups. The present paper is an outgrowth of attempts to identify, and determine the relationships of, ambystomatid salamanders represented by remains recovered from various Pliocene and Pleistocene fossiliferous deposits. Manuscript submitted 13 May 1958.—Ed.

<sup>2</sup> This emendation of the familiar name Ambystomidae is mandatory under Paragraph 50 (1), Sections (a) and (b), of the 1953 "Copenhagen Decisions on Zoological Nomenclature" (page 34). Section (a) prescribes the method of forming Family-Group names based on generic names of Greek or Latin origin; its provisions require in the present instance that *-stomat-* be used as the root to which the ending *-idae* is affixed. Section (b) requires "automatic" correction of a Family-Group name which, when first published, was incorrectly formed in contravention of (a). The emendation Ambystomatinae must similarly be used for the subfamily name. Though the "Copenhagen Decisions" made these provisions specifically applicable only to Family-Group names, from subfamily to superfamily, consistency requires that the subordinal name also be emended, to Ambystomatoidea.

southern Labrador southward to the southern part of the central plateau of Mexico, and temporally from possibly the late Mesozoic, certainly from the very early Tertiary, to the present. No fossil records are known from outside of the present range of the family; it has probably been confined to North America throughout its entire geological history.

The family, including fossil forms, contains between 30 and 35 currently recognized species. Certain broad relationships have generally been recognized at various supraspecific levels, but there has been little effort to define these supraspecific categories accurately, to delimit them clearly, and to determine their relative significance. The present study will treat such supraspecific groupings as they are indicated by their osteology. Such a restricted approach naturally has its limitations, and the conclusions reached must be considered tentative, subject to modification on the basis of evidence from other sources. On the whole, however, I believe the interrelationships to be rather accurately recognizable on the basis of osteology. No attempt has been made to investigate problems bearing on the status or definition of individual forms; only the supraspecific relationships will be considered. Subspecific or specific status in the listings given is based for the most part only on the apparent current consensus, and not on any additional evidence derived from the present study. In this respect and in matters such as synonymies, ranges, genotypes, and references to original descriptions I have drawn freely on the check lists of Schmidt (1953) and Smith and Taylor (1948).

I wish to acknowledge my indebtedness to the following persons for assistance in procuring the skeletal material for study: C. M. Bogert of the American Museum of Natural History; Herndon G. Dowling of the University of Arkansas; Denzel E. Ferguson of Mississippi State College; Coleman J. Goin and Arnold B. Grobman of the University of Florida; Wilfred T. Neill of the Ross Allen Reptile Institute; the late Karl P. Schmidt of the Chicago Natural History Museum; Hobart M. Smith of the University of Illinois; Edward H. Taylor of the University of Kansas. C. W. Hibbard of the University of Michigan Museum of Vertebrate Paleontology and Robert Wilson of the University of Kansas Museum of Vertebrate Paleontology have kindly permitted the examination of fossil material in the collections of their respective institutions. I am also grateful to Goin, Smith (who also provided radiographs of certain Mexican forms), Taylor, and to Walter Auffenberg of the University of Florida for their assistance in numerous other respects during the course of this study.

In order to facilitate the preliminary discussion, the classification that I have adopted is outlined below. An asterisk following the name of a form indicates that I have seen only immature (nonneotenic) larval specimens of that form; a double asterisk indicates that I have not been able to obtain any specimens for examination, a dagger (†) indicates that no skeletons have been seen, but that soft-ray radiographs have been examined. Subspecies are not included in this preliminary classification.

Suborder: Ambystomatoidea	<i>Ambystoma fluvinatum</i> **
Family: Ambystomatidae	<i>Ambystoma granulosum</i> †
Subfamily: Dicamptodontinae	<i>Ambystoma hibbardi</i>
Genus: Ambystomichnus	<i>Ambystoma lacustris</i> **
<i>Ambystomichnus</i>	<i>Ambystoma ordinarium</i>
<i>montanensis</i> **	<i>Ambystoma rosaceum</i> **
Genus: Dicamptodon	<i>Ambystoma subsalsum</i>
<i>Dicamptodon ensatus</i>	<i>Ambystoma tigrinum</i>
Subfamily: Rhyacotritoninae	The opacum group
Genus: Rhyacotriton	<i>Ambystoma opacum</i>
<i>Rhyacotriton olympicus</i>	<i>Ambystoma talpoideum</i>
Subfamily: Ambystomatinae	The maculatum group
Genus: Rhyacosiredon	<i>Ambystoma gracile</i>
<i>Rhyacosiredon altamirani</i>	<i>Ambystoma jeffersonianum</i>
<i>Rhyacosiredon leorae</i>	<i>Ambystoma laterale</i>
<i>Rhyacosiredon rivularis</i>	<i>Ambystoma macrodactylum</i>
<i>Rhyacosiredon zempoalensis</i> **	<i>Ambystoma maculatum</i>
Genus: Ambystoma	Subgenus: Linguaelapsus
Subgenus: Ambystoma	<i>Ambystoma annulatum</i>
The mexicanum group	<i>Ambystoma cingulatum</i>
<i>Ambystoma kansense</i>	<i>Ambystoma mabeei</i>
<i>Ambystoma lermænsis</i>	<i>Ambystoma schmidt†</i>
<i>Ambystoma mexicanum</i>	<i>Ambystoma texanum</i>
The tigrinum group	Subgenus: Bathysiredon
<i>Ambystoma amblycephalum</i> *	<i>Bathysiredon dumerili</i>
<i>Ambystoma bombypellum</i> *	

The family is characterized by the rather frequent occurrence of partial or complete neoteny. Neoteny may occur in occasional individuals of many of the species, in large populations of some forms, and is apparently universally obligatory in certain forms. Some discussion of certain of the morphological consequences seems desirable.

In general, the term neoteny is used here to refer to a situation in which sexual maturity is attained, even though the individual involved retains the external gills and other essentially larval features. Loss of the gills is frequently used as the sole criterion of metamorphosis, but it is, of course, only one of many aspects of the metamorphic process. All systems of the body undergo extensive metamorphic

changes. Retention of any larval feature, even though the individual may be typically adult in all other respects, can be considered as a sort of partial neoteny.

It is often assumed, probably correctly, that a number of morphological features of the larvae of existing forms are at least roughly comparable to the adult condition in some ancestor of these forms. For example, in the Hynobiidae and some primitive Ambystomatidae, the columella is free, not fused with the otic elements. The same condition occurs in the larvae of all Ambystomatidae, but in adults of most forms a fusion with the otic does occur. This fusion is clearly a characteristic which has developed phylogenetically within the family and develops ontogenetically within individuals of certain forms. Other similar examples could be cited.

Since neoteny, or partial neoteny, is itself usually a secondary development—a specialized characteristic, so to speak—it is easy to conceive of situations in which retrograde evolution of a particular feature might appear to occur. In the example given, if some form of *Ambystoma* should exhibit partial neoteny only in respect to this one feature, then, in that particular case, the failure of the columella to fuse with the otic represents an evolutionary stage beyond the fused condition. In general, when neoteny and partial neoteny occur in a group, the direction of evolution of individual features of this sort (i.e., those in which ontogeny more or less parallels phylogeny) cannot be definitely determined per se, but must be inferred from evidence from other sources concerning the direction of evolution in the series of forms being compared. A form appearing to be primitive may actually be so, with progressive modification leading to more specialized conditions in related forms. But it might also be possible, that the apparently most specialized form is actually, as regards this particular group, the most primitive, with progressive partial neoteny leading to the conditions found in the other forms. As a further complication, it is even conceivable that an intermediate condition is ancestral, with progressive partial neoteny leading along one line to the apparently more primitive conditions, while progressive modification leads along another line to the more specialized conditions.

Because of these considerations, features in which there is, or is presumed to be, a very close parallel between phylogenetic history and ontogenetic history do not of themselves provide much information concerning the phylogeny of the forms involved. Conclusions concerning phylogeny should be based, insofar as possible, on characteristics that can be shown to be relatively independent of this problem. For example, the parasphenoid varies from one group to another

within the family; in other words, there has been phylogenetic modification of the shape of that element. However, in individuals of any given group, the parasphenoid assumes its characteristic shape even in very young larvae; there is no corresponding ontogenetic modification in the development of the individual. A neotenic individual, or form, of a group would, therefore, still retain the parasphenoid shape characteristic of that group, rather than apparently reverting to a condition comparable to that in ancestral forms.

Despite the extensive and productive experimental studies of various physiological and chemical factors involved in neoteny and normal metamorphosis, the interaction of different environmental and genetic influences to produce neoteny in nature is still largely unexplained. And it is by no means certain that the factors involved in partial neoteny are always identical with those involved in complete neoteny.

In the Ambystomatidae, neotenic populations seem to be concentrated in regions of high altitude or low temperature or both, and perhaps in regions of iodine deficiency. The phenomenon is not, however, limited to such regions nor universal within them. That genetic factors are involved has been clearly demonstrated (e.g., Geyer and Fréytag, 1949; Twitty, 1941). It is equally clear that environmental factors also are frequently involved. In many instances, at least in certain subspecies of *tigrinum*, metamorphosis can be induced simply by transference of individuals from the natural environment to an aquarium. In other cases, and other forms, it is very difficult or impossible to induce metamorphosis by any experimental means. Within a limited area in southwestern Kansas, it appears that the changing environments of the glacial and interglacial stages during the Pleistocene were accompanied by corresponding changes in the mode of living of populations of *tigrinum* inhabiting that area. Populations from deposits associable with major glacial advances were apparently neotenic, while those associable with the interglacial stages underwent normal metamorphosis (cf. Tihen, 1955).

Large neotenic populations are pretty much limited to the *A. tigrinum* - *mexicanum* - *Bathysiredon* complex, but situations interpretable as representing partial neoteny occur throughout the family. Occasional neotenic individuals have also been reported in several other forms, such as *Dicamptodon* (DeMarco, 1952), *A. gracile* (Slater, 1936), and *Rhyacosiredon* (Taylor and Smith, 1945). It is not certain whether the individuals reported in these three forms would have remained neotenic throughout their life cycle under natural conditions, or whether they represent instances of what might better be termed

delayed metamorphosis, perhaps passing one extra season in the unmetamorphosed form but still with the expectation of normal metamorphosis to follow.

#### DISCUSSION OF CHARACTERS

Several of the characteristics that vary from group to group within the family exhibit only two possible conditions; for example, an independent lacrimal is either present or it is not. In such cases, and in the case of features relatively uniform throughout the family excepting in one particular group, the characteristics are best treated in connection with the group or groups involved.

In other instances, where the variation is of a progressive, continuous, or diversified nature, a preliminary discussion of the conditions found is preferable to a piecemeal presentation by individual groups. The present section is limited to features exhibiting variation of this latter sort. Detailed descriptions need not then be repeated in connection with the various groups; mention of the condition will be made, and further details can be obtained by reference to this preliminary section.

The composition of the various supraspecific categories, as used in this discussion, has been outlined in the introduction.

#### Teeth

In animals such as these, having continuous tooth replacement, there will be some variation in the form of individual teeth due to their varying stages of development. There is also some slight variation according to the position in the jaw. But the great majority of teeth in any given (mature) individual are of a form characteristic of the taxonomic category to which it belongs (fig. 1). The teeth of the Hynobiidae are conical, rather sharply pointed, with the tips slightly bifid but scarcely or not at all expanded. A similar condition occurs in immature larvae of all Ambystomatidae, although advanced larvae usually exhibit an approach towards the adult condition in their respective species. It is presumed that the teeth of the ancestral ambystomatids were similar to those of the hynobiids. Whether these teeth are best described as having a bifid tip or as developing a lateral cusp is debatable, but that question seems primarily a matter of terminology. In what I have assumed to be the primitive condition, the two portions (lingual and labial) of the tip seem nearly equal, but the lingual is perhaps slightly more fully developed.

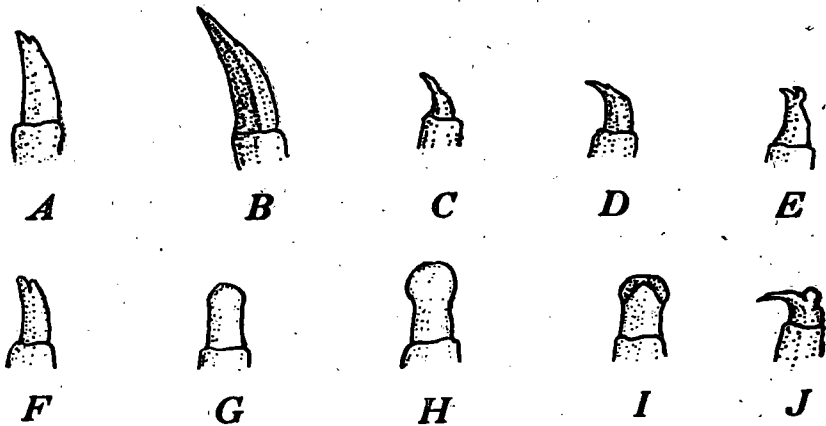


Figure 1.—Characteristic forms of individual teeth in various ambystomatid groups. (A) A typical hynobiid, *Batrachuperus pinchoni*, for comparison. This general form of tooth is also characteristic of the developing larvae of all ambystomatids. (B) *Dicamptodon ensatus*. Antero-lingual aspect. (C) *Rhyacotriton olympicus*. Anterior aspect. (D-E) *Rhyacosiredon altamirani*; showing some variation in form. (F-I) Anterior (F), lingual (G, H) and labial (I) aspects of the type of tooth found in all members of the subgenus *Ambystoma*. (J) *Ambystoma (Linguaelapsus) texanum*. Antero-lingual aspect.

In *Rhyacotriton* and *Rhyacosiredon* the inner cusp is usually somewhat elongated, forming the actual tooth tip, the outer one being represented by only a slight projection. The tooth tip itself is usually slightly, sometimes rather strongly, curved or hooked inward.

