SYSTEMATICS OF THE CAECILIANS

(AMPHIBIA: GYMNOPHIONA)

by

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ABSTRACT

Determining the higher level relationships of the modern amphibian order Gymnophiona (caecilians) poses a number of methodological problems. A cladistic methodology is outlined by which the phylogenetic relationships of this group can be determined objectively. Among the possible sister groups analyzed, which include dissorophid temnospondyls, aïstopods, nectrideans, lysorophoids, microsaurs, anurans and urodeles, the microsaurs of the families Gymnarthridae and Goniorhynchidae are the most plausible sister group of caecilians, based on cranial osteology. Hence, the three modern orders of amphibians, caecilians, anurans and urodeles, do not constitute a monophyletic assemblage exclusive of all other groups. Ingroup analysis indicates that the Ichthyophiidae is the most primitive living caecilian family. The cladistic analysis suggests that features of the unique jaw apparatus define two groups of caecilians which diverged, phylogenetically, early in the group's history. Morphometric analysis reveals that elements of the jaw apparatus compose a functional suite of features. Aspects of the development, function, and significance of the jaw to miniaturization of the caecilian skull are inferred from the morphometric analysis.

RESUME

Les affinités phylogenetiques de l'ordre moderne des amphibiens Gymnophiona (caeciliens) posent premièrement les problèmes méthodologiques. On présente une méthodologie par laquelle on peut déterminer objectivement les affinités phylogenetique des caecilians. Parmi des 'groupes-frères'potentiels, y compris les temnospondyles dissorophides, les aïstopodes, les nectrideans, les lysorophöides, les microsaurs, les anoures et les urodèles, les microsaurs de les familles Gymnarthridae et Goniorhynchidae sont le 'groupes-frère' le plus plausible, selon les caractères du crânes. Alors, les trois ordres modernes des amphibiens ne constituent pas un groupe monophyletique, non compris de tout les autres taxa. L'analyse cladistique de la Gymophiona lui-même sugget que les Caractères de la mâchoire définent deux groupes fondamentals dans les caeciliens, qui ont divergé tôt dans l'histoire de les caeciliens. L'analyse morphometrique rèvèles que les caractères de la mâchoire constitutuent une suite fonctionelle. On déduit quelques aspectes de l'ontologie, de la fonction et de la significance de la structure de la mâchoire selon l'analyse morphometrique.

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Figures 6,7 and 8 of this work were drawn by Mrs. Pamela Gaskill. Figure 31 was taken from drawings also originally made by Mrs. Gaskill.

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Not merely in the realm of commerce but in the world of ideas as well our age is organizing a regular clearance sale... Every speculative price-fixer who conscientiously directs attention to the significant march of modern philosophy,... is not content with doubting everything but goes further. Perhaps it would be untimely and ill-timed to ask them where they are going, but surely it is courteous and unobtrusive to regard it as certain that they have doubted everything, since otherwise it would be a queer thing for them to be going further. This preliminary movement they have therefore all made with such ease that they do not find it necessary to let drop a word about the how...

Søren Kierkegaard.

CHAPTER I.

GENERAL INTRODUCTION

I. THE PROBLEM

Since the first description of a caecilian by Linneaeus in 1749 (see Lescure 1985), there has been continual debate concerning their higher level relationships, a subject that has received heightened interest in the last number of years. The majority of workers have allied the caecilians (also known as gymnophionans or apodans) with the two other orders of extant amphibians, anurans and urodeles, based on a number of morphological, physiological, and behavioural similarites. There are, however, a welter of dissenting proposals concerning caecilian relationships, based on various morphological characters that caecilians share with other tetrapod assemblages.

Ascertaining the relationships of caecilians has continued to be a perplexing problem owing in part to the fact that that caecilians have a distinctive morphology and lifestyle. Anatomically, caecilians are highly derived, exhibiting features found in no other tetrapods. They have also modified many of the typical tetrapod structures in ways that are unique. Many of these features have no discernible

analogue or precursor in known tetrapod groups. The problem is exacerbated by the dearth of fossil material. On the basis of modern members alone it is exceedingly difficult to differentiate primitive from derived features, which in turn makes it impossible to predict with any degree of certitude, what characteristics the close relatives of caecilians might possess. Furthermore, although it has long been recognized that caecilians exhibit similarities to an array of tetrapod groups, there is at present no generally accepted higher level phylogeny that adequately describes the interrelationships of the tetrapods. The individual groups are easily recognized, but they are not readily ascribable to a robust, well supported phylogenetic scheme. It is therefore difficult to assess the significance of whatever similarities caecilians do share with other tetrapod lineages.

The advent of cladistics has brought a new conception of the significance of similarity in determining phylogenetic relationships. It is now recognized that organisms must be united by a particular kind of similarity, synapomorphy, in order that they be designated as members of a monophyletic group. A synapomorphy is simply a derived or advanced feature (apomorphy) that is shared between two or more groups. It is taken to be evidence of recent common ancestry (Hennig 1966 :91). Symplesiomorphies, or shared primitive characters, have no phylogenetic significance in cladistic systematics. Many of the characters that traditonally have been used to unite caecilians with various

other tetrapod groups may indeed be symplesiomorphies. The reliance on synapomorphies exclusively makes it imperative that the methods employed in distinguishing apomorphies from plesiomorphies are valid, robust and unbiased.

This study concerns itself primarily with determining the sister group relationships of the caecilians (Order Gymnophiona). The sister group is the group sharing the largest number of synapomorphies with the group in question. Any attempt to do so must address the three problems alluded to above. Specifically, these are establishing the nature of the primitive caecilian, determining the significance of the morphological similarities shared between caecilians and other tetrapod groups and, ascertaining how the groups with whom caecilians display similarities are related to the caecilians and to each other.

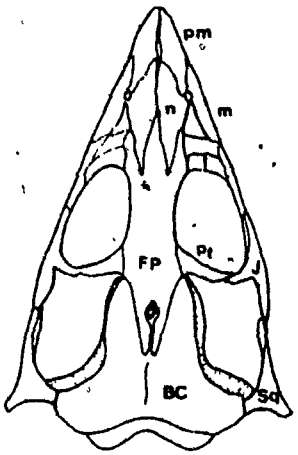
The Choice of Potential Sister Groups

The intial step is to delimit the set of plausible sister groups. In the case of caecilians, this is neither a simple nor trivial matter because the problem of discerning the primitive from advanced for caecilian characters (i.e. polarizing characters) and that of determining caecilian sister group relationships are intimately connected. In fact, it will be shown that the choice of potential sister groups determines which characters of caecilians can be polarized. In a sense I hope to make clear in Chapter II, there exists a

trade-off between the number of potential sister groups analyzed and the robustness of the inferences made about ingroup polarity. If a large number of groups are taken as potential sister groups, only a small number of caecilian characters can be polarized, yielding a non-robust inference about the primitive condition in caecilians. On the other hand, the fewer potential sister groups that are chosen, the lower will be the likelihood that the correct one is among them.

I have limited the analysis of sister groups to the following: Aïstopoda, Order Nectridea, Order Lysorophia, Order Microsauria, Family Dissorophidae, Order Anura and Order Caudata (Figure 1). The reasons for the choice of these groups concern the special methodological requirements of this particular study, and will be discussed in detail in Chapter two. Only two of these groups, Anurans (frogs) and Caudata (salamanders), are represented by living members. It is noteworthy that that the extinct orders, Aïstopods, Nectridea, Lysorophia and Microsauria are commonly united in the Subclass Lepsospondyli, while the modern orders are themselves usually united, with caecilians, in the subclass Lissamphibia (Romer 1966). The dissorophids are usually considered as a family of temnospondyl labyrinthodonts. A detailed discussion of the anatomy of these groups is deferred until the actual cladistic analysis but a brief outline of the various hypotheses of caecilian affinities is given below.

Figure 1. Representatives of the possible sister groups of caecilians. A, the Aïstopod Phlegethontia (from McGinnis 1967). B. the nectridean Ptyonius (from Bossy 1976). C. The lysorophoid Brachydectes (from Wellstead 1985). D. The dissorophid temnospondyl Doleserpeton (from Bolt 1969). E. the goniorhynchid microsaur Rhynchonkos (from Carroll and Gaskill 1978) F. the anuran Rana (RM uncatalogued). G. the urodele Ambystoma (RM 2362). Scale bars equal 1mm unless otherwise stipulated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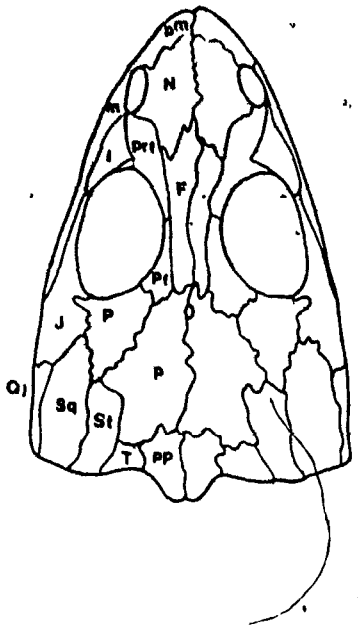
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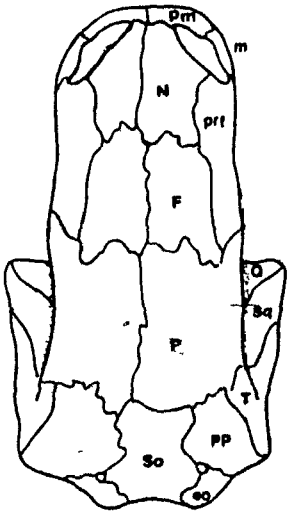
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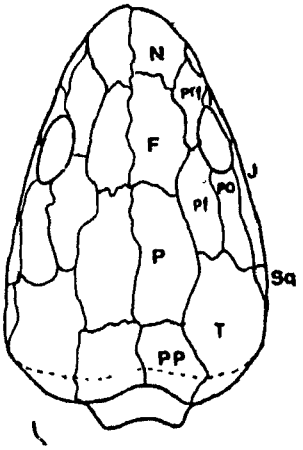
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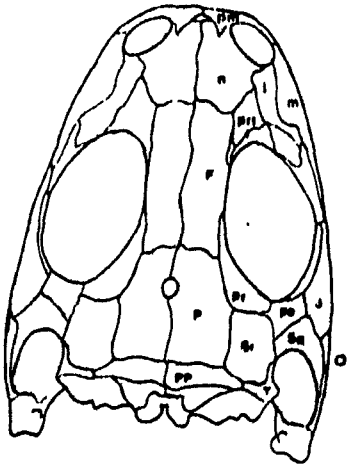
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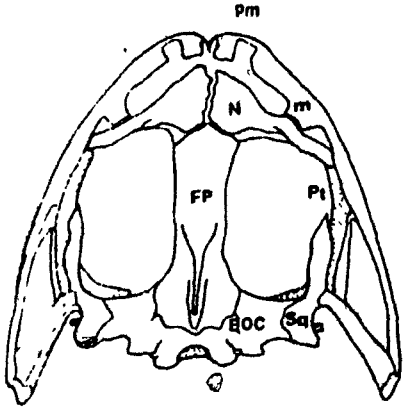
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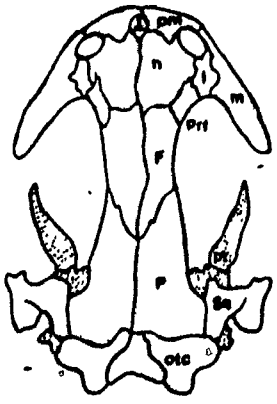
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Previous Hypotheses

An issue that has received much attention is the question of the monophyly or polyphyly of the extant amphibian orders (the Lissamphibia). The implication of lissamphibian monophyly for caecilians is that if the three modern orders represent a monophyletic assemblage, then caecilians share a more recent ancestor with Anura (anurans, or frogs) and the Caudata (urodeles, or salamanders) than with any other group. Lissamphibian monophyly was proposed by Gadow (1901), and has come to be the received view (Duellman and Trueb 1986). Parsons and Williams (1963) have provided the most complete formulation of this argument, citing the common possession of green rods in the retina, papilla amphibiorum of the inner ear (see also Lombard and Bolt 1979), pedicellate teeth (Parsons and Williams 1962), skull fenestration, and similar palatal structure, among other characters, as indications of close relationships between caecilians, frogs, and salamanders. Subsequent studies based on inner and middle ear morphology (Lombard and Bolt 1979; Bolt and Lombard 1985), vertebral structure (and other characters, Gardiner 1983), reproductive biology (Parker 1956), and karyotype (Morescalchi 1973) have supported this contention. Other reviews that favour lissamphibian monophyly include Szarski (1962), Romer (1966), Cox (1967) and Duellmann and Trueb (1986).

A less frequently encountered view has been put forward most recently by Carroll and Currie (1975). They

VI. Primitive tetrapods

#	Genus	Species	description
	Ichthyostega		cast skull, palatal view
CMNH 11090	Greererpeton	burkemorani	skull.

Abbreviations:

1. INSTITUTIONS

AMNH	American Museum of Natural History
BM(NH)	British Museum (Natural History)
CMNH	Cleveland Museum of Natural History
CNMH	Chicago Natural History Museum
KU	Kansas University
MCZ	Museum of Comparitive Zoology Harvard
LSUMZ	Los Angeles University, Museum of Zoology
MHW	Collection of Dr. Marvalee Wake Berekeley
RM	Redpath Museum McGill University
UCMP	University of California Museum of Paleontology
UCMVZ	University of California, Museum of Vertebrate Zoology
UF	University of Florida
UIMNH	University of Illinois Museum of Natural History

2. CONDITIONS OF SPECIMENS

C & S	Cleared and stained
D	Dried skull
W	Whole specimen

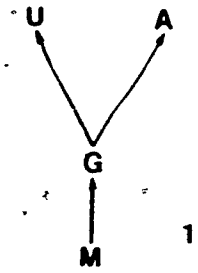
Bolt (1969) described a Paleozoic temnospondyl, Doleserpeton, as the most probable ancestor of the lissamphibians. At that time, this genus was the sole member of the Family Doleserpetontidae. It is now evident from a study by Bolt and Lombard (1985), that Doleserpeton is considered a member of the Dissorophidae.

The previous hypotheses of caecilian relationships are summarized in Figure 2.

Character Choice

With myriad characters that can be chosen, it is important to limit the analysis to characters that are pertinent to the question at hand. Behavioural, physiological, karyological, developemental, and soft anatomical characters have been used in the past to unite the three modern orders but the distributions of these characters among fossil groups is nearly always impossible to ascertain. Where possible, I have avoided the use of such characters. Characters such as the arrangement of dermal bones posterior to the parietals among lepospondyls, are not of use in establishing relationships in groups that lack these bones entirely, such as the modern forms. Use of characters such as these is minimized in the analusis. The caecilian vertebrae are quite distinctive and there are no traces of appendicular skeleton, so there are very few relevant postcranial features available for analysis. Hence I have restricted the analysis to cranial features that are relevant to all groups. In resolving characters of caecilians themselves, some soft

Figure 2. Previous hypotheses of caecilian relationships. Phylogenies with arrows represent phylogenetic trees. Rectilinear phylogenies are cladograms. A= Anura, Ai= Aïstopoda, D= Dissorophidae, G=Gymnophiona L= Lysorophoidea, M= Microsauria, N = Nectridea, P= Hypothetical "protolissamphibian ancestor", T= Temnospondyl amphibians, U= Urodela.



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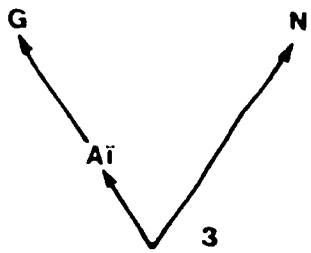
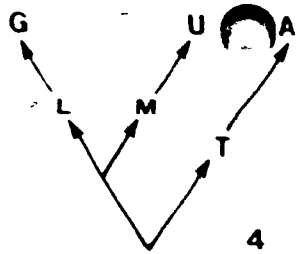
GADOW 1901

MOODIE 1909



3

MARCUS et al
1935



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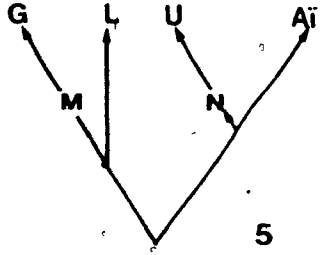
ROMER 1945



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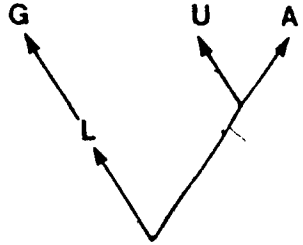
GREGORY et al
1956



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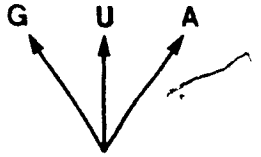
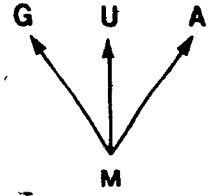


(PARKER 1956)

7

*PARSONS and WILLIAMS
1963



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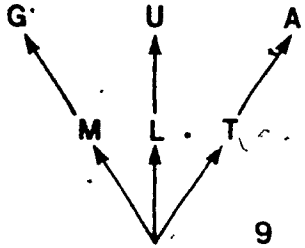
COX 1967



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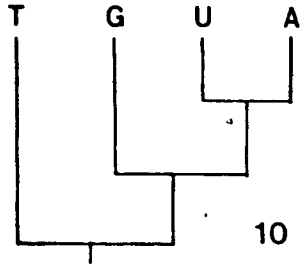
SCHMALHAUSEN 1968



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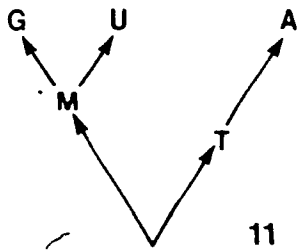
LOMBARD and BOLT 1979



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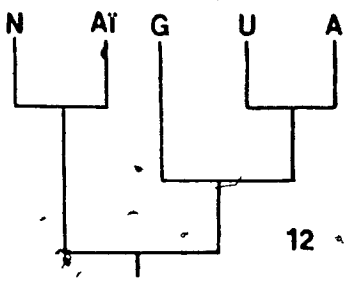
CARROLL and HOLMES
1980



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GARDINER 1982/3

anatomical features are considered but the analysis of the higher level relationships relies strictly on cranial osteology.

In a way, the view of character choice presented here is diametrically opposed to the criteria for character choice outlined by Løvtrup (1977: ch 2). The argument I have used to justify the use of cranial osteology only, viz. that soft anatomical features are not relevant to fossil groups, is the same argument used by Løvtrup to justify the exclusion of fossil groups from cladistic analysis. He claims that extinct groups cannot be analyzed because too little information can be gained from them. However, if fossil assemblages were excluded from this study, it would be trivially true that caecilians, anurans and urodeles constitute a monophyletic assemblage among those mentioned in this study.

II. SYSTEMATIC AND EVOLUTIONARY STUDIES

In studying any evolutionary aspect of a group of organisms, the observer brings some preconception, however tacit or inchoate, of the interrelatedness of that group. It is desirable, therefore, that a phylogenetic analysis precedes any other type of evolutionary study if the preconception is to be based on substantive knowledge. It is equally imperative that the phylogenetic study itself neither predetermines nor presupposes the results of subsequent

studies. The latter desideratum is the major reason for this work's uncommon preoccupation with systematic methodology.

In what follows, I present a methodology that provides an objective way of answering the questions at hand. In formulating the methodology, I attempt to minimize the number of contingent assumptions about the underlying phylogenetic process so that later, if desired, inferences about the process of evolution can be made without fear of tautogical, or self-contradictory argumentation. I also attempt to minimize the number of assumptions about the interrelationships of caecilians and the other groups in question. In this way no particular relationship is made, a priori, more likely than any other. A particularly important goal is to enunciate an objective, unbiased way to discern primitive from derived characters both within the caecilians and between the groups under study. This provides me with an opportunity to discuss some of the methods for ascribing polarity that are currently in use and to evaluate their validity and the assumptions involved. The methodology is formulated specifically for the problem of caecilian relationships but it is hoped that it can be generalized to other similar problems.

Chapter II contains the discussion of systematic methodology. In the discussion of methodology I claim that cladistics finds its justification in the reductionist programme. A similar point is made independently by Rieppel (1987). Phylogenetic problems are solved by reducing

organisms to a set of characters which are then designated as being primitive or derived. A cladogram is a parsimonious grouping of advanced characters. The assertion that an organism has the same phylogenetic history as its constituent parts allows the information in a cladogram, a grouping of characters, to be extended to a grouping of the organisms that possess those characters.

While the reductionist method justifies cladistics for organising taxa, it may also be the source of cladistics' principal inadequacy. Cladistics deals with characters and their transformations and as such does not yield an understanding of organisms as wholes. Organisms are 'concrete systems'. This means that the component parts of an organism interact, resulting in the emergent properties of that organism (Bunge 1978). Biological functions are classic examples of emergent properties of organisms; they are necessarily the result of interactions of an organism's constituent parts. The reliance of cladistics on characters, rather than on organisms, does not permit one to make inferences about the ways in which characters interact. It is often, however, of considerable interest to biologists to determine how an organism's components function and how those functions confer on the organism its capacity to survive and reproduce.

The final chapter of this work, Chapter IV, attempts to redress the inadequacies of the cladistic analysis. In Chapter IV, the interrelationships of some of the characters used in the actual cladistic analysis, presented in Chapter

III, are quantified. A morphometric study of the unique caecilian jaw and jaw adductor system is undertaken. It is hoped that from this analysis some inferences can be made about the function of the jaw system and its significance in the origin and evolution of caecilians as a group.

CHAPTER II.

SYSTEMATIC METHODS

The first rule was never to accept anything as true unless I recognized it to be evidently such: that is, carefully to avoid precipitation and prejudgement, and to include nothing in my conclusions unless it presented itself so clearly and distinctly to my mind that there was no reason to doubt it.

The second was to divide each of the difficulties which I encountered into as many parts as possible, and as might be required for an easy solution.

The third was to think in an orderly fashion, beginning with the things that were simplest and easiest to understand , and gradually and by degrees reaching toward more complex knowledge, even treating, as though ordered, materials which were not necessarily so.

The last was always to make enumerations so complete, and reviews so general, that I would be certain that nothing was omitted.

Rene Descartes.

I. INTRODUCTION

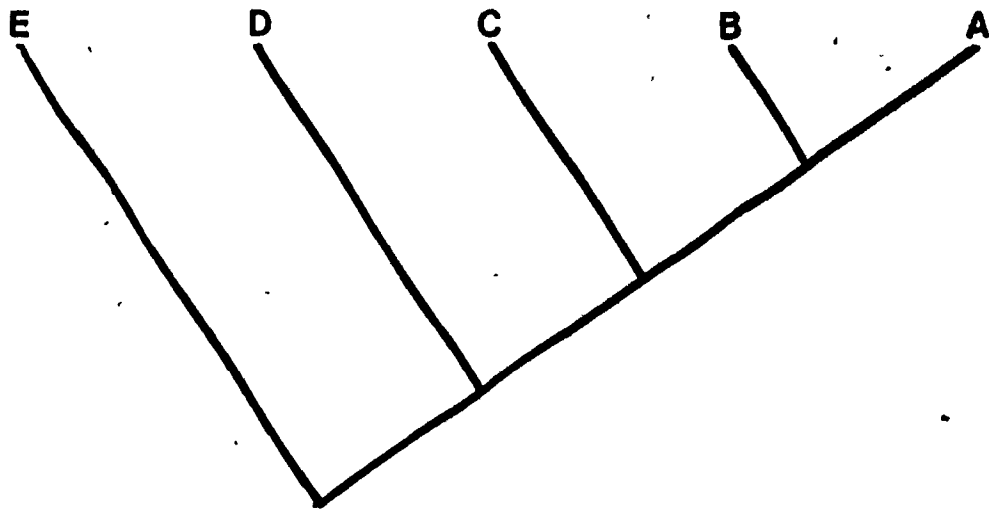
Précis of Cladistics

The principles of cladistics are extremely simple but the recent proliferation of opinions on the method, the meaning, and the utility of cladistics has tended to obscure the central issues. It is a daunting proposition for the non-specialist to abstract a unifying theme from the mass of cladistic literature. For this reason, and because of the plurality of opinions about cladistics within the systematic community, I present an epitome of the systematic method as it is used in this study.

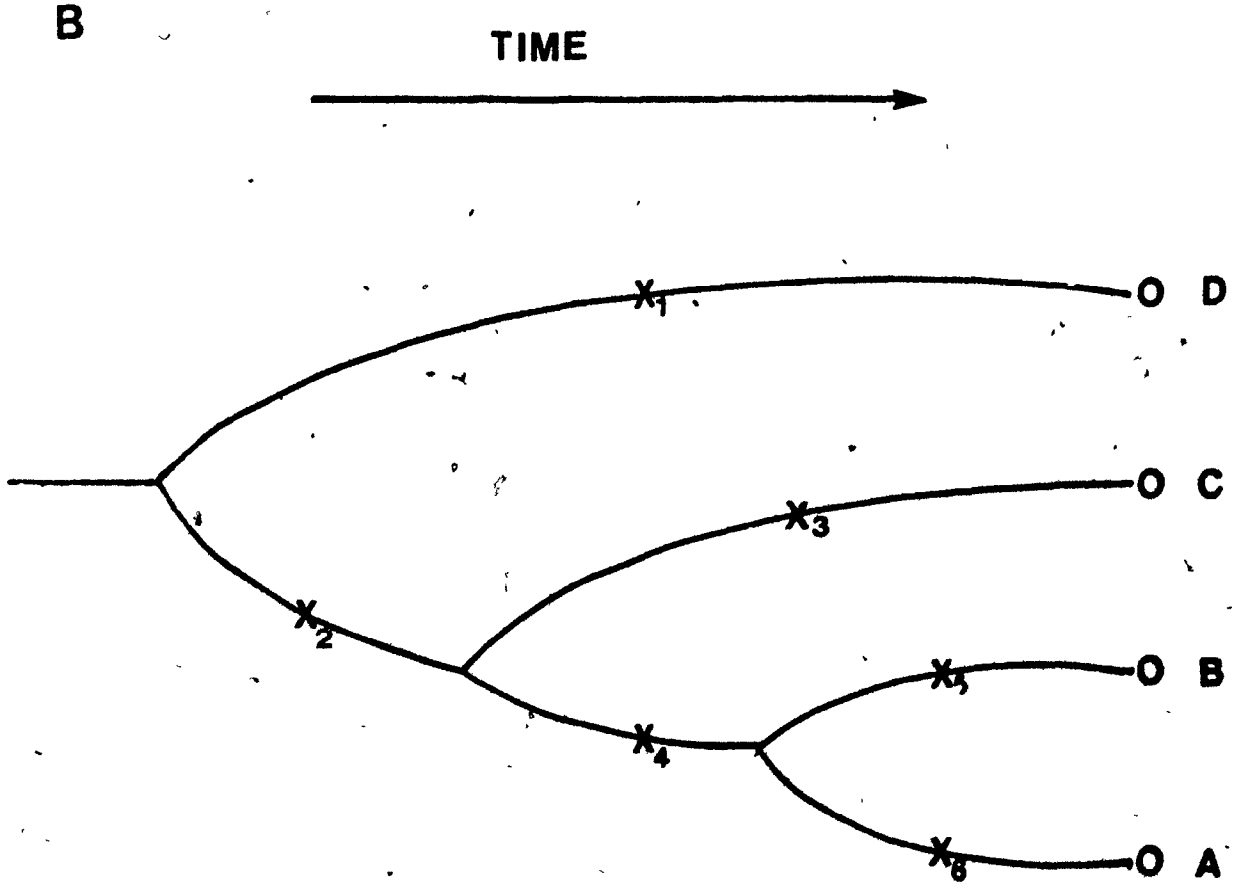
The goal of cladistics is to organise taxa under investigation into a hierarchy of nested sets of increasing exclusiveness (fig. 3a). Unlike other systematic methods, the objective is not to arrange the taxa into genealogies that incorporate ancestry and descent. The nested sets of cladistics are monophyletic groups. The members of a monophyletic group are demarcated by their possession of advanced features known as apomorphies. The significance of apomorphies is that they are inverse indices of generality. This can be clearly explained diagrammatically. Figure 3b shows a set of open-ended, irreversible branching trajectories for objects A, B, C and D. The poihts marked 'X'

Figure 3 A. A cladogram of taxa A,B,C,D and E. A&B comprise a monophyletic group exclusive of all other taxa. B. A set of open-ended, non-reversible branching trajectories for objects A,B,C and D. X marks a point on a trajectory at which a particular attribute of all objects on that trajectory changes.

A



B



designate places where changes occur in particular attributes of all objects on that trajectory. At any given time, those objects that share the largest number of changed attributes are those whose trajectories have diverged the most recently. If the objects in figure 3b are organisms, and the attributes are heritable characteristics, then figure 3b is a cladogram. The changed attributes are the apomorphies. Organisms A and B share apomorphies that are less general than those shared between A, B and C, and so on. Apomorphy X_4 is sufficient to demarcate A & B as a monophyletic group that is exclusive of C and D. Because shared apomorphies (synapomorphies) are indicators of the relative recency of divergence of the trajectories, they, rather than the amount of overall similarity, are the important properties uniting monophyletic groups.

A cladistic analysis is the process of reconstructing the most likely set of branching trajectories for a set of organisms. It comprises the steps of recognising characters, discerning the apomorphies and, grouping organisms on the basis of shared apomorphies.

Cladistics as Reduction

The epigraph of this chapter is a quotation from Descartes' seminal work on the method of scientific inference. This treatise saw the inception of the reductionist research strategy. It is particularly germane to a clear exposition of cladistic analysis. Each of Descartes'

four rules has an analogue in the stages of a cladistic analysis.

First, one establishes the minimum set of assumptions about the nature of the underlying process being reconstructed - "...carefully to avoid precipitation and prejudgement." There are two levels of assumptions needed. The first is the set of minimum assumptions about cladistic inference in general; this needs only to be outlined once. The second is the set of assumptions concerning the phylogenetic relationships of the groups in question and needs to be formulated for each investigation.

The second step, "divide each of the difficulties ... into as many parts as possible", is the analogue of dividing organisms into series of characters. It is the characters that are dealt with directly in cladistic analysis, and not the entire organisms.

The third step is that of resolving characters into apomorphies and plesiomorphies (primitive characters), "beginning with the things that are simplest and easiest to understand." This is the methodologically complex procedure of ascribing polarity. It receives considerable discussion in this paper.

The final step entails choosing between the set of phylogenetic hypotheses suggested by the resolved characters in such a way that one chooses the hypothesis with the maximum likelihood relative to the set of observations - "always make enumerations so complete that nothing [is] omitted." This is

the controversial stage of applying the principle of parsimony. A detailed discussion is beyond the purview of this work, but a cursory overview is given here to describe and justify the type of parsimony argument employed in the systematic analysis.

I shall outline each of these steps below, paying particular attention to the critical step of ascribing polarity. It is first necessary to distinguish cladistics from synthetic systematics in order to explain how the two systems can be compared and to justify my adherence to one in preference to the other.

Synthetic Versus Cladistic Systematics

Most previous hypotheses of higher order relationships of caecilians, and indeed those of lissamphibians and lepospondyls, have been couched in the terminology of evolutionary (synthetic) systematics, although some (Gardiner 1982, 1983; Bolt and Lombard 1985) have taken a cladistic approach. This raises some ambiguity when attempting to compare the conclusions of different authors. It is especially acute when dealing with the make-up of monophyletic groups. For example, the proposal of lissamphibian monophyly put forward by Parsons and Williams (1963) does not specify an appropriate ancestral group although a range of possible candidates is mentioned, nor does it suggest any resolution of ingroup relationships of the Lissamphibia. The contention by

Bolt (1969, 1977) that anurans have descended from dissorophoid temnospondyls fails to discuss explicitly whether urodeles and caecilians are to be included in a monophyletic group with anurans as descendants of temnospondyls. Later works by Lombard and Bolt (1979) and Bolt and Lombard (1984) either hypothesize or assume that this is the case. Carroll and Currie (1975) identify what they believe to be an ancestral-descendant lineage between microsaurs and caecilians but fail to identify what other groups, if any, would be included with the caecilians in a monophyletic assemblage. It is apparent from later works though (Carroll and Holmes 1980; Carroll and Gaskill 1978), that at least one of these authors (Carroll 1987: ch 9) holds that the three extant orders of amphibians are independently derived. Likewise, although Eaton's (1959) hypothesis of caecilian relationships to the lysorophoids specifically excludes the anurans and urodeles as being members of a monophyletic group with caecilians, those of Nussbaum (1983) and Moody (1909) do not. Most of the proposals put forward by synthetic systematists are consistent with a number of cladistic relationships for the groups in question because they either do not specify a primitive sister group (ancestral group) or do not resolve ingroup relations, or both.

Much of this problem stems from the fact that in a synthetic hypothesis of phylogenetic relationship it is sufficient to identify only two taxa, the ancestor and the descendant. It is acceptable to say "A is the ancestor of B".

In cladistics, on the other hand, any proposition of phylogenetic propinquity between two taxa must be a made relative to a third. "A and B constitute a monophyletic group" is uninformative, whereas "A and B constitute a monophyletic group exclusive of C" is informative. (Often "A and B constitute a monophyletic assemblage" is stated with the tacit understanding that this is true relative to all other groups.)

The study of caecilians undertaken here differs from most of its predecessors in its attempt to exploit the methods and principles of cladistic analysis. This raises a problem in that the precepts of cladistic and evolutionary systematics are incommensurable. Cladistics produces cladograms and synthetic systematics produces phylogenetic trees that incorporate ancestry and descent. As hypotheses about the phylogenetic history of a set of organisms, phylogenetic trees and cladograms may appear at first to be much the same thing; they are not. The most important concepts that differ between the two systems are the respective meanings of monophyly, and the distinction between ancestral-descendant sequences on one hand, and sister group relationships on the other.

Monophyly

The standard cladistic definition of a monophyletic group is an assemblage comprising an ancestor and all its descendants (Eldredge and Cracraft 1980). Monophyletic groups are defined by synapomorphies. They are the canonical unit of

cladistic systematics, and only groups meeting the cladistic definition of monophyly can be recognized as natural (Nelson and Platnick 1981). In contrast, the synthetic definition of monophyly does not require that all the descendants of a given ancestor are included in the same monophyletic group. The genealogical tree can be cut arbitrarily and still meet the synthetic requirement of being based on monophyletic groups (Simpson 1961). This produces paraphyletic groups, groups that do not include all the descendants of a given ancestor.The Class Reptilia, in the sense of amniote tetrapods minus mammals and birds, is a classic example of a paraphyletic group.

While cladists rely exclusively on synapomorphy for delineating natural groups, evolutionary systematists employ a component of overall similarity in their classification schemes, recognizing paraphyletic groups as natural assemblages. A monophyletic group, for syntheticists, shares a common ancestor but also is united by a set of adaptive features (Ashlock 1971; Mayr 1974). The major distinction then between the criterion for a monophyletic taxon in cladistic and synthetic systems is that the synthetic system requires common ancestry whereas the cladistic system requires exclusive common ancestry.

Common ancestry in synthetic systematics, as a requirement of membership within a natural group, is clearly subordinate to the requirement of overall similarity. This is evidenced by the fact that if common ancestry had primacy over adaptive unity, the synthetic definition of a natural

group (Ashlock 1971: encompassing both paraphyly and cladistic monophyly), could not exist. The genealogical nexus could not be cut (Mayr 1974) such that an ancestor and its descendants occupied different (non-nested) monophyletic groups (Nelson and Platnick 1981). The utility of the requirement of common ancestry in synthetic systematics is to ensure that the similarities by which groups are defined are homologous.

Ancestors and sister groups

It is generally recognized in cladistics that character phylogenies do not have inherent in them the type of information by which ancestors can be identified (Hull 1979; Platnick 1979) but a group can be designated as a plesiomorphic sister group. The reason for this is that a species or monophyletic group is defined by the emergence of a new taxonomic character (Løvtrup 1977). All other groups, including the ancestor, will lack that character, barring convergence. As a result, the ancestor cannot de distinguished from any other taxon on the basis of the character that defines the descendant. The absence of this character in any group is clearly insufficient evidence for it being designated as ancestor. Evolutionary systematists contend, in contrast, that ancestors can, and should, be identified (Mayr 1974; Szalay 1977).

Choosing between methods

A question arises: if synthetic and cladistic systems

are incommensurable, and the majority of existing studies have been formulated in terms of the former, why choose the latter? There are two reasons for this, the information content inherent in a phylogenetic tree compared to that in a cladogram, and the extent to which each system yields to thorough methodological codification.

The relationship between a cladogram (synapomorphy scheme) and a phylogenetic tree (incorporating ancestral-descendant series) has been discussed by Platnick (1978), and by Sober (1983a, 1985, 1986). The relationship is not reciprocal. Whereas a phylogeny implies one cladogram only, the converse is not true. A cladogram implies a number of phylogenies. A grouping of three taxa resolved by synapomorphies implies a single cladogram. A three taxon cladogram, in turn, circumscribes six possible fully resolved phylogenetic trees (fig. 4).

Both systems employ character similarities in defining groups. It was shown in figure 3b that advanced characters impart information concerning recency of divergence, to a set of taxa. The information content of an array of characters resolved into primitive and derived states suffices only to generate a synapomorphy scheme, not a phylogenetic tree. Additional information concerning the type of tree topology (one of the six shown in fig. 4) and the probabilities of evolutionary change on each branch is required to specify a tree from a character distribution of this sort (Sober 1985). It is evident then that for a given number of taxa, a

Figure 4. The relationship between a cladogram and a set of trees for three taxa. Arrows are ancestral descendant lineages. o=unknown ancestor. Arrows denote ancestral-descendant transitions.

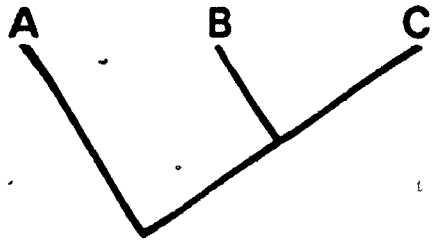
A CHARACTER PHYLOGENY

	A	B	C
STATE	0	1	1

0 = Plesiomorphy
1 = Apomorphy

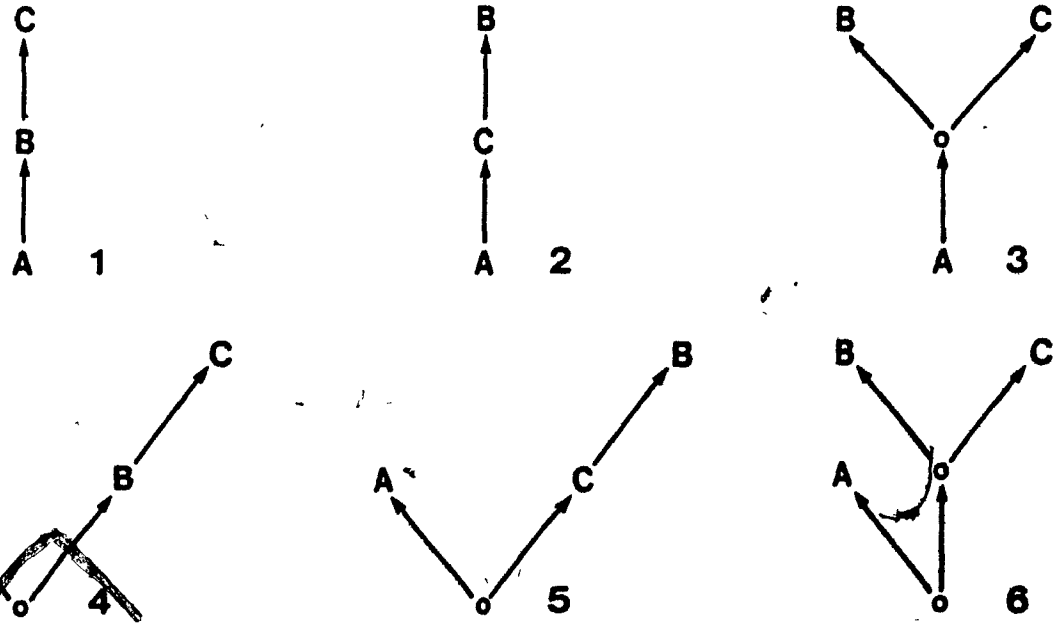
implies

1 CLADOGRAM



implies

6 PHYLOGENETIC TREES



phylogenetic tree has considerably more information content than a cladogram; (where that information might come from is another question entirely). If cladistic and synthetic hypotheses are to be compared, they must be reduced to some commensurable format. Although the precepts of these systems differ, their results can be reduced to a common format, specifically that which contains less information, a cladogram.

The other reason for choosing to present this work in cladistic terms rather than adhering to the methodology of synthetic systematics, is that the method of synthetic systematics has never been rigidly codified. Indeed one of its most ardent proponents, Simpson (1961), claims that the methodology of systematics (his "taxonomy" (pp 9-11)) "is really a combination of a science, most strictly speaking, and of an art" (p 110). The steps by which a phylogenetic hypothesis is arrived at, given knowledge of the anatomy, physiology (etc) of a group are seldom discussed, and when they are it is evident that the methods are largely intuitive and ad hoc. For the plethora of papers extolling evolutionary systematics, none has been able to prescribe precisely how a series of variable characters can be resolved into a most parsimonious phylogenetic tree.

II. PERFORMING A CLADISTIC ANALYSIS

1. Assumptions

One of the often proposed advantages of cladistics is that in reconstructing a phylogenetic history, it makes very few contingent assumptions about the underlying process. According to Sober (1983a,b), there are three assumptions. These are: 1) that probabilities of evolution on each branch are between 0 and 1 (noninclusive). This simply implies that evolution (change of character state) is neither inevitable nor impossible on any branch. 2) Branches evolve independently of one another. This is a relatively innocuous assumption except in the case of character displacement by sister species. 3) On any phylogenetic tree, Pr(1->1) > Pr(0->1) (i.e. that the probability of a branch terminating with the advanced condition (1) of any character is greater if it begins with that character state than if it begins with the primitive (0) condition). Contrary to many criticisms (Felsenstein 1978), the last assumption does not imply either that homoplasy (the independent attainment of advanced features) is rare, or that stasis is more prevalent than evolutionary change (Sober 1985). I see assumption three as making only scant requirements on the process of evolution. It seems simply to be a justification for grouping by synapomorphy. If common possession of derived features were not an indication of probable common ancestry (i.e. if Pr(0->1) $\geq$ Pr (1->1)) then synapomorphy would be invalid as a basis

on which to define monophyletic groups; cladistics would reduce to phenetics. Moreover, assumption three appears to me to be the equivalent of the assumption made by Platnick (1979), and Patterson (1982) that evolutionary histories can best be represented by a hierarchy of nested sets. Granted, this assumes a continuous, irreversible process such as we commonly perceive organic evolution to be (Hull 1979; Beatty 1982; Brooks and Wiley 1985) (fig 3b), but makes no further assumptions concerning the nature or deployment of change within or between groups.

If we are to be able to infer the particulars of the evolutionary process from the reconstructed phylogeny, it is essential that our systematic methodology be as little encumbered as possible by contingent assumptions about that evolutionary process. This is the main advantage of the minimal assumptions required by cladistics.

2. Character Recognition

The characters of cladistics are treated as independent entities. It is not required of characters that they transform independently; it is simply advisable not to constrain, *a priori*, the ways in which characters can associate in a cladogram.

Character weighting has been a much discussed issue in cladistics (Hecht and Edwards 1976, 1977; Neff 1986; Sober 1985; Shaffer 1986). It consists of assigning characters differential values according to their capacity to yield correct phylogenetic inference. The value is usually based on

either the evolutionary lability of a character, or its propensity to transform in association with other characters. Both of these properties, lability and association, can only be determined in an a posteriori way (Sober 1985), but character weighting is a strictly a priori technique. I have chosen not to weight characters. All characters are taken to have equal potential value in reconstructing a cladogram.

3. Character Polarities

A variety of methods have been proposed for determining polarity. I will consider some of the more common ones here. More exhaustive discussions are provided by deJong (1980), and Stevens (1980), both of which differ in many respects from the general approach taken here. My intent is to determine which methods are justified given the assumptions made about cladistic inference. The methods deemed justifiable will be valid for both ingroup and outgroup analysis but some modifications will be necessary for their use in ingroup analysis. The procedures I shall discuss were suggested by Luckett (1980). They include indirect and direct methods of character analysis (after Nelson 1973). The indirect method is outgroup analysis. The direct methods comprise stratigraphic sequence, ontogeny, and functional suites of features. Within the systematic community there is no consensus on the relative merits of each these procedures, so they will be dealt with in some detail.

Indirect observation

Perhaps the most common method of of determining polarity is outgroup comparison, as described by Watrous and Wheeler (1981) and Farris (1973). The outgroup rule states that given a series of homologous character states in a monophyletic group, that state which is found in its plesiomorphic sister group is taken as primitive (i.e. plesiomorphic), whereas that state (or those states) found only in the ingroup are advanced (i.e. apomorphic) (modified from Wiley 1981:139). The assumptions are: that an appropriate outgroup is chosen, and that any character under question has not transformed within the outgroup.

Outgroup analysis is widely practiced in cladistics. Among all methods for inferring character polarities it has received the most complete formulation (Watrous and Wheeler 1980; Maddison et al 1984).

Direct Observations

In addition to outgroup comparison, direct observation of the ingroup can be used to ascribe polarities to characters. Luckett (1980) suggests three criteria: stratigraphic sequence of characters, ontogenetic sequence of characters, and functional suites of features.

Stratigraphic Sequence.

The sequence in which homologous character states occur in the fossil record has been widely employed in differentiating primitive from advanced character states, an

approach strongly advocated by Simpson (1961 :83)

> ...when based on sequences in geological time or when relatable to recent forms, paleontological studies do have a true time dimension and the data are directly historical. In spite of deficiencies in other respects (biased samples, incomplete anatomy, no physiology etc.) fossils provide the soundest basis for evolutionary classification when data adequate in their own field are at hand".

That contention was addressed directly by Schaeffer et al (1972), who maintain that the utility of the fossil record lies solely in attaching a time frame to evolutionary events and that it cannot be used in their reconstruction; "... it is simply wrong to use biostratigraphy to determine polarity a priori. It should not be incorporated into the methodology just because it may be right" (pg. 43; emphasis in the original). But they also state that "the congruence of morphocline and chronocline polarities increases our confidence in the hypothesized phylogeny" (pg. 44). If, as these authors contend, it is wrong to use biostratigraphy "just because it may be right", the congruence of morphocline and chronocline polarities says nothing more than that morphocline polarities also "may be right". If only because of its historical significance, the utility of the fossil record in ascribing polarity deserves more than a facile dismissal.

In contrast to Schaeffer et al (1972), I accept stratigraphic sequence as a legitimate criterion for ascribing polarity, or as a valid potential falsifier of character phylogenies arrived at by other means. The

justification goes as follows. The first appearance of a plesiomorphic state necessarily occurs before the first appearance of its respective apomorphic state or states. One interprets the cladistic grouping (AB)C as stating that taxa A and B share a more recent common ancestor than either shares with C, or more correctly, that the characters that unite A and B exclusively have emerged after their respective states in C. Løvtrup (1977:24) expresses this idea as two of the theorems of cladistics. " No taxonomic character defining the taxon T_j can have originated later than any of those defining the taxa T_{j+1} included in T_j;" and "No taxonomic character defining the taxa T_{j+1} included in T_j can have originated earlier than any of those defining T_j." Cladograms based on character phylogenies derived by non-paleontological methods (e.g. outgroup comparison) have implicit in them a time component, that is recency of common ancestry (Hennig 1966) or, perhaps more accurately, relative recency of emergence of apomorphies (Hull 1979). The time component of a cladogram generated by such a method is not a result of direct observation but is a function of the distribution of character states. The time component in a character polarity taken from the fossil record is independently derived; it is read directly from the stratigraphic sequence of characters. In this respect, the stratigraphic sequence of characters is an appropriate, independent means of designating polarity.

Stratigraphic position (the 'paleontological argument') as a criterion for ascribing polarity was also

disparaged by Nelson (1978) as not being falsifiable and thereby having no information content. I do not see the relevance of Nelson's (1978) contention that the paleontological argument is protected from falsification by ad hoc hypotheses. As one example of such, he seems to claim that given the notorious incompleteness of the fossil record, it is highly unlikely that the correct earliest character state can be known. He maintains, furthermore, that cases in which a previously held polarity based on the fossil record is overturned by the discovery of new fossil material are adequate to falsify the paleontological argument. This is an erroneous conclusion. A method of phylogenetic inference is not impugned by the fact that an incorrect observation can favour an incorrect hypothesis (Sober 1985). Elementary deductive logic tells us that a valid argument may have a false premise and a false conclusion. The recognition of this potential source of error is not an ad hoc hypothesis in its defence. The admission that an observation may be misleading is not an admission that the form of argumentation is invalid. Nelson appears to conflate the ideas of the legitimacy of a method of phylogenetic inference and the reliability of the observations on which the inference is made. For the paleontological argument itself to be fallacious would require that given the correct sequence of characters in the fossil record, the method could favour an incorrect hypothesis about which is primitive and which is derived.

Any merit to be found in Nelson's criticism of the

use of paleontology, then, must revolve around the question of the reliability of the fossil record itself. It is widely acknowledged that the fossil record is incomplete. This does not necessarily imply that it is more often than not misleading. Paul (1982) convincingly demonstrates that there is a high probability of species and, by extension, characters being preserved in the correct temporal sequence in the fossil record, irrespective of its completeness. This allows one to postulate that those states of clinal characters that occur earlier in the stratigraphic sequence are the actual precursors of those appearing later.

I do not claim that the paleontological argument is infallible. I do claim that a valid method needn't be. It is sufficient grounds for rejecting a method of phylogenetic inference if the observations are 'positively misleading' (Felsenstein 1978). That is that as the number of observations become indefinitely large, they tend not to favour the correct hypothesis (Felsenstein 1978; Sober 1983b). I infer from Nelson's scepticism of new fossil evidence that he would impute this property to the fossil record. However, Paul (1982) demonstrates that more often than not the fossil record will yield the correct polarity, and will do so increasingly frequently as it becomes more complete.

It was proposed by deQuieroz (1985), that polarizing characters by the use of the fossil record is a special case of outgroup comparison and should be subsumed under it. The

paleontological argument, unlike outgroup comparison, does not require an assumption of relationships beyond the ingroup in question. Quite simply, within a monophyletic assemblage, those character states occuring first in the fossil record are postulated to be the genealogical antecedents of cognate character states appearing later. I conclude that the stratigraphic sequence of characters is an appropriate criterion for ascribing polarity. I do not accord it primacy. The evidence of the fossil record vis a vis individual character polarities does not take precedence over countervailing evidence provided by outgroup comparison. Similarly, outgroup comparison does not take precedence over stratigraphic sequence.

Ontogenetic sequence

The utility of the ontogenetic criterion has been one of the most discussed aspects of phylogenetic reconstruction of late (Nelson 1973, 1978, 1985; Stevens 1980; deJong 1980; Fink 1982; Patterson 1982, 1983; Bonde 1984; Brooks and Wiley 1985; Kluge 1985; deQueiroz 1985). Nelson (1978) and Patterson (1982, 1983) have argued for the primacy of the ontogenetic criterion in polarizing characters based on Von Baer's second law, which states that development proceeds from the more general to the less general (Garstang 1922; Gould 1977: 61-3). Nelson (1978) claims that if development proceeds from more general to less general, then:

> "given an ontogenetic character transformation, from a character observed to be more general to a

character observed to be less general, the more general character is primitive and the less general character is advanced."

In contrast, Kluge (1985) has contended that the ontogenetic criterion is simply a special case of outgroup comparison. Brooks and Wiley (1985) also claim that "[d]irect observation of ontogeny does not resolve any cases of evolutionary change in ontogeny that outgroup comparisons fail to resolve and outgroup comparisons resolve cases which direct observations fail to resolve." A somewhat similar interpretation is given by Stevens (1980). The use of ontogeny is rejected outright by deJong (1980), except as a provisional method of polarizing characters when none other is applicable.

These issues require further discussion, but for the purposes of this paper it should be noted that the literature pertaining to caecilian cranial anatomy, and to that of fossil and recent amphibians is predominantly concerned with the instantaneous morphology of adults ("semaphoronts" sensu Hennig 1966). This restricts the characters available for analysis to adult morphologies. The issue here in assessing the utility of the ontogenetic criterion is the confounding effects of heterochrony when phylogenies are based on instantaneous morphologies. During development of an organism, ontogentic sequences can be altered in any of a number of ways such that the resultant final morphology is different from that of its ancestors. The types of changes have been formalized in slightly different ways by DeBeer (1940), Løvtrup (1974: 305) and Alberch et al (1979). Without

direct observation of both ancestral and descendent ontogenies, it cannot be determined which type of heterochronic event has brought about the change. Contrary to Nelson's (1978) proposition, heterochrony (his neoteny) cannot be assumed a priori, thereby nullifying all criteria except ontogeny. Rather, as Kluge (1985) points out, heterochrony can only be discerned if a phylogeny is presumed.

Examples of the problem heterochrony poses to ascribing polarity to instantaneous characters are given by Rieppel (1979) for the articulation of vertebral centra, and the configuration of the trabeculae in the braincase of squamates (his views are rebutted by Bonde 1984). An apt illustration is also found in the development of the caecilian skull roof. The dermatocranium can be observed, in some forms, to undergo closure during development (Wake and Hanken 1982) as a result of the concrescence of dermal anlagen (DeBeer 1935), yielding the closed (stegokrotaphic) condition in adults. In others closure does not occur, resulting in the open (zygokrotaphic) condition. Thus in all closed-skull forms zygokrotaphy has existed at some stage in development. The open skull condition is more general as it is present in the development of both skull types and must have been manifest in the latest common ancestor at some stage in development. By Nelson's (1974) dictum, the open skull roof is correctly taken to be plesiomorphic. That does not make it plesiomorphic for all semaphoronts. The question

becomes one of whether the ontogenetic transformation zygokrotaphy -> stegokrotaphy is plesiomorphic, and zygokrotaphy -> zygokrotaphy the result of terminal deletion, or conversely, whether zygokrotaphy -> zygokrotaphy is plesiomorphic and zygokrotaphy -> stegokrotaphy the result of terminal addition. If, as argued by de Queiroz (1985), the ontogenetic transformation (rather than the instantaneous state) is the character, then we have two characters of equal 'generality': i.e. 1) zygokrotaphy -> stegokrotaphy and, 2) zygokrotaphy -> zygokrotaphy.

The implicattion of the skull roof example is that when concentrating on the phylogenies of instantaneous adult morphologies, direct observation of ontogenies itself has no utility in ascribing polarity. It is not necessarily a special case of outgroup comparison (Kluge 1985), nor as Fink (1982) asserts, can it be used to augment taxonomic information gained by outgroup comparison. More correctly, ontogenetic transformations are themselves characters which must be polarized by other methods. The method is usually, but not necessarily, outgroup analysis, as ontogenetic series are exceptionally rare in the fossil record. The ontogenetic method as usually outlined (for example by Szalay 1977) will not be employed in this study. Developmental sequences will only be used in cases where it is important to distinguish between loss and fusion of elements, or differential patterns of fusion of elements.

Functional suites of features

Hecht and Edwards (1976,1977) maintain that closely integrated characters, or covarying suites of features have high information content in reconstructing phylogenies. In their weighting system functional suites are considered as having high weight because they reduce the probability of misinterpreting a transformation series as a result of homoplasy. The rationale behind this, presumably, is that if features are seen to correlate closely, or form an integrated functional unit, and polarity can be ascribed to one such component, then the other constituents of the suite can also be differentiated into primitive and advanced states. Frost (cited by Sporne 1956) ascribed the propensity for advanced states of functionally related characters (his "homogeneous tissues") to be correlated with one another to the fact that their evolutionary rates would be coupled.

There are a number of problems with this approach. The first, and most crucial, is that it is not by itself a method for determining polarities of transformation series. At least one character of the suite must be amenable to some other method of analysis in order that plesiomorphies and apomorphies be distinguished. The second criticism involves the demarcation and weighting of characters. In terms of functional suites, if what are perceived as separate characters are inextricably linked such that a change in one character necessarily effects a concomitant change in the

others, they are more correctly considered as composing a single character. Repeated use of that character would be redundant. If the constituent characters of a suite do not covary exactly but simply are seen to correlate somewhat closely with one another then they cannot be considered simultaneously as a suite of features. In fact, by doing so, one would ensure that eventually a transformation series would be assigned the wrong polarity. In this sense functional suites of features are 'positively misleading' (Felsenstein 1978).

Adaptive suites of features are dealt with by Sporne (1956) in a discussion of the 'principle of correlation' (see Congruence Characters below), who points out, furthermore, that adaptive suites of features are particularly susceptible to convergence.

My contention is that integrated suites of features have no special utility in ascribing polarity to transformation series. If features are linked, but only in a probabilistic way, then they should be treated as independent characters. If they are inextricably linked, they should be treated as one character. The argumentation used in polarizing functional suites of features is not valid but its obverse, the congruence method discussed below, is valid.

Summary of polarity methods

In summary of the character analysis phase, outgroup comparison, and the stratigraphic sequence of character states are acceptable, independent criteria for polarizing

characters. They will be applied whenever possible in distinguishing primitive from advanced states in caecilians. Direct observation of ontogenetic sequences is not a method of polarizing characters but instead is one of demarcating them. Polarity cannot be established by use of what is standardly called the ontogenetic criterion. Functional suites of features have no special claim to high information content, and have no utility in ascribing polarity.

4. Cladogram Construction

When all character transformations univocally support one cladogram, constructing a cladogram from a set of transformation series poses no problem. This, unfortunately, is seldom the case. When there is conflicting evidence from character transformations, it is necessary to choose between the cladograms suggested by the observations. The principle of cladistic parsimony is employed in doing so.

Parsimony was proposed as an auxilliary principle of phylogenetic inference by Hennig (1966: 122). He argued that homoplasy (the independent derivation of advanced character states) should not be invoked unless evidence requires it. Hennig's auxilliary principle is often misconstrued as requiring that homoplasy is rare and hence represents an unwarranted restriction on the evolutionary process (Felsenstein 1978). There is, however, a distinct difference between minimizing the required homoplasies and requiring that homoplasies are rare (Farris 1983). The former, Hennig's

principle, is the sense in which parsimony is applied here.

In a series of papers, Sober (1983a,b. 1985, 1986) has developed a likelihood justification for parsimony that requires only the minimal assumptions of cladistics. It states that the most parsimonious hypothesis is the one that confers maximum likelihood on the observations (Sober 1983a). Cladistic parsimony is strictly a methodological concept that addresses the amount of evidential support of an hypothesis relevant to a set of observations. It does not make contingent statements about the process of evolution. The way in which evidential support for a cladogram is assessed is by determining the number of homoplasies. The cladogram requiring the fewest homoplasies is the most parsimonious and is therefore the most likely given the set of observations.

III. SPECIAL METHODOLOGICAL CONSIDERATIONS IN CAECILIAN SYSTEMATICS

Determining the phylogenetic relationships of caecilians actually requires two separate cladistic analyses. Customarily, when one wishes to determine the higher level relationships of a monophyletic group, the known ingroup relationships are employed in determining the morphotype (or stem species) of the group (Novacek 1980), which is then compared to the potential sister groups. The morphotype is simply the totality of plesiomorphic features. It may or may not be coextensive with any known member. Conversely, if one wishes to estimate the nature of the stem species of a monophyletic group, or resolve the ingroup relationships, the known or presumed sister group is employed in ascribing polarity to ingroup characters. The particular problem in caecilian systematics is that neither the morphotype nor the primitive sister group is known. Hence cladistic analyses of both the ingroup and the outgroup are necessary and they must be performed sequentially. The ingroup analysis will be performed first. From it, the cranial anatomy of the stem species caecilian will be inferred. The stem species caecilian will then be compared to the potential sister groups. It is of particular importance that the ingroup analysis neither presupposes nor predetermines the outgroup results, and vice versa. This requires some methodological

modifications to the techniques outlined in this chapter. Previous studies of caecilian relationships, both outgroup and ingroup, have not paid due attention to this problem.

Modifications of Outgroup Comparison

The outgroup method was discussed above as a widely used and powerful technique for ascribing polarity. Despite its apparent robustness it does presuppose knowledge of the primitive sister group in order that ingroup polarities can be resolved (Stevens 1980). In the case of caecilians, though, the sister group is not known. Clearly, the required progression from known (sister group) to unknown (polarities of ingroup characters) is the reverse of that outlined above for outgroup analysis, where ascription of polarity must precede designation of a sister group.

The fact that the outgroup chosen predetermines the polarity of characters, which in turn is used to designate a plesiomorphic sister group, has been overlooked in taxonomic studies of caecilians thus far. When utilized in this manner, there is an inherent circularity in outgroup comparison. As an example, should the investigator choose to assign a lissamphibian or protolissamphibian outgroup as have Parsons and Williams (1963), the fenestrated (open) condition of the skull would be taken as primitive (Wake and Hanken 1982). Conversely, if Paleozoic microsaurs are nominated (Carroll and Currie 1975), stegokrotaphy (the closed-skull condition),

would just as correctly be chosen as the primitive state. These are equally plausible, if opposite, designations of polarity but in each case the outgroup chosen proscribes the eventual designation of the other as the sister group.

Notwithstanding the problems that outgroup comparison pose to the type of study proposed here, the method is sufficiently robust that with some modification it can be used in establishing polarities for the purpose of stem species reconstruction. In cases such as this, where there are a number of hypothesized sister groups, outgroup comparison can be salvaged by making two modifications. First one need only assume a higher level relationship (Nelson 1973) rather than a sister group relationship, thereby designating a larger than usual outgroup and, second, restrictions must be placed on the types of characters that outgroup comparison can be used to polarize. I shall attempt to explain these modifications in some detail.

Modification 1: For the purposes of this study, the phylogenetic assumptions will be: 1) tetrapods are a monophyletic assemblage (Szarski 1977), 2) rhipidistian crossopterygins are the plesiomorphic sister group of the tetrapods (Holmes 1985). Within these assumptions, the anamniote tetrapods minus caecilians are the most appropriate outgroup for both the character analysis and the subsequent designation of sister groups. Thus, for any clinal character within caecilians, that state present in the anamniote tetrapods can be taken as the primitive condition for caecilians.

It might be argued that the anamniote tetrapods minus caecilians encompasses such a diversity of forms that almost all caecilian character states, both primitive and derived, would be represented in one outgroup member or another, and that those character polarities that could be resolved would simply be tetrapod plesiomorphies shared with rhipidistians. An enumeration of tetrapod plesiomorphies would appear to be of little assistance to a taxonomic study of such a derived group as the caecilians. These problems can be circumvented. The choice of this outgroup is defensible for two reasons. Given the assumptions about tetrapod relationships, the anamniote tetrapods are the most exclusive outgroup known: 1) to encompass the proposed sister groups and, 2) to form a sister group relationship with the lineage in question. The validity of the latter point, that a group and its outgroup should constitute a natural assemblage is self evident. That the outgroup should encompass all proposed sister groups is a special requirement of the problem at hand, and requires further explanation. Normally in a procedure where outgroup comparison were employed, the outgroup would circumscribe the set of possible sister groups (usually a set of one). Any group falling outside the outgroup could not be considered a potential sister group. The specific problem as formulated in this study is one of comparing the relative likelihoods of a number of alleged sister group relationships. As the anamniote tetrapods are the most exclusive taxon that includes all proposed sister groups, it is the appropriate

outgroup.

Modification 2: Notwithstanding the legitimacy of the anamniote tetrapods as the outgroup, the inherent circularities have not yet been removed. Furthermore it still leaves us with a huge and unwieldy outgroup. The tendency for the outgroup method to resolve only tetrapod plesiomorphies introduces a bias in the character analysis. This bias would favour the most plesiomorphic putative sister group when later ascribing relationships. Once again to use the example of skull fenestration, assume that lissamphibians are a natural assemblage, and that the open skull condition is a lissamphibian synapomorphy, making zygokrotaphy plesiomorphic for caecilians and stegokrotaphy derived. The type of outgroup analysis advocated here would result in the reversal of the true polarity, i.e. the closed condition of the skull would be taken to be primitive on the basis of the closed (stegocephalian) skull of the primitive tetrapods. The open skull condition would be taken as an apomorphy shared between anurans and salamanders but not with caecilians. Zygokrotaphy in caecilians would be seen as convergent, thereby obscuring the true polarity. For this reason a caveat is required: no character state can be designated as the primitive caecilian condition by application of the outgroup rule unless it is present, or is universally absent, in all proposed sister groups. In the above example the condition of the skull roof is disallowed. This stricture substantially reduces the number of characters available for outgroup analysis but it is necessary in order to preserve the objectivity of the

method.

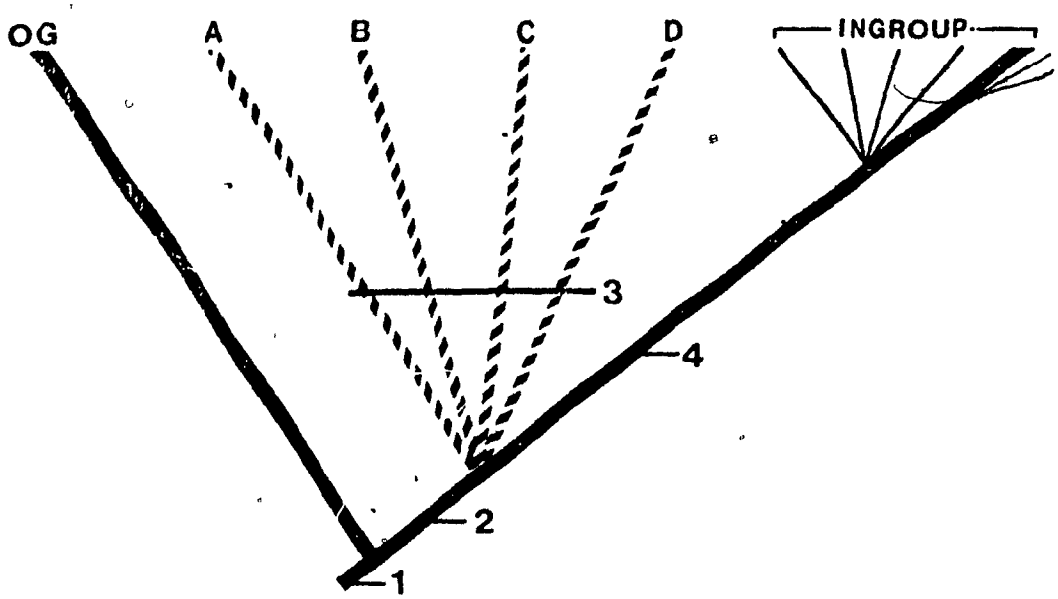
In effect, the modified outgroup procedure serves only to enumerate four categories of characters (fig. 5a): 1) tetrapod plesiomorphies of caecilians shared by all proposed sister groups, 2) tetrapod plesiomorphies of caecilians shared by none of the proposed sister groups, 3) synapomorphies of caecilians and all proposed sister groups above the level of primitive tetrapods and, 4) caecilian autapomorphies. The types of characters that can be polarized are uninformative in resolving the relationships between the potential sister groups (A,B,C,D) and the ingroup. The fact that these characters do not have any information content in resolving relationships between outgroups, ensures the method's objectivity in establishing polarities of the ingroup, without predetermining sister group relationships.