In *Dicamptodon* the teeth are strongly laterally compressed, with a sharp, simple tip. This gives the tooth the general form of a slightly curved double-edged blade, quite different from the teeth of any other member of the family.

The typical form for other members of the family is a bluntly rounded, definitely bifid tip; many have each of the two cusps, particularly the inner, expanded into a disclike structure. The tooth as a whole thus exhibits a spade-shaped, or at least a peg-shaped, form. Such a form is characteristic for adults (and mature neotenic larvae) of all members of the subgenera *Ambystoma* and *Bathysiredon*. In the subgenus *Linguaelapsus*, the tooth form is rather variable. In *annulatum* the essential form seems similar to that of the subgenus *Ambystoma*, but the tooth itself is rather short and the tip, though bifid, extremely blunt; the arrangement of the teeth is, however, characteristic of *Linguaelapsus*. In *mabeei*, most of the maxillary-premaxillary teeth are of the typical *Ambystoma* type, while many of the mandibular teeth exhibit the pointed, hooked condition described

below for *texanum*, the teeth are arranged almost entirely in a single row on each dentigerous element, as in the subgenus *Ambystoma*. In *texanum* the inner fork, or cusp, of the tip is long, sharply pointed, and strongly hooked inwards. There is apparently some geographic variation within the species in respect to the extent of development of the medial and lateral cusps. The species *cingulatum* is unique in having a capstan-shaped tooth, with the tip exhibiting a nearly flat surface. This tip may have been developed from the lateral cusp of a tooth such as that in *texanum*, the inner cusp having been reduced to the point of elimination. There is no indication of a bifid tip in this species, nor of the development of secondary cusps.

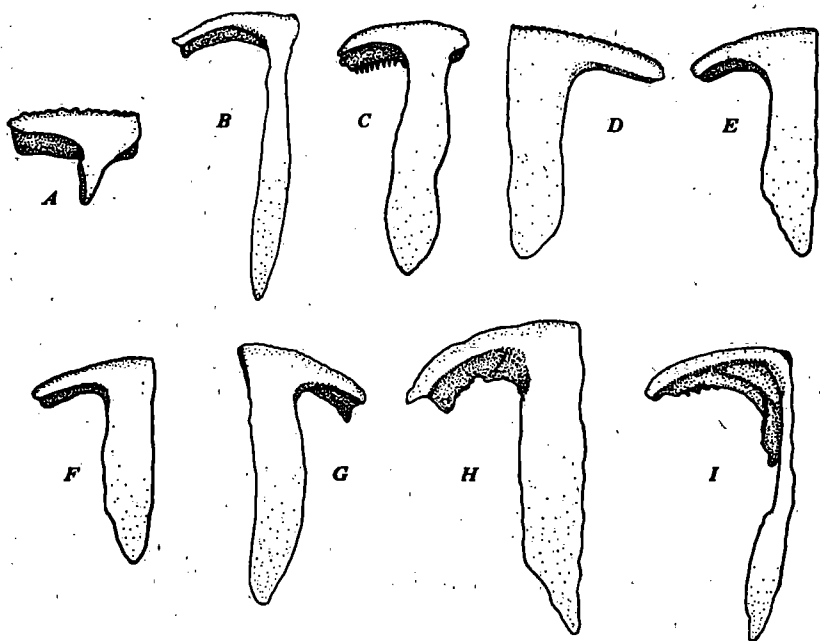


Figure 2.—Anterodorsal aspects of the premaxillae of various adult ambystomatids and hynobiids. (A) A typical hynobiid, *Batrachuperus pinchoni*. (B) *Rhyacotriton olympicus*. (C) *Rhyacosiredon altamirani*. (D) *Ambystoma tigrinum*. (E) *Ambystoma taipoideum*. (F) *Ambystoma opacum*. (G) *Ambystoma maculatum*. (H) *Ambystoma mabeei*. (I) *Ambystoma cingulatum*.

The neotenic larvae of the *A. mexicanum* - *tigrinum* - *Bathysiredon* complex have the same type of teeth as do metamorphosed adults, so the ontogenetic development of this character appears there to be a matter of age of the individual rather than of metamorphosed or non-metamorphosed condition.

## Premaxillae

In the hynobiids the nasal processes of the premaxillae are rather short and are well separated from each other; in all ambystomatids, these processes are elongated (figs. 2 and 3). In larval ambystomatids the processes are widely separated, embracing a large fontanelle; in adults of all members of the family excepting *Rhyacotriton* and *Rhyacosiredon* the processes are closely approximated in the midline, nearly or completely obliterating the fontanelle. It is likely, though not certain, that the persistence of a broad fontanelle in the two genera named represents in each case an example of partial neoteny, rather than retention of a primitive condition.

The nasal processes vary greatly in proportions, from the very broad and relatively short processes of the *Dicamptodon* premaxilla to the very long, slender ones of *Rhyacotriton* and *A. texanum*. Their proportions are, to some extent, correlated with the general proportions of the cranium.

Typically, the nasal process is a simple, flat blade. In members of the subgenus *Linguaelapsus* a vertical thickening occurs just above the dentigerous portion, forming a sort of partial septum in the nasal cavity. Both the longitudinal and vertical extent of this thickening vary from form to form within the group, and it may be represented either by a thickening of the entire blade, or only by the development of a lamina along the medial edge. In the region where this lamina or thickening develops, the lateral extent (that is, the surface exposed dorsally) is usually greatly reduced.

Customarily there is no palatal process of the premaxilla, and thus no sutural connection between the premaxillae and prevomers. In *Dicamptodon*, however, a definite palatal shelf is present, and there is an extensive, firm, sutural connection between this shelf and the prevomer (fig. 9B). This contributes to the general solidity and rigidity of the *Dicamptodon* skull, particularly the palate; this matter will be discussed more fully in connection with that genus.

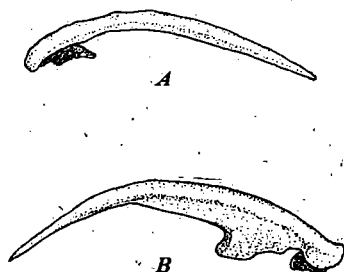


Figure 3.—Medial aspects of the premaxillae of *Ambystoma maculatum* (A) and *A. cingulatum* (B), showing the flat-bladed character of the spine in the former, and the vertical extension in the latter, characteristic of the more specialized members of the subgenus *Linguaelapsus*.

## Prevomers

In adults of both the Hynobiidae and Ambystomatidae the prevomers (figs. 4 and 5) are rather extensive bones, approaching but usually lacking firm sutural connections with the premaxillae and maxillae on the floor of the skull. *Rhyacosiredon* is unique in having prevomers in the larval position and of only slightly greater than the usual larval extent. The prevomerine teeth in that genus are, in contrast to the larval condition, reduced to a single row. The situation is comparable with a metamorphic stage in other forms, rather than with a true larval stage; it is almost certainly the result of a partial neoteny, since no similar condition occurs in any known adults of either family.

The evidence that the palatine bone contributes to the adult prevomer is tenuous, but there is a process (usually dentigerous) in the adults of most ambystomatids forming part of the posterior choanal border and extending lateral to the choana. It is probable that this process represents the palatine bone; whether it is actually homologous with the palatine or not, it is conveniently referred to as the palatine and such usage is followed here. In what is considered to be the most primitive condition, both the palatine and the prevomer proper bear teeth, those of the palatine being directly continuous with those of the prevomer. In many forms of the genus *Ambystoma* there is a very definite diastema between the palatine and the prevomerine teeth; occasionally the palatine teeth are completely lacking, and in some forms of the subgenus *Linguaelapsus* the palatine itself is greatly reduced or lacking.

In hynobiids the prevomerine teeth of each side are usually in a curved series, convex anteriorly, so that the teeth of the two sides form a somewhat M-shaped pattern. In most ambystomatids the medial end of the tooth row on each side is usually located at least as far anteriorly as the portion lateral to it, so that the pattern is transverse, A-shaped, or W-shaped. In *Dicamptodon* and *Rhyacotriton* there is a tendency, not strongly marked, towards the M-shaped pattern of the hynobiids. In adults of most ambystomatids the prevomerine teeth are situated along the extreme posterior edge of that element; in *Dicamptodon*, *Rhyacotriton*, the *tigrinum* group, and *A. mabeei* there is a small postdentigerous process extending a short distance onto the ventral surface of the parasphenoid.

The anterior, medial, and posteromedial borders of the choanae are formed by the prevomers, with the palatine forming most of the posterior border. In hynobiids and the presumably more primitive ambystomatids there is no bony lateral border. In some groups of the genus

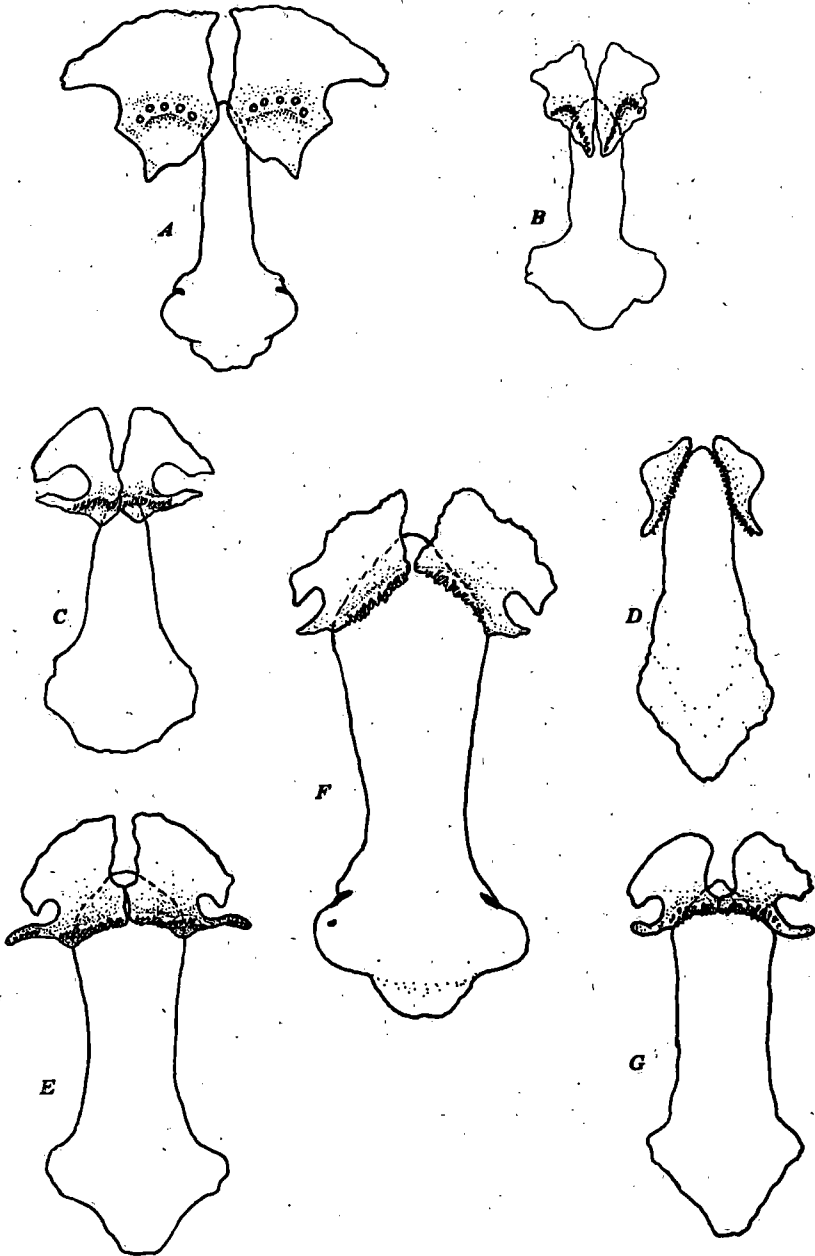


Figure 4.—Prevomers and parasphenoids of various ambystomatids and hynobiids. (A) *Batrachuperus pinchoni*. (B) *Hynobius leechi*. (C) *Rhyacotriton olympicus*. (D) *Rhyacosiredon altamirani*. (E) *Ambystoma mabeei*. (F) *Ambystoma annulatum*. (G) *Ambystoma cingulatum*.

*Ambystoma* there is a projection of the posterolateral corner of the prevomer, forming a partial lateral border for the choana; in some forms the bony border is nearly complete.

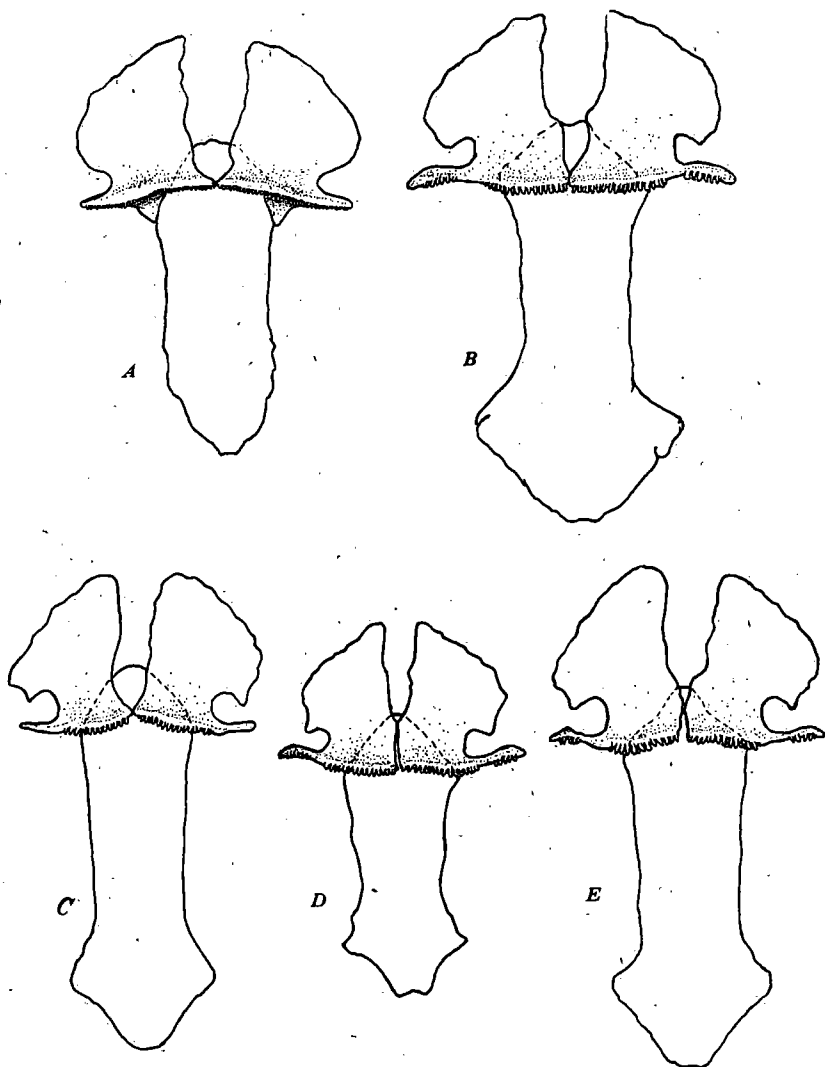


Figure 5.—Prevomers and parasphenoids in members of the subgenus *Ambystoma*. (A) *Ambystoma tigrinum*. (B) *Ambystoma opacum*. (C) *Ambystoma macrodactylum*. (D) *Ambystoma maculatum*. (E) *Ambystoma jeffersonianum*.

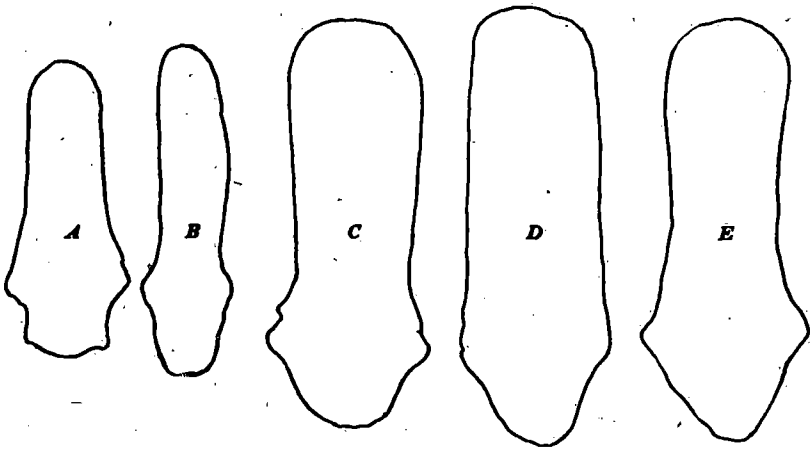


Figure 6.—Examples of variation in the form of the parasphenoid in certain groups. (A) *Rhyacosiredon altamirani* (compare with fig. 4D). (B) *Ambystoma amblycephalum* (larval). (C) *Ambystoma lermaensis*. (This represents as extreme a departure from the more typical *tigrinum* form as will normally be encountered in specimens from either the *tigrinum* or *mexicanum* groups. Variation is intra-specific; the figured specimen is not typical of the species *lermaensis*.) (D) *Ambystoma kansense*, showing clear affinity with the *mexicanum-tigrinum* complex. (E) *Ambystoma kansense*. Example of variation.

#### Parasphenoid

In hynobiids the parasphenoid is a relatively straight-sided element, with the part underlying the otic region markedly expanded (figs. 4, 5, and 6). The parasphenoid of *Dicamptodon* is virtually identical with these; that of *Rhyacotriton* is markedly expanded under the otic region, but the sides diverge more or less regularly from the anterior end posteriorly, and the expansion underlying the otic region is less marked.

In *Ambystoma* the amount of expansion of the posterior part of the parasphenoid varies but is, in general, decidedly less marked than in the hynobiids, *Dicamptodon*, and *Rhyacotriton*. In most forms the sides of the parasphenoid anterior to the expanded posterior portion are distinctly concave. In the *tigrinum* and *mexicanum* groups there is a good deal of individual variation, but typically the posterior portion is only slightly or not at all expanded, and the sides of the element are nearly parallel rather than concave.

As has been mentioned, the characteristic form of the parasphenoid can be discerned relatively early in larval development; there is little ontogenetic variation.

### Hyobranchium

The hyobranchium is consistently cartilaginous in larvae; in adults (and mature neotenic larvae) the os triangulare is consistently ossified. This is the only ossified portion of the hyobranchium in most members of the family, excepting for occasional small, scattered and isolated centers of ossification in one or more of the other elements. In the Hynobiidae, in *Dicamptodon*, and in *Rhyacosiredon* virtually the entire hyobranchium is ossified. The fact that it is ossified in hynobiids, supported by the fact of its ossification in *Dicamptodon*, leads to the conclusion that, insofar as the Ambystomatidae are concerned, the bony hyobranchium is a more primitive type than the cartilaginous.

There is considerable infraspecific variation in the form of the os triangulare. There is a tendency for this element to be equally triradiate, or to have the anterior-posterior branch elongated, in the *tigrinum* and *mexicanum* groups and *Rhyacosiredon*. In the other forms the three arms are frequently equal, but departures from this form are in the direction of a shortening of the anterior arm, and a more transverse orientation of the two posterior arms.

The majority of specimens I have examined have been dried skeletons, with the cartilaginous hyobranchium missing or, at best, shrunken and distorted. Various accounts in the literature do not seem to be in complete agreement as regards details, but there appears to be rather general agreement as to the presence of an annulus, or ring-shaped otoglossal, in certain forms. This was the primary basis of Cope's (1887) attempt to define the ambystomatid genera. He there retained in the genus *Ambystoma*, defined in part as having an annular otoglossal (in adults—no larvae possess an annular otoglossal), the species *maculatum*, *talpoideum*, *opacum*, *tigrinum*, and *macroductylum*. There is fairly general agreement that this element is typically present in forms that I have referred to the genus *Ambystoma*—excepting, of course, those forms that are always neotenic and, possibly, *A. gracile*. An annular otoglossal also occurs in *Rhyacotriton*, according to both the original definition given by Dunn (1920) and the figure provided by Hilton (1946).

The two genera *Chondrotus* and *Linguaelapsus* differed, according to Cope, in details of hyobranchial structure, but at least were in agreement in respect to the absence of an annular otoglossal. Since he placed "*lepturus*" (= *cingulatum*) in the latter genus and the unquestionably very closely related "*microstomum*" (= *texanum*) in the former, it is clear that the other features involved in his definition must be of minor significance. In these two genera were included, beside the above two forms, *ensatus*, *annulatum*, and suprisingly.

*gracile*. The absence of an annular otoglossal in *ensatus* (i.e., *Dicamptodon*) has been supported by a number of subsequent observations. I know of no other recorded observations on the condition in *annulatum*, *cingulatum*, or *texanum*, but my own observations of the absence of an annulus in *mabeei* lends support to the conclusion that this is indeed a characteristic feature of the subgenus *Linguaelapsus*. I am inclined to question Cope's observation concerning *A. gracile* until it is confirmed.

In neotenic members of the *mexicanum* and *tigrinum* groups the hyobranchium is of typically larval form, and so lacks an annulus. Such an element is present in adult *tigrinum*, and would presumably be present in adults of forms at present known only as neotenics. According to Hilton (1946) there is no annulus in *Rhyacosiredon*. This could conceivably be the result of partial neoteny, but the hyobranchium is otherwise of typical adult form. The osseous condition of the hyobranchium in that genus definitely represents a primitive, rather than a neotenic, condition; this is probably also true of the absence of an annulus.

#### Vertebrae

The vertebral column consists of a single cervical vertebra, or atlas, a varying number of trunk vertebrae (this number being constant for a given species within narrow limits of variation), a single sacral vertebra, and a varying number of caudal vertebrae (this number being quite variable even intraspecifically). The number of trunk vertebrae is very closely correlated with costal groove count (Hilton, 1957). Since the latter is a readily determinable external feature, the costal groove count (provided the method of counting is standardized) is a more utilizable characteristic than the direct vertebral count. Because of different methods employed in making the costal groove count, however, the literature records cannot always be taken as directly comparable with each other.

Allowing for this factor, it is still possible to determine costal groove numbers very closely in the various species and to compare them throughout the family. Variation in the number of costal grooves is relatively slight. Twelve seems to be a fairly typical number, with nearly all forms having, most frequently, between 11 and 13. Exceptions include *A. talpoideum* which may have as few as 10, *Rhyacotriton* with 14, and members of the subgenus *Linguaelapsus* in which the number varies from 13 to 15. Occasional individuals of the *tigrinum* group may have as many as 14, but this number is not typical for any species.

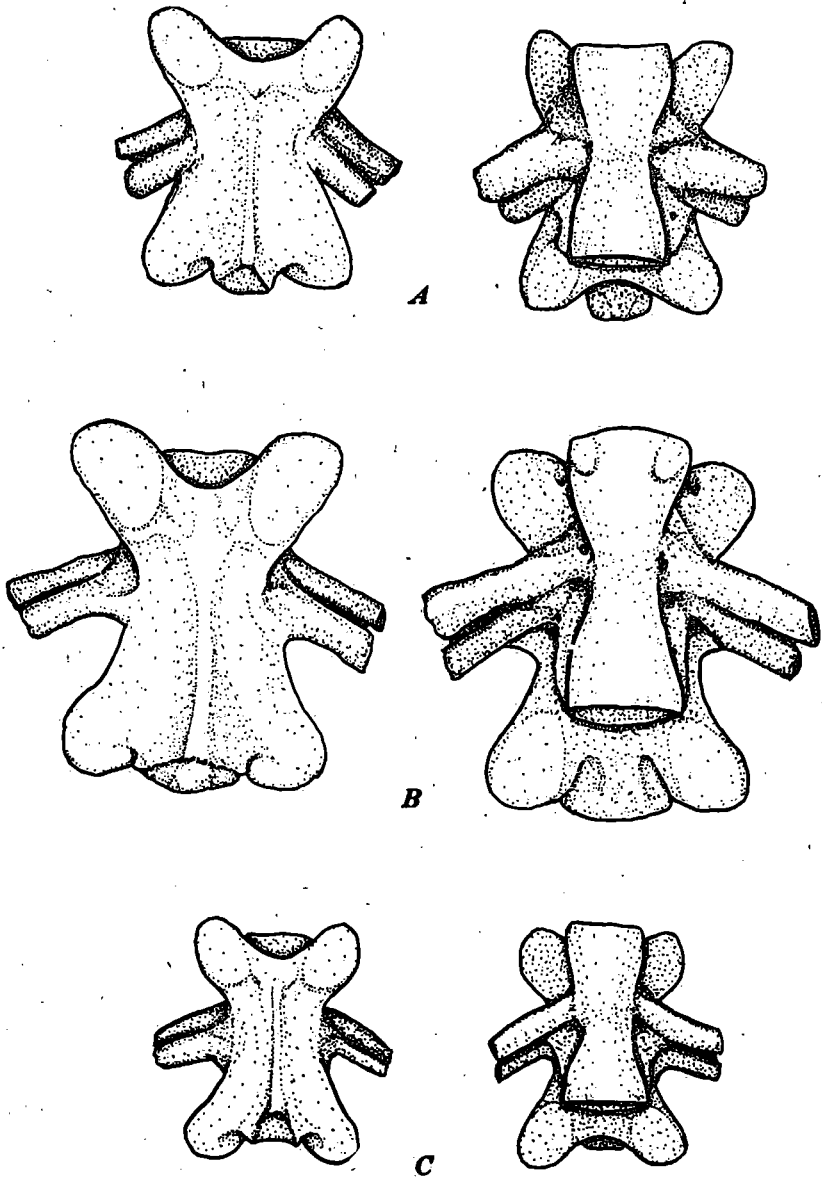


Figure 7.—Dorsal and ventral views of vertebrae of various ambystomatids. (A) *Rhyacostiredon altamirani*. (B) *Ambystoma tigrinum*, as typical of all members of the *tigrinum* and *mexicanum* groups. (C) *Ambystoma opacum*. Note that general proportions are similar to the above.

There is little variation in basic structure of the trunk vertebrae from different portions of the column within a given species, but there is usually a decided positional difference in proportions. The vertebrae of the anterior portion of the trunk are relatively high, broad, and short, becoming progressively lower, narrower, and relatively longer in the posterior portion of the trunk. In *Rhyacotriton* the proportions are essentially similar throughout the entire series (Stokely and Holle, 1953).

Certain phylogenetic trends in vertebral proportions can be noted, but because of the linear variation just mentioned, along with individual intraspecific variation, a much larger number of specimens than have been available to me must be examined before any accurate statistical comparisons can be made. Some of the more marked trends are fairly obvious, though the extent of overlapping variation is not accurately determined. The vertebrae of *Rhyacosiredon*, *Rhyacotriton*, and the *mexicanum* and *tigrinum* groups of *Ambystoma* are similar in proportions. Using this as a comparative basis, those of the other members of the family are elongated to a greater or lesser extent, the elongation being most marked in the *maculatum* group of *Ambystoma* (figs. 7 and 8). A number of comparative ratios might be given, but two will be probably the most useful. One is a comparison of the length of the centrum with its width at the anterior end; figures are presented in table 1. The range of variation could probably be lessened if only one specific vertebra of each specimen were used, but also, so would the usefulness of the character. In general, I have used vertebrae only from the middle part of the trunk, excluding only the anteriormost three or four and a similar number posteriorly. In respect to this particular ratio, it would appear from the figures in the table that the vertebrae of *cingulatum* and *texanum* are relatively short and wide; other vertebral measurements make it clear that this results from a tendency towards flaring of the ends of the centrum rather than a broadening of the vertebra as a whole.