Modification number two also explains the necessity of limiting the number potential sister groups to be considered. In Figure 5a, the potential sister groups (A,B,C, and D) are depicted as representing a polychotomy. This is not an hypothesis of their interrelationships, rather it is a graphical convention designating that their interelationships are not known. Their true phylogenetic relationships can be any possible permutation, as long as all groups are connected, directly or indirectly, to the main axis (the line extending from the root to the ingroup).

When the condition found in the ingroup is variable, three of the four types of characters that the outgroup

Figure 5. The modified outgroup argument. Taxa A,B,C and D are potential sister groups of the ingroups, whose interrelationships are unknown. A. Characters with the distributions given for 1,2,3 and 4 are the only types of characters that can be polarized by this outgroup comparison. Note from the distribution of character states that these characters have no information content in discerning relationships between the outgroups. OG=outgroup IG=character state in stem species of ingroup.
B. The effect on ingroup polarity determination of the addition ofan extra potential group E. As for A, where E. IG=distribution of character states within the ingroup. 1' and 1" are alternate apomorphic states of character 1.

A



Character State Distribution

	OG	A	B	C	D	IG
1	0	0	0	0	0	0
2	0	1	1	1	1	1
3	0	1	1	1	1	0
4	0	0	0	0	0	1

B

Character State Distribution

	OG	A	B	C	D	E	IG
1	0	0	0	0	0	1	0,1
2	0	1'	1'	1'	1'	1"	1',1"
3	0	1	1	1	1	0	0,1
4	0	0	0	0	0	0	1

comparison can resolve are directly affected by the number of potential sister groups chosen. These are characters 1, 2 and 3 in figure 5a. If an extra unknown group (E) were added that had the plesiomorphic state for character 3 (fig. 5b), then character 3 could not be used in the analysis, not because taxon E would be linked with the ingroup, but because on the basis of taxon E, character 3 would be discounted as a possible apomorphy of A,B,C and D with the ingroup, whether or not the apparent zero states in E and the ingroup are homologous. This is the same argument given earlier for disqualifying the character of skull roof condition in caecilians from outgroup comparison. If taxon E (fig. 5b) had an alternative apomorphic state of character 2, character 2 would be disqualified because the condition in the stem species of the ingroup could not be discerned. And similarly, if taxon E were to possess the the same apparent apomorphic state of character 1 as found in some ingroup members, then the apparent apomorphic states (1) would be taken as being homoplasies and the zero state of the ingroup taken as primitive, whether or not the 1 states of E and the ingroup are the result of common ancestry.

The foregoing discussion shows that any character for which all the potential sister groups do not share the same character state is to be disqualified. The addition of an extra potential sister group diminishes the probability that this condition will be met by any character. Every character for which the condition is violated by the addition of an extra sister group is one less outgroup character that can be

utilized in polarizing ingroup characters. For that reason it is advisable to restrict the set of potential sister groups.

In circumscribing the set of potential sister groups, I have relied upon previous hypotheses of caecilian relationships. As discussed in chapter I, there are a number of studies that document the characters shared between caecilians and a variety of other tetrapod groups, and propose their close relationships. All of the groups that I have chosen as plausible sister groups of caecilians have been proposed as such by previous authors. For each group, one or more of the following three conditions obtains. 1) The proposed group has been hypothesized to be ancestral to, or the primitive sister group of caecilians. 2) The proposed group and caecilians are hypothesized to be members of a monophyletic group whose interrelationships are not resolved. 3) The proposed group is part of a cladogram, and is the sister group of a monophyletic group containing caecilians, where caecilians are the sister group of all other members. (unless the proposed group is the outgroup that has been used for ascribing polarity). The criteria for sister group choice do not imply that this study intends to test the relative merits of all previous hypotheses. Rather, the criteria themselves were chosen to delimit the set of groups with the highest likelihood of being the caecilian sister groups, based on what is known of their cranial anatomy. The arbitrary addition of any other group would tend to undermine

the strength of the inference made about the nature of the primitive caecilian.

Congruence Method

The principle of congruence was formulated (although not so named) by Kluge and Farris (1969). It claims that "[t]he primitive state is likely to be associated with states of other characters known from other evidence to be primitive" (pg. 5). It is considered distinctly less robust than outgroup comparison and the statigraphic sequence of characters by most authors. Although it has fallen into disrepute with most systematists (deJong 1980; Stevens 1980 and references therein), I shall reformulate and employ the congruence principle as a secondary method. Its utility comes in further refining the reconstructed stem species and in further resolving ingroup relationships. It can be used only after a stem species and, if different, a most primitive known ingroup member are designated. As a secondary method it can not overturn any polarities arrived at during the morphotype reconstruction.

Sporne (1948, 1956) showed empirically that the inferred primitive states of characters were significantly more likely to be found with other primitive characters than with derived characters. This he called the 'principle of correlation.' Unlike previous authors, Sporne interpreted this simply as a reflection of the fact that in any monophyletic lineage there is at least one member that

possesses only and all plesiomorphies for that lineage. Whereas the probability of plesiomorphies being associated is a necessary condition of phylogenetic relationships and will obtain in any monophyletic group, the same is not true of apomorphies.

The rationale for employing what I shall call the congruence principle is similar in some respects to Sporne's probability argument. If morphotype construction decisively favours one ingroup member as being close to the plesiomorphic condition, then the supposition can be made that the character states that it manifests, in addition to those resolved by stem species reconstruction, are also primitive. It functions essentially by designating the morphotype and, if different, the most primitive known member as a new outgroup and the rest of the lineage as the ingroup. It requires the assumption of no transformation between the morphotype and the most primitive known member for the character in question. In this regard it is as robust as outgroup comparison. It carries the same assumptions as outgroup comparison and is undermined by the same conditions (i.e. that an inappropriate outgroup is chosen, that the character state in the outgroup is an apomorphy, or the character transforms between the outgroup and the ingroup). It is less robust than outgroup comparison only to the extent that it involves two inferences of polarity applied sequentially. The first can be either a stratigraphic sequence argument or an outgroup argument. The second is, in

effect, an outgroup argument. The soundness of the second argument (congruence method) is predicated on the soundness of the first. In light of the restrictions placed on outgroup comparisons for this study, there will be a number of disqualified characters that can be polarized by this method.

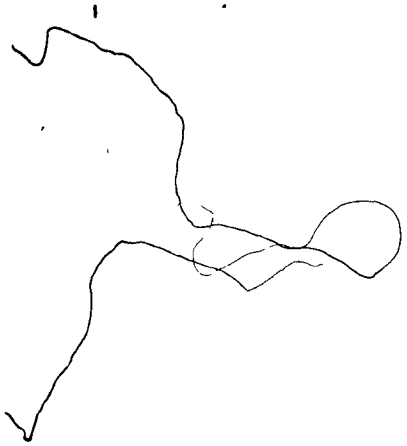
IV. SUMMARY

A phylogenetic analysis is performed in four stages. The assumptions are first outlined. The taxa in question are divided into characters. The characters are polarized. Cladistic groupings are then made from the shared apomorphies. As such the method of cladistic analysis fits the paradigm established by Descartes for conducting scientific enquiry.

The critical stage of cladistic analysis is that of ascribing polarity. The outgroup method and the stratigraphic sequence of characters are designated as the correct methods for polarizing characters of instantaneous morphologies.

Caecilian systematics actually poses two distinct problems, one of discerning ingroup relationships and the other of determining outgroup relationships. Neither analysis, ingroup nor outgroup, must be permitted to predetermine or presuppose the results of the other. In light of this, the outgroup method for polarising characters

requires two modifications. In addition, a secondary method of ascribing polarity, the congruence method, is adapted for the purpose of reconstructing the putative stem species and further refining ingroup relationships.



CHAPTER III.

THE PHYLOGENETIC RELATIONSHIPS OF THE GYMNOPHIONA

INTRODUCTION

The methods of polarizing characters recommended in chapter two are applied to the characters of the cranial osteology of caecilians and the proposed sister groups. The phylogenetic assumptions required for this process are: 1) that tetrapods are monophyletic, and 2) that all groups employed in the analysis are monophyletic.

An introduction to the anatomy and classification of caecilians will be followed by an overview of the anatomy, classification and stratigraphic range of the proposed sister groups.

I. CAECILIANS

Caecilians are the least well known of the modern amphibian orders. They are pantropical in their geographic distribution. They are usually fossorial or semifossorial but one family, Typhlonectidae, is entirely aquatic. The body is extremely elongate, with a large number of annuli. There are no traces of limbs or girdles. The vertebrae are unipartite, and unique in their possession of paired odontoid-like processes projecting anteriorly from their ventral margins.

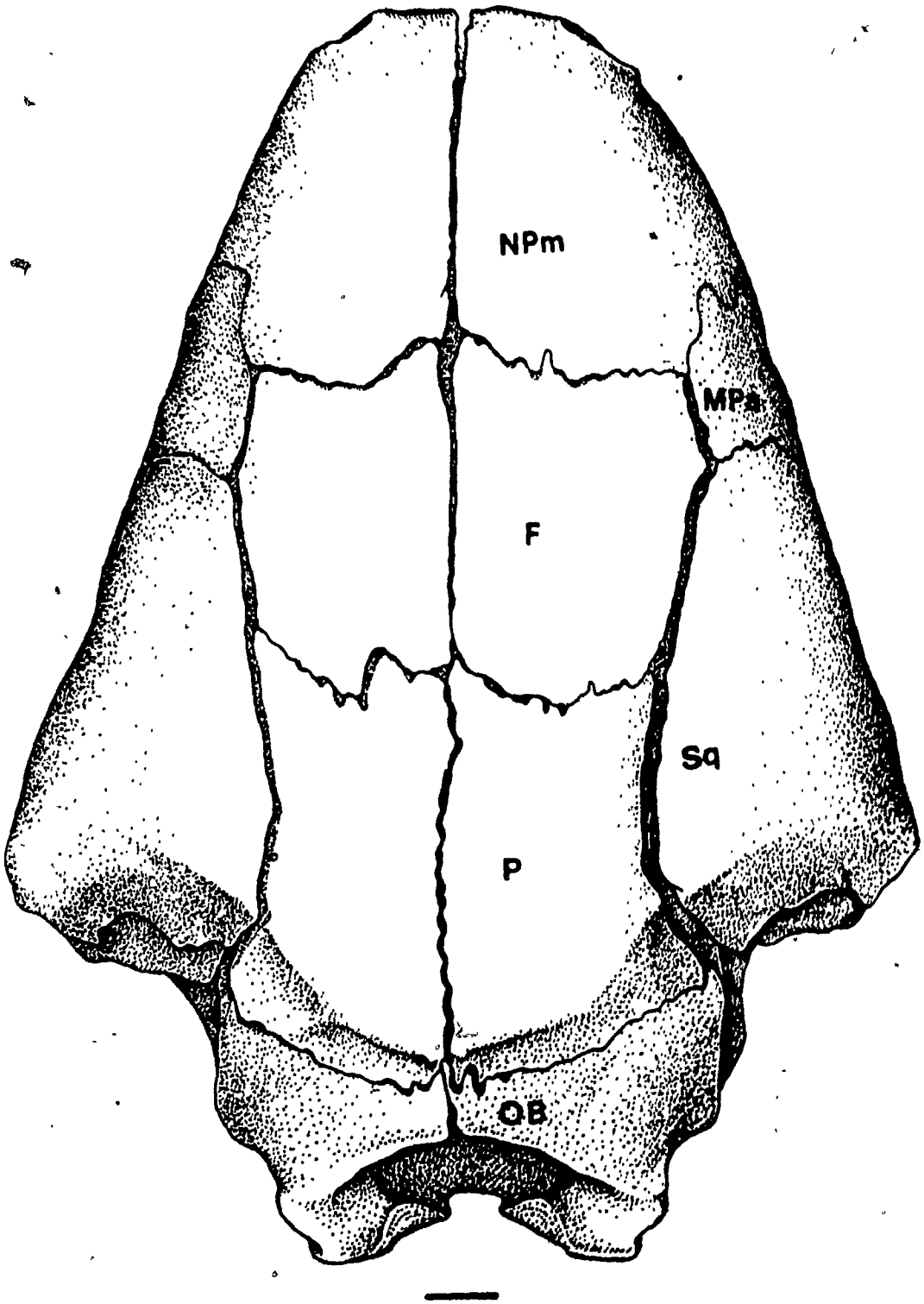
The highly derived cranial anatomy is structurally and functionally divergent from that of any other tetrapods.

Cranial Anatomy

Several thorough descriptions of caecilian cranial anatomy are available (Weidersheim 1879; Marcus et al 1935; DeVilliers 1932, 1938; dejaeger 1938,1939a,b,c; Ramaswami 1941, 1948 a,b; Brand 1956; Els 1963; Visser 1963: Taylor 1969). Straub (1985) gives a concise review of the descriptive literature. Thus, I shall provide only a general overview.

In general appearance, the caecilian skull is small and terete. It tapers gently anteriorly from its widest point at the craniomandibular joint, usually ending in a rounded or slightly flattened snout. Loss and fusion of elements is a major feature of caecilian cranial anatomy. The posterior border of the skull table is formed by the large paired parietals. There is no parietal foramen. Paired frontals are found anterior to the parietals. A mesethmoid element may or may not intervene between the paired frontals at their anterior extremities. Paired frontals and parietals are present in all caecilians (Figure 6). Here the uniformity of the skull roof ceases. The rest of the dermal skull roof is highly variable between genera. The anterolateral portion of the skull roof is usually formed by a nasopremaxilla, which is thought to incorporate the nasal, premaxilla (as the name implies) and sometimes the septomaxilla. In some genera all

Figure 6. Caecilian skull, dorsal view.
Gymnopis multiplicata CNHM 15026
Scale bar = 1mm


NPm
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OB

three elements are separate and border the external naris. In others, the septomaxilla is fused with the nasopremaxillary unit. A combination of the maxilla and palatine, the maxillopalatine, forms the lateral and ventrolateral (palatal) portion of the skull. Fusion of the maxilla and the palatine is universal in the order. Brand (1956) thought that they were discrete elements in Scolecomorphus, but this is evidently not so (Nussbaum 1985). The maxillopalatine may or may not include the prefrontal. The prefrontal, when present, is a larger structure than its counterpart in most tetrapods. Behind the maxillopalatine is a large cheek unit called the squamosal. It usually reaches from the parietal dorsally to the ventral cheek margin, but there are exceptions such as Rhinatrema and Epicrionops (Nussbaum 1979a). The cheek unit is bordered posteriorly by a lateral exposure of the quadrate.

A fenestra sometimes intervenes between the squamosal and the parietal. It is often quite extensive and in one family, Rhinatrematidae, permits the extrusion of the jaw adductor musculature. As will be discussed, the nature and significance of this fenestra are the subject of considerable controversy (fig. 6).

The palate of caecilians is highly derived (fig. 7). Most conspicuously, there are two well developed rows of teeth separated by a space. The lateral row on the maxillopalatine and nasopremaxilla corresponds with the marginal dentition of other tetrapods. The inner row, shared by the maxillopalatine and vomer, is developed to a degree not

Figure 7. Caecilian skull dorsal view. *Gymnopis multiplicata* CNHM 15026 Scale bar = 1mm.

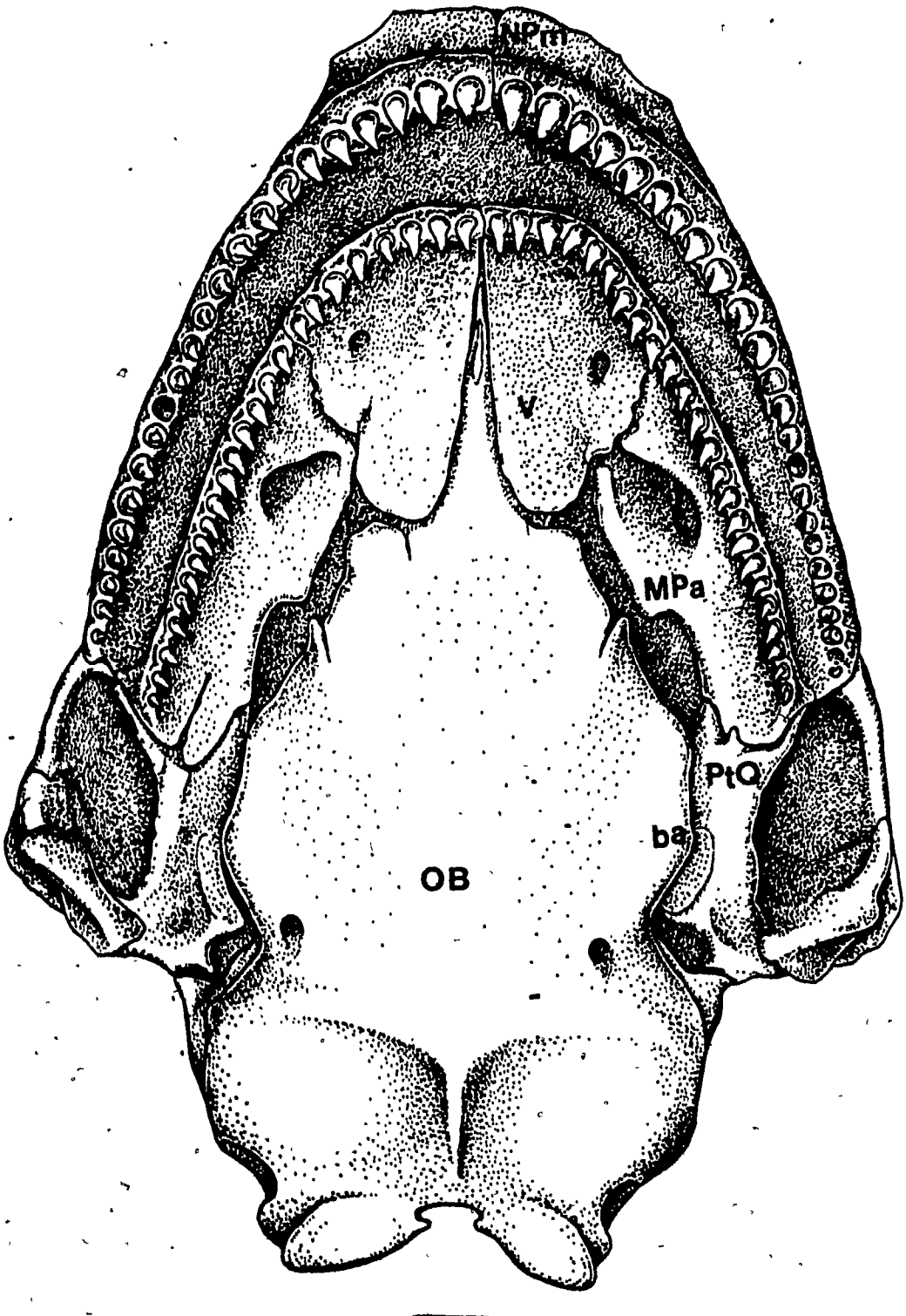
NPtt
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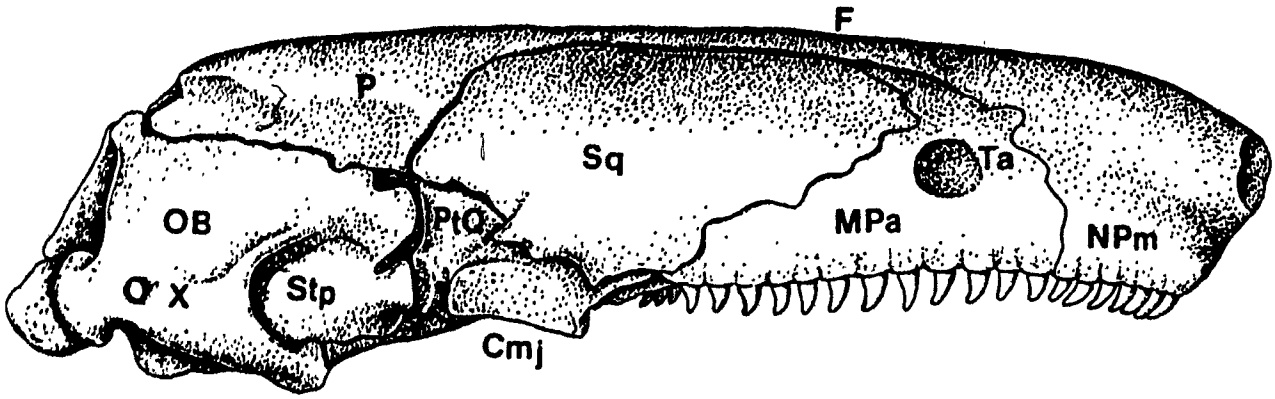
Figure 8. Caecilian skull, lateral view (Top) and posterior view (Bottom)
As in fig. 6 and 7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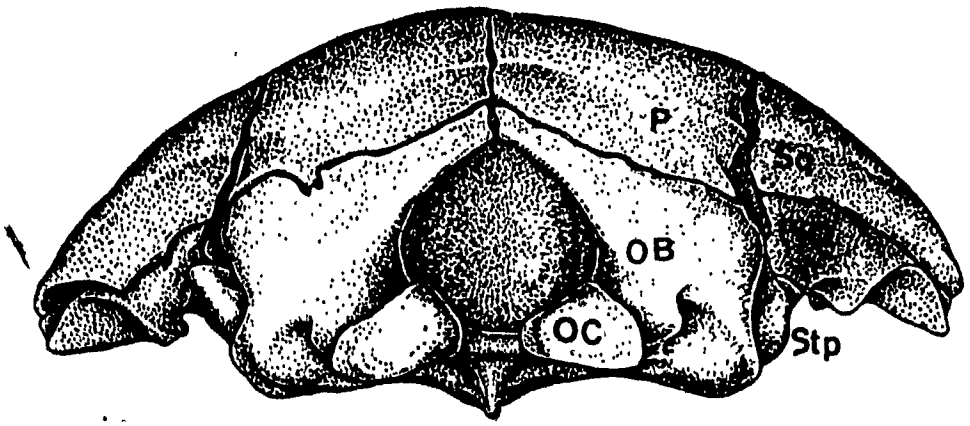
NPm
Stp
Cmj


P
SO
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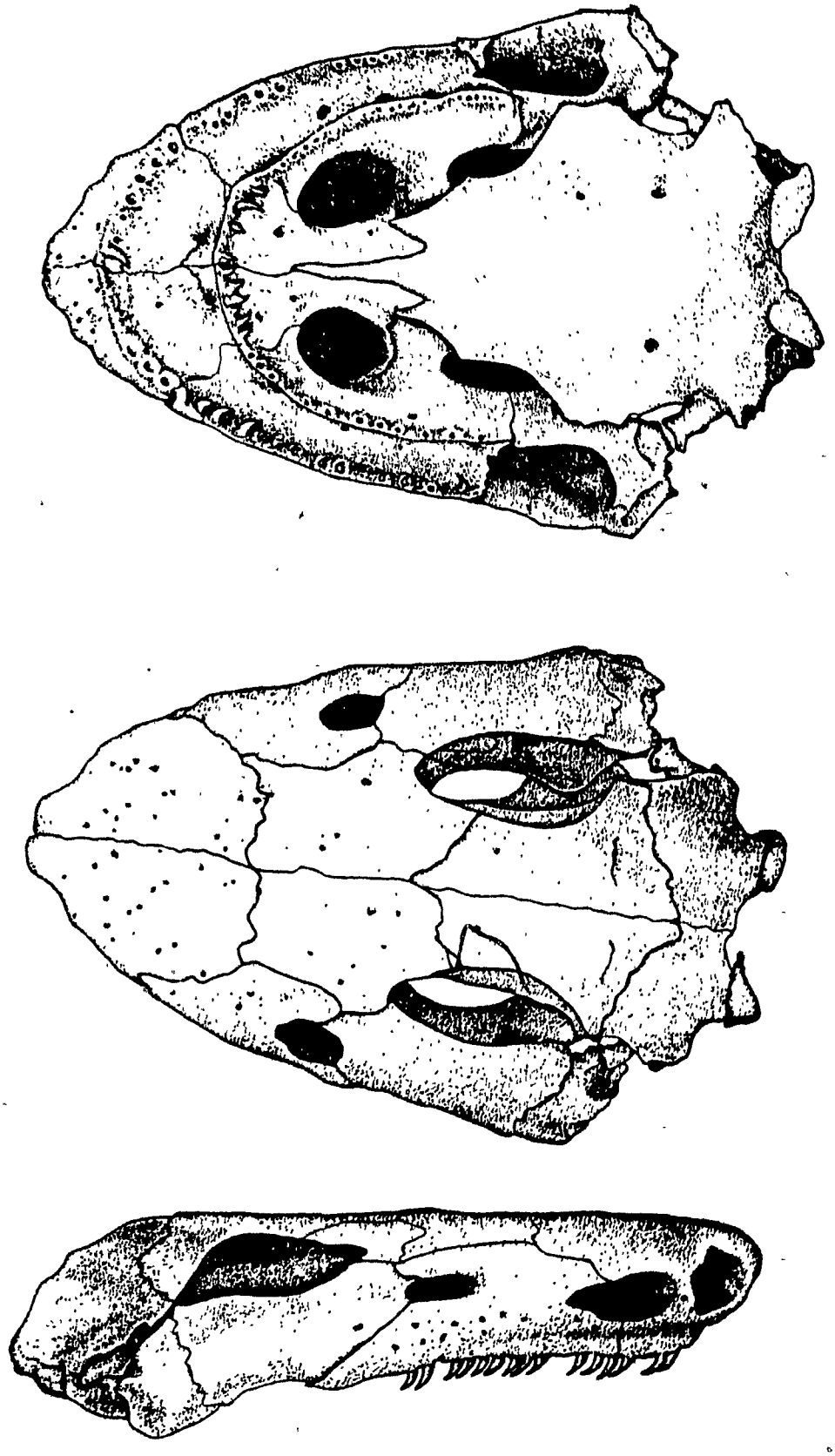
seen in other tetrapods. The vomers are large, being the only other dermal elements in the anterior portion of the palate. The internal nares are bordered either by the vomer alone or by the vomer and maxillopalatine but are peculiarly located, being mesial to the inner tooth row. The pterygoid is variously fused to the quadrate or distinct, the former condition being the most common. In one family, the Scolecomorphidae, the pterygoid and quadrate are fused as one unit with the stapes (Brand 1956).

The braincase posteriorly is a single ossified unit, the os basale. There are two occipital condyles. The large cultriform process tapers rapidly anteriorly, usually ending in a point between the vomers. Two large fenstrae ovale open laterally on the otic capsules. The stapes has a large footplate and a style that continues anterolaterally to appose the suspensorium.

The connection of the braincase and the dermal skull and quadrate ventrally is highly derived in caecilians(deJager 1939c; Ramaswami 1942). A synovial joint usually exists between the pterygoquadrate (or pterygoid) and the os basale. Another synovial joint occurs between the quadrate and the distal end of the stapes style (figs. 7 and 8). These joints permit considerable mesiolateral kinesis between the posterior portion of the cheek and the braincase (DeVilliers 1936; Straub 1985). This type of kinesis is unique to caecilians.

The orbit is sometimes completely occluded by bone (fig.8). When it is open, it is unusually small. It is most

Figure 9. *Typhlonectes*. sp. An open-skulled, caecilian Redrawn from Taylor (1969a).



often defined by the maxillopalatine or by the maxillopalatine and the squamosal. The alternative to those two states is the presence of a small ring or crescent of bone around the orbit called the postfrontal.

While vision seems to have been de-emphasized in caecilians, a novel sensory structure called the tentacle has been elaborated. The tentacle is a tactile organ that exits the skull usually anterior to the orbit. It is a combination of the Harderian gland, the nasolacrimal duct, the M. retractor bulbi, and Jacobson's organ (Badenhorst 1978). It is unique to caecilians, having no analogue in any other tetrapods.

Another unique, highly derived system is found in the caecilian lower jaw/jaw musculature complex. The lower jaw is extremely solid, built of two strong bones, the pseudodentary and pseudoangular, joined by a long transverse scarf joint just anterior to the quadrate condyle. The pseudodentary extends posteriorly far beyond the jaw joint as a huge retroarticular process. The process is often inflected mesially or dorsally (or both). The adductor chambre of most caecilians is severely confined by the skull roof. Uniquely in caecilians, the gular musculature, the M. interhyoideus posterior, augments the standard adductor by pulling downwards (and inwards) on the retroarticular process, closing the jaw in the manner of a first order lever (Nussbaum 1983). The unique gular musculature is frequently quite large and originates on the fascia of the outer trunk.

The jaw and jaw musculature appear to constitute a highly complex, and strange functional suite of features. It varies in its morphology both ontogenetically and phylogenetically but is fully formed in all species. There do not appear to be any adequate morphological intermediates between the condition found in caecilians and the condition found in other tetrapods so it has been difficult to determine in what manner, or by what selective pressure, this system has come about. It is often thought to be associated with the extremely small size of the caecilian skull.

The fossil record of caecilians is meagre to say the least. Two vertebrae, one from the Paleocene (Estes and Wake 1973), and one from the Upper Cretaceous (Maastrichtian) (Rage 1986) have been positively identified as caecilian. They are essentially modern in structure and demonstrate only that the gymnophionan vertebral pattern had already been established by the late Cretaceous.

I must avoid any charges of disingenuousness by stating my knowledge of some presumed fossil caecilian skull material from the Kayenta formation (Liassic, Lower Jurassic) of Arizona. It has been tentatively identified as caecilian by Dr. A.L. Panchen (Pers. comm.). I have seen this material and concur with Dr. Panchen that it appears to be caecilian, essentially modern in aspect. The material has not been used here in generating hypotheses of character polarities except to extend the stratigraphic range of the order. Based on the discussion of the paleontological criterion , I consider that, when described in detail, these specimens will provide

independent tests of the character phylogenies derived by other methods.

Classification

The first recognized caecilian genus, Ichthyophis, was described by Linnaeus in 1749 (cited in Lescure 1985). Since then, in various configurations of higher taxa, caecilians have been allied with fish, snakes (as members of a group comprising 'legless amphibia'), and reptiles. The modern conception of the caecilians as a distinct order began with the creation of the Order Gymnophia by Raffinesque-Schmaltz in 1814 (cited in Lescure 1985). The name was later emended to O. Gymnophiona by Muller (1831). The recognition of this assemblage as a component of the Class Amphibia, as distinct from the Class Reptilia, followed in 1825 with the publication of a monograph by Gray. In this same work, the first of the modern families, the Family Caeciliidae, was erected. The Caeciliidae of Gray is a slightly different assemblage from that of the same name proposed most recently by Laurent (1984) and very different from that of Lescure et al (1985). Gray's Caeciliidae encompassed all known forms and in fact continued as the sole caecilian family for almost one hundred and fifty years.

The modern trend in caecilian classification is marked by a proliferation of higher taxa and taxonomic ranks. Its inception came with the painstaking descriptions by Taylor

(1968a). Taylor (1968a) erected two new families by removing two genera, Ichthyophis and Caudacaecilia, from the Caeciliidae and uniting them in the new family Ichthyophiidae. The family Typhlonectidae was created to differentiate the aquatic forms Typhlonectes, Potamotyphlus, Chthonerpeton and Nectocaecilia. Later (Taylor 1969a), the genus Scolecomorphus was raised to the family level (Scolecomorphidae). In a further study (Taylor 1969b), the remaining caeciliids were divided into two subfamilies, Caeciliinae comprising Caecilia and Oscaecilia, and the Dermophinae encompassing all other genera.

Further refinements on Taylor's classification scheme have been added by Nussbaum (1977, 1979a). Two genera, Rhinatrema and Epicrionps, were removed from the caeciliids and placed in a new family Rhinatrematidae (1977). The size of the caeciliidae was further diminished by the removal of the genus Uraeotyphlus (Nussbaum 1979a), which was placed in the family Ichthyophiidae as a monogeneric subfamily (Uraeotyphlinae). This change required the formation of the subfamily Ichthyophiinae to accomodate the already existing ichthyophiids. These alterations left the order divided into five families, Rhinatrematidae, Ichthyophiidae, Caeciliidae, Typhlonectidae, and Scolecomorphidae. Two families are further divided into subfamilies. The Ichthyophiidae contains two subfamilies, Ichthyophiinae and Uraeotyphlinae. The Caeciliidae comprises the subfamilies Caeciliinae and Dermophinae.

The last few years have seen a resurgence in the alpha-

level taxonomy, and the classification has been further split. The formerly monogeneric family Scolecomorphidae was divided into two genera (Nussbaum 1985). The subfamily Caeciliinae was expanded to include the new genus Minascaecilia (Wake and Campbell 1983), as well as the formerly dermophine genera Microcaecila, Parvicaecilia (as suggested by Savage and Wake 1972) and the members of the invalid genus Copeotyphlus (Nussbaum 1979b). More recently, Laurent (1984) raised the subfamilies Dermophinae and Caeciliinae to family level, although his conception of the make up of these two groups differs from that of Wake and Campbell (1983). Lescure et al (1985) added a profusion of higher taxa in their attempt to generate a cladistic classification of the caecilians. In total, they generated 67 suprageneric taxa (below the level of order) at 12 different ranks, all within two suborders.