The other ratio used is that of combined zygapophyseal width as compared with the zygapophyseal length. The term "combined zygapophyseal width" is used to denote the distance between the lateral borders of the prezygapophyses plus the distance between the lateral borders of the postzygapophyses. "Zygapophyseal length" is the longitudinal distance between the anterior tips of the prezygapophyses and the posterior tips of the postzygapophyses. In general, the proportions as reflected by this ratio correspond, from one group to another, with those reflected by the central measurement; the

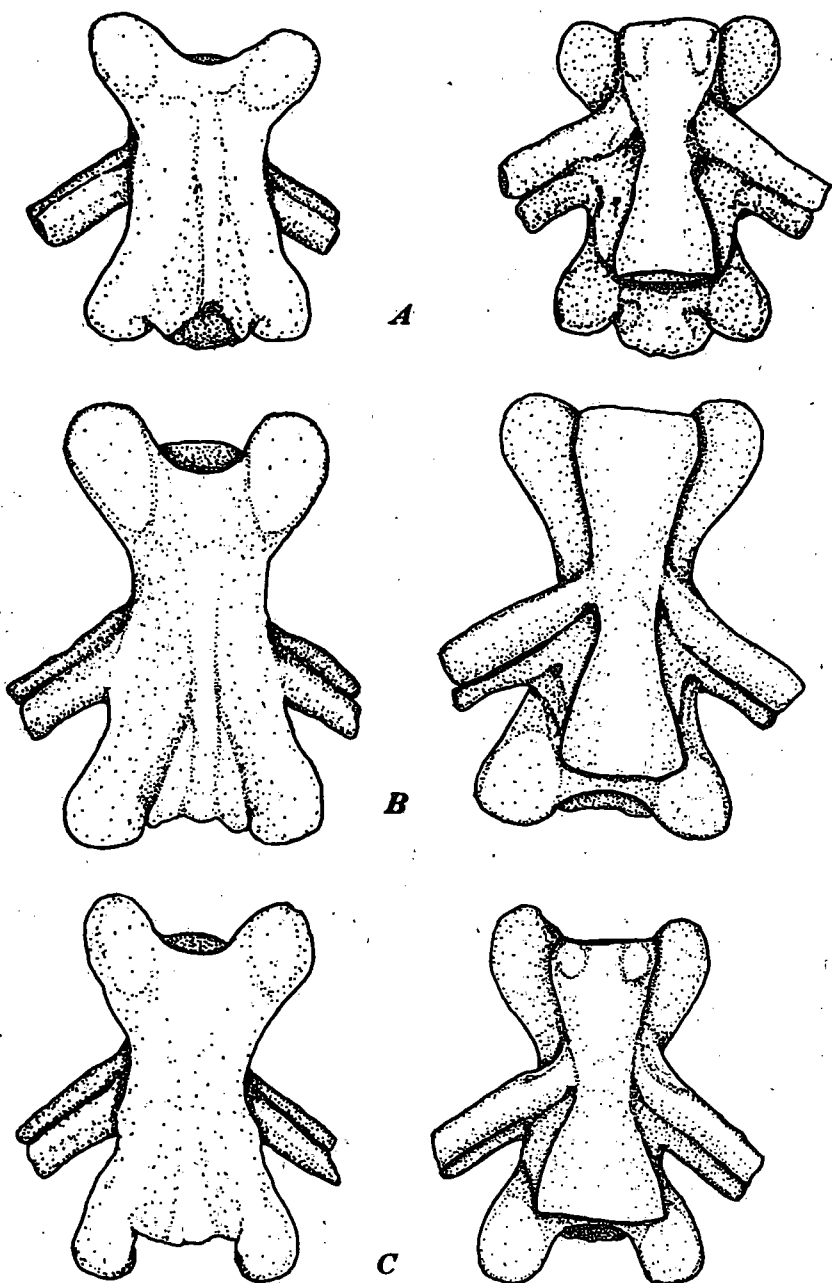


Figure 8.—Dorsal and ventral views of vertebrae of various ambystomatids. (A) *Ambystoma gracile*. (B) *Ambystoma maculatum*. (C) *Ambystoma texanum*.

elongation of the vertebrae of *texanum* and *cingulatum* is clearly shown.

TABLE 1

VERTEBRAL RATIOS IN VARIOUS GROUPS OF AMBYSTOMATIDS

Forms	Length of centrum	Combined zygapophyseal width
	Width of centrum at anterior end	Zygapophyseal length
<i>Rhyacosiredon</i>	2.0 - 2.2	1.4 - 1.7
<i>Dicamptodon</i>	2.2 - 2.5	1.4 - 1.6
<i>A. mexicanum</i> group	1.9 - 2.2	1.3 - 1.6
<i>A. tigrinum</i> group	1.8 - 2.3	1.3 - 1.7
<i>A. opacum</i> group	2.0 - 2.6	1.3 - 1.5
<i>A. maculatum</i> group	2.2 - 2.9	1.1 - 1.4
<i>A. mabeei</i> and <i>annulatum</i>	2.3 - 2.7	1.0 - 1.3
<i>A. texanum</i> and <i>cingulatum</i>	1.9 - 2.3	1.0 - 1.3

In most forms the posterior end of the neural arch projects definitely posterior to the level of the posterior border of the postzygapophyses. In the *maculatum* group and the subgenus *Linguaelapsus*, at least in the posterior portion of the trunk, the postzygapophyses extend at least as far, usually definitely farther, posteriorly than does the neural arch. An exception is found occasionally in *A. gracile*; in general, the vertebrae of that species seem to approach those of the *tigrinum* group more closely than do those of any of the other species in the *maculatum* group.

In normal (i.e., not neotenic) larvae, and frequently in recently metamorphosed adults, the notochord is continuous. In mature adults and mature neotenic larvae a septum develops at the middle of each centrum, interrupting the notochord. From my observations this feature, depending as it apparently does on the age or state of maturity of the animal rather than on metamorphic condition, is a fairly reliable gauge of the maturity or immaturity of the individual. The single specimen of *Bathysiredon* that I have seen possesses a continuous notochord, and it is a large specimen, almost certainly sexually mature. All of the specimens of the *mexicanum* group that I have seen that are noted to be mature have the notochord interrupted, but two specimens of about the same size, with no notation as to whether or not they were mature, have a continuous notochord.

The vertebrae of ambystomatids are, in general form, very similar to those of the hynobiids, except that in the latter family the articular facet of the transverse process is often not sharply divided into dorsal

and ventral portions; the ribs are, correspondingly, unicipital. This is not a diagnostic family characteristic; some hynobiids have transverse processes with the dorsal and ventral articular facets completely separated, indistinguishable from those of ambystomatids. I have seen neither a sufficient number of specimens nor forms of the hynobiids to determine whether the variation in this respect is at an infraspecific, specific, or supraspecific level.

#### SYSTEMATIC ARRANGEMENT

##### Suborder AMBYSTOMATOIDEA new emendation

Ambystomoidea Noble, 1931, *The biology of the amphibia*, p. 471.

**DEFINITION.**—Salamanders having the angular fused with the prearticular; second epibranchial lost; premaxillary spines elongated; prevomers without extensive processes extending over the parasphenoid region; vertebrae amphicoelous; skull without a frontosquamosal arch; fertilization internal.

**DISCUSSION.**—This group is to some extent morphologically intermediate between the more primitive Cryptobranchoidea and the more specialized Salamandroidea. It appears to have been derived from one section of the former but is in no sense ancestral to the latter, which is believed to have arisen entirely independently from a different cryptobranchoid stock. The fusion of the angular and prearticular, the loss of the second epibranchial, the elongation and approach of the premaxillary spines, and internal fertilization are features shared with at least some salamandroids. The short prevomers, without extensive posterior processes, the amphicoelous vertebrae, and the lack of a frontosquamosal arch are among the features distinguishing this group from various members of the Salamandroidea.

##### Family AMBYSTOMATIDAE Hallowell

Ambystomidae Hallowell, 1856, *Proc. Acad. Nat. Sci. Phila.*, vol. 8, p. 11.

**DEFINITION.**—Essential family characteristics the same as those of the suborder.

**DISCUSSION.**—In the past, this family has been most frequently associated with the Hynobiidae and is almost certainly derived from a hynobiid stock that presumably migrated from Asia to North America via the Bering land bridge very early in the Tertiary, possibly even in the late Mesozoic. It is true that there is no direct fossil record of the family prior to the middle Pliocene, but trackways from the Paleocene of Montana have been referred to this family (Peabody, 1954). The absence of specimens from intervening geologic stages is not sur-

prising, even if we assume that the family was widespread and relatively abundant throughout most of the Tertiary. Wherever techniques for collecting microvertebrate fossils have been intensively applied to Pliocene and Pleistocene deposits, and to many earlier ones, urodele remains have been recovered. It is to be expected in the near future, as these techniques are developed and more extensively applied to older deposits, a much better fossil record of this and other salamander families will be obtained.

Several features not mentioned in the definition of the suborder also serve to distinguish the Ambystomatidae from the Hynobiidae. The universally bicipital ribs of ambystomatids, as compared with the most frequently unicipital ribs of the hynobiids, have already been mentioned. The pterygoid and quadrate are fused with each other in all specimens I have seen of the Hynobiidae (cf. also Villiers, 1936), never in the Ambystomatidae. According to Dunn (1923) the Hynobiidae possess an additional small carpal and tarsal element, possibly representing the vestiges of a prehallux and prepollex, not present in the Ambystomatidae. A number of minor differences can be observed, many of which may not be absolutely consistent.

All of the members of the suborder Ambystomatoidea are included within this one family. Differences within the family, although involving only a limited number of species, are so extensive that I believe recognition of three separate subfamilies to be desirable. Recognition of three separate subfamilies to accommodate only five separate genera may appear to be rather drastic procedure. Yet the great number of differences involved, and the magnitude of some of these differences can, in my opinion, only be interpreted by assuming a differentiation into three distinct lines early in the phylogenetic history of the family.

#### Subfamily DICAMPTODONTINAE new subfamily

**DEFINITION.**—Ambystomatids having an independent lacrimal bone; exoccipital and prootic independent; columella independent; skull exceptionally solid (see discussion for details); individual teeth compressed, having somewhat the shape of a curved, double-edged blade; nasal bones present; premaxillary spines short and broad, embracing no, or at most a small, fontanelle; a decided linear variation in the proportions of the trunk vertebrae; lungs, eyes, and ypsiloid cartilage normal.

**DISCUSSION.**—It has long been recognized that *Dicamptodon* shares with *Rhyacotriton* several primitive features not occurring elsewhere in

the family. Most significant of these are, in my opinion, the failure of the prootic and exoccipital to fuse into a single periotic bone on each side, the presence of an independent lacrimal, and a fairly close resemblance of the parasphenoid to that of hynobiids. There are also other points of resemblance. Although the prevomerine tooth pattern is greatly different, each shows a tendency towards an M-shaped pattern, rather than the A-shaped to W-shaped one of other members of the family. In both, the characteristic number of phalanges in the fourth toe is three, as compared with four in nearly all other forms. Both usually lack an enclosed procoracoid foramen in the pectoral girdle (Stokely and Holle, 1954). In the larvae of both, the dorsal fin is limited to the tail, not extending up onto the trunk.

Despite these many resemblances each form, particularly *Rhyacotriton*, has so many unique characteristics that the two are no more similar to each other than to the remainder of the family. All of these resemblances represent apparently primitive features; none of the specialized characteristics of either form are found in the other. The points of similarity do not, then, denote any close relationship between the two, but simply indicate that the lines leading to these two forms were derived from the ancestral proto-Ambystomatidae at an early stage, prior to the development of the specializations characterizing the remainder of the family.

The most distinctive feature of the skeleton of *Dicamptodon* is the solidity and rigidity of the skull. In the evolution of salamanders the tendency has been, generally, towards a less rigid skull. Whether the condition in *Dicamptodon* represents the retention of a primitive condition, or represents a secondary development from a type of structure more nearly typical of other ambystomatids, is not certain. I am inclined to the opinion that it is a secondary development, possibly associated with habits or habitat, since a similar solidity is not encountered in any other known ambystomatid or hynobiid.

Among the features contributing most strongly to this solidity, particularly of the palatal region, are the firm, relatively extensive sutural connections of the prevomers with the premaxillae and the maxillae. This involves the presence of a distinct palatal shelf on the premaxilla, not found in other forms, and of a more extensive palatal portion of the maxilla than is customary in other forms. Also, the pterygoid is heavy and extensive. In all individuals I have seen this element actually abuts against the posterior end of the maxilla; some figures of the *Dicamptodon* skull (e.g., Hilton, 1946) indicate only that the pterygoid approaches the maxilla very closely, without actually being in contact with it, so there may be some variation in this respect. All

of the bones of the skull are relatively heavy, with firm and solid sutures.

The shape of the individual teeth is a unique and undoubtedly specialized feature. *Dicamptodon* seems to be an exceptionally voracious salamander (cf. Graf, 1949), and it is possible that the tooth shape is to some extent correlated with its feeding habits. The extensive parieto-squamosal crests indicate a strongly developed jaw musculature, also perhaps associable with feeding habits.

The hyobranchium is largely ossified, as in the Hynobiidae, and the otoglossal cartilage is not annular. The carpus and tarsus are cartilaginous in larvae, ossified in adults; there are eight carpal elements.

### Genus *Dicamptodon* Strauch

*Dicamptodon* Strauch, 1870, Mém. Acad. Sci. St. Pétersbourg, sér. 7, 16 (4) : 68.

Type species *ensatus* Eschscholtz, 1833, by monotypy.

*Chondrotus* Cope, 1887, Amer. Nat., 21 : 88. Type species *tenebrosus* Baird and Girard, 1852 = *ensatus* Eschscholtz, 1833.

DEFINITION.—Essential generic characteristics the same as those of the subfamily (fig. 9).

RANGE.—The Pacific coast, from southwestern British Columbia to Santa Cruz County, California; also known from northern Idaho. Trackways referred to this form are known from the lower Pliocene of California (Peabody, 1954).

DISCUSSION.—This genus is generally considered, correctly, I believe, to be the most primitive existing representative of the family. The numerous primitive features shared with *Rhyacotriton* have already been mentioned. With the exception of the shape of the teeth and probably the rigidity of the skull, most of the points of difference between the two forms represent specializations in *Rhyacotriton*, with *Dicamptodon* retaining a primitive condition frequently shared with other members of the family.

REFERRED FORMS.—*Dicamptodon ensatus* (Eschscholtz), 1833, Zool. Atlas pt. 5 : 6, pl. 22.

### Genus *Ambystomichnus* Peabody

*Ambystomichnus* Peabody, 1954, Jour. Paleont., 28 (1) : 80. Type species *montaniensis* Gilmore, 1928.

DEFINITION.—Known only from trackways. I quote from the diagnosis given by Peabody: "... Comparable in body form with ... *Dicamptodon*, ... but twice as large and slightly longer in the

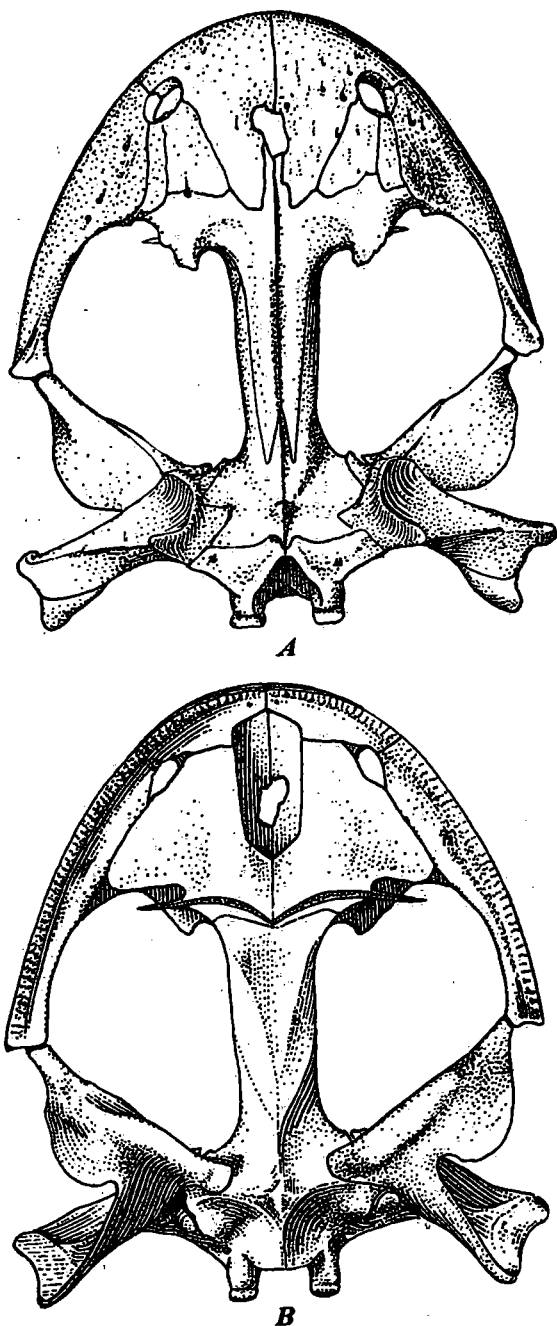


Figure 9.—Skull of *Dicamptodon ensatus*. (A) Dorsal aspect. (B) Ventral aspect.

trunk region. Details of the footprints agree closely with footprints of living and Pliocene ambystomids, and the bilobate palm of the manus is exactly as in living *Dicamptodon ensatus*. Stride 18 cm. maximum; pace angulation . . . 77 degrees maximum; manus 3.1 cm. wide, pes 3.7 cm. wide overall; both relatively distant from midline."

RANGE.—Known only from the Paleocene of Bear Butte, Sweetgrass County, Montana.

DISCUSSION.—Since this form is known only from trackways, reference to any subfamily must be tentative. Peabody's discussion places emphasis on the bilobate palm of *Ambystomichnus* and *Dicamptodon*, and also mentions certain other items indicating an affinity between these two genera. Geographic and temporal considerations at least do not discredit such an association.

REFERRED FORMS.—*Ambystomichnus montanensis* (Gilmore), 1928, Proc. U.S. Natl. Mus., 74 (5) : 1.

#### Subfamily RHYACOTRITONINAE new subfamily

DEFINITION.—Ambystomatids with an independent lacrimal bone; prootic and exoccipital independent; columella independent; skull not exceptionally rigid; individual teeth conical; nasal bones lacking; premaxillary spines long and narrow, embracing a fontanelle; only slight linear variation in the proportions of the trunk vertebrae; eyes large, protuberant; lungs and ypsiloid cartilage much reduced.

DISCUSSION.—The primitive features shared by this subfamily and the Dicamptodontinae have already been described. Despite these similarities, *Rhyacotriton* is so distinct, not only from *Dicamptodon*, but from all other members of the family, that recognition of a separate subfamily seems essential.

*Rhyacotriton* is unique in the absence of a nasal bone; to judge from appearances this element is actually lacking, not simply fused with one of the adjacent bones. This may be the result of a partial neoteny, since the nasal is one of the last bones to ossify during larval development, but the element is present in neotenic larvae of other members of the family. The extreme length of the premaxillary spines (=nasal processes) is approached only by some members of the subgenus *Linguaelapsus*, in which the form of this bone is otherwise quite different, and which completely lack a fontanelle. The contrast with the short, broad nasal process of the *Dicamptodon* premaxilla is especially marked. The pterygoid is greatly reduced, and is less extensive than in any other member of the family; again this is in particularly strong contrast to the condition in *Dicamptodon*. The skull as a whole

is less rigid, and with perhaps relatively less bone, than in other members of the family; again, the most extreme contrast is with *Dicamptodon*. The abortive development of the lungs is unique among the Ambystomatidae; as in most other lungless salamanders, the ypsiloid cartilage is correspondingly reduced.

The small size, body proportions, protuberant eyes, and coloration all contribute to a strikingly distinctive external general appearance. It is the only member of the family in which the carpus and tarsus remain cartilaginous in adults, and in which the number of carpal elements is reduced to six (Hilton, 1948). It is distinctive in the almost complete lack of linear differentiation in the trunk vertebrae. In this genus alone of the ambystomatids the musculus levator scapulae is incompletely differentiated anteriorly from the m. dorsalis trunci in the adult, though such a condition is found in the larvae of all forms (Dunn, 1941). *Rhyacotriton* is also unique in breeding habits; the eggs are large, laid singly, and the total complement averages only about 10 or 12 eggs (Noble and Richards, 1932; Stebbins and Lowe, 1951).

In addition to these unique features, the Rhyacotritoninae differ from the Dicamptodontinae in several respects in which they resemble at least some of the Ambystomatinae. These include the conical shape of the teeth, which may be slightly hooked at the tip, the loss of the palatine teeth, the cartilaginous condition of the adult hyobranchium, the presence of an annular otoglossal cartilage, the presence of a premaxillary fontanelle, and numerous details of form and proportion.

A number of the features of this group might be interpretable as the result of a partial neoteny, though such an interpretation might

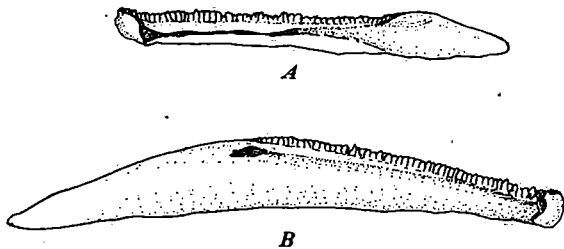


Figure 10.—Dentaries of typical ambystomatids. (A) *Ambystoma gracile*. This sort of dentary, with a prominent flange of bone on the lingual surface, is typical of all forms of the subgenus *Ambystoma*, and is also found in *A. mabeei*. (B) *Ambystoma mexicanum*, neotenic larva. This general type of dentary, lacking the flange on the lingual surface, is characteristic of the larvae of all ambystomatids, and resembles that of adults of *Dicamptodon*, *Rhyacotriton*, *Rhyacosiren*, and most members of the subgenus *Linguaelapsus*.

well be questioned in most of the instances. These features would include the presence of the premaxillary fontanelle, the relatively unspecialized teeth, the absence of the nasals, the cartilaginous condition of the carpus and tarsus, the independent columella, and minor details in the form of certain other elements, such as the dentary (fig. 10). In any event, whether or not ascribable to partial neoteny, the conditions in *Rhyacotriton* differ in detail from those found in any other member of the family, larval or adult. It is interesting to note that these features occur in a form that is largely aquatic, and is, in this aquatic environment, subject to relatively low temperatures. It is active at temperatures of from 5° to 10° C.

### Genus *Rhyacotriton* Dunn

*Rhyacotriton* Dunn, 1920, Proc. New Engl. Zool. Club, 7: 56. Type species *olympicus* Gaige, 1917.

**DEFINITION.**—Essential generic characteristics the same as those of the subfamily.

**RANGE.**—Pacific coastal region from the Olympic Mountains south to southern Humboldt County, California. No fossil record.

**DISCUSSION.**—As indicated above, this genus is the most distinctive member of the family. The primitive features shared with *Dicamptodon* indicate an early origin, but the subsequent modification has been extensive. It cannot be considered a derivative of *Dicamptodon*, as has sometimes been suggested.

Eaton (1933) has described a condition which he interpreted as a sort of streptostyly in this genus and in the Pacific forms of *Ambystoma*, and has postulated a derivation from *A. macrodactylum* or an extinct related form on that basis (1934). The existence of such a condition has been strongly questioned by Villiers (1938a, 1938b) and others. There is no other evidence for such a derivation of the genus, and a great deal of evidence that no close relationship exists between *Rhyacotriton* and the genus *Ambystoma*. I am of the opinion that the Rhyacotritoninae were derived from an early stock, the line leading to *Rhyacotriton* becoming established prior to the appearance of the genus *Ambystoma* as such.

### REFERRED FORMS.—

*Rhyacotriton olympicus olympicus* (Gaige), 1917, Occ. Pap. Univ. Mich. Mus. Zool., no. 40: 2, pl. 1.

*Rhyacotriton olympicus variegatus* Stebbins and Lowe, 1951, Univ. Calif. Publ. Zool., 50: 471.

## Subfamily AMBYSTOMATINAE Hallowell

DEFINITION.—Ambystomatids lacking an independent lacrimal bone; prootic and exoccipital fused into a single periotic bone, with which the columella is also usually fused in adults; skull not exceptionally solid; individual teeth essentially conical, though the tips may be modified in various ways; nasal bones present; premaxillary spines varying in proportions, embracing no appreciable fontanelle in metamorphosed adults (excepting in *Rhyacosiredon*); a linear variation in proportions of trunk vertebrae; lungs, eyes, and ypsiloid cartilage normally developed.

DISCUSSION.—Major specializations of this subfamily include the loss of the independent lacrimal and the fusion of the exoccipital with the prootic. In most forms the columella is also fused with the resulting periotic. The prefrontal of the Ambystomatinae has almost exactly the form and relationships of the prefrontal plus the lacrimal of the other subfamilies, and may well represent a fusion of these two elements. However, no trace of an independent lacrimal is observable macroscopically even in very young larvae. Fusion of the exoccipital and prootic occurs very early in ontogeny—as soon as these bones really begin to take form—but fusion of the columella with the periotic does not occur until metamorphosis; it remains independent in neotenic individuals, and occasionally also in metamorphosed adults of some species.

The parasphenoid is always clearly distinguishable from that in either of the other subfamilies, though it has been modified somewhat differently in the different groups of Ambystomatinae. Variation in this element will be discussed more fully in connection with these groups.

The prevomers are usually completely free of the premaxillae, and narrowly or not at all in contact with the maxillae; there is never a solid sutural connection with either of these elements. Similarly, although the pterygoid may in some species approach the maxilla closely, it never abuts against that bone as it appears to do in *Dicamptodon*. The cranial sutures generally are moderately firm; the skull lacks the extreme solidity of the *Dicamptodon* skull, though it is typically more solid than in *Rhyacotriton*.

The premaxillary spines are well separated and embrace a large fontanelle in all larvae including mature neotenic individuals, but in adults of all forms excepting *Rhyacosiredon* the spines are closely approximated in the midline and the fontanelle is virtually or completely obliterated. In general, the spines are of moderate proportions, with

only minor variation between species except in some members of the subgenus *Linguaelapsus*. The premaxillae do not possess a true palatal shelf, such as is found in *Dicamptodon*.

The hyobranchium is variable within the subfamily, both as to extent of ossification and details of morphology. The carpus and tarsus are cartilaginous in larvae, including neotenic larvae, and ossified in metamorphosed adults. There are eight carpal elements.

### Genus *Rhyacosiredon* Dunn

*Rhyacosiredon* Dunn, 1928, Proc. New Engl. Zool. Club, 10 : 85. Type species *altamirani* Dugès, 1895.

DEFINITION.—Ambystomatinae in which the metamorphosed adults retain the prevomerine teeth in approximately the larval position and retain a large premaxillary fontanelle; maxillae much reduced in extent; hyobranchium extensively ossified; tooth tips not strongly bifid, but pointed, often recurved; parasphenoid typically diverging from anterior end to posterior expanded portion; four phalanges in fourth toe; metamorphosis customary, but neoteny may occur.

RANGE.—The high mountains at the southern edge of the main Mexican plateau.

DISCUSSION.—Several of the characteristics of this genus probably represent a partial neoteny. The position of the prevomerine teeth is almost certainly such a feature, as is probably the persistence of a premaxillary fontanelle, and possibly the limited extent of the maxillae and the relatively simple form of the individual teeth. At the time the genus was proposed, Dunn suggested that it was derived from, or at least had affinities with, the *tigrinum* group of *Ambystoma*, with the implication that partial neoteny was an important factor in producing the generic differentiation. This view has been generally assumed to be correct.