It is difficult to present the definitive classification of an order that has gone from containing a single suprageneric taxon (one family) to 67 (in 12 ranks) in 18 years. I have tried to adhere to a fairly conservative classification system here, one that conforms most closely to Nussbaum's (1979a, 1985) and Wake's (1985), recognizing that additional refinements are in order. I have followed the lead of Laurent (1984) in treating the Dermophinae and Caeciliinae at the family level (Dermophidae and Caeciliidae), thereby abandoning the original concept of the Caeciliidae as unifying these groups. They appear to be sufficiently easily

distinguished from one another (Taylor 1969c; Laurent 1984) that this is justifiable. Should they prove to constitute a monophyletic group, they could be accommodated in a new Superfamily Caecilioidea, or resume their status as subfamilies of the Caeciliidae. Subsequent studies will probably further divide the Family Dermophidae. Additionally, I have taken licence to treat the subfamilies Ichthyophiinae and Uraeotyphlinae as distinct entities, as have Duellman and Trueb (1986) rather than consider them collectively under the family Ichthyophiidae, because the latter subfamily had been moved *en masse* from one family (Caeciliidae *sensu* Taylor) to another (Ichthyophidae) (Nussbaum 1979a).

Although I treat the interrelationships of these groups cladistically, I do not feel impelled to follow the convention outlined by Griffiths (1976) and adhered to by many cladists (McKenna 1975; Lescure *et al* 1985) in which each dichotomy is assigned a taxonomic rank, either numbered (Griffiths) or named (McKenna). McKenna (1975), while defending his use of this convention, admits its shortcomings. He refers to the "bugaboo of instability" (pg. 22), meaning that addition of any new taxon requires a complete rearrangement of the classification scheme. He also admits to the necessary proliferation of taxonomic ranks, but is rather more sanguine than Panchen (1982) about the actual number required. My opinion on this issue is that if the primary function of classification (in contradistinction to phylogeny reconstruction [Kitts 1978]) is one of information storage and retrieval, the proliferation of redundant taxonomic ranks is

TABLE 1

CLASSIFICATION OF LIVING CAECILIANS

FAMILY CAECILIIDAE (24 genera)

SUBFAMILY CAECILIINAE (5 genera)

- *Caecilia*
- *Microcaecilia*
- *Minascaecilia*
- *Oscaecilia*
- *Parvicaecilia*

SUBFAMILY DERMOPHINAE (19 genera)

- *Afrocaecilia*
- *Boulengerula*
- *Brasilotyphlus*
- *Cryptopsophis*
- *Dermophis*
- *Gegeneophis*
- *Geotrypetes*
- *Grandisonia*
- *Gymnopis*
- *Herpele*
- *Hypogeophis*
- *Idiocranium*
- *Indotyphlus*
- *Luetkenotyphlus*
- *Mimosiphonops*
- *Praslinia*
- *Pseudosiphonops*
- *Schistometopum*
- *Siphonops*

FAMILY ICHTHYOPHIIDAE (3 genera)

SUBFAMILY ICHTHYOPHIINAE (2 genera)

- *Caudacaecilia*
- *Ichthyophis*

SUBFAMILY URAEOTYPHLINAE (1 genus)

- *Uraeotyphlus*

FAMILY RHINATREMATIDAE (2 genera)

- *Epicrionops*
- *Rhinatrema*

FAMILY SCOLECOMORPHIDAE (2 genera)

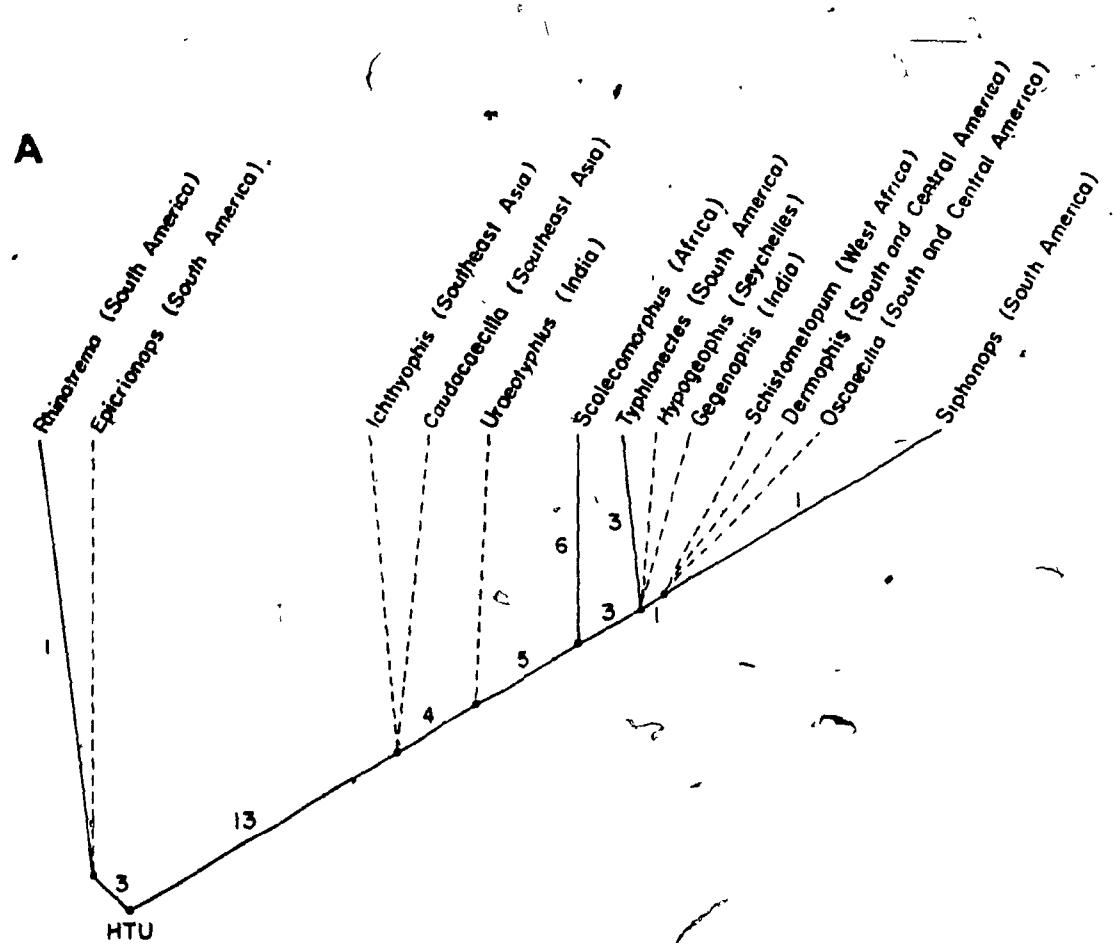
Crotaphatrema
Scolecomorphus

FAMILY TYPHLONECTIDAE (4 genera)

Chthonerpeton
Nectocaecilia
Potamotyphlus
Typhlonectes

-SOURCES: Nussbaum 1977, 1979a,b 1985
Taylor 1968, 1969a
Savage and Wake 1982
Wake 1985
Wake and Campbell 1982

Figure 10. Two currently accepted ingroup phylogenies of the caecilians A. from Nussbaum (1979). B. from Duellmanm and Trueb (1986:466)


A
Rhinotrema (South America)
Epicrionops (South America)
Ichthyophis (Southeast Asia)
Caudacaecilia (Southeast Asia)
Uraeotyphlus (India)
Scolecomorphus (Africa)
Typhlonectes (South America)
Hypogeophis (Seychelles)
Gegenophis (India)
Schistometopum (West Africa)
Dermophis (South and Central America)
Oscaecilia (South and Central America)
Siphonops (South America)
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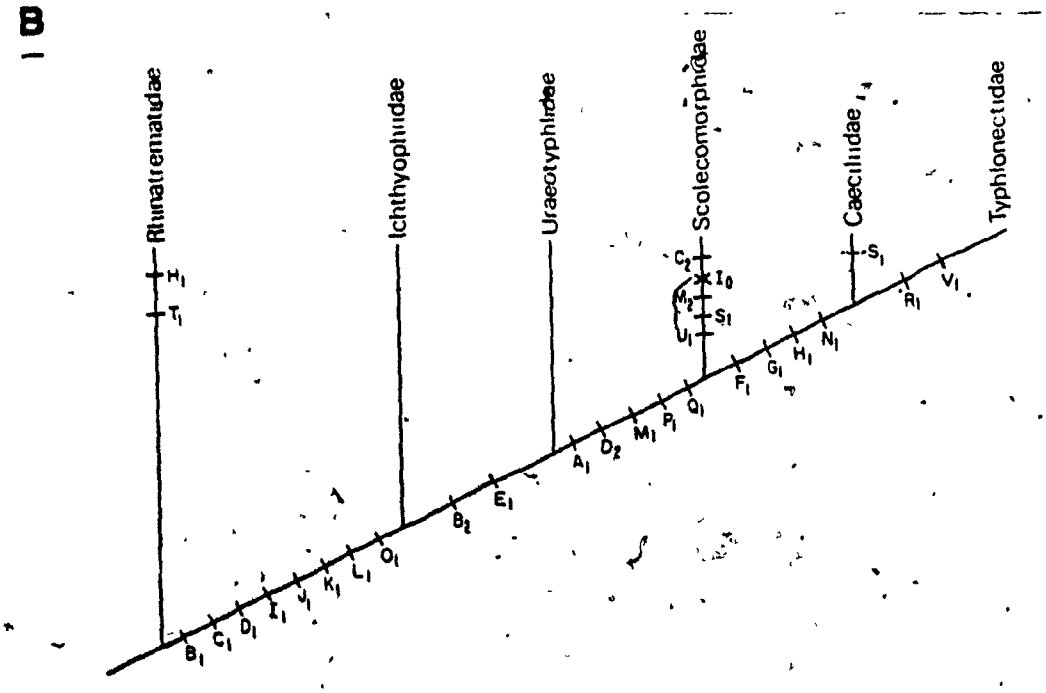

B
Rhinatrematidae
Ichthyophiidae
Uraeotyphlidae
Scolecomorphidae
Caeciliidae
Typhlonectidae

unnecessarily cumbersome. A classification of caecilians is given in Table 1.

The Skull Roof Controversy

A brief discussion of a current controversy in caecilian systematics will serve to illustrate the importance of discerning the primitive from the derived features of the caecilians. The inability to distinguish primitive from derived is an impediment not only to an understanding of ingroup relationships, but also to outgroup relationships.

The majority of previous studies of caecilian systematics discuss the structure of the skull roof as an important character or suite of characters. The skull roofs of anurans, urodeles and lysorophoids are widely fenestrated (gymnokrotaphic). In living forms the fenestrations of the skull permit the expansion of the adductor musculature of the lower jaw through the skull roof. It is presumed also to have been the condition in lysorophoids (Wellstead 1985). Microsaurs and nectridians, like primitive labyrinthodonts, have solidly closed (stegocephalian) skull roofs.

The caecilian skull roof exhibits variability in this respect. An open skull condition (zygokrotaphy) is found in four out of the five currently recognised families (Nussbaum 1979a) (fig. 11). The closed skull roof (stegokrotaphy) is more widely distributed among genera. When present, the

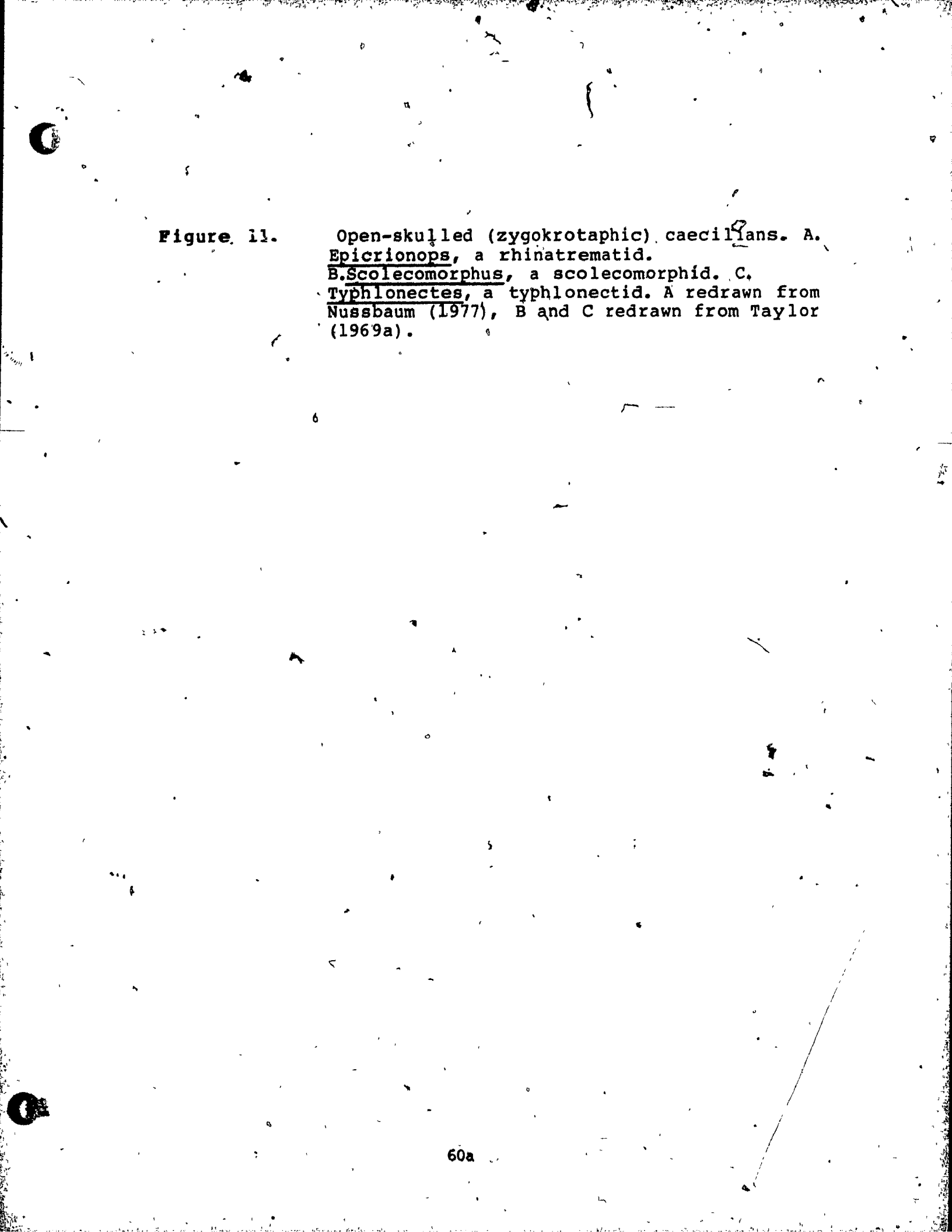
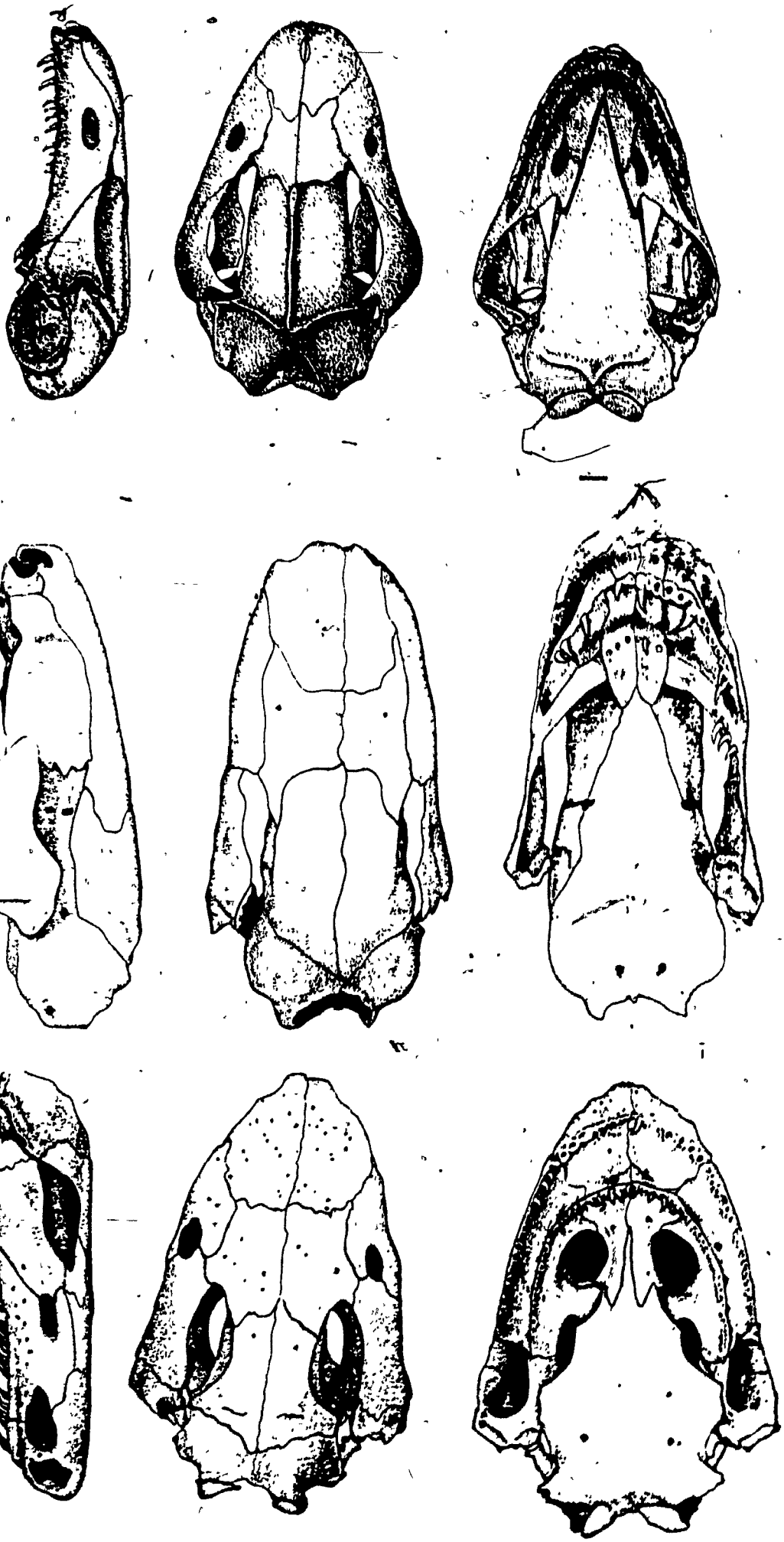


Figure 11. Open-skulled (zygokrotaphic) caecilians. A. *Epicrionops*, a rhinatrematid. B. *Scolecomorphus*, a scolecomorphid. C. *Typhlonectes*, a typhlonectid. A redrawn from Nussbaum (1977), B and C redrawn from Taylor (1969a).



fenestration occurs between the parietal and squamosal units. In all stegokrotaphic caecilians the parietal-squamosal suture is weak (Wake and Hanken 1982). There are intermediates between the typical zygokrotaphic and stegokrotaphic conditions. The presence of the closed skull roof condition has been adduced as evidence of caecilian relationships to the microsaurs (Romer 1945; Gregory et al 1956; Schmalhausen 1968; Carroll and Currie 1975). Alternatively, the open skull roof has been cited as evidence of the relationship of caecilians to anurans and urodeles (Parsons and Williams 1963; Nussbaum 1977; 1979a) and to lysorophoids (Moodie 1909; Eaton 1959; and Nussbaum 1983). Clearly it is important to determine the polarity of the skull condition in caecilians before it can be utilised in ascribing relationships of the group. The structure of the skull roof in living amphibians is of considerable systematic and functional significance (Carroll and Holmes 1980); its implications for the taxonomy, and functional morphology of caecilians will be discussed in some detail.

II. PROPOSED SISTER GROUPS

The criteria for the choice of the potential sister groups of caecilians were outlined in chapter two. The purpose of establishing these criteria was to delimit the set of probable potential sister groups, while at the same time excluding unlikely groups from the analysis. The groups that meet these criteria are the aïstopods, nectrideans, lysorophoids, gymnarthrid and goniorhynchid microsaurs, dissorophid temnospondyls, anurans and urodeles.

Aïstopods

The aïstopods are the oldest of the lepospondyl groups. The earliest known member dates from the Visean of Scotland ca. 340 ma. (Wellstead 1982). The most recent aïstopods have been found in the Lower Permian of North America (Arroyo formation ca. 270 ma). Although they are represented by only five genera, there is a considerable diversity in cranial anatomy within the order (fig. 12). The five genera are distributed into three families: Lethiscidae (Wellstead 1982) comprising the Visean genus Lethiscus, Ophiderpetontidae which, while containing only one genus, probably encompasses most of the known specimens, and Phlegethontiidae, which currently contains three genera, Phlegethontia (including Dolichosoma), Aornerpeton, and Sillerpeton (Lund 1972).

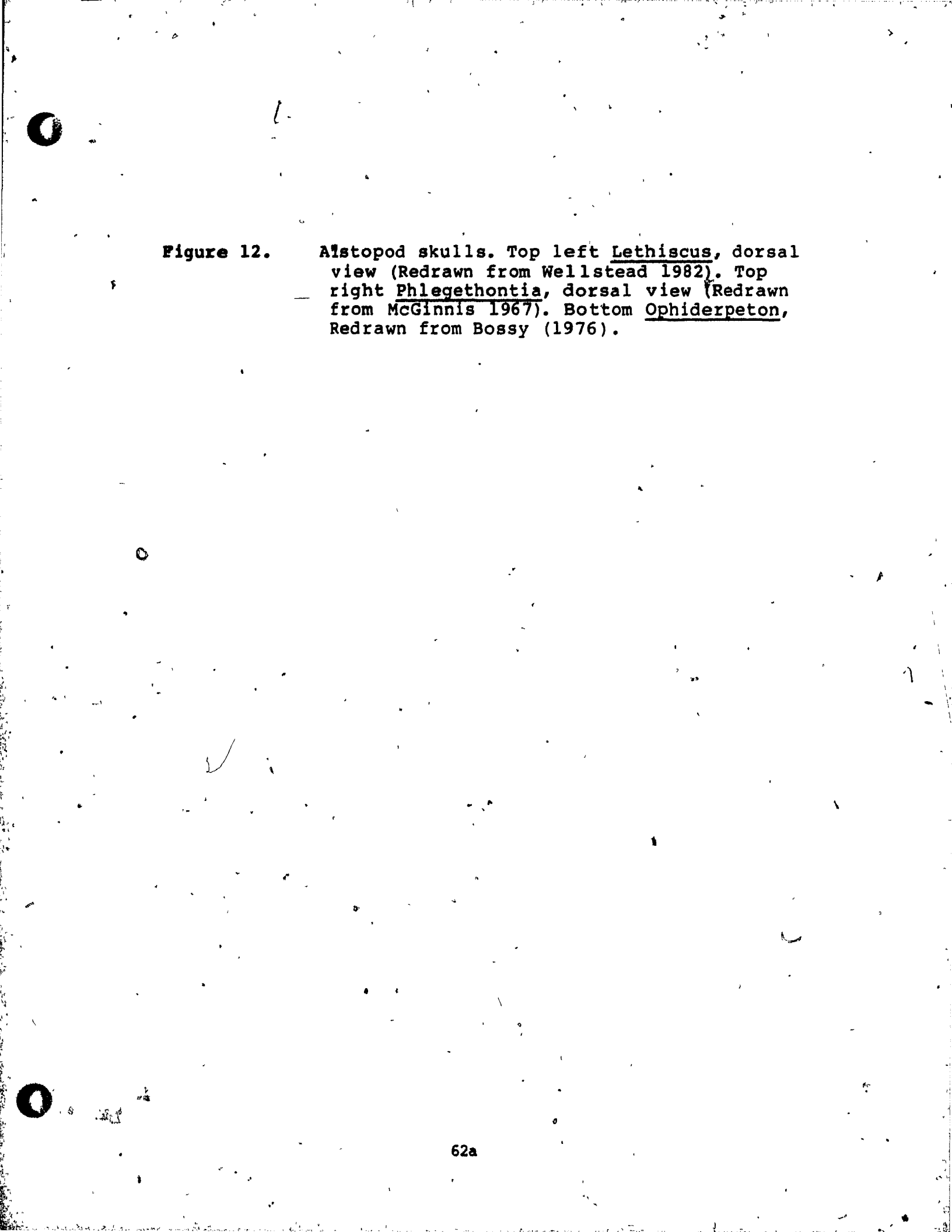
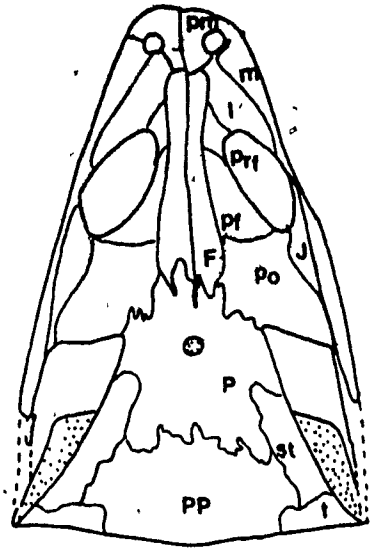


Figure 12. Aïstopod skulls. Top left *Lethiscus*, dorsal view (Redrawn from Wellstead 1982). Top right *Phlegethontia*, dorsal view (Redrawn from McGinnis 1967). Bottom *Ophiderpeton*, Redrawn from Bossy (1976).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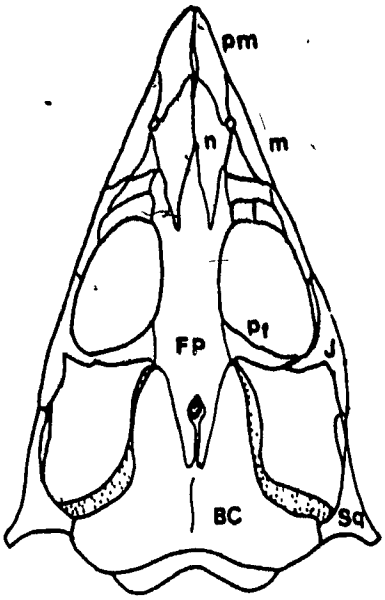
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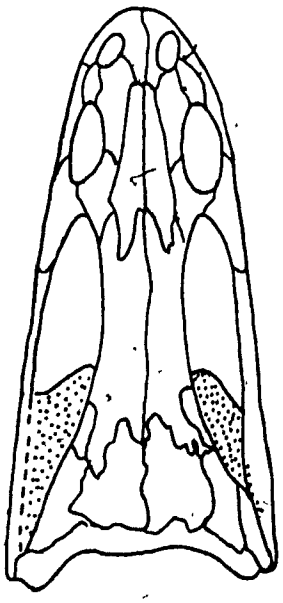

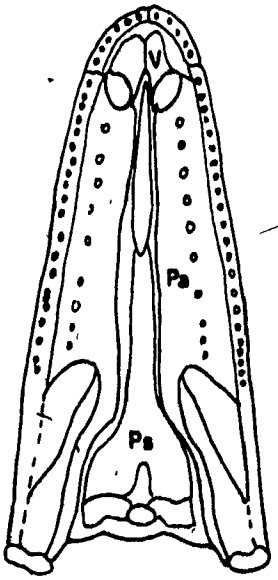
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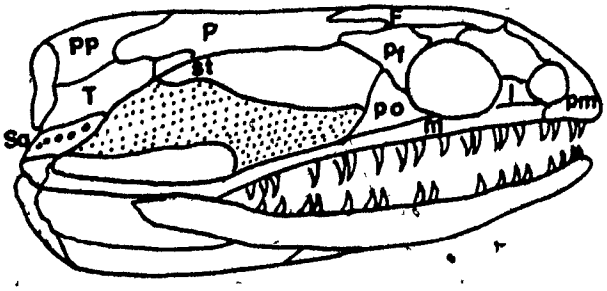
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Aïstopods have a general appearance not unlike caecilians. They are limbless and elongate, some with 100 or more vertebrae. Most of the characters that diagnose the group are postcranial. Baird (1964, 1965) lists six common elements of the rib, vertebral and hyoid structure that unite all genera. A general description of the features of the skull is possible despite its variability between genera. In palatal or dorsal view it describes a long isosceles triangle with its apex anterior. The cheek region is fenestrated in all genera but the ventral margin is complete. The skull roof of Lethiscus exhibits a full complement of circumorbital bones as well as distinct parietals, supratemporals, tabulars and a large median postparietal. The palate and the braincase, as inferred from X-rays, appear similar to the primitive tetrapod condition as seen in early temnospondyls (Wellstead 1982).

The cranial structure of the better known families Phlegethontiidae and Ophiderpetontidae is divergent from that of Lethiscus. The skull of Ophiderpeton is considerably narrower than that of Lethiscus or phlegethontiids. The quadrate condyle is in the primitive tetrapod location, approximately at the level of the occiput, or slightly behind it. The orbits are exceedingly small and are located relatively far forward in the skull. There appears to be a full complement of circumorbital elements. The cheek is elongate and widely fenestrated . It is fairly apparent from the number of small osteoderms that cover the opening that the jaw adductor musculature did not extrude through the cheek

(Bossy 1976). The braincase, to the extent that it is known, is of the primitive tetrapod type. The cultriform process is long and slender and the interpterygoid vacuities are narrow.

By far the best studied aïstopod group is the Phlegethontiidae. The phlegethontiid skull is marked by the loss and fusion of elements, particularly in the posterior portion. Some of the designations of the skull elements are disputed. I have chosen to follow primarily McGinnis (1967). The frontals are usually fused bilaterally, and send two posteriorly directed lappets to surround the parietal foramen, when present (Steen 1931, 1938). There is no distinct parietal. It is usually taken to be fused to the frontal (McGinnis 1967), or to be incorporated into the roof of the braincase (Gregory 1948: Turnbull and Turnbull 1955). There are no elements behind the parietal. There is a large cheek fenestration bordered anteriorly by the postfrontal, postorbital and jugal (but see Lund 1972), ventrally by the jugal and quadratojugal, and posteriorly by the squamosal. The squamosal has a unique triradiate structure and is thought by Lund (1972) to have been highly kinetic. The craniomandibular joint is conspicuously anteriorly located, being just anterior to the foremost portion of the anterior semicircular canal. The lower jaw in aïstopods has two compound elements that meet at a large, oblique scarf joint.

The description of aïstopod braincase structure is taken from the phlegethontiids. A single beautifully preserved specimen from the Fort Sill locality is described by McGinnis

(1967) (fig. 24c). The braincase has undergone complete fusion. Its occipital surface is unique in possessing a single, well formed notochordal pit as the craniovertebral joint. The fenestrae ovale are extremely large and open ventrally. The phylogenetic affinities of aïstopods are puzzling. Most authors have refrained from allying them with other groups. Apart from being associated with the caecilians (Marcus et al 1935; and in part Gardiner 1982), they were considererd by Romer to be related to lysorophoids (Turnbull and Turnbull 1958). Bossy (1976) considered them to be closely related to the nectrideans.

Nectrideans

Like the aïstopods, nectrideans are characterised largely by postcranial features. There are elaborate neural spines on the vertebrae, with accessory articulating surfaces. The most distinctive feature is the large haemal spines on the caudal vertebrae that attach to the middle of the centra and closely resemble neural arches. The presacral series is relatively short for small Paleozoic amphibians. All have fewer than twenty seven presacral vertebrae. The limbs are diminutive, prompting suggestions that they were aquatic. Nectrideans range in time from the lowermost Pennsylvanian (Westphalian A ca. 310 ma) to the Lower Permian. In all, fourteen genera are grouped into three families. They are generally small skulled, stegocephalian amphibians. The pattern of dermal bones of the skull roof usually approximates the primitive labyrinthodont arrangement, though there is

appreciable variation between the three families (fig. 13).

Perhaps the most primitive family is the Urocordylidae. It contains six genera split evenly into two informal subgroups, one characterized by the genus Sauropleura, the other by Ptyonius. The skull of Sauropleura is extremely long anteroposteriorly, whereas that of Ptyonius is somewhat shorter. The snout and skull roof are thought to have been highly kinetic (Milner 1980).

The little known family Scincosauridae appears to be intermediate between the urocordylids and the highly derived keraterpetontids. Scincosaurus has a relatively stout skull that expands slightly posteriorly. There are neither supratemporals nor postparietals so the skull is bordered posteriorly by the parietals. Scincosaurus has unusually well developed limbs for a nectridean. It was probably terrestrial.

Keraterpetontids include the 'classic nectrideans', characterized by the dorsoventrally flattened skull with elaborate extensions of the squamosal and tabular (called 'tabular horns'). The orbits are small, and located far forward in the skull. The palate of later keraterpetontids (except Batrachiderpeton) is derived relative to that of urocordylids in having large interpterygoid vacuities. The moveable basicranial articulation becomes fused. The craniomandibular joint is far forward, the mandibles short. Some possess a dorsally inflected retroarticular process (Milner 1978). What is known of the braincase suggests that it conforms to the type found in early labyrinthodonts, such as

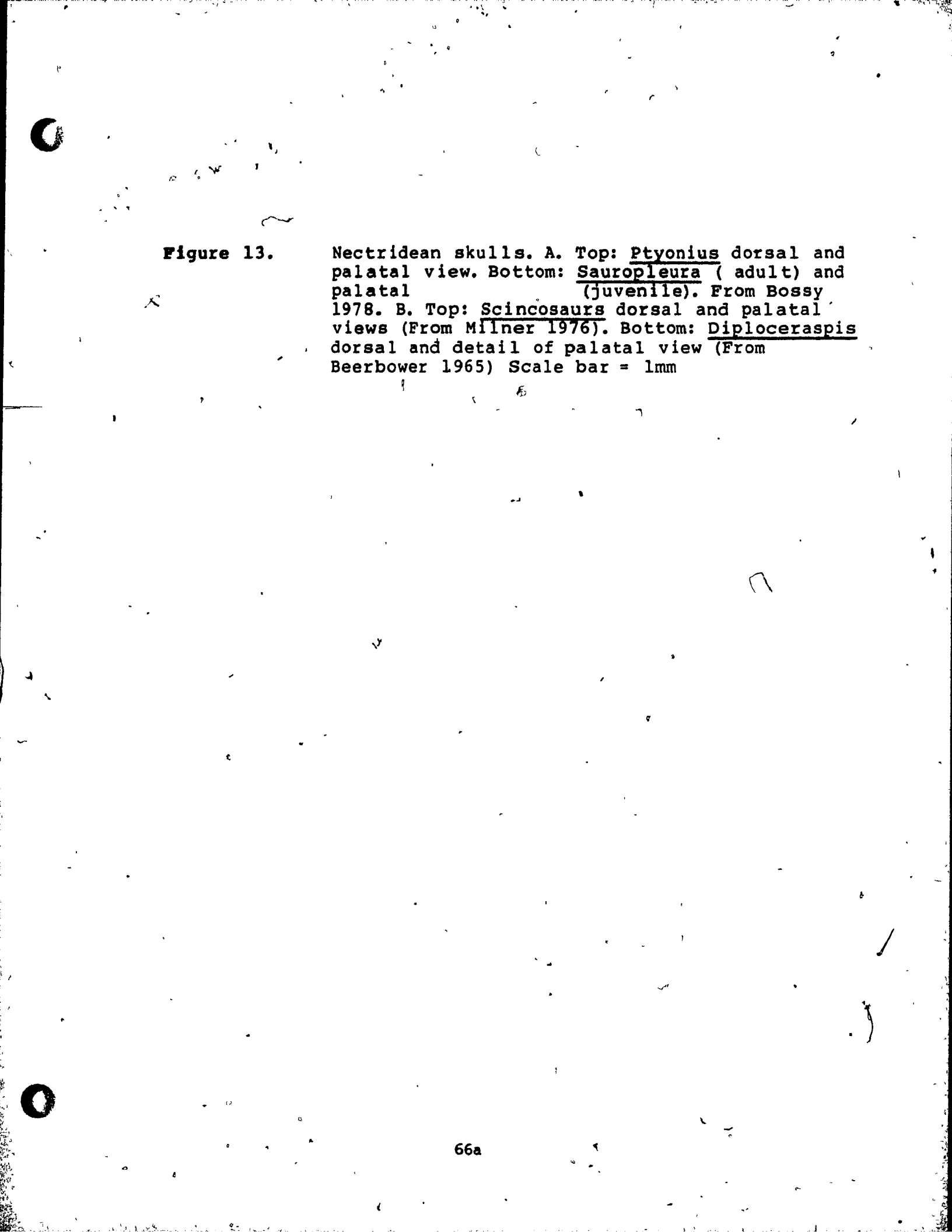
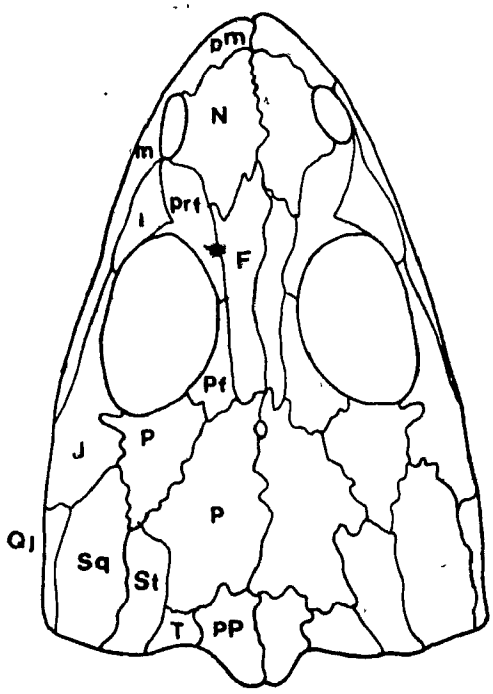
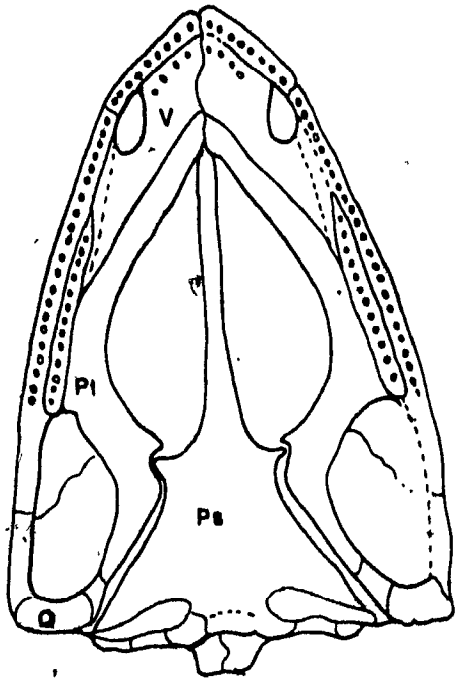
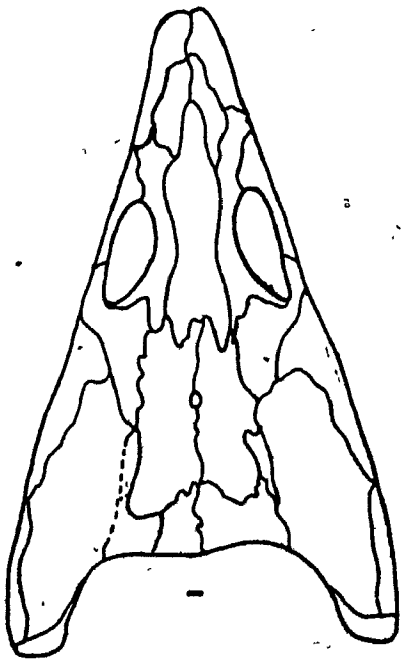


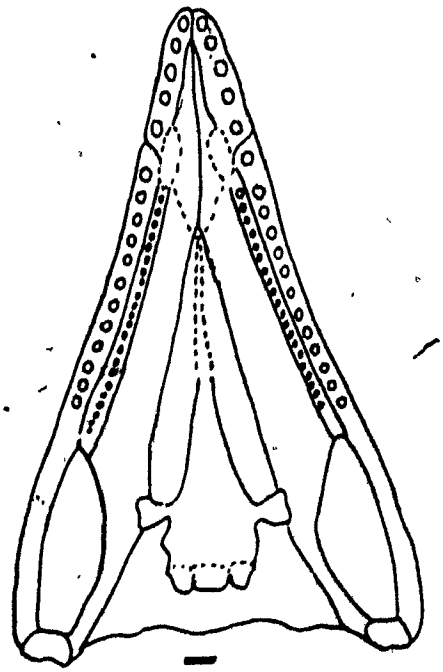
Figure 13. Nectridean skulls. A. Top: Ptyonius dorsal and palatal view. Bottom: Sauropleura (adult) and palatal (juvenile). From Bossy 1978. B. Top: Scincosaurs dorsal and palatal views (From Milner 1976). Bottom: Diploceraspis dorsal and detail of palatal view (From Beerbower 1965) Scale bar = 1mm

A









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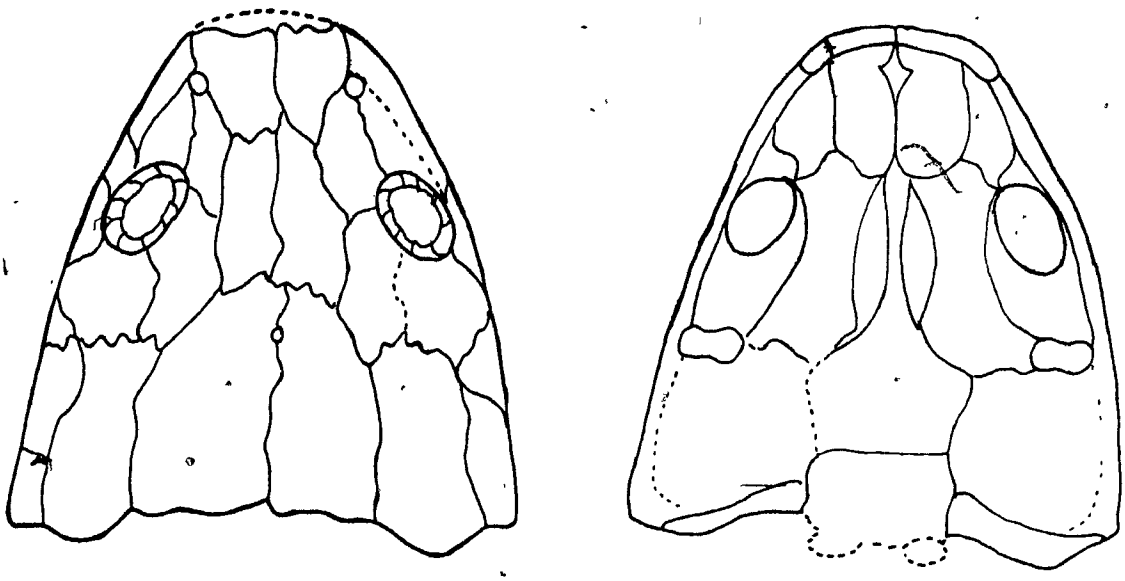
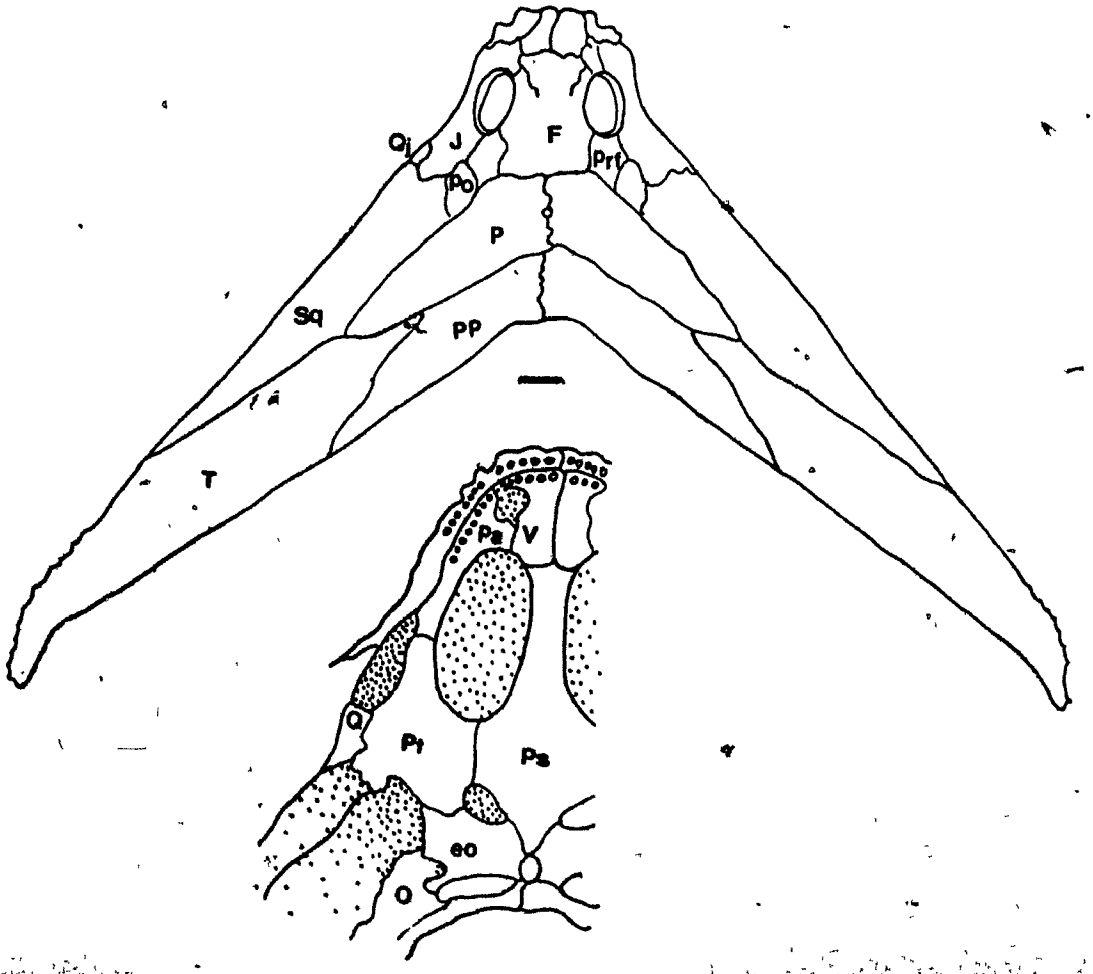




colosteids. There are however minor exceptions. The best known braincase material is that of the highly specialized keraterpetontid Diploceraspis. Most braincase observations will be taken from this description (Beerbower 1963).

The relationships of nectrideans are enigmatic. They display a number of highly specialized features, such as the kinesis of the urocordylid skull roof and the tabular horns of keraterpetontids, superimposed on an essentially primitive tetrapod pattern of the skull. They have been associated with the anthracosaurs (Romer 1945) on the basis of the contact of the tabular with the parietal. They have also been allied with temnospondyls based on the structure of the palate (Smithson 1982). Schmalhausen (1968) associates the nectrideans with aïstopods, as do Gardiner (1982) and Thomson and Bossy (1970), and points out that these two groups were thought by Marcus et al (1935) to comprise a monophyletic group with caecilians. It is significant to note that in Parsons and Williams' (1963) proposal of lissamphibian monophyly, their presumed 'protolissamphibian' ancestor was claimed to resemble Scinosaurus more closely than any other known Paleozoic amphibian (Bossy 1978). Schmalhausen (1968) notes that certain authors have hypothesized nectrideans as possible ancestors of urodeles but does not cite any studies specifically.

Lysorophoids

The lysorophoids are another discrete group of Paleozoic amphibians. Like the aïstopods they have elongate bodies

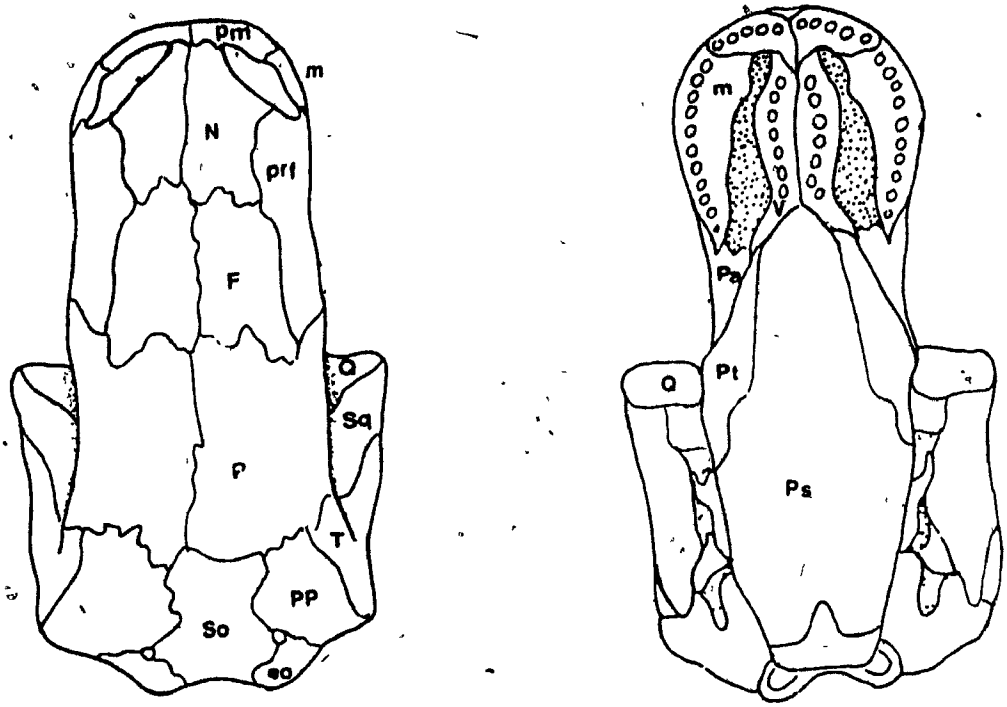
and holosponylous vertebrae. They range in time from the mid-Pennsylvanian (Westphalian D) to the Lower Permian (Wellstead 1985).

In a recent taxonomic revision Wellstead (1985), recognised four genera Brachydectes, Pleuroptyx, Lysorophus, and Molgophis. Brachydectes is the best known. Morphologically, the lysorophoids are less diverse than aistopods and nectrideans (fig.14).

The lysorophoid skull is distinctive in the structure of the cheek and suspensorium. The cheek is widely fenestrated, lacking postorbital bones and ventral margin. The braincase and otic capsule are clearly visible in lateral view. The suspensorium is an anteroventrally sloping pillar comprising three bones: the tabular (which has been called the supratemporal by Sollas (1920) and Bolt and Wassersug (1975)) and the squamosal, and the quadrate. The tabular and squamosal form the outer surface of the pillar and surround the quadrate for most of its length. The craniomandibular joint is located far anteriad of the occiput. As Wellstead (1985) points out, it is anterior to the basipterygoid process.

In dorsal view, the dermal skull roof is made up of a series of paired elements: nasals, frontals and parietals medially. A pair of large prefrontals extends the length of the lateral border of frontals and parietals. Most of either posterolateral corner of the skull roof is occupied by a large postparietal (alternatively labelled the supratemporal

Figure 14. Lysorophoid skull. Brachydectes (Redrawn from Wellstead 1985). Bar equals 1 cm.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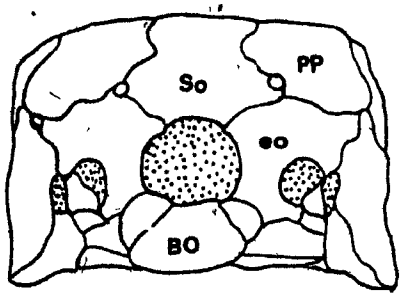
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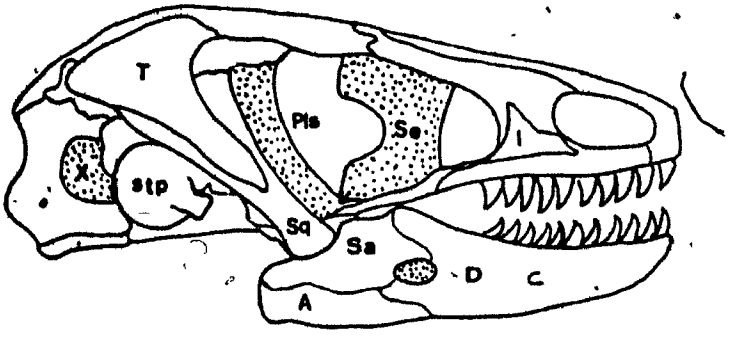
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Bolt and Wassersug (1975)). A large supraoccipital element extends up from the border of the foramen magnum onto the dorsal surface of the skull and intervenes between the two postparietals.

With the exception of the basisphenoid, all the elements of the primitive tetrapod braincase are distinct in lysorophoids. The occipital condyle is a convex strap shared by the basioccipital and the exoccipitals. Separate pleurosphenoid and sphenethmoid elements are apparent.

The palate is highly derived. The ectopterygoid is absent. The maxilla is very short. There is a well developed row of teeth on the large vomers. The vomers are in contact medially throughout most of their length. The parasphenoid, which presumably incorporates the basisphenoid, is a wide, flat structure in palatal view, that tapers gradually anterior to the basipterygoid processes. The pterygoids are small and closely appressed to the lateral margins of the parasphenoid. There is no appreciable interpterygoid vacuity.

The mandible is very short with a correspondingly small retroarticular process. The dentary, surangular, and angular surround a large lateral mandibular fossa on the outer surface of the mandible. The mesial surface is made up of a prearticular and a single splenial (Wellstead 1985).

Like the previously discussed groups, lysorophoid relationships are difficult to determine. Wellstead (1985) associates them with the microsaurs on basis of the structure of the craniovertebral joint. They have also been suggested as urodele ancestors (Schmalhausen 1968) and as relatives of

temnospondyls (Smithson 1982).

Microsaurs

Among the Paleozoic groups being analyzed here, the microsaurs are the most common and the best known. Positively identified specimens range in time from the Lower Pennsylvanian, Westphalian B (Joggins, Nova Scotia) to the Upper Permian. They are small, generally with elongate presacral vertebral columns, and have small limbs. There are exceptions however. Some microsaurs approach the appendicular and vertebral proportions of early reptiles (Gregory 1965; Westoll 1942, 1943; Romer 1950). The most thorough review of microsaur anatomy and phylogeny to date is that of Carroll and Gaskill (1978).

Microsaurs exhibit considerable variation in skull structure (fig. 15). The skull roof is essentially primitive, retaining the closed condition and a number of original elements found posterior to the parietal in early tetrapods. Carroll and Gaskill (1978) recognize two suborders, the Microbracomorpha and the Tuditanomorpha, differentiated by the expansion of the parietal (Microbrachomorpha) or the postorbital (Tuditanomorpha) into the area primitively occupied by the intertemporal. All previous hypotheses of microsaurian affinities with caecilians, except one, have identified a single family, the Gymnarthridae, as the most likely ancestor. The single exception is that of Carroll and

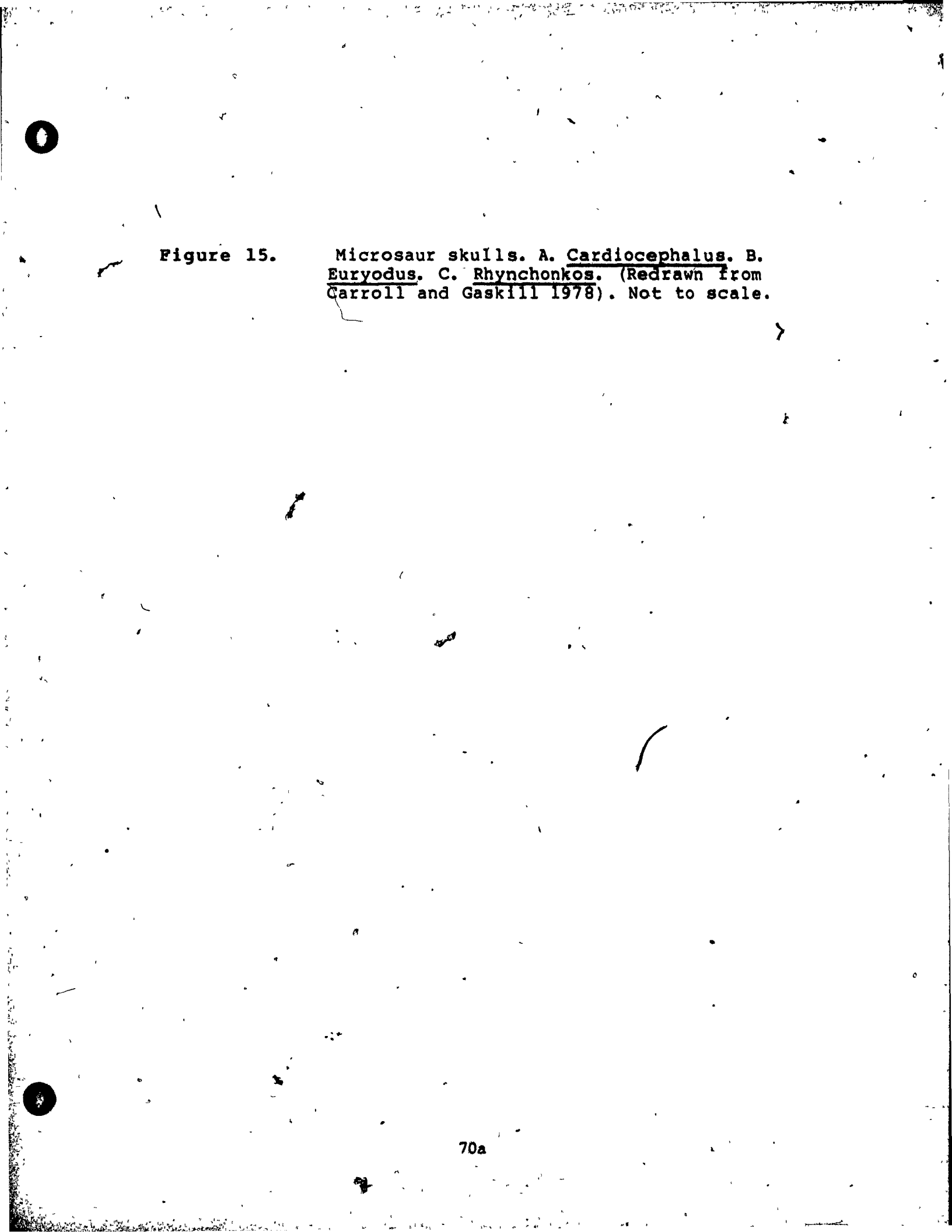
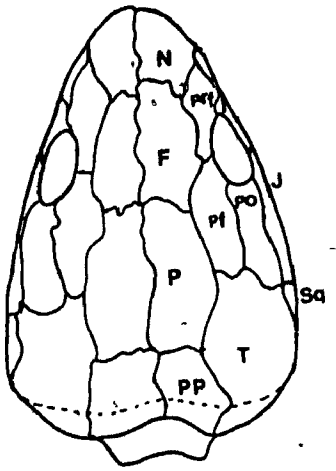


Figure 15. Microsaur skulls. A. Cardiocephalus. B. Euryodus. C. Rhynchonkos. (Redrawn from Carroll and Gaskill 1978). Not to scale.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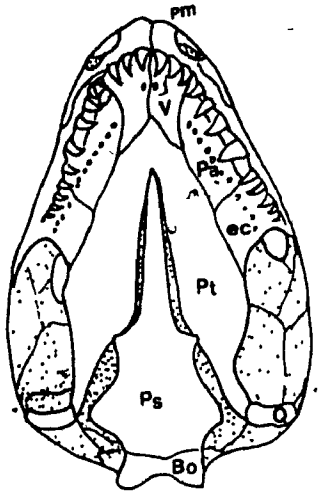
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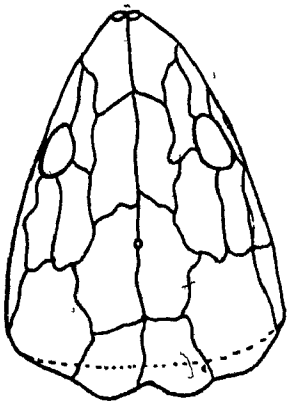
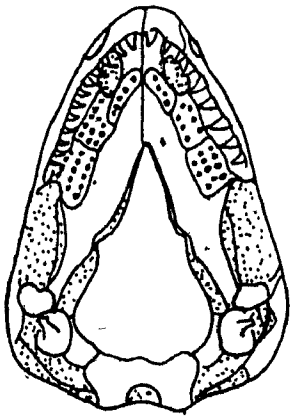
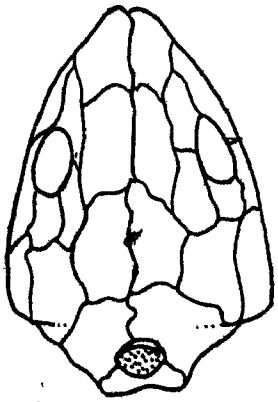
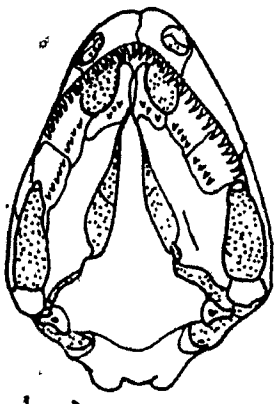
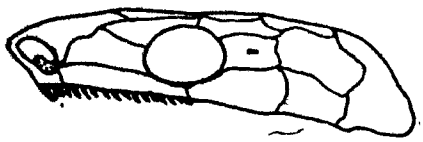










Currie (1975) who proposed the monotypic family Goniorhynchidae as the most appropriate ancestral family. While there is no assurance that microsaurs as a whole constitute a monophyletic group, cladistic analysis of the tuditanomorphs has shown quite convincingly that the Goniorhynchidae and the Gymnarthridae are monophyletic (Schultze and Foreman 1981). This study will restrict the discussion of microsaurs to the Gymnarthrid/Goniorhynchid complex as it is a natural assemblage, and the only microsaur group that has been proposed as caecilian ancestors.

The goniorhynchids and gymnarthrids encompass ten genera ranging in time from the Lower Pennsylvanian to the Permian. The Goniorhynchidae contains one genus, Rhynchonkos. The gymnarthridae comprises nine. A large tabular occupies the posterolateral corner of the skull table. In palatal view, the parasphenoid is a large structure that tapers quite rapidly anteriorly. The dermal bones of the palate are primitive in their arrangement, except for the rather wide V-shape formed by the mesial margins of the pterygoids which accommodates the tapering braincase. There is an inner row or shagreen of small palatal teeth paralleling the marginal dentiton. The lower jaw is subterminal, and the craniomandibular joint is distinctly anterior to the occiput, with the exception of Euryodus and Parioticus (Schultze and Foreman 1981). The parietal foramen is lost in members of the genera Euryodus, Pariotichus, and Cardiocephalus (see Carroll and Gaskill 1978, Fig. 31; Broili 1904 Plate 6 Fig. 5-5a).

The best known braincase is that of Rhynchonkos. It is a

well ossified structure that includes all primitive occipital arch and otic capsule elements of the primitve tetrapod skull. Rhynchonkos alone has a very small supraoccipital bone (Schultze and Foreman 1981). Carroll and Gaskill (1978) identify a large pleurosphenoid element anterior to the foramen for nerves V and VII.

The postcranium of Rhynchonkos is incompletely preserved, but that of typical gymnarthrids is long (>30 presacral vertebrae) (Carroll 1965; Carroll and Gaskill 1978). The limbs are diminutive.

Like the other lepospondyl groups, microsaurs have been linked with a wide variety of tetrapods. They were originally thought to be reptiles, a supposition that has recurred in the literature (1948, Westoll 1942a, b; Gregory 1965, but see Romer 1950 and Baird 1965; Carroll and Baird 1968). They have also been associated with two other lepospondyl groups as yet unmentioned, the adelogyrinids and the acherontiscids. Romer (1945) considered microsaurs to be related to lysorophoids and to be ancestral to urodeles. Carroll and Holmes (1980) have proposed the derivation of urodeles from tuditanomorph microsaurs, but not specifically from gonlorhynchid/gymnarthrids. Wellstead (1985) and Gregory et al (1956) suggested lysorophoid-microsaur affinities. While the Wellstead did not specify a particular microsaur family, Gregory et al singled out the gymnarthrids. They have been considered derivatives of both major labyrinthodont groups, anthracosaurs (or batrachosaurs) (Schultze and Foreman 1981)

and temnospondyls (Smithson 1982).

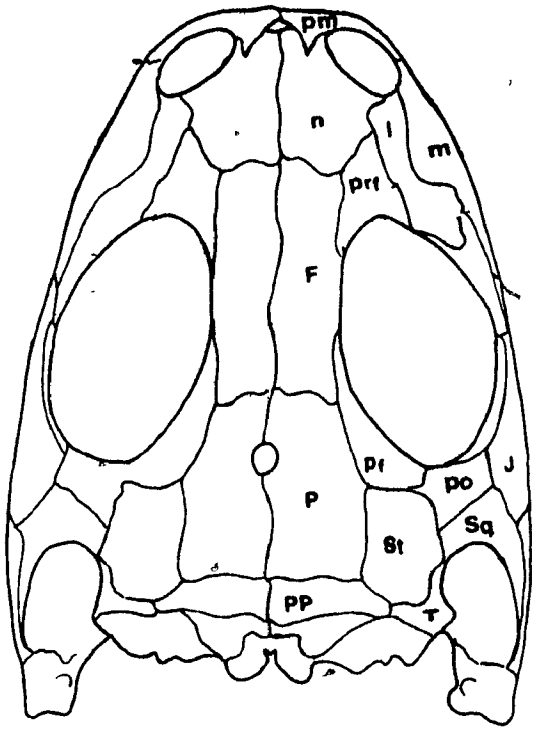
Dissorophidae

The dissorophids are a group of Pennsylvanian to Lower Triassic temnospondyls amphibians. They are generally small with dermal armour. There are usually taken to be twelve genera. In addition, Bolt (1969) described a very similar temnospondyl, Doleserpeton, which he placed in a new family Doleserpetontidae. The Doleserpetontidae was presumed to be very closely related to the dissorophidae. It is apparent in later works, however, that Bolt (Bolt and Lombard 1985) considers Doleserpeton to be a member of the Dissorophidae. The two most completely described genera are Tersomius (Carroll 1964) and Doleserpeton (Bolt 1969, 1977) (fig. 16). Most of the characters will be taken from the descriptions of these two genera.

One of the most striking features of this group is the presence of a presumed otic notch. Doleserpeton has a small rod-like stapes directed towards the squamosal embayment that probably acted as an impedence matching device, very similar in its structure to that found in most frogs.