Partial neoteny has probably played a part in the development of the genus, but there is considerable evidence that it is derived from a primitive ambystomatine stock entirely independently of the derivation of the *tigrinum* group. The ossified condition of the hyobranchium in *Rhyacosiredon* is considered primitive; elsewhere in the family it occurs only in *Dicamptodon*; it certainly cannot be interpreted as retention of a larval condition. The shape of the parasphenoid is unique, and quite dissimilar from the rather specialized parasphenoid of the *tigrinum* group. The pointed teeth might conceivably be a neotenic feature, but in the *A. mexicanum-tigrinum-Bathysiredon* complex the

tooth tips of all mature neotenic larvae are strongly bifid and often expanded, exactly as those of adults; it is more likely, then, that the pointed, scarcely bifid teeth of *Rhyacosiredon* are primitive rather than neotenic. The reduced extent of the maxilla is somewhat comparable with that of small larvae of *tigrinum*, but not with that of larvae approaching metamorphosis nor with that of mature neotenic larvae.

The position of the prevomerine teeth is a neotenic feature. The prevomer itself is, however, more extensive than the typical larval prevomer, and the teeth are reduced to a single row. In these respects, the *Rhyacosiredon* prevomer resembles a metamorphic stage in *Ambystoma* rather than a true larval stage. The pterygoid has lost its connection with the palatine and is of relatively limited extent, decidedly smaller than is typical for the *tigrinum* group. In general form it bears a marked resemblance to the pterygoid of *Batrachuperus* and *Hynobius*, perhaps another indication of a primitive origin for the genus.

The number of mandibular teeth is relatively small. The dentaries bear only a slight ridge on their lingual surface, as is true in the preceding subfamilies and in larval *Ambystoma*, rather than a strong flange of bone completely surrounding Meckel's cartilage such as occurs in most adult *Ambystoma*. The prearticular has only a low, indistinct coronoid process, again resembling *Ambystoma* larvae (and adult hynobiids); adult *Ambystoma* have a rather high, distinct coronoid process. Many of these features could be the result of partial neoteny; most might equally well or better represent retention of an ancestral condition.

The trunk vertebrae are short and broad, with proportions similar to those of the *tigrinum* group, but probably even slightly shorter than in that group. In both this genus and *Ambystoma* there are occasional vertebrae with a pair of protuberances ventrolaterally at the anterior end of the centrum (accessory basapophyseal processes). These do not appear to be limited to, nor consistently characteristic of, any particular species or group of species, nor any specific portion of the vertebral column. A few specimens have been seen in which these processes were found at the posterior, instead of the anterior, end of the centrum of some of the vertebrae. In brief, the presence, absence, location in the column, extent, and position on the centrum of these processes are all highly variable features throughout the subfamily. This fact, parenthetically, casts some doubt on the validity of the assignment of the fossil genus *Dehmiella* from Europe to the family Plethodontidae on the basis of the position of the basapophyseal processes.

## REFERRED FORMS.—

*Rhyacosiredon altamirani* (Dugès), 1895, Description d'un axolotl des Montagnes de las Cruces (*Amblystoma altamirani*, A. Dugès): 1, pl. 1.

*Rhyacosiredon leorae* Taylor, 1943, Univ. Kan. Sci. Bull., 29 : 345, pl. 26.

*Rhyacosiredon rivularis* Taylor, 1940, Herpetologica, 1 : 171, pl. 17.

*Rhyacosiredon zempoalensis* Taylor and Smith, 1945, Proc. U.S. Natl. Mus., 95 : 527.

Genus *Ambystoma* Tschudi

*Siredon* Wagler, 1830, Naturl. Syst. Amphib.: 209. Type species *axolotl* Cuvier = *mexicanus* Shaw, 1789.

*Ambystoma* Tschudi, 1838, Mém. Soc. Sci. Nat. Neuchâtel, 2 : 92. Type species *subviolacea* Barton = *maculatum* Shaw, 1802.

*Xiphonura* Tschudi, 1838, Mém. Soc. Sci. Nat. Neuchâtel, 2 : 95. Type species *jeffersonianum* Green, 1827.

*Salamandroidis* Fitzinger, 1843, Syst. Rept. : 33. Type species *subviolacea* Barton = *maculatum* Shaw, 1802.

*Axolotl* Owen, 1844, Ann. Mag. Nat. Hist., 14 : 23. Type species *guttata* Owen = *mexicanus* Shaw, 1789.

*Amblystoma* Agassiz, 1846, Nomenclator Zool. Rept., p. 2. Emendation.

*Heterotriton* Gray, 1850, Cat. Batr. Grad. Brit. Mus. : 33. Type species *ingens* Green = *tigrinum* Green, 1825.

*Plagiodon* Duméril, Bibron and Duméril, 1824, Erpét. Gén., 9 : 101. Substitute name for *Ambystoma*.

*Desmlostoma* Sager, 1858, Penin. Jour. Méd., 5 : 428. Type species *maculatum* Shaw, 1802.

*Camarataxis* Cope, 1859, Proc. Acad. Nat. Sci. Phila., 11 : 122. Type species *maculatum* Shaw, 1802.

*Pectoglossa* Mivart, 1867, Proc. Zool. Soc. London, 1867 : 698. Type species *persimilis* Gray = *jeffersonianum* Green, 1827.

*Sirenodon* Desor, 1870, Bull. Soc. Sci. Nat. Neuchâtel, 8 : 269. Type species *lichenoides* Baird = *mavortium* Baird.

*Linguaelapsus* Cope, 1887, Amer. Nat., 21 : 88. Type species *annulatum* Cope, 1886.

*Phioambystoma* Adams and Martin, 1929, Amer. Jour. Sci. (5th ser.), 17 : 504. Type species *kansense* Adams and Martin, 1929.

*Bathysiredon* Dunn, 1939, Not. Nat., no. 36 : 1. Type species *dumerili* Dugès, 1830.

?*Lanebatrachus* Taylor, 1941, Kans. Geol. Surv. Bull., 25 (18) : 180. Type species *martini* Taylor (= *kansense* Adams and Martin, 1929 ?).

?*Ogallalabatrachus* Taylor, 1941, Kans. Geol. Surv. Bull., 25 (18) : 181. Type species *horarium* Taylor (= *kansense* Adams and Martin, 1929 ?).

**DEFINITION.**—Ambystomatinae in which metamorphosed adults have the prevomerine teeth in a typically adult position; premaxillary fontanelle nearly or completely obliterated in adults; maxillae of normal extent; hyobranchium almost entirely cartilaginous; tips of teeth definitely bifid, often very blunt or even expanded, occasionally pointed but very sharply hooked inwards; sides of parasphenoid parallel or concave, not diverging; four phalanges in the fourth toe in most forms; metamorphosis is customary, but neoteny may occur in some species and is apparently obligatory in a few.

**RANGE.**—The range of the genus is virtually coextensive with that of the family.

**DISCUSSION.**—I am fully aware of the violence being done to the law of priority by the use of the name *Ambystoma* for this genus while retaining in it the species *mexicanum*. I can, however, find no morphological basis for separating the genera *Siredon* and *Ambystoma*, and the physiological basis, if any, is certainly extremely tenuous. As Schmidt (1953) has pointed out, the substitution of the earlier name of *Siredon* for *Ambystoma* has long been avoided by American authors as too flagrant a disregard of usage, although most of them are well aware that a generic distinction between the two is more imaginary than real. The only logical solution of the problem appears to be an action by the International Commission on Zoological Nomenclature to invalidate the name *Siredon* and place *Ambystoma* on the list of *nomina conservanda*. On the assumption that such action will at some time be taken, I have chosen for the present to disregard priority in preference to disregarding either usage or the biological evidence.

The genus *Ambystoma* is a widespread and rather variable one, containing the great majority of the known species in the family. Three subgenera and several species groups are discernible within the genus, although the grouping is not always so clearly indicated as might be desired. Comparisons between *Ambystoma* and *Rhyacosiredon* have been discussed in connection with the latter; details of structure and, more particularly, variation within the genus will be discussed under the various subgroupings.

#### Subgenus *Ambystoma* Tschudi

**DEFINITION.**—Members of the genus *Ambystoma* in which the premaxillary spines are not exceptionally long and narrow, and lack a vertical lamina or thickening; tongue with longitudinal plicae, or plicae radiating from a posterior field; teeth of each dentigerous element arranged in a single row in adults; otoglossal cartilage annular

in adults; dentary of adults with a prominent flange of bone on the lingual surface; costal grooves 10 to 13 (rarely 14).

RANGE.—The range of the subgenus is coextensive with that of the genus.

DISCUSSION.—Most of the species are included in this subgenus. There is close general agreement among all the forms in regard to the major osteological features, but variation in details suggest the existence of four species groups. As has been stated, the distinctions between the groups are not always sharp and clear-cut, but certain generalizations can be made and apparent evolutionary tendencies noted. The proper assignment of some of the species to a species group is open to question, particularly in the case of some of the rarer Mexican forms.

#### The *tigrinum* group

DEFINITION.—Members of the subgenus *Ambystoma* with the trunk vertebrae relatively short and broad (see the section on vertebrae); premaxillary spines tend to be rather short and broad; parasphenoid typically straight-sided, or with sides only very slightly concave, and without or with only a slight posterior expansion underlying the otic region; no extensive diastema between prevomerine and palatine teeth; a postdentigerous process on the prevomers; choanae without a lateral bony border; os triangulare tending to be longitudinal; neoteny occasional to common in many, perhaps all, species.

RANGE.—Southeastern British Columbia and the southern half of Alberta to New York, south throughout most of the United States and Mexico to the southern edge of the Mexican plateau, excepting only the Pacific Northwest, Baja California, part of the Florida peninsula, and the Mexican coastal lowlands. Fossil representatives are known from the upper Pliocene of Kansas and from the Pleistocene of various localities in the central and western United States and northern Mexico.

DISCUSSION.—The characterization of this group is based primarily on the species *tigrinum*. Several of the Mexican forms are poorly known, especially with respect to skeletal characteristics. All have been referred tentatively to this group, largely on a geographic basis, but it is possible that some either should not be so referred or that, when they become better known, it will be necessary to modify the definition of the group.

This would appear to be the most primitive group of the genus, and is characterized primarily by the absence of specializations found

in members of the other groups. The form of the parasphenoid is somewhat variable, in some cases even approaching the condition in the *maculatum* and *opacum* groups, but there is a strong tendency towards a reduction, even loss, of the posterior expansion, and a lack of concavity of the sides. The great majority of individuals possess a parasphenoid that can be recognized as the *tigrinum* type without difficulty. This particular feature is considered to be a development that has occurred within the line leading to this group, and is about the only osteological feature in which this group is considered to be more highly modified from an ancestral condition than are the other groups.

The *os triangulare* is frequently about equally triradiate, that is, the three rami are of about equal length. There is a tendency in some forms for an elongation of the anterior ramus, and a reduction of the other two, so that the element becomes  $\Lambda$ -shaped. This is rather variable even intraspecifically, so is probably not a matter of great significance.

The proportions of the premaxillary spines are also subject to some variation, but there is a definite tendency in most forms for these spines to be relatively short and broad, at least as compared with those of the *maculatum* group (cf. figs. 2D, E). In occasional specimens there may be a slight diastema between the prevomerine and palatine teeth; when such a diastema is present it is of limited extent as compared with the wide diastema usually found in other groups. Palatine teeth are always present. As mentioned in the introductory section, the posterolateral corner of the prevomer proper is not produced posteriorly to form a lateral choanal border. This, so far as has been observed, seems to constitute a constant, though minor, distinction between the *tigrinum* group and all others. The retention of a small postdentigerous process on the prevomer also would appear to be a constant characteristic.

The majority of species are relatively large forms, with snout-vent lengths of 90 to 100 mm. being common for adults. In some neotenic larvae the total length exceeds 300 mm., with a snout-vent length of somewhat over half of this total. They are, in general, rather heavy-bodied forms, with well-developed limbs that overlap strongly when adpressed. The tail is typically heavy but fairly long, usually between 40 and 50 percent of the total length. Individual tail length is, even within a species, a highly variable feature, and useful only in a general way. The number of costal grooves is usually 12 or 13, occasionally 11, rarely 14. The color pattern is variable, but yellow and black are the predominating colors in the group.

Neoteny is a common phenomenon in the *tigrinum* group, particularly in those subspecies of *tigrinum* inhabiting the Rocky Mountains and northern Plains region, and some forms of the Mexican plateau. The neotenic populations usually produce individuals of decidedly greater size than those which metamorphose normally. Mature neotenic larvae can be distinguished from normal immature larvae by the development of vertebral septa interrupting the notochord, the development of strongly bifid and blunt or somewhat expanded tooth tips, the larger number of maxillary-premaxillary and mandibular teeth and, frequently, simply by size. If the characteristics of the upper Pliocene *A. hibbardi* have been correctly interpreted, specifically the apparent poor ossification of certain cartilage bones, the diagnostic features may be a result of partial neoteny, though there is good evidence that the species consistently underwent metamorphosis, and was not neotenic in the full sense of the term.

REFERRED FORMS.—As pointed out above, many of the Mexican species are poorly known, and can be only tentatively referred to this group. There is, I believe, special reason to question such a reference for the Chihuahuan *A. fluvinatum*. Although no adult individuals are known, it seems likely that this species differs rather markedly from the typical members of the *tigrinum* group in size, proportions, number of costal grooves, and possibly in number of teeth. It is, however, along with one or two other forms of questionable affinity, referred to the *tigrinum* group for the time being on the basis of geographical probability.

*Ambystoma* (*Ambystoma*) *amblycephalum* Taylor, 1940, Univ. Kans. Sci. Bull., 26 (for 1939) : 420, pl. 45.

*Ambystoma* (*Ambystoma*) *bombypellum* Taylor, 1940, Univ. Kans. Sci. Bull., 26 (for 1939) : 418, pl. 45.