The skull roof is closed; there is no cheek fenestration. The interpterygoid vacuities are extremeley wide. The cultriform process is long and narrow. An ectopterygoid is present in Tersomius and most other dissorophids, but is lost in Doleserpeton. The presence of pedicellate teeth in Doleserpeton was cited as possible

Figure 16. Dissorophids. Top Doleserpeton. (Redrawn from Bolt 1969). Bottom Tersomius, palatal view. (Redrawn from Carroll 1964). Scale bar = 1mm.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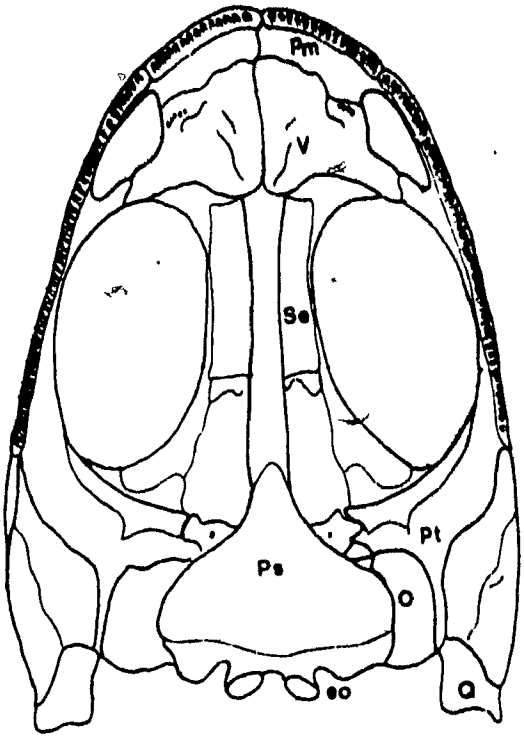
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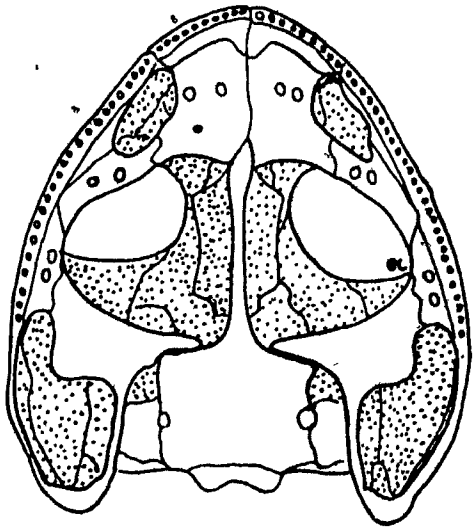


evidence of lissamphibian relationships by Bolt (1969, 1977).

The relationships of the dissorophids among the temnospondyls is not known. They have often been cited as a plausible sister group for anurans (Bolt 1977; Lombard and Bolt 1979; Bolt and Lombard 1985). They have also been proposed as a possible sister group of the lissambphibia as a whole (Bolt 1969; Rage and Lescure 1984).

Extant Groups

The living groups are generally better known than the Paleozoic lepospondyls. Both the anurans and the urodeles encompass a large amount of anatomical variation. However, as the earliest fossil record of caecilians predates that of urodeles and is contemporaneous with that of frogs (Liassic), it is possible to use only the primitive states of characters for anurans and urodeles. There are a number of alternate ingroup phylogenies for anurans (see Inger 1967; Kluge and Farris 1969; Duellman 1975) and for urodeles (Hecht and Edwards 1977; Duellman and Trueb 1986 and references in both). For either order, where there is a general consensus on the primitive state of a character between authors, the plesiomorphic condition will be taken as representative of that group.

Anurans

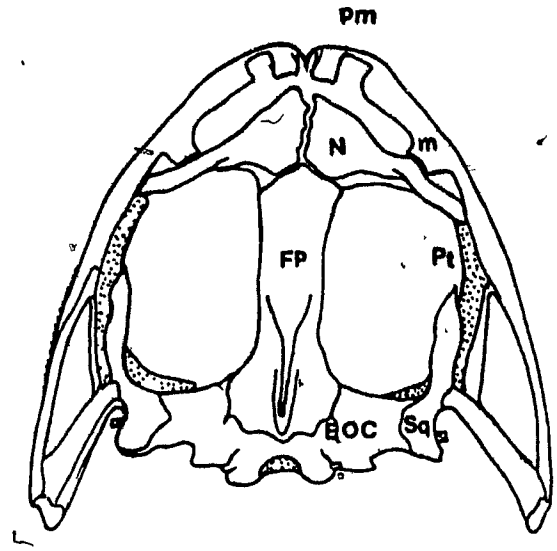
Anuran ingroup relationships have been reviewed extensively, particularly during a period from the early 1960's to the mid 1970's. Unfortunately, few if any of these

relied to any great great extent on cranial anatomy. Griffiths (1963 :247-8) in fact decries the "taxonomic unreliability of osteocranial characters" in his discussion of salientian phylogeny.

There are currently 339 recognized genera of frogs, divided into twenty two families, one of which, Paleobatrachidae is wholly extinct (Duellman and Trueb 1986). The earliest known true anuran, Vieraella, dates from the Lower Jurassic (Liassic) (Estes and Reig 1973). It has been placed in the family Leiopelmatidae (Duellman 1975) with the genera Leiopelma and Ascaphus.

The most conspicuous osteocranial character of the anurans is the fenestration of the cheek and skull roof (figs. 17 and 18). Frontals and parietals are fused into a single frontoparietal. The skull roof possesses none of the postparietal series of dermal elements found in primitive tetrapods. The wide cheek fenestra is bordered posteriorly either by the paroccipital process of the otic capsule or by the squamosal. The ventral cheek margin is complete. There may or may not be a distinct quadratojugal. The dermal palatal elements are much reduced and there is a wide interpterygoid vacuity. The vomers are highly variable in size and shape (Griffiths 1963), but constitute the major portion of the anterior dermal palate. The palatine is either small or absent. When present, it does not contact the pterygoid. The pterygoids are small, usually triradiate structures, one ramus extends to the suspensorium, another

Figure 17. Anurans. Top and Bottom Rana catesbeiana. Rm uncatologued. Scale equals 1cm. MiddleLeptodactylus. (Redrawn from Trueb 1973).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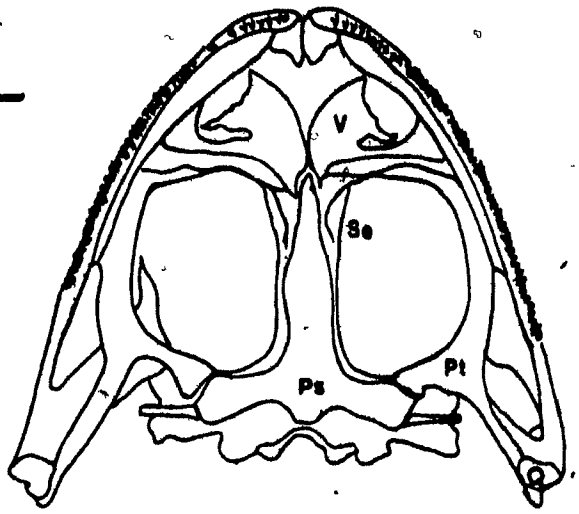
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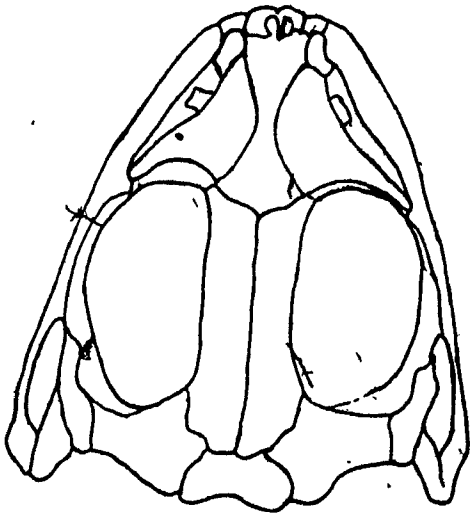
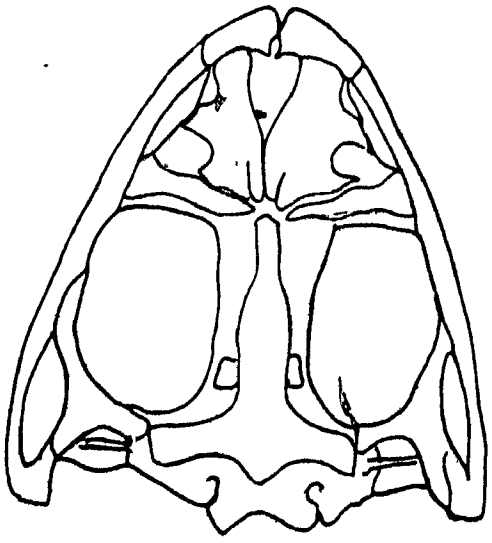




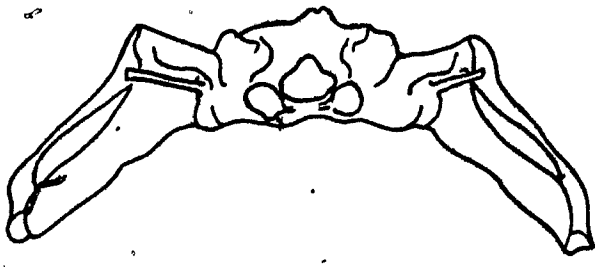
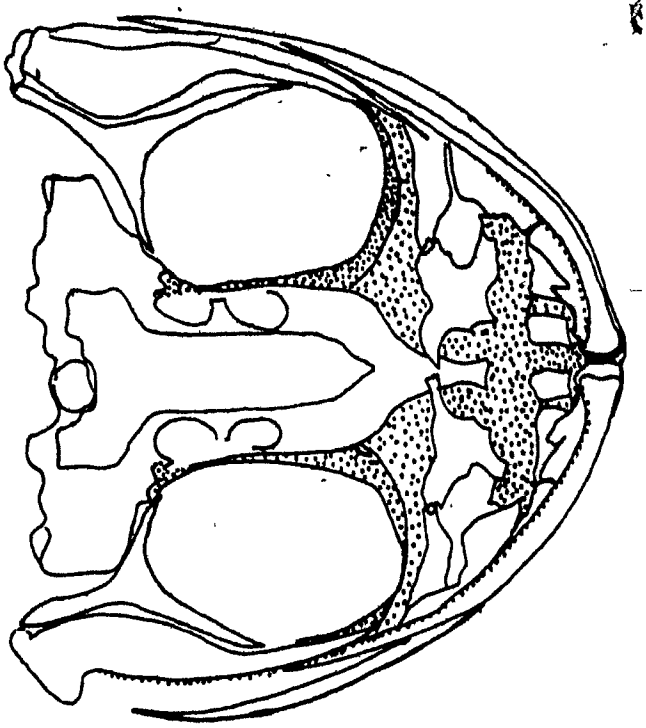
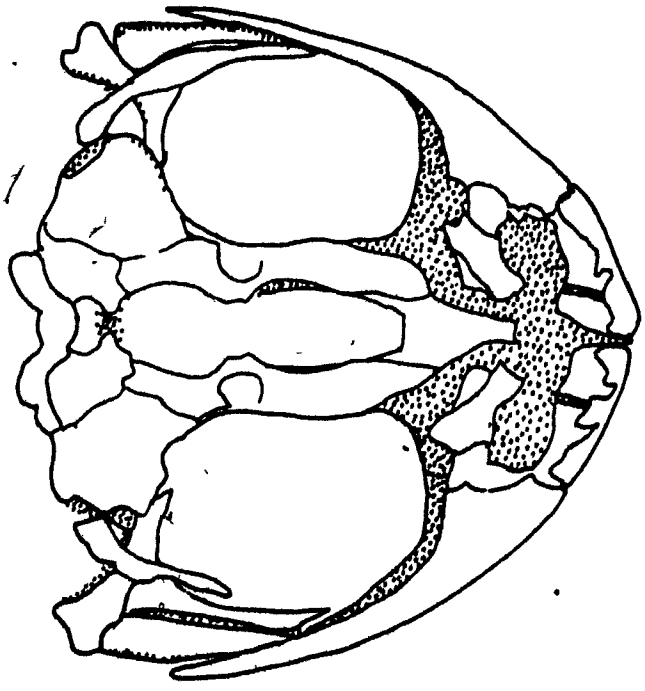


Figure 18. The primitive anuran Leiopelma hamiltoni NMNS 29597-5; left palatal view, right dorsal view. oarse stippling denotes cartilage





meets the maxilla, and a third, if present, extends toward the otic capsule of the braincase.

The braincase is a unified structure. It is essentially T-shaped in palatal view. The 'spar' of the T is made up of the cultriform process of the parasphenoid, forming the ventral surface of the braincase, bordered on either side by a ventromedial extension of the sphenethmoid. The arms of the T are formed by the laterally expanded otic capsules. The otic capsule comprises the opisthotic, which is indistinguishably fused to the exoccipital and the large prootic. The prootic and opisthotic are often indistinguishably fused. There is usually an impedence matching ear involving a long slender stapes and plectrum.

Anuran teeth are pedicellate (except in Xenopus) when they are present. The lower jaw contains two (mostly) dermal elements, the dentary and the angulosplenial, as well as an ossification of Meckel's cartilage, the mentomeckelian, at the mandibular symphysis. The hyolaryngeal apparatus is a highly derived and variable structure. The foregoing brief attempt to characterize the anuran skull belies the wide range of anatomical variation within the group (see Trueb 1973).

There is slightly more general agreement on the outgroup relationships of anurans than there is for the other groups considered. They are most commonly allied with the urodeles (Eaton 1959), or with urodeles and caecilians (Gadow 1901; Parker et al 1956; Parsons and Williams 1963; Cox 1967; Lombard and Bolt 1979; Gardiner 1982), although to my knowledge, anuran/caecilian relationship exclusive of the

urodeles has never been proposed. Whether or not associated with salamanders or caecilians, they are usually perceived to have been derived from temnospondyl labyrinthodonts. Among the hypotheses considered here, it is only those of Gadow (1901), Cox (1967), and Gardiner (1982, 1983) that do not permit the direct descent of anurans from temnospondyls. The reason for the concordance, presumably, is the existence of what are usually taken to be morphological intermediates between temnospondyls and anurans. Triadobatrachus (Protobatrachus) of Madagascar is considered a proanuran and shows a number of typically temnospondyl features (Piveteau 1937; Watson 1940). It has been proposed as a morphological intermediate between anurans and labyrinthodonts (but see Hecht 1962, 1963). A credible argument is made by Bolt (1969, 1977) for the evolution of frogs from a Doleserpeton or Tersomius-like ancestor.

Urodeles

There is considerably less agreement over the relationships of the urodeles. There are currently 96 recognized genera, 34 of which are extinct. They are arranged in 13 families, four of which are wholly extinct. The earliest known salamander is Karaurus from the Upper Jurassic of the USSR (Ivakhnenko 1978)

Like the anurans, urodele cranial anatomy can be characterized quite easily but it must be recognised that the

urodele 'bauplan' incorporates a wide range of variation. Urodele skulls are marked by the possession of significantly fewer distinct elements, both dermal and endocranial, than are found in primitive tetrapods (fig. 19). The temporal region is widely fenestrated. Carroll and Holmes (1980) interpret this as an extensive emargination of the cheek, their viewpoint owing to the fact that the ventral margin of the cheek is incomplete. There are no circumorbital elements behind the eye, and no postparietal elements. Generally there is no palatine in adults, with the exception of genera such as Pseudobranchus and Siren. Lebedkina (1967) claims that the palatine is incorporated into the pterygoid during developement. The pterygoid is usually triradiate. The anterior ramus does not contact the dermal palate or the maxillary arch, either directly or indirectly. The basal ramus is associated usually with the otic capsule, and the quadrate ramus with the suspensorium. The suspensorium is a strut, directed ventrally from the skull roof, comprising the squamosal and the quadrate. Dorsally the squamosal contacts either the parietal or the otic capsule.

The neurocranium is formed usually of two large endochondral units. The orbitosphenoid anteriorly, and the oticoccipital posteriorly, both underlain by the wide parasphenoid. The anterior extension of the braincase is parallel-sided, the lateral margin formed largely by the orbitosphenoid. The oticoccipital moiety is extensively fused. There are no distinct basioccipital or basisphenoid elements. The otic capsule is also a single coossified unit in most

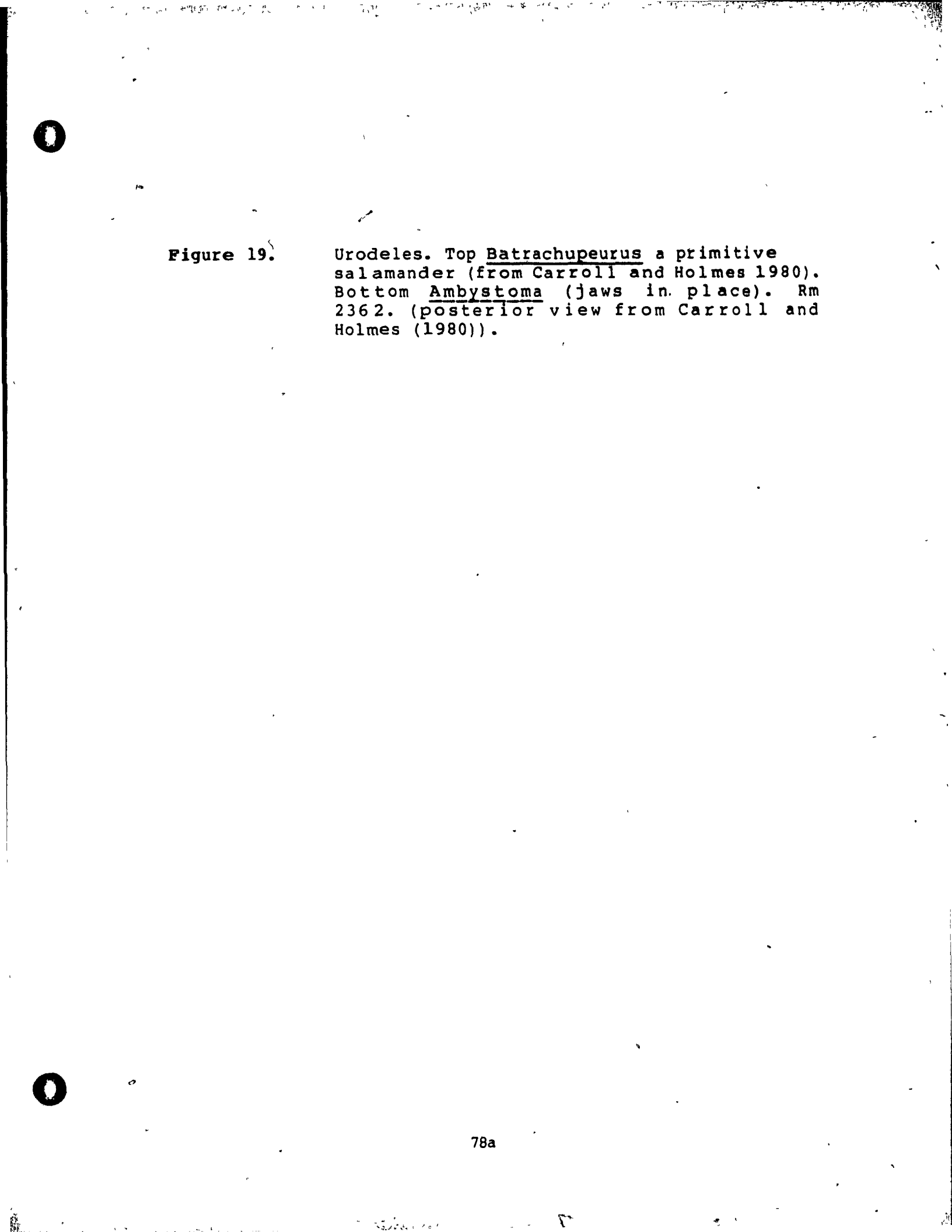
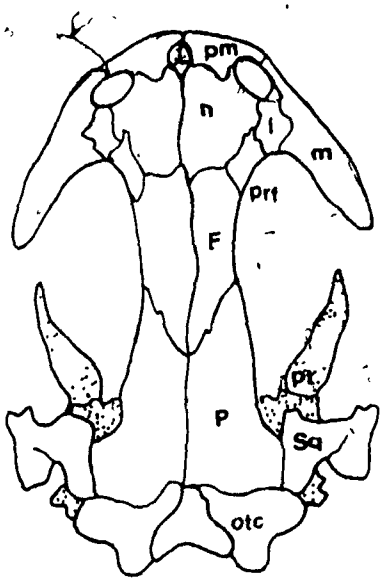


Figure 19. Urodeles. Top Batrachupeurus a primitive salamander (from Carroll and Holmes 1980). Bottom Ambystoma (jaws in place). Rm 2362. (posterior view from Carroll and Holmes (1980)).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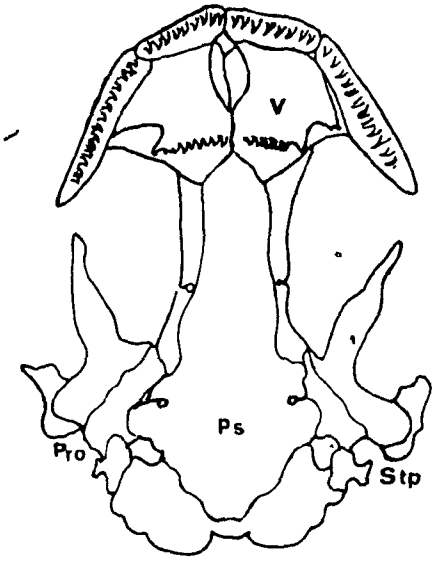
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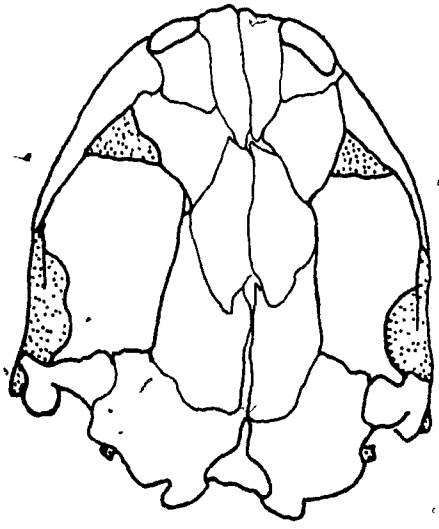
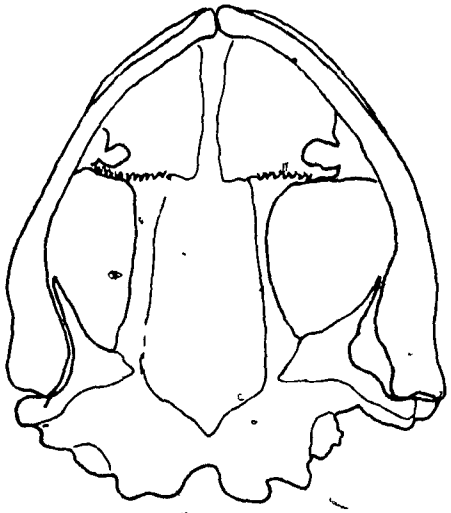
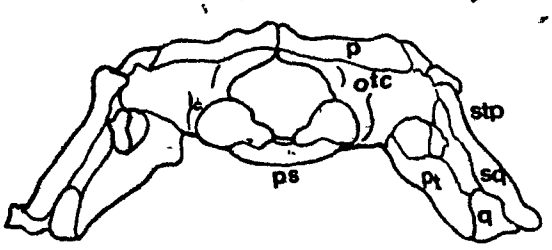





p
otc
stp
ps
pt
sq
q

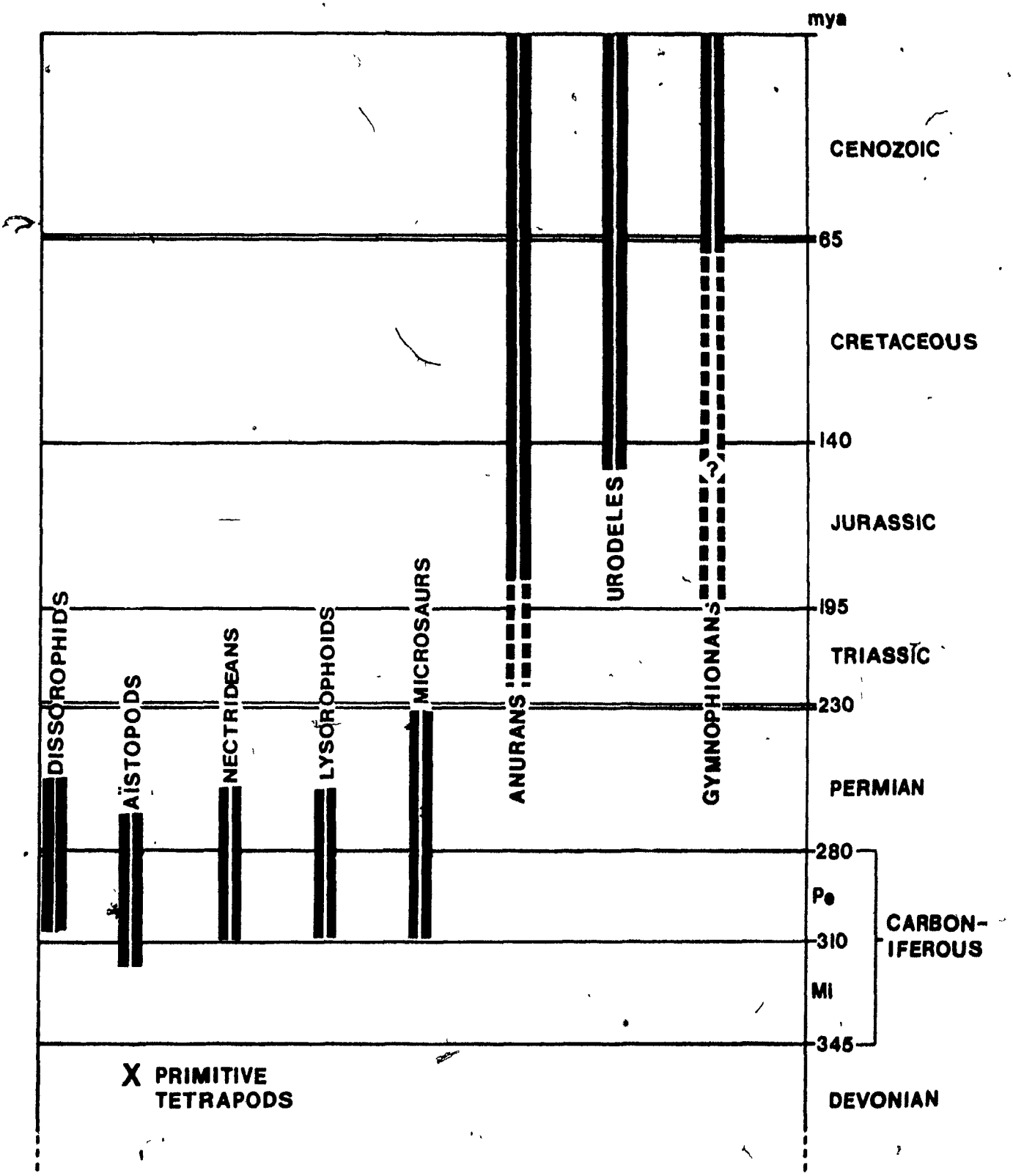
adults, although distinct prootic and opisthotic anlagen are discernible early in development (Bonebrake and Brandon 1970).

The lower jaw comprises essentially the dermal elements dentary and prearticular. There is a separately ossified articular and, in addition, an ossification of Meckel's cartilage at the region of the mandibular symphysis. The hyoid apparatus is highly variable

Most authors unite urodeles with anurans, caecilians, or both. Romer (1950) allied the urodeles with the microsaurs alone. Carroll and Holmes (1980) proposed tuditanomorph microsaurs such as Llistrofus, in which the cheek is emarginate, as probable ancestors. Gregory et al (1956) concluded that urodeles are derived from nectrideans (see also Parsons and Williams (1963) for the similarity between their 'protolissamphibian' and Scincosaurus. They were thought by Schmalhausen to be derived from the lysorophoids, and by Estes (1965) to have evolved from labyrinthodonts.

The stratigraphic ranges of the groups discussed here are given in figure 20. A synopsis of their proposed interrelationships is shown in figure 2.

Figure 20. Stratigraphic ranges of the potential sistergroups.


mya
CENOZOIC
65
CRETACEOUS
140
JURASSIC
195
TRIASSIC
230
PERMIAN
280
Pe
310
MI
345
CARBON-
IFEROUS
DEVONIAN
DISSOROPHIDS
AÏSTOPODS
NECTRIDEANS
LYSORPHOIDS
MICROSAURS
ANURANS
URODELES
GYMNOPHIONANS
X PRIMITIVE TETRAPODS

METHODS AND MATERIALS

Cleared and stained specimens, dried skulls, and whole preserved caecilian specimens were observed. The dried specimens and some of the cleared and stained specimens were drawn with a camera lucida attached to a Wild M5 or M6 microscope and measured either from the drawings or, whenever possible, from the drawings and through an ocular micrometer. Most of the cleared and stained specimens were photographed using a Wild binocular microscope and camera attachment. Kodak Pan-X film was used for the photography. It was exposed at 50 ASA and developed using microdol developer.

A complete listing of the specimens observed and their mode of preservation is given in appendix 1. In total 173 caecilian specimens were available for study. The sample encompasses twenty two of the thirty four known living genera, and thirty seven of the 167 described species are identified. The compositon of these specimens among the major taxonomic groups considered in this study is as follows:

- Ichthyophiinae (10 specimens):

  Ichthyophis beddomei (1), I. kohtaoensis (3), unidentified (2).

  Caudacaecilia nigroflava (1), C. larutensis (1), C. asplenia (1) C. weberii (1).

- Uraeotyphlinae (2 specimens):

Uraeotyphlus narayani (2)

- Caeciliinae (20 specimens):

Caecilia ochrecephala (1), C. occidentalis (10), C. tentaculata (2), C. nigricans (1), unidentified (4).

Microcaecilia albiceps (2)

- Scolecomorphidae (5 specimens):

Scolecomorphus uluguruensis (2), S. kirkii (2), S. vittatus (1).

- Typhlonectidae (19 specimens):

Typhlonectes obessum (1), T. compressicauda (4), T. natans (3), unidentified (9).

Chthonerpeton indistinctum (1), S. viviparum (1)

- Rhinatrematidae (14 specimens):

Epicrionops petersii (5), bicolor (9).

- Dermophinae (93 specimens):

Afrocaecilia taitana (4).

Boulengerula boulengerii (1), B. titanus (1).

Dermophis mexicanus (48), unidentified (3).

Gegeneophis ramaswamii (2).

Geotrypetes seraphini (16), G. grandisonae (1) *.

Grandisonia alternans (2).

Gymnopis multiplicata (5).

Herpele squalostoma (1).

Hypogeophis rostratus (5).

Idiocranium russeli (1)

Indotyphlus battersbyi (1).

Scistometopum thomensis (1), S. gregorii (1).

Siphonops annulatus (1), unidentified (1).

(* generic designation of this specimen is being changed (Wake Pers. comm))

I have haye had access to a number of specimens of fossil and living tetrapods. These are also listed in appendix 1.

Primitive tetrapods:
Greererpeton burkemorani:
Ichthyostega sp.

Lysorophoids:
Brachydectes tricarinatus:

Cocytinus sp.

Aïstopods:
Ophiderpeton

Phlegethontia

Microsaurs:
Microbrachis and other unidentified specimens

Dissorophids:
casts of Amphibamus

The entire Redpath Museum teaching collection of modern amphibians was also available for inspection. Additionally, a beautifully preserved specimen of the rhipidistian Eusthenopteron foordi (RM 14.234) was available for inspection.

Cladogram construction

I have used a phylogenetic inference program for IBM PC (PHYLIP version 2.8, mixed parsimony program (MIX); Felsenstein 1978). Characters are coded as being primitive (0) or derived (1). For the majority of characters, I have used the 'Camin-Sokal' parsimony option which considers (0 -> 1)

transitions as being more likely than (1 -> 0). The program recognizes only binomial input (0 and 1). Characters with more than two states (e.g. 0,1',1") must be coded as more than one character. MIX requires that a character phylogeny be designated. For instance, if the series 0 -> 1' -> 1" were presumed, then the correct coding would be: 0=00, 1'=01, 1"=11, meaning that any transition ending at 1" (11) would have to pass through 1'(01). Except where it is impossible or inapplicable, I have tried not to predetermine the phylogenies of alternative apomorphic states. In order to maintain maximally unconstrained character phylogenies, for all multi-apomorphic characters I have coded all alternate apomorphic states as divergent from the plesiomorphic state (i.e. 0=00, 1'=01, 1"=10), and have employed the 'Wagner' parsimony option. The Wagner parsimony considers 0 -> 1 and 1 -> 0 transitions as equally possible. The result is not a fully unconstrained phylogeny. The transition from 1' -> 1" actually requires a 1' -> 0 -> 1" phylogeny, and is therefore <u>a priori</u> only half as likely as any single (0 -> 1 or 1 ->0) transition. This is the best way available in the PHYLIP program to keep the multi-apomorphic characters relatively unconstrained.

RESULTS

I. CHARACTER POLARITIES

Ingroup Characters

The polarities of twenty nine cranial characters, with 33 apomorphic states, are resolved for the ingroup analysis. The characters and the distribution of their states among caecilians are tabulated in Table 2. The states are described briefly in Table 3. The polarities and their resolution are discussed at greater length in the discussion section.

Outgroup Characters

Forty characters, with 62 apomorphic states, distributed among the caecilians and their proposed sister groups are polarized. The distribution of the character states groups is tabulated in Table 4. They are briefly described in Table 5.

II.RELATIONSHIPS

Ingroup Relationships

In general appearance the resultant cladogram (fig. 21) of the ingroup analysis is not greatly dissimilar from that

Figure 21. Ingroup cladogram for caecilians. Character numbers are as for tables 2 and 3.

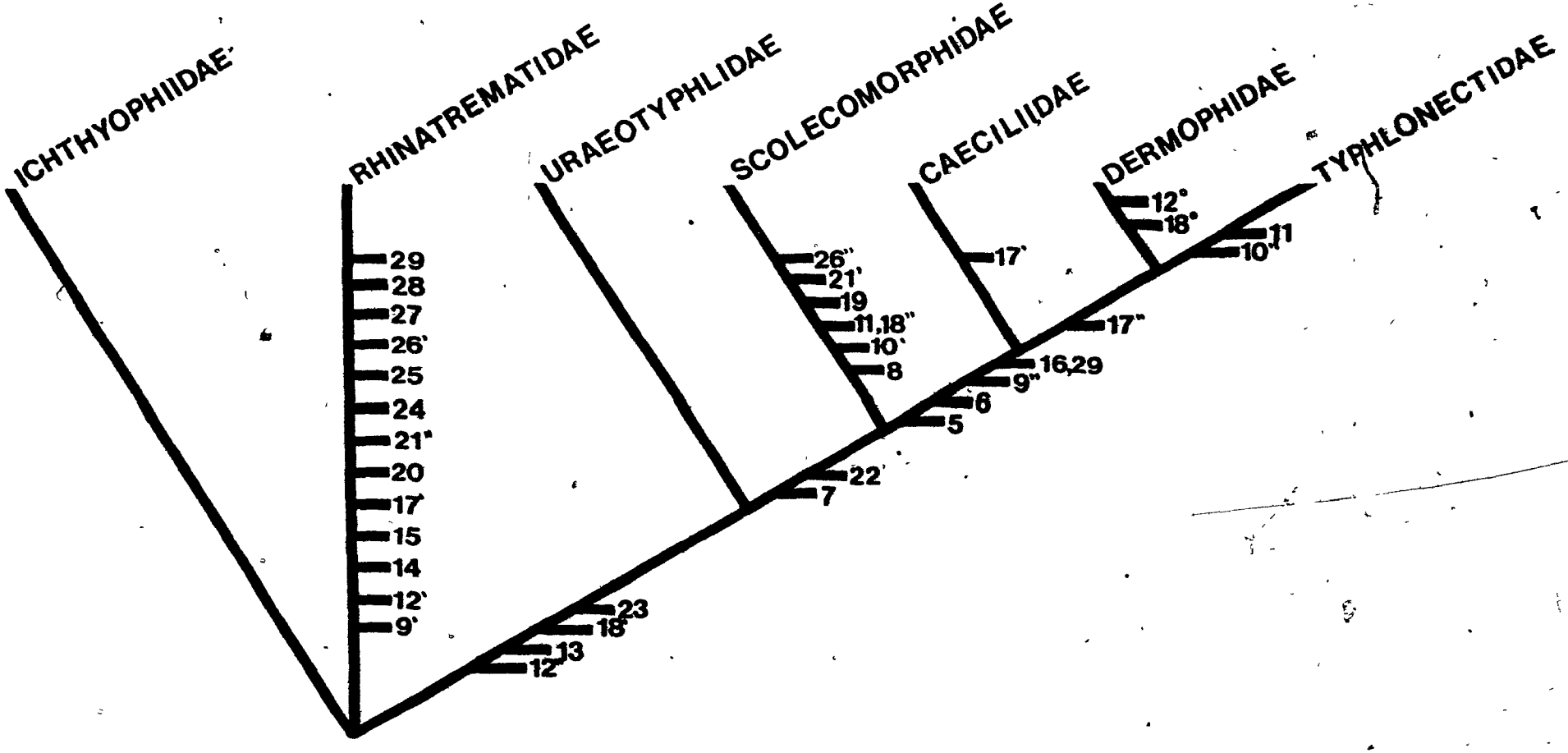

ICHTHYOPHIIDAE
RHINATREMATIDAE
URAEOTYPHLIDAE
SCOLECOMORPHIDAE
CAECILIIDAE
DERMOPHIDAE
TYPHLONECTIDAE
29
28
27
26'
25
24
21*
20
17'
15
14
12'
9'
23
18
13
12
22'
7
26"
21'
19
11,18"
10'
8
5
6
9"
16,29
17'
17"
12°
18°
11
10

TABLE 2a.

DISTRIBUTION OF INGROUP CHARACTERS
(outgroup comparison)

-- CHARACTER -- #	NAME	ICHTHY	URAEO	RHINA	SCOLE	DERMO	CAECI	TYPHL
1	Os Basale	0	0	0	0	0	0	0
2	Tentacle	0	0	0	0	0	0	0
3	Lower jaw	0	0	0	0	0	0	0
4	Double row teeth	0	0	0	0	0	0	0
5	Nasal	0	0	0	0	1	1	1
6	Premaxilla	0	0	0	0	1	1	1
7	Pterygoquad	0	0	0	1	1	1	1
8	Stapes	0	0	0	1	0	0	0
9	Vomers	0	0	1	0	0,1"	1"	1"
10	Internal naris	0	0	0	1'	0	0	1"
11	Orbit (O/C)	0	0	0	1	0,1	0,1	0
12	Tentacle/ orbit	0	1"	1'	1"	0	1"	1"
13	Tentacle/ orbit	0	0,1	0	na	0,1	1	1
14	Cheek attachment	0	0	1'	0/1"	0	0	0

TABLE 2b.
(continued)

DISTRIBUTION OF INGROUP CHARACTERS
(congruence characters)

-- CHARACTER -- # NAME	ICHTHY	URAEO	RHINA	SCOLE	DERMO	CAECI	TYPHL
15 Squamosal	0	0	1	0	0	0	0
16 Septomax.	0	0	0	0	1	1	1
17 Circumorb. bones	0	0	1'	na	1"	1'	1"
18 Tentacle. aperture	0	1"	0	1'	0	1"	1"
19 Kinesis	0	0	0	1	0	0	0
20 Basal articulation	0	0	1	0,1	0	0	0
21 Braincase	0	0	1'	1"	0	0	0
22 Occipital condyles	0	0	0	1	1	1	1
23 Perforate stapes	0	0,1	0	?	1	1	1
24 Mouth opening	0	0	1	0	0	0	0
25 Retroart. inflection	0	0	1	0	0	0	0
26 Hyoid	0	0	1'	1"	0	0	0
27 M.Interhy. posterior	0	0	1	0	0	0	0
28 MAMI	0	0	1	0	0	0	0
29 Prefrontal	0	0	1	0	1	1	1

TABLE 3.

INGROUP CHARACTER STATE DESCRIPTIONS

Character	Plesiomorphy	Apomorphy
1 Os Basale	Braincase elements fused	
2 Tentacle	Present	
3 Lower jaw	Pseudoangular and Pseudodentary	
4 Double row teeth	Palatal teeth	
5 Nasal	Present as discrete element	Fused or lost
6 Premax	Present as discrete element	Fused or lost
7 Pterygoid/ quadrate	Separate units	Combined unit
8 Stapes	Present	Fused or lost
9 Vomers	Bilateral contact extensive	1' divergent 1" apposed, os Basale intervenes
10 Internal naris	Present	1' indistinct 1" enlarged
11 Orbit	Open	Closed
12 Tentacle/ orbit	Anterior and adjacent	1' Within orbit 1" aperture removed from orbit
13 Tentacle/ orbit	Contiguous	Separated by dermal bone
14 Cheek attachment	synostosis	1' peg-in-socket 1" absent
15 Squamosal	At ventral cheek margin	Not at ventral cheek margin
16 Septomaxilla	Present	Lost or fused

INGROUP CHARACTER STATE DESCRIPTIONS (Continued)

Character	Plesiomorphy	Apomorphy
17 Circumorbital bones	Postfrontal (ocular)	1' Within maxpal. 1" between maxpal. and squamosal
18 Tentacle aperture	Anterior to orbit	Within orbit
19 Kinesis	Present	Absent
20 Basal articulation	Present	Absent
21 Braincase	Tapering	Parallel sided
22 Occipital condyles	Contiguous	Separate
23 Stapes	Perforate	Imperforate
24 Mouth opening	Subterminal	Terminal
25 Retroart. process	Inflected	Straight
26 Hyoid	Cb 3&4 fused	1'Cb 3&/or 4 lost 1"Cb 3&4 expanded
27 M. Interhy. post.	Two bundles	One bundle
28 MAMI	Within adductor chamber	Beyond adductor Chamber
29 Prefrontal	Present	Lost or fused

Figure 22. Outgroup cladogram. Character numbers are as for table 4.

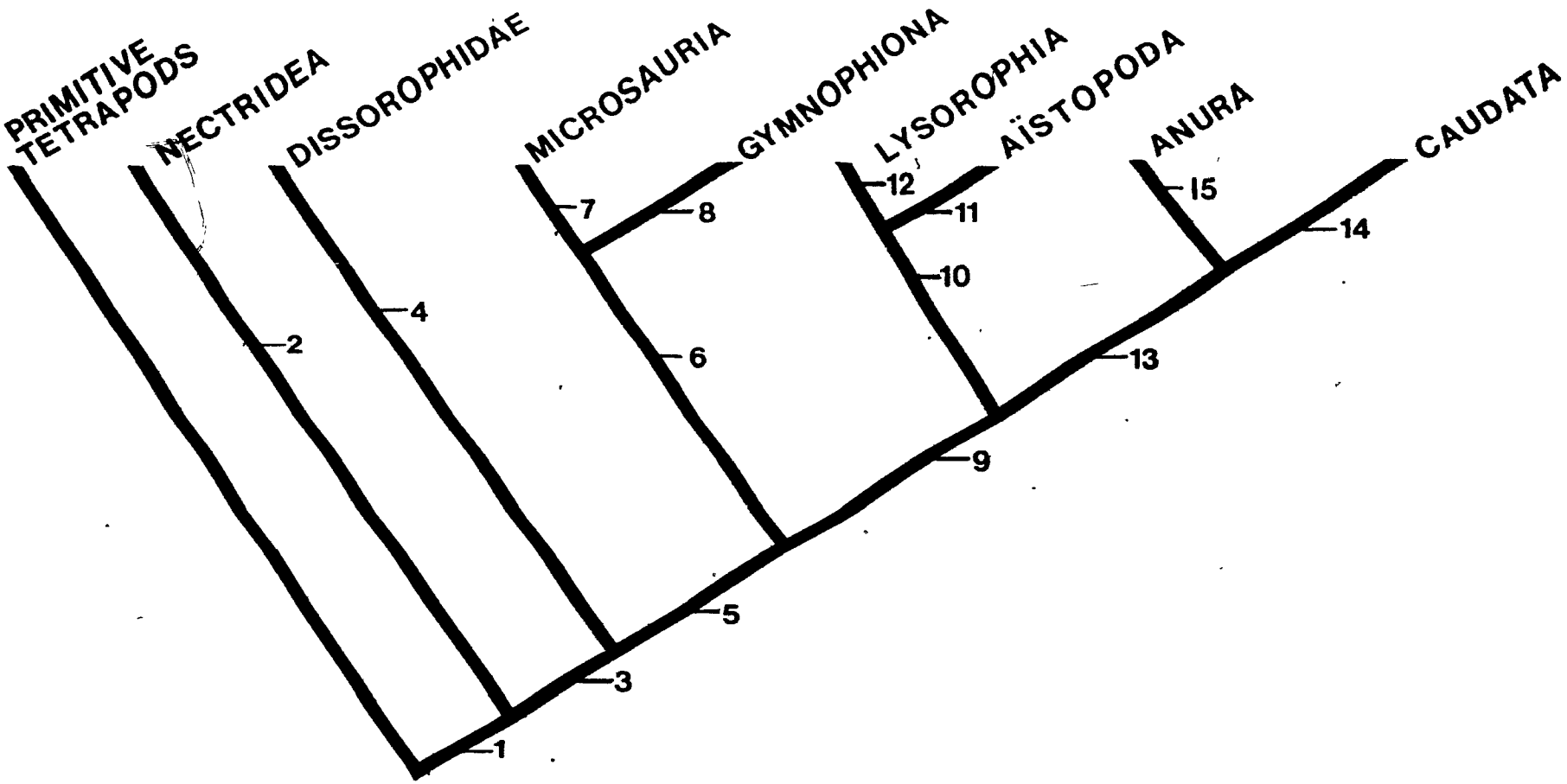

PRIMITIVE TETRAPODS
NECTRIDEA
DISSOROPHIDAE
MICROSAURIA
GYMNOPHIONA
LYSOROPHIA
AÏSTOPODA
ANURA
CAUDATA
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15

TABLE 4

CHARACTER STATE DISTRIBUTION FOR OUTGROUP RELATIONSHIPS

#	Character.	Group: AISTOPODA	NECTRIDEA	LYSOROPHIA	ANURA	URODELA	GYMNOPHIONA	MICROSAURIA	DISSORPHIDS
1	Braincase fusion	1'	0	0	1"	1'	1'	0	0
2	Prootic/Opisthotic	0/1	0	0	0	0	1	0	0
3	Synotic Tectum	0	?	?	0	0	1	1	?
4	Supraoccipital	1	0	1	0	0	0	1/0	0/1
5	Operculum	0	0	0	1	1	0	0	0
6	X Nerve Foramen	1"	0	1"	1'	1'	1"	1"	0
7	Craniovertebral Joint	1'	1'''	0	1'''	1'''	1"/1'''	1"/1'''	1'''
8	Stapes Morphology	1'''	?	1'	1"	1'	1'	1'	1"
9	Stapes Perforation	?	?	0	1	1	0	0	0
10	Paroccipital Process	1'	0/1"	1'	1"	1"	1'	1'	0
11	Pleurosphenoid	0	0	0	0	0	1	1	0
12	Parasphenoid	0/1	0	0	0	0	1	0	0
13	Cultriform Process	0	0	1"	1'	1'	1'''	1'''	0
14	Sphenethmoid	0	0	0	0	1	1	0	0
15	Interpterygoid Vacuities	0	0/1'/1"	0	1"	1"	1'	1'	1"
16	Pterygoids bilateral contact	1	0/1	0	1	1	1	1	1

TABLE 4 (Continued)

CHARACTER STATE DISTRIBUTION FOR OUTGROUP RELATIONSHIPS

#	Character.	Group: AISTOPODA	NECTRIDEA	LYSOROPHIA	ANURA	URODELA	GYMNOPHIONA	MICROSAURIA	DISSOROPHIDS
17	Basicranial Articulation	0	0/1"	0	1	1	0	0	0
18	Pterygoid/Maxillary Arch	1'	0	1'	1"	1	0	0	0
19	Epipterygoid	0	0	0	1	0/1	1	0	0
20	Ectopterygoid	0/1	0/1	1	1	1	1	0	0/1
21	Palatal Teeth	1'''	0/1'''	1"	1'''/1"	1"	1'	0	0/?
22	Pedicellate Teeth	0	0	0	0/1	0/1	1	0	0/1
23	Post Parietal Elements	0/1	0	0	1	1	1	0	0
24	Frontoparietal	0/1	0	0	1	0	0	0	0
25	Parietal Foramen	0/1	0	1	1	1	1	0/1	0
26	Squamosal/Parietal contact	0/1"	0/1'	1'	1'/1"	1'/1"	1'	0	0
27	Otic Notch	0	0	0	1	0	0	0	1
28	Post Orbital Elements	0	0	1"	1"	1"	1'	0	0
29	Septomaxilla	1	1	1	0	0	0	0	0/1
30	Quadratojugal	0	0	1'	0/1"	0/1"	1'	0	0

TABLE 4 (Continued)

CHARACTER STATE DISTRIBUTION FOR OUTGROUP RELATIONSHIPS

#	Character.	Group: AISTOPODA	NECTRIDEA	LYSOROPHIA	ANURA	URODELA	GYMNOPHIONA	MICROSAURIA	DISSOROPHIDS
31	Quadrate Kinesis	0	0	0	0	1	1'	0	0
32	Cheek Fenestration	1	0	1	1	1	0	0	0
33	Ventral Cheek Margin	0	0	1	0	1	0	0	0
34	Craniomandibular Joint	0/1'	0/1'	1'	0/1'	1'	1'	1'	0
35	Jaw Closure	0	0	0	0	0	1	1	0
36	Bones in Lower Jaw	0/1'	0	0	1"	1'''	1'	0	0
37	Mentomeckelian	0	0	0	1	1	0	0	0
38	Splenial Teeth	0	0/1	0	0	0	1	1	0
39	Retroarticular Process	0	0/1'	0	0	1'	1"	1'	0
40	Hyoid Structure.	0	?	1'	1"	1'	1'	1'	?

TABLE 5

OUTGROUP CLADOGRAM TRANSFORMATIONS

Internode	Taxa	Character	Transformations
1	All Outgroups	7'''	Double occipital condyle
2	Nectrideans	29	Loss of septomaxilla
3	All minus Nect	16	Loss bilateral contact pteryg.
4	Dissrophids	8"	Impedence matching stapes
		15	Wide interpterygoid vacuities
		27	Otic notch
5	Ly, Al, An, Mi, Gym.	8'	Stapes morphology
		25	Loss parietal foramen
		34	Jaw joint anterior to occiput
		40	3 or 4 ceratobranchials
6	Microsaurs & Gymnophionans	3	Loss synotic tectum
		13"	Tapering parasphenoid
		10'	Paroccipital process (none)
		11	Pleurosphenoid
		15'	Interpterygoid vacuities
		16"'	Vagus nerve foramen
		35	Subterminal jaw
		38	Two rows teeth -lower jaw
		39'	Retroarticular process
		(7")	Craniovertebral joint
7	Microsaurs	26°	Squamosal-parietal non-contact
8	Gymnophionans	1'	Fusion post. portion braincase
		2	Otic capsule fusion
		12	Parasphenoid
		14	Sphenethmoid fusion
		19	Loss of epipterygoid
		20	Loss of ectopterygoid
		21'	Palatal teeth
		22	Pedicellate teeth
		23	Loss of postparietal elements
		26	Squamosal-parietal contact
		28	Single circumorbital element
		30'	Fused quadratojugal
		31'	Quadrate kinesis
		36	Pseudodentary, pseudoangular
		39"	Retroarticular process

TABLE 5 (continued)

OUTGROUP CLADOGRAM TRANSFORMATIONS

Internode	Taxa	Character Transformations
9	Ly & A?/ An & Ur.	21"' Palatal teeth
		26 Squamosal-parietal contact
		28 Loss of postorbital elements
		32 Cheek fenestration
10	Lysorophoids & A?stopods	4 Supraoccipital
		10' Loss of Paraoccipital process
		29 Loss of Septomaxilla
11	A?stopods	1' Braincase fusion-posterior
		2 Otic capsule fusion
		6" Vagus Nerve Foramen
		7' Craniovertebral joint
		8"' Stapes morphology
		21"' Loss of Palatal teeth
		28° Postorbital element
12	Lysorophoids	11 Pleurosphenoid
		13" Cultriform process
		30" Loss of quadratojugal
		33 Loss of ventral cheek margin
13	Anurans & Urodeles	1" Braincase fusion -posterior
		2 Otic capsul fusion
		5 Operculum
		6' Vagus nerve foramen
		9 Stapes imperforate
		10" Paraoccipital process to cheek
		15" Wide interpterygoid vacuities
		13' Loss of postparietal elements
		(22) Pedicellate teeth
		(26") Squamosal-parietal contact
		(30) Loss of Quadratojugal
		37 Mentomeckelian
14	Urodeles	18 Loss Pterygoid-maxilla contact
		31" Quadrate kinesis
		33 Ventral cheek margin
		36"' Bones in mandible
15	Anurans	8" Stapes morphology
		24 Frontoparietal
		27 Otic notch
		36" Bones in mandible
		40" Hyoid

produced by Nussbaum (1979) by use of clique analysis or that reported for the same data by Duellman and Trueb (1986:466) employing the WAGNER 78 program. Except for the fact that the Caeciliidae is treated as two separate taxa in this study (Caeciliidae and Dermophidae), the cladogram produced by this study and that reproduced in Duellman and Trueb are Wagner-equivalent (Cartmill 1981). This means that the topologies are equivalent. There are rooted in different places however. The previous studies (Nussbaum 1979a; Duellman and Trueb 1986) (fig. 10) relied on what is largely a different suite of characters, including a significant proportion of postcranial features. Some of the cranial characters employed here do overlap with those of Nussbaum's studies (1977, 1979a). Due to the methodological differences between those studies and this, some of the transformation series are ascribed different polarities. The current study suggests that a number of minor modifications to the previously proposed classification schemes are in order.

The genus Uraeotyphlus is currently subsumed under the Family Ichthyophiidae as a separate subfamily, Uraeotyphlinae (Nussbaum 1979). It appears from this analysis that although ichthyophiines (the other subfamily of the Ichthyophiidae) can be said to be a plesiomorphic sister group of the uraeotyphlines, the two subfamilies do not constitute a discrete monophyletic assemblage in themselves. Rather the uraeotyphlines would be included in a monophyletic assemblage that would include all other caecilians except the

ichthyophiines and the Family Rhinatrematidae. Uraeotyhlines are united with these groups by the structure of the tentacle and tentacular aperture, and the possession of an imperforate stapes. The stapes of Uraeotyphlus shows what may be considered an intermediate stage as it is notched for the passage of the stapedial artery. It is interesting to note though that two of these tentacular characters (12 and 18") are not shared with the dermophids.

Additionally, the groups commonly united under the Family Caeciliidae (Subfamily Caeciliinae and Subfamily Dermophinae) appear not to comprise a monophyletic group. They can be differentiated on the basis of the configuration of the bones surrounding the orbit (17). The orbit in caeciliines, when present, is located entirely within the maxillopalatine, a condition apparently independently derived in rhinatrematids, whereas the orbit in dermophines, when open, is bordered by both the maxillopalatine and the squamosal. A number of anatomical differences have been cited by Taylor (1968a), Wake and Campbell (1983), and Laurent (1984) to differentiate further the caeciliines from the dermophines. These include the extremely large teeth of caeciliines as compared with dermophines (Wake and Campbell 1983), and the notch at the anterior extremity of the caeciliine vomers, not found in the dermophinae (Taylor 1968a). The caeciliines (sensu Wake and Campbell 1983) and the dermophines are treated here as separate families, Caeciliidae and Dermophidae respectively.

The Typhlonectidae, the (here termed) Dermophidae and Caeciliidae appear to compose a monophyletic assemblage

united by the common fusion of the nasal (5) and premaxillary (6), the loss of the prefrontals (29), a narrow, but variable, extension of the os basale between the vomers (9") and the loss of the septomaxilla (16), or its incorporation into the nasopremaxillary complex (Wake and Hanken 1982). This conclusion is implied in the results of the clique analysis and Prim Network analysis performed by Nussbaum (1979)

The most striking difference between the results of this analysis and others is not the number of distinct families or the distribution of characters between them; it is the relationship between two particular families, Ichthyophiidae and Rhinatrematidae. In Nussbaum (1979), Duellman and Trueb (1986) and in this study these two families have a sister group relationship. However, in this study the Ichthyophiidae are by far the more primitive group. Since Nussbaum's (1977) study of the Rhinatrematidae it has been considered to be the most primitive assemblage. In contrast with that view, the rhinatrematids here appear to be quite derived. Out of the twenty nine characters considered they exhibit a total of 13 apomorphies, none of which is shared with any other caecilian group. Only the highly specialized typhlonectids and the caeciliids (a total of 9 genera) have equal numbers of apomorphic features. None has as many autapomorphies. Apart from the convergence cited above (17'), and the independent loss of the prefrontal, rhinatrematids share only caecilian plesiomorphies with the other groups.

On the basis of their possession of the plesiomorphic state for the fourteen characters polarized by outgroup comparison, the ichthyophiids (Ichthyophis and Caudacaecilia) are taken to represent the most primitive living caecilian assemblage. Like the rhinatrematidae, they share only plesiomorphies with the rest of the order. Unlike any other group, they manifest no apomorphic states of the 29 characters considered here. This, in part, is a requirement of the methodology for characters 15 through 29, as a result of the rather stringent constraints put on the outgroup comparison. It is significant though that for the 14 characters resolved by outgroup comparison the primitive condition for all is found in the ichthyophiids. The eventual description of the caecilian fossil material will provide an independent test of these polarities.

The relative primitiveness of these two families warrants a closer look because of its bearing on the skull fenestration controversy. The two rhinatrematid genera are distinctly zygokrotaphic. Uniquely in these forms, the jaw adductor muscle mass extends dorsally beyond the adductor chamber and takes its origin on the lateral skull roof surface. The presumed primitive nature of this family lent creedence to the interpretation of zygokrotaphy as primitive for caecilians, although it should be noted that this character was used in assigning the rhinatrematids their primitive status on the assumption of lissamphibian monophyly (Nussbaum 1977). The skull is essentially closed in the ichthyophiids, but a line of weakness or a small temporal

fenestra is observable in such species as Ichthyophis kohtaoensis (Taylor 1969a). The condition of the skull roof has not been coded as a character on the cladogram given, but it is evident that zygokrotaphy must have arisen a number of times within the order. A minor gap between the cheek and skull roof is found in Uraeotyphlus narayani (Nussbaum 1979a), and U. oxyurus (Taylor 1969). Full temporal fenestration appears to have evolved independently within the Scolecomorphidae (Scolecomorphus only), once in the Dermophidae (Geotrypetes), and in the Typhlonectidae.

There are a number of characters that undergo what, in the context of the cladogram proposed here, must be considered convergences or reversals. The most labile characters appear to be associated with the tentacle and the orbit/tentacle relationship. Character 13, with only one discernible advanced state (tentacle not confluent with orbit), is seen to undergo three character state reversals, one in each of the Uraeotyphlidae and Dermophidae which are polymorphic for this state, and once in the internode before the emergence of the Uraeotyphlidae. Character 12 (spatial relation of tentacle and orbit), with two apomorphic states is seen to diverge from the primitive condition, found in Ichhtyophiids, independently in rhinatrematids and the suite comprising all other families. The contribution of dermal bones to the tentacular aperture (18) undergoes reversion to the plesiomorphic state in dermophids. If, as Nussbaum (1977) and Badenhorst (1978) note, the forward migration of the tentacle is a common feature in

the ontogeny of caecilians, a retardation of the rate of forward migration could produce the condition found in rhinatrematids, and its acceleration would yield a condition such as that in scolecomorphids and Uraeotyphlus. The attainment of the orbit wholly within the maxillopalatine (17') appears to have been derived independently in caeciliids and rhinatrematids. The absence of a discrete prefrontal (29) is a homoplasy occuring within rhinatrematids and all groups distal to the divergence of the scolecomorphids.

Outgroup Relationships

The most parsimonious cladogram for the forty characters analysed is shown in Figure 22. Character transformations are listed in the accompanying table (Table 5). The cladogram lists as characters only those that fully transform. Characters that transform between some members of a terminal taxon and its nearest node are not denoted.

One of the immediately striking results of the cladistic analysis is the number of autapomorphies that define terminal taxa. This indeed is the crux of the longstanding conundrum over amphibian interrelationships. Although the groups are easily discerned, they are not easily allied with one another. The nectridea are the minor exception, as a group they bear only one autapomorphy. They independently lose the primitive septomaxilla (29). Many of the trends that

characterize later assemblages, though, are attained independently within the nectrideans. Despite their early appearance, the aïstopods as a whole exhibit a considerable number of autapomorphies (6). These include the extensive fusion of the posterior portion of the braincase (as in Phlegethontia) (1'), as well as the fusion of the otic capsule elements (2), the concave median craniovertebral joint (7'). The stapes morphology (8''') of Phlegethontia, as restored by Turnbull and Turnbull (1958), is unique. The dermal skull roof is reduced as an independent advancement within the aïstopods. The palatal teeth (21''') are lost independently.

The lysorophoids exhibit sixteen apomorphic features. Four of these are derived independently from all other groups. The braincase of lysorophoids maintains many of the primitive tetrapod features. The shape of the cultriform process (13") is a unique feature. The cheek is emarginate ventrally (33).

The anurans exhibit five autapomorphies. The slightly-built stapes (8") and the otic notch (27), although shared with dissorophids, are independently derived. The hyoid in anurans (40") is a highly specialized structure (Trueb 1973). Fusion of the frontoparital (24), and the configuration of the elements of the lower jaw (36") are also independently derived.

There are six autapomorphies of urodeles. The fusion of the orbitosphenoid elements of the ethmoid moiety (14), and the unique style of quadrate kinesis (31") are distinguishing features. The ventral cheek margin is independently lost in

urodeles (33). Pterygoid-maxilla contact is lost (18). The structure of the lower jaw (36''') is derived in urodeles.

The highly derived, distinctive nature of the caecilian skull is best evidenced by its possession of fourteen autapomorphic features among thirty apomorphies. The braincase and the otic capsule elements are extensively fused (1 and 2). Although this resembles the condition seen in aistopods it appears to have occurred convergently. The extensively fused ethmoid moiety of the braincase is unique (14), as is the complete fusion of the parasphenoid with the endochondral braincase (12). The form of quadrate kinesis (31'), the contact of the squamosal and the parietal (26'), the independent loss of the postparietal elements (23), and the reduction to one, of the postorbital series (28) and the developmental fusion of the quadratojugal anlage to the surrounding squamosal element, all mark the caecilian skull roof and cheek unit as unique among the tetrapods. Quite significantly, pedicellate teeth (22) are acquired independently, as is the row of palatal teeth (21"). There is no epipterygoid (19). The structure of the lower jaw, with its long retroarticular process (39'), and its obliquely joined pseudodentary and pseudoarticular also serve to distinguish this group (36').

In addition to the autapomorphies, distinguishing all members of a group from any other, characters are seen to undergo transformation independently within lineages. There are fully nine of these within the nectridea. These are:

expansion of the paroccipital process (10"), squamosal-parietal contact (26'), the loss of palatal teeth (21'''), the absence of the ectopterygoid (20), the fusion of the pterygoid with the parasphenoid at the basicranial articulation (17'), the location of the craniomandibular joint anterior to the occipital condyle (34); a row of teeth in the lower jaw (38); a relatively elongate retroarticular process (36'); pterygoids not contacting their bilateral counterparts medially (16); both alternate apomorphic states of the pterygoid vacuity (15' and 15"). Most of these derived characters are manifest in the family Keraterpetontidae.

Six characters transform within the Aïstopoda. Two of these are partial reversals. The partial reversals are in characters 34, the craniovertebral joint at the level of the occipital condyle and, 20, the parietal foramen. The apomorphies attained within the aïstopods are: fusion of the parasphenoid with the oticoccipital portion of the braincase (12), contact of the squamosal solely with the otic capsule dorsally (26"), loss of postparietal elements (23), the possession of two dermal elements in the lower jaw, joined by an oblique squamous joint (36') and, fusion of the frontal and parietal to form a frontoparietal (24).

There is a partial reversal within the gymnarthrid/goniorhynchid lineage involved with the presence of a parietal foramen (25). There is also a partial 0 -> 1 transformation, the possession in Rhynchonkos of a supraoccipital (4).

One character transforms within the urodeles. It is the

possession of pedicellate teeth (22). Tooth pedicelly also transforms within the anurans. It is equiprobably independently derived in some anurans and urodeles, or independently lost. Other characters changing within the anurans are: possession of a quadratojugal (30), the most parsimonious phylogeny requires this to be a reversal when it occurs. Vomerine teeth are both present and absent in the urodeles (27" -> 27'''). The craniomandibular joint (32) is located posterior to, anterior to, or level with the occipital condyle.

The synapomorphies that support sister group combinations are of the greatest significance. These are the presumed derived characters that indicate and order the relative recency of common ancestry among the groups in question. The phylogeny in Figure 22 delimits seven monophyletic groups in addition to the terminal taxa. These are: 1) all groups above the level of the primitive tetrapods, 2) all groups in 1, minus nectrideans, 3) the microsaur/gymnophionan + lysorphoid/alstopod + anuran/urodele assemblage; 4) the lysorophoid/alstopod + anuran/urodele assemblage, 5) the lysorphoids and alstopods, 6) the group comprising just anurans and urodeles, and, 7) the group made up of reciprocal sister groups microsaurs and gymnophionans.

One character unites all groups above the level of primitive amphibians. This is the possession of double occipital condyles. One character unites these groups above the level of nectrideans, the lack of bilateral contact of the

pterygoids anterior to the parasphenoid (16).

The microsaurs and gymnophionans plus the lysorophoids alstopods, urodeles, and anurans share four apomorphies. The stapes is composed of a large footplate (in relation to the overall size of the element) and a short, stout style projecting toward the suspensorium (8'). It subsequently transforms, becoming the impedence matching structure of anurans (8' > 8"). The parietal foramen is absent (25). This character is reversed in Rhynchonkos and some gymnarthrids. The craniomandibular joint is located anterior to the level of the occipital condyle (34). It reaches its most anterior location in the lysorophoids, where it is anterior to the level of the basicranial articulation. Once again, this character is reversed in a number of anuran genera. The structure of the hyoid apparatus comprising paired basibranchials and four (less commonly three) ceratobranchials unites these members (40'). Anurans further modify the hyobranchial skeleton (40"). The resultant character phylogeny is 40' -> 41".