*Ambystoma* (*Ambystoma*) *fluvinatum* Taylor, 1941, Copeia, 1941 (3) : 144.

*Ambystoma* (*Ambystoma*) *granulosum* Taylor, 1944, Univ. Kans. Sci. Bull., 30 : 57, pl. 8.

*Ambystoma* (*Ambystoma*) *hibbardi* Tihen, 1955, Contrib. Mus. Paleont. Univ. Mich., 12 (11) : 230.

*Ambystoma* (*Ambystoma*) *lacustris* Taylor and Smith, 1945, Proc. U.S. Natl. Mus., 95 : 532, pl. 18.

*Ambystoma* (*Ambystoma*) *ordinarium* Taylor, 1940, Univ. Kans. Sci. Bull., 26 (for 1939) : 422, pl. 46.

- Ambystoma* (*Ambystoma*) *rosaceum rosaceum* Taylor, 1941, Copeia, 1941 (3) : 143.
- Ambystoma* (*Ambystoma*) *rosaceum nigrum* Shannon, 1951, Proc. U.S. Natl. Mus., 101 : 466.
- Ambystoma* (*Ambystoma*) *rosaceum sonoraensis* Shannon, 1951, Proc. U.S. Natl. Mus., 101 : 468.
- Ambystoma* (*Ambystoma*) *subsalsum* Taylor, 1943, Copeia, 1943 (3) : 151.
- Ambystoma* (*Ambystoma*) *tigrinum tigrinum* (Green), 1825, Jour. Acad. Nat. Sci. Phila. (ser. 1), 5 : 116.
- Ambystoma* (*Ambystoma*) *tigrinum californiense* (Gray), 1853, Proc. Zool. Soc. London, 1853 : 11, pl. 7.
- Ambystoma* (*Ambystoma*) *tigrinum diaboli* Dunn, 1940, Copeia, 1940 (3) : 160.
- Ambystoma* (*Ambystoma*) *tigrinum mavortium* Baird, 1850, Jour. Acad. Nat. Sci. Phila. (2), 1 : 284.
- Ambystoma* (*Ambystoma*) *tigrinum melanostictum* Baird, 1860, Expl. Surv. R.R. Miss. Pacific, 12, pt. 2 : 306.
- Ambystoma* (*Ambystoma*) *tigrinum nebulosum* Hallowell, 1854, Proc. Acad. Nat. Sci. Phila., 6 : 209.
- Ambystoma* (*Ambystoma*) *tigrinum stebbinsi* Lowe, 1954, Proc. Biol. Soc. Wash., 67 : 243.
- Ambystoma* (*Ambystoma*) *tigrinum velasci* Duğès, 1888, La Naturaleza (ser. 2), 1 : 142.

#### The *mexicanum* group

DEFINITION.—Members of the subgenus *Ambystoma* virtually indistinguishable morphologically from the members of the *tigrinum* group, but differing in being usually or consistently neotenus under natural conditions; parasphenoid sometimes straight-sided and unexpanded as in the *tigrinum* group, but frequently approaching a form more typical of the other groups of the genus; members of this group tend to be larger than those of the *tigrinum* group, but do not exceed the maximum size of neotenic larvae of that group.

RANGE.—The ancient lakes of the southern Mexican plateau. One species from the middle Pliocene of Kansas is also tentatively referred to this group.

DISCUSSION.—There is some question as to whether the forms assigned here should even be placed in a group separate from *tigrinum*, but a few very minor features of morphological difference, in conjunc-

tion with the apparently usually obligatory neotenic mode of life, have induced me to consider them a separate group.

I have previously (1955) pointed out the possibility that the middle Pliocene *Plioambystoma kansense* is not a distinct genus, but a neotenic form of *Ambystoma*. In that paper it was suggested that the name *Plioambystoma* be tentatively retained pending some information concerning the adult condition. Since that time I have examined a larger number and variety of larval skeletons of Recent forms, and am convinced that when distinctions of superspecific taxonomic significance exist, they can usually be discerned in the larvae. In the absence of any evidence to the contrary, I am now of the opinion that *Plioambystoma kansense* does not differ in any important respect from Recent members of the *tigrinum-mexicanum* complex. Since, so far as can be determined from the known fossil populations, this species was consistently neotenic, it is referred to the *mexicanum* rather than to the *tigrinum* group.

I am also of the opinion that *Lanëbatrachus* and *Ogallalabatrachus* are most probably based on aberrant specimens of *kansense*, and have therefore placed these genera in the synonymy of *Ambystoma*. Admittedly this must be a matter of conjecture, based on the limited number of specimens available, but I believe it is the most likely interpretation of the currently known material.

#### REFERRED FORMS.—

*Ambystoma (Ambystoma) kansense* (Adams and Martin), 1929, Amer. Jour. Sci. (5th ser.), 17: 504.

*Ambystoma (Ambystoma) lermaensis* (Taylor), 1940, Univ. Kans. Sci. Bull., 26 (for 1939): 427, pl. 48.

*Ambystoma (Ambystoma) mexicanum* (Shaw), 1789, Nat. Misc., 9: pls. 343, 344.

#### The *opacum* group

DEFINITION.—Members of the subgenus *Ambystoma* with vertebral proportions somewhat intermediate between those of the two preceding and those of the following group; parasphenoid with concave sides and a definite alate expansion posteriorly; a wide diastema between the prevomerine and palatine teeth; no postdentigerous process on the prevomers; a partial lateral bony border to the choanae; os triangulare tending to be transverse; neoteny unknown.

RANGE.—Most of the United States east of the Great Plains.

DISCUSSION.—This group is very similar to the *maculatum* group in most respects, but the vertebral proportions are somewhat inter-

mediate between that group and the *tigrinum* group. Also, the members of the *opacum* group have a somewhat more rounded, less oval skull, and the proportions of the premaxillae resemble those of the *tigrinum* group more closely than they do the *maculatum* group, although in both the vertebrae and the premaxillae there is overlapping variation in both directions.

Only two species are included in this group, *opacum* and *talpoideum*. Both are small forms with stout bodies, well-developed limbs, wide heads, and moderately short tails. The total length never exceeds 120 to 125 millimeters, and is usually decidedly less. Although the color patterns differ markedly, in both forms there is a brown to black ground color with whitish or grayish markings. In correlation with the short bodies, the number of costal grooves is low, only ten or eleven in *talpoideum*, eleven or twelve in *opacum*. Neoteny is unknown in either form.

The skull of *talpoideum* is particularly short and broad, with these proportions reflected in most of the individual cranial bones. It is further characterized by a particularly strong development of the various crests for muscle attachment. A *opacum* is apparently devoid of any unique osteological features, but is distinctive in being the only member of the family that lays its eggs on land.

#### REFERRED FORMS.—

*Ambystoma* (*Ambystoma*) *opacum* (Gravenhorst), 1807, Vergl. Uebersicht Zool. Syst. : 431.

*Ambystoma* (*Ambystoma*) *talpoideum* Holbrook, 1838, N. Amer. Herp., ed. 1, 3 : 117, pl. 29.

#### The *maculatum* group

DEFINITION.—Members of the subgenus *Ambystoma* with the vertebrae definitely elongated; premaxillary spines relatively longer and narrower than in the preceding groups; parasphenoid with concave sides and a definite alate expansion posteriorly; usually a wide diastema between the prevomerine and palatine teeth (occasionally lacking in *maculatum*); no postdentigerous process on the prevomers; a partial lateral bony choanal border; os triangulare tending to be transverse; neoteny may occur rarely in *A. gracile*, but is not known in any of the other species.

RANGE.—Divisible into two disjunct areas. Along the Pacific coast from southern Alaska to northern California and east into Montana; in the east from southern Labrador to southeastern Manitoba and south throughout most of the United States east of the Great Plains.

DISCUSSION.—This is not a compact group, the five species referred to it being rather diverse, but they appear nevertheless to be more closely related to each other than to any other member of the genus. The primary distinguishing feature of the group is the elongation of the vertebrae. In *gracile* and to a lesser extent *macrodictylum*, this elongation is somewhat less marked than in the eastern forms. Both *gracile* and *maculatum* are large, heavy-bodied forms, resembling the members of the *tigrinum* group in general habitus; *maculatum* also resembles that group in the possession of a yellow and black color pattern. *A. jeffersonianum*, *laterale*, and *macrodictylum* are smaller forms, with more slender bodies and limbs. The tail is moderately long, usually approximating 50 percent of the total length.

The parasphenoids frequently possess a characteristic small process on the anterior end, but this is not universally present even in a given species. The pterygoids tend to be somewhat reduced, with a constriction shortly behind the tip of the anterior process, so that this process appears to terminate in a knob rather than tapering to a point. The number of costal grooves is typically 11 in *gracile*, 12 or 13 in *macrodictylum*, and 12 (occasionally 11 or 13) in the other species.

This may be thought of as a northern group, each of the forms excepting *laterale*, which has a rather limited range, having a more northerly distribution than does any member of any other group occupying a similar type of habitat, although *tigrinum* may range nearly as far northward in the more arid Canadian Plains.

#### REFERRED FORMS.—

*Ambystoma* (*Ambystoma*) *gracile gracile* Baird, 1859, Pacific R. R. Surv., Rept., 10, Williamson's Route, pt. 4, no. 4 : 13, pl. 44.

*Ambystoma* (*Ambystoma*) *gracile decorticatum* Cope, 1886, Proc. Amer. Philos. Soc., 23 : 522.

*Ambystoma* (*Ambystoma*) *jeffersonianum* (Green), 1827, Contr. Mac-lurean Lyc., 1 : 4, pl. 1.

*Ambystoma* (*Ambystoma*) *laterale* Hallowell, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 3 : 355.

*Ambystoma* (*Ambystoma*) *macrodictylum macrodictylum* Baird, 1849, Jour. Acad. Nat. Sci. Phila., ser. 2, 1 : 299.

*Ambystoma* (*Ambystoma*) *macrodictylum croceum* Russell and Anderson, 1956, Herpetologica, 12 : 137.

*Ambystoma* (*Ambystoma*) *maculatum* Shaw, 1802, Gen. Zool., 3 (pt. 1) : 304.

Subgenus *Linguaelapsus* Cope

DEFINITION.—Members of the genus *Ambystoma* in which the premaxillary spines are typically long and narrow, and have a ventral lamina or thickening just above the dentigerous ramus; tongue with plicae branching from a median groove; teeth (except in *mabeei*) arranged in more than one row on all dentigerous elements; palatine teeth lacking (except in *mabeei*); no annular otoglossal cartilage; dentary of adults lacking a prominent flange of bone on the lingual surface in most forms, resembling closely the larval dentary of members of the subgenus *Ambystoma*; costal grooves 13 to 15.

RANGE.—Southeastern United States, west to Texas, Oklahoma and Kansas; north to Illinois, Indiana, Ohio and North Carolina; most of peninsular Florida excluded. A single form apparently referable to this subgenus is known from the Mexican state of Mexico.

DISCUSSION.—The more specialized members of this group are so distinctive that they might well be considered as representing a genus distinct from *Ambystoma* were it not for the existence of intermediate forms. There is, within the group, a gradation from a nearly typical *Ambystoma* condition to these highly modified forms. For this reason, subgeneric status seems preferable to full generic status.

All of the species are of small to moderate size, with slender bodies and slight limbs that do not meet when adpressed. The tail tends to be relatively short, frequently less than 40 percent of the total length. The color pattern is variable, but blacks, grays, and whites predominate. The number of costal grooves is consistently rather high, as compared with the subgenus *Ambystoma*. There is a strong tendency for the cranial sutures to be extremely irregular. The parasphenoid is consistently strongly expanded posteriorly. Interspecific variation is considerable, and is discussed in the following paragraphs.

*A. mabeei* is scarcely recognizable as belonging to the subgenus *Linguaelapsus*, excepting for the condition of the tongue and the lack of an annular otoglossal cartilage. The premaxillary spines are relatively short and broad; the vertical lamina is very limited in extent, its development being so slight that probably no significance would be attached to it in the absence of other resemblances to *Linguaelapsus*. There is, however, a definite irregularity to the cranial sutures, and at least some of the individual teeth are of the form occurring in other species of *Linguaelapsus*—that is, the inner fork of the bifid tip is long, sharp-pointed, and very strongly bent inwards, the outer fork becoming nearly obsolete. In contrast to conditions in the more typical members of the subgenus, *mabeei* possesses palatine teeth, all

teeth are arranged in single rows, the dentary has a prominent flange of bone on the lingual surface, the premaxillary spines are relatively short and broad, the vertebral proportions are very similar to those of the *maculatum* group, and all skeletal elements are very similar in form and proportions to those in members of the *maculatum* group. The prevomer bears a postdentigerous process—a condition found otherwise in the genus only in the *tigrinum* group (and presumably in metamorphosed individuals of the *mexicanum* group).

In *annulatum* the premaxillary spines are longer, and the vertical expansion somewhat more extensive. The teeth are multirowed (usually three rows) and the palatine teeth lacking, the palatine itself being greatly reduced in extent. In this and the succeeding species, the prevomer has a less transverse, more diagonal, orientation, reminiscent of the larval position, though by no means identical with it (cf. figs. 4K-L). The dentary is relatively short; there is a flange of bone on the lingual surface, but it is much reduced in extent. The vertebrae are still similar to those of the *maculatum* group; the dorsal surface of the atlas is slightly flattened. The cranial sutures are definitely irregular. Minor differences in form and proportions of a number of skeletal elements (as compared with the *maculatum* group) can be observed.

In most respects *cingulatum* and *texanum* are very similar to each other. In both the premaxillary spines are long and narrow, the region between the nares frequently being so narrow that, because of the vertical thickening, the bone in this region appears to have a primarily vertical orientation. The ends of the vertebral centra are widened as compared with the two preceding species (see the section on vertebral variation), and the dorsal surface of the atlas is definitely flattened. There is only a slight ridge on the lingual surface of the dentary, which thus resembles, in this respect, the larval dentary of other members of the genus. The palatine is edentulous, of variable extent in *cingulatum*, always greatly reduced or apparently lacking in *texanum*. The cranial sutures are irregular, perhaps not so markedly so in *cingulatum* as in *texanum*. Nearly all cranial elements are distinguishable in details of form from those of the members of the *maculatum* group. The teeth, in both species, are in three or four rows on all dentigerous elements; the individual teeth of the two species differ markedly in form, as described in the preliminary discussion.

The osteology of *A. schmidtii* is virtually unknown, except for the fact that the teeth are in multiple rows. Radiographs (fig. 11) of the type are not clear as to details, but the apparent vertebral proportions, the apparently long and slender premaxillary spines, and the ar-

range of the prevomerine teeth support the idea that this species is properly referable to the subgenus *Linguaelapsus*.

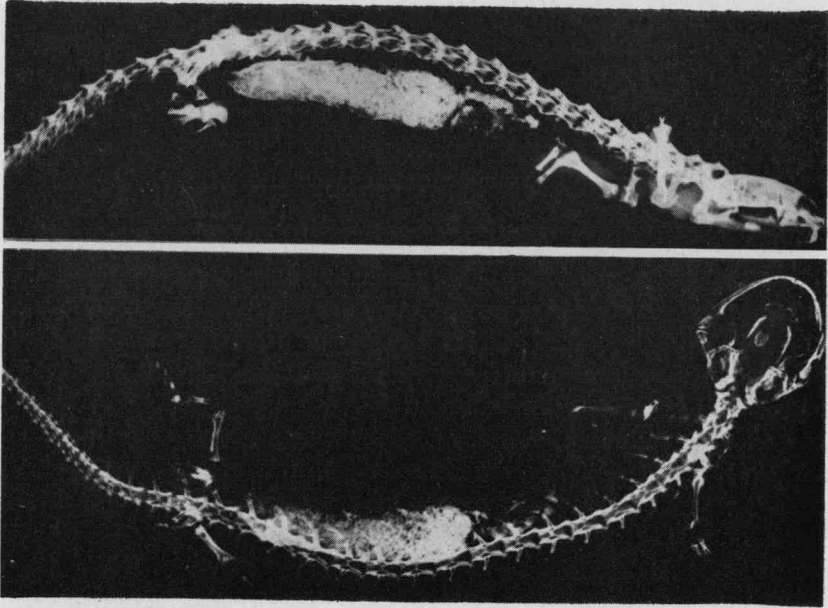


Figure 11.—Radiographs of the type specimen of *Ambystoma schmidtii*.

If only the forms *cingulatum* and *texanum* were considered, it would be tempting to postulate a primitive origin for this group. The absence of a lingual flange on the dentary, the strongly expanded parasphenoids, the lack of an annular otoglossal cartilage, and several minor details, are all points of resemblance with the presumed condition in primitive members of the family. The affinities of *mabeei* with *Linguaelapsus* are, however, strongly indicated by the condition of the tongue and by the apparent rudiments of other specializations characterizing the more modified forms, and *mabeei* is unquestionably a member of the genus *Ambystoma*. Most of the features mentioned above, instead of representing a retention of primitive conditions, could be the result of partial neoteny; this must be the case if *Linguaelapsus* is to be derived from a stock that could already be considered as belonging to the genus *Ambystoma*. The often somewhat diagonal orientation of the prevomers might also be considered a neotenic feature.

In general, *mabeei* resembles very strongly the *maculatum* group. It does, however, share with the *tigrinum* group the apparently primi-

tive feature of a postdentigerous process of the prevomer. The assumption is that the subgenus *Linguaelapsus* was derived from the *maculatum* group (or the line leading thereto) after most of the *maculatum* group characteristics had been established, but before the postdentigerous process had been lost, at least in all members of the group.

REFERRED FORMS.—

*Ambystoma* (*Linguaelapsus*) *annulatum* Cope, 1886, Proc. Amer. Philos. Soc., 23 : 525.

*Ambystoma* (*Linguaelapsus*) *cingulatum cingulatum* Cope, 1867, Proc. Acad. Nat. Sci. Phila., 19 : 205.

*Ambystoma* (*Linguaelapsus*) *cingulatum bishopi* Goïn, 1950, Ann. Carnegie Mus., 31 : 300, pl. 1.

*Ambystoma* (*Linguaelapsus*) *mabeei* Bishop, 1928, Jour. Elisha Mitchell Sci. Soc., 43 : 157, pl. 23.

*Ambystoma* (*Linguaelapsus*) *schmidtii* Taylor, 1939, Univ. Kans. Sci. Bull., 25 (for 1938) : 263, pl. 26.

*Ambystoma* (*Linguaelapsus*) *texanum* (Matthes), 1855, Allg. deutsche naturh. Seitschr. (new ser.), 1 : 266.

Subgenus *Bathysiredon* Dunn

DEFINITION.—A neotenic ambystomid, similar in general to the *mexicanum* group of the subgenus *Ambystoma*, but differing in the following respects: Only three phalanges in the fourth toe (four in nearly all other Ambystominae); digits short, webbed (unwebbed in larvae of other forms); gill branches with filaments to near base (none arising near base in other forms); 8 to 10 gill rakers on the anterior face of the third arch (twelve or more in most members of the *mexicanum* and *tigrinum* groups); head strongly depressed.

RANGE.—Known only from Lake Pátzcuaro, Michoacán, Mexico.

DISCUSSION.—This form is still rather imperfectly known. As a whole, the skeleton offers little with which to distinguish this group from the *mexicanum* group of *Ambystoma*, though some minor differences in proportions of individual cranial elements can be found. These are perhaps associated with the depression of the skull, though this depression is by no means as obvious in the skull itself as it is in the intact fleshed individual. I have seen only a single skeleton of *Bathysiredon*, so have no idea as to the extent of variation in the minor proportional differences noted.

The parasphenoid, at last in this one individual, is somewhat more greatly expanded posteriorly than is typical for the *mexicanum* and

*tigrinum* groups, though not at all beyond the range of variation in these groups. Its affinities with the *mexicanum-tigrinum* complex can scarcely be questioned.

Generic differentiation, then, seems to be based on the following features:

(a) Only three phalanges in the fourth toe. This varies infraspecifically in some members of the *tigrinum* group—for example, it is a subspecific characteristic for *A. rosaceum nigrum* (Shannon, 1951), and may well be subject to individual variation in other forms.

(b) Digits short and webbed. This apparently is a valid distinction between *dumerili* and other species, but not one that I can consider to be of generic importance.

(c) Gill branches with filaments to near base. Again this distinction, even if valid, seems scarcely to be one of generic importance.

(d) Eight to ten gill rakers on the anterior face of the third arch. If all members of the *mexicanum* group and *Bathysiredon* were put in a single group, the total variation within that group, in respect to the number of gill rakers on the anterior face of the third arch, would be less than the corresponding variation among forms all assigned to the single species *tigrinum* (Dunn, 1940).

(e) Head strongly depressed. Proportions of the head are somewhat variable within the genus *Ambystoma*, and some of these variations are much more clearly reflected in the skull (e.g., comparing *A. talpoideum* with *jeffersonianum*) than is any difference between *dumerili* and members of the *mexicanum* group.

It does not appear to me that, at least on the basis of present knowledge, generic status for this form is fully warranted. On the other hand, some differences do exist between *dumerili* and the members of the *mexicanum* group. I suggest, therefore, that the category be considered a subgenus of the genus *Ambystoma* rather than a distinct genus.

#### REFERRED FORMS.—

*Ambystoma* (*Bathysiredon*) *dumerili dumerili* (Dugès), 1870, La Naturelle, 1 : 241, pl. 5a.

*Ambystoma* (*Bathysiredon*) *dumerili queretarensis* Maldonado-Koerdell, 1948, Mem. Acad. Nat. Cien. Mexico, 56 : 196.

#### DISTRIBUTIONAL CONSIDERATIONS

A large part of the present range of many species occupies areas that were glaciated during Wisconsin time. Even many of the forms

whose range is outside of the glacial limits probably have had their range greatly altered by climatic and ecologic changes associated with the various glacial advances and retreats. It is, in such a case, rather presumptive to speculate on past distributions, particularly in a group that has apparently been in existence throughout the Tertiary, but for which fossil records are extremely limited. Nevertheless, a possible arrangement can be postulated.

The ancestral ambystomatids or proto-ambystomatids probably entered North America from Asia by a northern route in the very early Tertiary or perhaps in the late Mesozoic. It seems likely that very early in the history of the family there was a split into two groups. One such group became isolated west of the Rockies (or an equivalent western barrier, depending partially on the actual period of entry into North America). It is assumed that this group retained a number of characteristics of the ancestral stock, specifically, the independent prootic and exoccipital, the strongly expanded parasphenoid, the relatively simple tooth structure, the independent lacrimal, and perhaps to a limited extent, a disposition of prevomerine teeth resembling that of hynobiids. This ancestral stock, must at this time, have already developed the essential family characteristics that distinguish the ambystomatids from the hynobiids. It was from this western group that the Dicamptodontinae and the Rhyacotritoninae are thought to have been derived.

The primary center of dispersal for the other section of the ancestral stock, giving rise to the Ambystomatinae, seems to have been in the eastern half of the continent, possibly in the general vicinity of what is now the Great Lakes region. There is no direct evidence as to the route by which this area was reached, but it was likely through a northern forested region in what is now Canada, during a period of relatively mild climate, rather than across the less humid, generally less wooded, present Plains area further to the south. Parallel instances of distribution or migration are known in a large number of animal and plant groups—the salamandrids, to cite another example from the Amphibia. The time of establishment of this group in eastern North America is also a matter of speculation but, if the further postulations to be made are correct, it must have been no later than the Miocene, and probably earlier.

This eastern section, either during the course of migration or after establishment, lost the independent lacrimal; the exoccipital and prootic were fused, and the other developments characterizing the subfamily Ambystomatinae appeared. We may assume an outward spread from this center. Northward dispersal, though perhaps oc-

curing to some extent, would be limited much of the time by temperature. The relatively arid, unforested condition of the Plains region through much of the Tertiary effectively prevented any extensive spread to the west. The major movement from this center must, then, have been southward. *Rhyacosiredon*, or its precursor, was probably an early entrant into Mexico that has survived only in the southern part of the plateau, near the periphery of the range of the family.

Approximately contemporaneously with the southward movement of the *Rhyacosiredon* stock, certain modifications, such as the chondrification of the adult hyobranchium, the development of more highly modified teeth, the development of a lingual flange on the dentary, and so on, were occurring in the central stock. A second wave of migration is represented by the *A. tigrinum* - *mexicanum* - *Bathysiredon* complex. This group, at some point, became adapted to relatively arid, unforested conditions and underwent a secondary dispersal northward from the Mexican region. The appearance of *kansense* in the middle Pliocene of Kansas, of *hibbardi* in the upper Pliocene of the same area, of *tigrinum* there and elsewhere in the early Pleistocene as well as throughout the entire northern and western portion of its present range, are postulated to represent northward movement from this secondary center, rather than direct dispersal from the original northeastern center. The *mexicanum* group and the related subgenus *Bathysiredon* are probably early derivatives of this line; they are, like *Rhyacosiredon*, now limited to the southern edge of the Mexican plateau.

It might be mentioned that the development of neoteny, or in some species, aquatic habits even for metamorphosed individuals, might be a factor in the adaptation of this group to arid conditions. These aquatic habits allow full utilization of such permanent water as is available. Food can be obtained in the aquatic habitat, and it is not necessary for the individual animals to be subjected to the rigorous terrestrial conditions of the arid areas in which they live. Taylor and Smith (1945) have suggested that the varying chemical composition of the different permanent bodies of water in the region may have been one of the factors involved in speciation in that region.

Simultaneously with the development of the *tigrinum*-*mexicanum* complex in Mexico, further differentiation was occurring in the region of the present eastern United States. *Linguaelapsus* may well have developed about this period, probably in the southeastern United States or the Gulf region. The retention of a postdentigerous process on the prevomer suggests that it was derived at a relatively early date from the *maculatum-opacum* group precursor stock, but not be-

fore most of the characteristics distinguishing those two groups from *tigrinum* had appeared. The *opacum* group may have arisen from a small section of the *maculatum* group in the southeast. We can postulate relatively mild, humid climate conditions at the time the *maculatum* group was developing, allowing an apparently early representative (*gracile*) to reach the Pacific region along some northward path as was postulated previously for the eastward movement of the ancestral Ambystomatinae. The appearance of *macroductylum* in the west is considered the result of a second such movement, rather than representing a development within the western region. Again, the time of these occurrences is conjectural.

I think it probable that this major pattern of distribution had been established before the close of the Pliocene, so that at the beginning of the Pleistocene the basic distribution of the major divisions of the family was much as it is today. That individual ranges were greatly altered by the advance and retreat of the glaciers during the Pleistocene is unquestioned, but this would not require any alteration in the basic pattern. At times, corresponding with glacial advance, the elements of this pattern were probably compressed and perhaps shifted southward; at other times they expanded and were shifted northward, but the relationships between the elements remained essentially constant.

The presence of *A. schmidti* in the southern Mexican plateau is explainable on the basis of one of these southward shifts, presumably coincident with a major glacial advance. The relatively primitive *mabeei* may have survived the glaciations in a coastal pocket corresponding closely to its present range. If it should be found that some of the now poorly known Mexican species are not actually referable to the *tigrinum* group, but are more properly placed with one of the other groups, their presence in Mexico is readily explainable on the same basis as that of *A. schmidti*.

In summary, the appearance of the family in North America, and the establishment of two major stocks, must have occurred in the late Mesozoic or very early Tertiary. The various species groups of *Ambystoma* were established before the Pliocene, and their distribution, in major aspects, established at least before the end of the Pliocene. Some, possibly most, of the extant species were in existence by the earliest Pleistocene; individual ranges may have been greatly altered from time to time, but the major relationships of distributional pattern have probably been maintained much the same since the close of the Pliocene.

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