That lysorophoids and alstopods share a sister group relationship with anurans and urodeles is a new proposal. It is supported in this hypothesis by five characters. Well developed rows of teeth on the vomers (21) are synapomorphic features. They are further transformed in the Alstopods. The contact of the squamosal with the parietal (26') is present in all three orders. As will be seen, it is equally probable that this character undergoes further transformation before or after the anuran/urodele node. The cheek region is highly

fenestrated in all four groups (32). There is no ectopterygoid (20), although it may be present in some alstopods (Bossy 1978). There are no remaining elements of the postorbital series (28"). The most parsimonious arrangement of this character is of one transformation, and a partial reversal, rather that three independent transformations. The ectopterygoid (20) is absent in all four assemblages but is present in Lethiscus, the earliest alstopod (Wellstead 1982). Although the tree shown in figure 22 is a strict consensus tree (rooted at the outgroup), trees generated by various subsets of these characters show the alstopods to be the most labile group. It is highly possible that additional characters would disrupt this putative sister group pairing.

The lysorophoids and Alstopods are united by four apomorphies, the presence of a supraoccipital (4), a reduced or lost paraoccipital process (10'), loss of pterygoid-maxilla contact, and lack of a septomaxilla (29).

The remaining groups, #7 and 8, are respectively the best supported sister groups in the entire cladogram. Their support is substantially stronger than that of all others. Group 7, anurans and urodeles, is defined by twelve synapomorphies (and possibly as many as fifteen) Group 8, caecilians and microsaurs, is supported by nine (possibly ten).

Those characters uniting anurans and urodeles (group 7) are the fusion of posterior braincase elements (1), prōotic/opisthotic fusion (2), imperforate stapes (9), a

laterally extended paroccipital process (10"), the parallel - sided structure of the anterior extension of the braincase (cultriform process) (13'), the widely divergent interpterygoid vacuities (15"), the possession of an operculum (5), the location of the vagus foramen (postotic foramen) (6'). The unique articulation of the pterygoid with the otic capsule (17'), and the loss of the epipterygoid (19) are also common features. Pedicellate teeth (22) are equiprobably a synapomorphy of urodeles and anurans, or independently derived within these groups. The absence of postparietal elements (23) unites these orders. The intervention of the otic capsule between the squamosal and parietal (or frontoparietal) (26") is equiprobably a synapomorphy, or independently derived. The loss of the quadratojugal (30) is equiprobably a synapomorphy or independently derived within the groups.

The last group to be considered is the order Gymnophiona and its sister group the gymnarthrid/goniorhynchid microsaurs, group 8. There are nine definite synapomorphies, and one possible one. The alternative apomorphies of the craniovertebral joint (7" or 7''') are equally likely as synapomorphies. The absence of a synotic tectum (3), the structure of the paroccipital process, and the presence of a pleurosphenoid element (11) in the braincase are distinctive features. Additional synapomorphies are, the shape of the interpteryogoid vacuities (15'), and the wide, tapering cultriform process (13'''). Finally, the structure of the lower jaw is seen as a unifying feature. The lower jaw is

subterminal in position (35). It bears an inner row or series of teeth (38), and a retroarticular process (39'). The last character is considerably more pronounced in caecilians, undergoing further transformation (39' -> 39").

DISCUSSION

Apart from the enunciation of an objective and robust methodology, the goal of this work has been to establish the most probable phylogenetic position of the caecilians within the tetrapods, most particularly, to choose the most likely of a number of putative caecilian sister groups. As a contingent result, this work permits one to propose a number of hypotheses concerning the interrelationships of other nonamniote groups, based on some fairly well supported sister group pairings.

Before a discussion of the implications of the cladograms shown in Figures 21 and 22, the rationale for the character polarities must be given. A discussion of the character state distributions within caecilians is followed by a discussion of the character states among the various sister groups.

I. Ingroup Characters

Outgroup Comparison (Characters 1-14)

The modified outgroup comparison resolves 14 characters. The distribution of character states among caecilian families, and subfamilies is summarized in the first portion of Table 2a.

Characters 1 through 4 are caecilian autapomorphies. These include the presence of an os basale (character 1), the possession of a tentacle (DeVilliers 1938; 1939) (character

2), the highly specialized lower jaw (3) and two parallel rows of pedicellate teeth on the palate (4) are present in all caecilian genera.

There is a great deal of variation in the number and configuration of the elements of the dermatocranium. Ontogenetically, the trends toward fusion of elements is clearly demonstrated, not only in the braincase but also in the dermal skull. The ontogenetic development of the skull has been observed for a number of genera, including: Ichthyophis (Peter 1898), Hypogeophis (Marcus et al 1933), Gegeneophis (Ramaswami 1948), Dermophis (Hanken and Wake 1982), Typhlonectes (chondrocranium only, Wake et al 1985) and Idiocranium (Wake and Savage 1986). Those elements of the dermal skull that can be observed to undergo fusion to adjacent elements in some genera include: nasal (5), prefrontal, septomaxilla, premaxilla (6), circumorbitals, quadratojugal (in Hypogeophis only), pterygoid (7), quadrate and in Scolecomorphus, the stapes (8). These elements are identified by topographical location only, and their homologies can not be established definitively. Those assigned character numbers occur as discrete units in the adults of at least one genus and can be polarized by outgroup comparison. The greatest number of separate units is found in the family Ichthyophiidae.

In primitive tetrapods, anurans, urodeles, microsaurs, nectrideans, and lysorophoids, the nasals (5), premaxillae (6), pterygoids (7), quadrates and stapes (8) all appear

primitively as separate units. This is taken to be the primitive condition for each of these elements within the caecilians. Circumorbital elements other than prefrontals are present in gymnarthrid microsaurs (Carrroll and Gaskill 1978), primitive urodeles (Hynobius) and dissorophids, but absent primitively in anurans (Estes and Reig 1973), and Lysorophoids (Bolt and Wassersug 1975). Anurans lack a prefrontal. The septomaxilla is present as a distinct element in urodeles, anurans (Duellmann and Trueb 1985), microsaurs (Carroll and Gaskill 1978) and nectridians, but is not represented in any of the known lysorophoid material (Bolt and Wassersug 1975), nor in Doleserpeton (Bolt 1969).

There are few characters of the dermal palate that exhibit much variation. Two such characters discussed by Nussbaum (1977, 1979a) are the configuration of the vomers (9), and the size and shape of the internal naris (10). The vomers range from being widely divergent posteriorly in rhinatrematids, to being bilaterally apposed along the midline throughout their length. The condition found in anurans, urodeles (Duellman and Trueb 1985), gymnarthrid microsaurs (Carroll and Gaskill 1978), primitive labyrinthodonts (Romer 1945), and lysorophoids (Bolt and Wassersug 1975), aïstopods and nectrideans (Milner 1978; Bossy 1976), and dissorophids (Carroll 1964), is one in which the vomers are apposed throughout all or most of their length; it is here considered primitive. The internal naris in caecilians is generally small and surrounded by the vomers and maxillopalatines. This is similar to the primitive

tetrapod condition and that in most anurans, salamanders, microsaurs nectridians and lysorophoids. The typhlonectids, uniquely, have greatly enlarged internal nares, which can be plugged by ossicles on the tongue. This is taken as being derived (10'). Another uniquely derived feature of the internal naris is found in the scolecomorphids, where the choanal border is indistinct (10") (Nussbaum 1979, 1985).

Primitively in tetrapods, and universally in the proposed sister groups of caecilians the orbit is open. This is the case in most caecilians, but in the scolecomorphidae (Brand 1956) and in some dermophids and caeciliids the orbit (11) has become occluded by dermal bone. The latter state is taken to be derived.

The relationship of the orbit (when present) and tentacle is subject to variation. The tentacle is usually taken to be the homologue of the nasolacrimal duct in other tetrapods (Weidersheim 1879 as cited in Badenhorst 1978). From a study of tentacular development by Badenhorst (1978) it appears that the tentacle structure incorporates the Harderian gland, the M. Retractor bulbi of the eye, the nasolacrimal duct, and is associated with Jacobsen's organ. Ontogenetically, the tentacle begins in front of the developing orbit in the familiar location of the nasolacrimal duct and usually migrates anteriorly. The development of this structure in rhinatrematids takes a different course. It is closely associated with the eye early in development, and in adults is located fully within the orbit (Nussbaum 1977). The adult

condition in the caecilians varies from one in which the tentacle is in front of the orbit and confluent with it (some ichthyophiids and dermophids), to one in which it is located far anterior to the orbit and separated from it by dermal bone (Uraeotyphlus, Scolecomorphids, and Typhlonectids), to one in which the tentacle is located fully inside the orbit. Judging by the position of the Harderian gland (Walls 1942) and the nasolacrimal duct in living tetrapods and the position of the nasolacrimal canal in primitive fossil tetrapods and rhipidistians (Jarvik 1980), the condition in which the tentacle is anterior to (12) and contiguous with (13) the orbit would appear to be primitive. The other conditions, the tentacle far anterior (12') or wholly within the orbit (12") are considered advanced. The condition in which the orbit and tentacular aperture are separated by dermal bone (13) is considered derived. Unfortunately, the condition of the nasolacrimal canal in lysorophoids is indeterminate (Bolt and Wassersug 1975; Wellstead 1985), but given the existence of a distinct lacrimal unit it will be assumed that the standard relationship obtains.

In all outgroups, and most caecilians, the connection of the cheek with the skull table or braincase is in the form of a wide synostosis (14). The cheek does not contact either skull roof or braincase in some scolecomorphids (e.g Scolecomorphus) (14"), but does in the normal manner in others (Crotaphatrema). Uniquely in rhinatrematids, a peg-in-socket articulation has evolved between the dorsolateral surface of the os basale and the squamosal. The rhinatrematid condition

is taken as derived (14').

Stratigraphic Sequence

The fossil record is of little assistance in reconstructing the caecilian morphotype. Two fossil vertebrae have been described, one from the Paleocene (Estes and Wake 1973), the other from the Uppermost Cretaceous (Rage 1986). They appear to be typical mid-dorsal vertebrae showing only minor variations on the modern caecilian pattern. Despite their holospondyly they do not bear any great deal of resemblance to the vertebrae of anurans, salamanders, gymnarthrid microsaurs, or lysorophoids, and especially not to that of the nectrideans. All that can be learned from these fossils is that the modern caecilian vertebral structure had been established by the Upper Cretaceous.

In summary, outgroup comparison allows discrimination of character states for 14 characters, four of which (Characters 1-4), are autapomorphies. These characters, and their distribution among families are summarized in Table 2a. Because of the dearth of caecilian fossil material, stratigraphic sequence of features is incapable of resolving any characters. This does not however diminish the validity of the paleontological argument in principle.

The Caecilian Stem Group

The Ichthyophiidae, standardly known as the Subfamily Ichthyophiinaeand comprising the genera Ichthyophis and Caudacaecilia, have the primitive condition of all 14 characters. The Uraeotyphlidae exhibits 12. Rhinatrematids display 11 of these plesiomorphies, dermophids 11. scolecomorphids 8, caecilliids 8, and Typhlonectids 7 (see Table 4a). On this basis, it is postulated that the ichthyophiids resemble most closely the latest common ancestor of all known living caecilians (fig. 23).

Having designated a most plesiomorphic known member, (the Ichthyophiidae), it is now possible to refine the putative morphotype, and to resolve further ingroup polarities. Note from the preceding section that, by chance alone, the ichthyophiines possess only plesiomorphic states of the characters polarized. This means that the putative morphotype, will be coextensive with the most primitive known member (namely the Ichthyophiinae). This is not a requirement of morphotype analysis, nor does it say anything about the veracity of the result. For the clinal characters listed below, the plesiomorphic state is taken to be that which is present in the Ichthyophiinae.

Congruence Characters (15-29)

Nussbaum (1979a) contended that the condition found

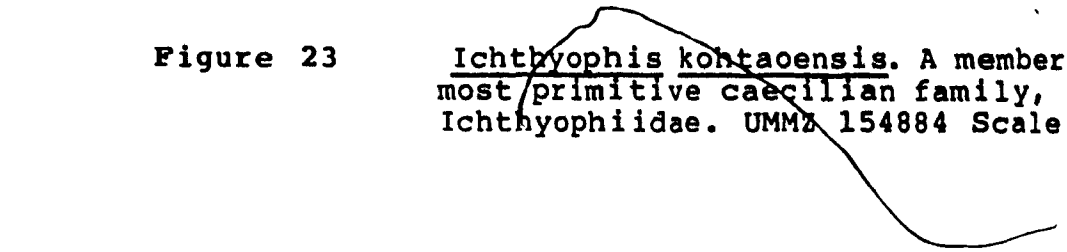
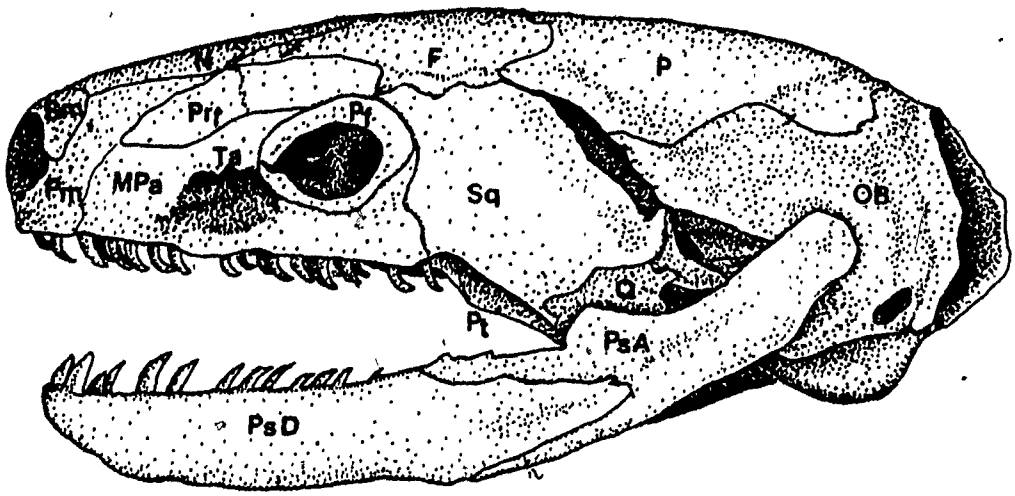


Figure 23 Ichthyophis kohtaoensis. A member of the most primitive caecilian family, Ichthyophiidae. UMMZ 154884 Scale bar = 1mm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uniquely in the rhinatrematids in which the contact of the maxillary portion of the maxillopalatine with the quadrate excludes the squamosal from the ventral border of the cheek is primitive for caecilians. The common condition, found in Ichthyophiids, and indeed all caecilians except rhinatrematids, is one in which the squamosal unit contributes to the ventral border of the cheek (15) (see fig.27a). A distinct septomaxilla (16) is present in the ichthyophiids, rhinatrematids and scolecomorphids; in typhlonectids, and caeciliids it is fused to the maxillopalatine (Laurent 1984). A distinct septomaxilla is also present in anurans, urodeles, nectridians and microsaurs, but not in lysorophoids, some dissorophids and aïstopods.

The orbit, when present, and tentacle vary in their spatial relationship to the dermal elements (17, 18). In the Rhinatrematid Epicrionops, the orbit is open and located entirely within the maxillopalatine. A similar relationship is found in the caeciliids with open orbits (17'). In the Dermophidae, the orbit, when present, is invariably defined by the maxillopalatine and the squamosal (17") (Taylor 1969). In both scolecomorphid genera the orbit is occluded. The primitive condition, found in ichthyophiines is one in which the orbit is surrounded by a circumorbital bone.

With one exception (rhinatrematids), the tentacle (18) in all families is anterior to the orbit (when the latter feature is present). In the Ichthyophiidae it is wholly

contained within the maxillopalatine, the probable primitive condition. The primitive condition is shared with the dermophines figured by Taylor (1969) except Idiocranium, Geotrypetes, and Herpele. Rhinatrematids are considered here to share this plesiomorphy as the tentacle/orbit is contained wholly within the maxillopalatine. In uraeotyphlines (Nussbaum 1979), typhlonectids and caeciliines, the tentacular aperture is shared by the nasopremaxilla and maxilla (18'). In scolecomorphids the tentacle exits ventrolaterally to the external naris, and is bordered by the maxillopalatine, prefrontal and septomaxilla (Nussbaum 1985) (see fig 27b) (18").

The cheek unit has a moveable articulation with the braincase (19) in all families except the scolecomorphids (Brand 1956). This latter state is considered advanced. In Ichthyophis, as in most caecilians, the squamosal is sutured, or closely apposed to the parietal (Visser 1963; Taylor 1969). In one genus of scolecomorphid (Brand 1956; Nussbaum 1985) the posterior attachment of cheek unit and skull table is evidently lost. In the other the primitive condition is retained. The basicranial articulation of caecilians is a synovial joint between the pterygoid (or the pterygoid portion of the pterygoquadrate) (20) (Marcus et al 1935; DeVilliers 1938). Despite its specialized function, it appears very similar to the basicranial articulation of primitive tetrapods above the level of the ichthyostegalians (Carroll 1980; Smithson 1982). It consists of a boss from the os basale which fits into a rugose pad covered with cartilage in

the pterygoquadrate. A similar basipterygoid process is found in the braincase of dissorophids, aïstopods, microsaurs urocordylid and scincosaurid nectrideans and lysorophoids, but not in anurans and urodeles. Evidently, this structure is not present in rhinatrematids Nussbaum (1979). Its absence is taken to be the derived state. Brand (1956) maintains that it has also been lost in scolecomorphids as a result of the extreme diminution of the suspensorium; this however is not supported by Nussbaum (1985).

The shape of the braincase (21) has been invoked as a lissamphibian synapomorphy (Parsons and Williams 1963; Nussbaum 1977). This character varies within the caecilians. The common condition, exhibited by ichthyophiids, is one in which the braincase tapers anteriorly. There are two unique variants on this. In the Rhinatrematidae, and the Scolecomorphidae the braincase is somewhat more parallel-sided (fig 27) approaching the strut-like configuration found in anurans and urodeles. It appears that this configuration has evolved independently in the two families. The rhinatrematid condition is formed by the enlargement of the parasphenoid portion of the os basale (21'). The scolecomorphid condition (21") is formed by the expansion of the orbitosphenoid (Brand 1956; Nussbaum 1985).

The occipital condyles of most ichthyophiids are joined medially by an isthmus (22), a condition shared with the rhinatrematids, uraeotyphlids and some dermophids. In other

forms the condyles are distinct; the latter state is here considered derived.

The structure of the stapes, when present, is relatively invariant. The single variable character is the relationship of the style to the stapedial artery (23). In ichthyophids, rhinatrematids, Hypogeophis and Gymnopis proxima (Taylor 1969a), the style is perforated for the passage of the artery. In caeciliines and typhlonectids the artery passes around the stapedial style. The stapes in scolecomorphids becomes fused with the quadrate ontogenetically (Brand 1956).

The lower jaw of caecilians is unique (24, 25). It is a highly specialized structure and function have been discussed by Nussbaum (1983). The ratio of the prearticular skull length: lower jaw length (24) varies from approximately 1.0 in rhinatrematids to between 1.4 and 1.5 in scolecomorphids. In most forms the mouth is slightly subterminal, as is the case in ichthyophiids. The terminal mouth of rhinatrematids is seen as a uniquely derived feature. Similarly, the inflection of the retroarticular process (25) varies from approximately 0° in rhinatrematids to approximately 58° (unpublished data) in Scolecomorphus. A slight inflection is found in Ichthyophis; it is taken to be the primitive condition.

Three basic types of hyoid structure (26) can be recognized in the gymnophionans (Nussbaum 1977). These are: the ichthyophiid type in which the ceratohyal and the ceratobranchial are subequal in length and breadth, and joined by a short basibranchial, with ceratobranchial 3 and 4 present and fused - the caeciliid and typhlonectid varient has a much

expanded Cb 3+4, the rhinatrematid type in which the ceratohyals are bulbous, and only two (Rhinatrema, Cb 3 and 4 lost), or three (Epicrionops, Cb 4 lost) ceratobranchials remain (26') and, the scolecomorphid type, where Cb 3 and 4 are fused posteriorly (26"). The ichthyophiid condition is considered plesiomorphic. It should be noted that the ichthyophiid condition resembles most closely the morphology of the hyoid apparatus in primitive (hynobiid) salamanders (Edgeworth 1935; Eaton 1937; Fox 1959), some tuditanomorph microsaurs (Pantylus Romer 1969), lysorophoids (Brachydectes Wellstead 1985), and where known in adult, albeit paedomorphic labyrinthodonts (Dvinosaurus Bystrov 1938; Kaurerpeton Olson and Lammers 1976). This is radically different from the hyoid structure of frogs (Trueb 1973).

As part of the highly derived jaw system of caecilians, the gular musculature has become expanded and assumes the function of an accessory jaw adductor (Nussbaum 1982). This is a feature of all caecilians but some variation is apparent in the degree of elaboration of the system. Nussbaum (1977) designates the primitive condition as being one in which the the M. Interhyoideus posterior and is a small, single bundle. In most other caecilians except rhinatrematids, the M. Interhyoideus is made up of two bundles and is considerably larger. As the latter is the condition in ichthyophiids, it is taken to be primitive here. These muscles are distinct units in most other tetrapod but their condition cannot be inferred for the fossil groups

In all caecilians except the rhinatrematids, the standard teleostome adductors are confined wholly within the primitive adductor chamber (28). Both of the rhinatrematid genera are zygokrotaphic. Uniquely, in this family, the M. Adductor mandibulae Internus muscle mass is greatly enlarged and passess through the temporal fenestra, finding its origin on the lateral surface of the braincase and on the skull roof. There is a small sagittal crest along the medial parietal suture. As it is not present in any of the ichthyophiidae, it is here considered derived.

A distinct prefrontal is present in ichthyophiines, uraeotyphlines and scolecomorphids. It is absent as a separate unit in rhinatrematids, although it is coded as being present by Nussbaum (1979a). The prefrontal is present as a distinct element in all potential outgroups except anurans. Because the ichthyophiids possess a separate prefrontal, that condition is considered plesiomorphic.

II. Outgroup Characters

Having arrived at an approximation of the latest common ancestor of all ingroup members, namely the family Icthyophiidae, the putative caecilian morphotype can now be used in establishing the higher order relationships of the group. There are a number of cranial features that have been

cited as evidence of caecilian relationships to the aforementioned groups. These and other characters are ascribed polarity on the basis of the primitive anamniote tetrapods as the designated outgroup. Any character state manifest in this latter group is designated as plesiomorphic. It should be noted that the paleontological criterion is valid for outgroup analysis also. It has not been implemented, however, due to the very poor time resolution between most of the proposed groups. The oldest lysorophoids, microsaurs and nectrideans are known from the same Lower Pennsylvanian stage (Westphalian D-lysorophoids, B-microsaurs, and A-nectrideans, B-C-dissorophids). The earliest true anuran Vieraella and the specimens tentatively identified as caecilians are both known from the Lower Jurassic (Liassic), the earliest Salamander from the Upper Jurassic (fig. 2).

Braincase (Figure 24).

Primitively in tetrapods, the braincase comprises a number of distinct elements. Separate elements compose the occipital arch: exoccipitals, basiocciptal, and sometimes a supraoccipital. The otic capsule is made up of separate opisthotic and prootic elements. Anurans, urodeles, caecilians and aïstopods exhibit variable degrees of fusion of the braincase. The posterior portion of the braincase, the otic-occipital moiety is totally fused as a single ossification in aïstopods (McGinnis 1967) and caecilians (1'). In anurans and urodeles generally the braincase is

Figure 24 Braincases. A. A microsaur, Rhynchonkos (Redrawn from Carroll and Gaskill 1978). B. A lysorophoid, Brachydectes (Redrawn from Wellstead 1985). C. An Aïstopod, Phlegethontia (UCMP 62580). D. An anuran, Xenopus (RM uncat.). and E. A caecilian Dermophis mexicanus (UCMVZ 897).

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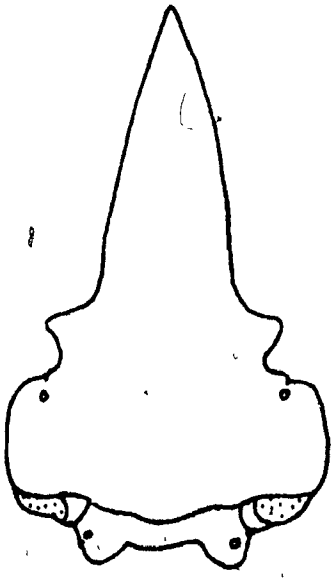

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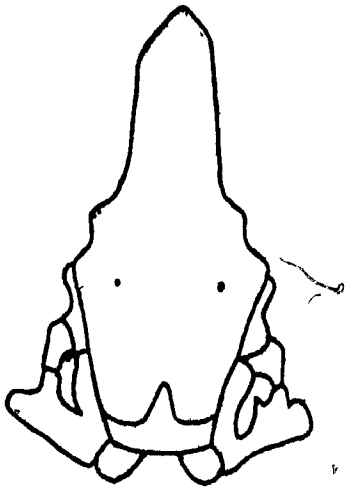

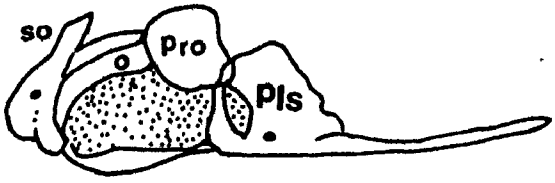

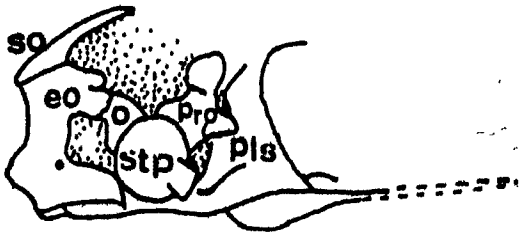

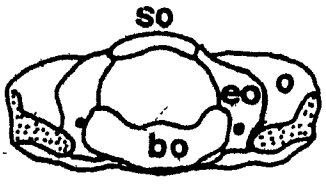

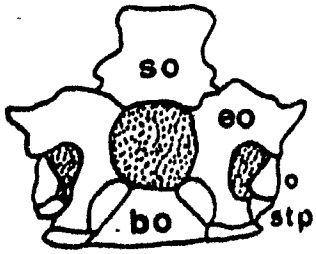

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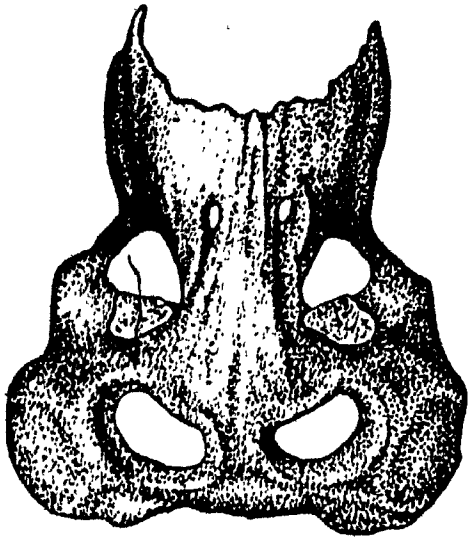

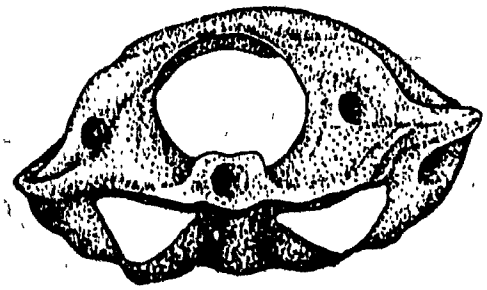

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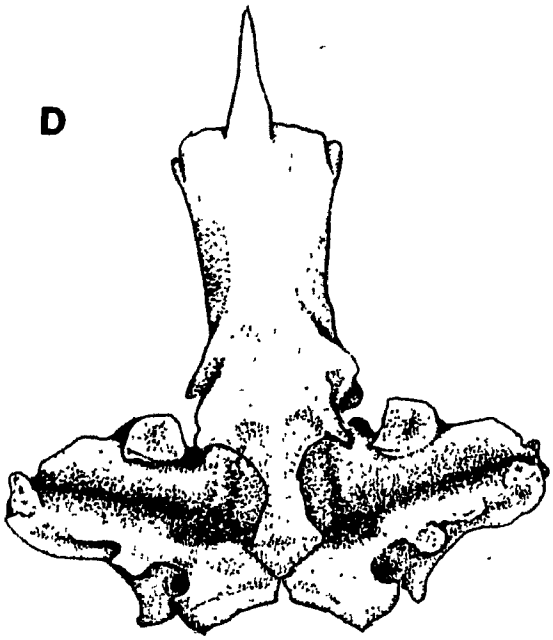

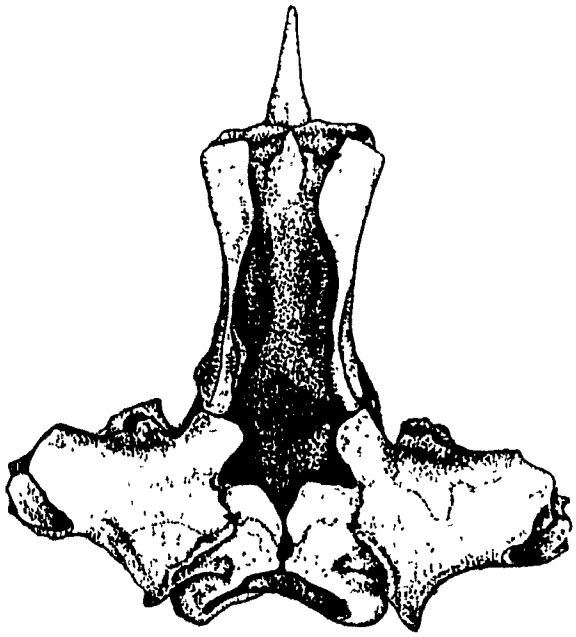

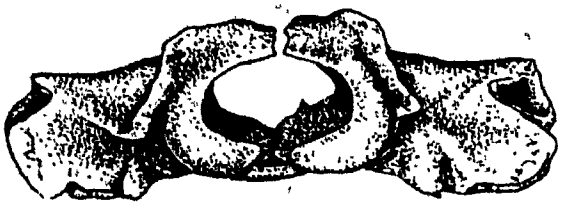

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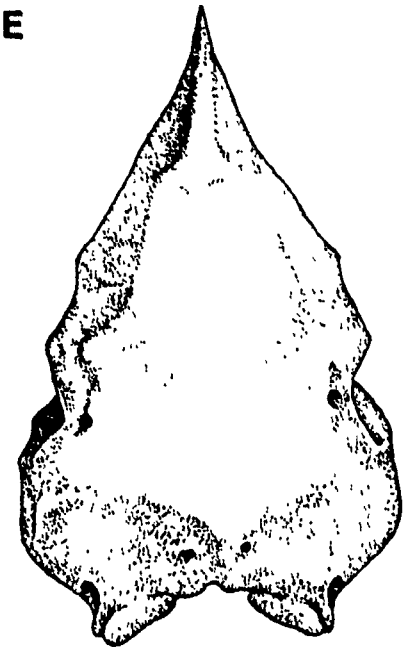
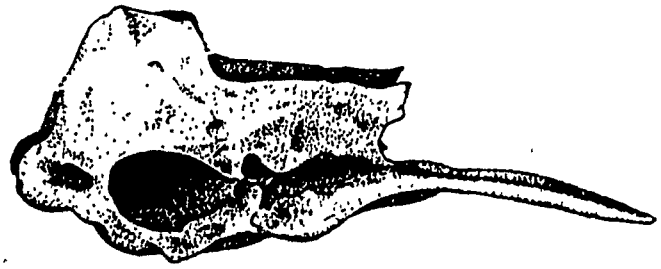
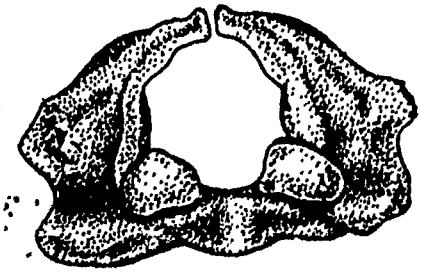






fully or partly co-ossified. Co-ossification occurs by the fusion of the occipital arch (and presumably the basisphenoid) with the opisthotic, and then in turn the fusion of this compound element with the prootic (1"). In some primitive salamander families, Karauridae, Cryptobranchidae, and Hynobiidae this fusion does not occur (Duellman and Trueb 1986). The braincase of anurans generally is made up of two paired elements, an exoccipital-opisthotic, and a large prootic (1"). In some anurans (Trueb 1973) and urodeles the prootic and opisthotic are distinct. The otic capsules of caecilians and aïstopods are fully fused. The elements of the otico-occipital moiety are totally fused in caecilians. In lysorophoids, and tuditanomorph microsaurs (with the exception of Cardiocephalus sternbergii Carroll and Gaskill 1978:172) they are distinct. The dissorophid braincase exhibits the primitive features (Carroll 1964).

A synotic tectum (3) is present primitively in tetrapods as the posteriormost element of the chondrocranial roof (DeBeer 1937: 393; Heaton 1980). This element is absent in all caecilians (Wake and Hanken 1982). It is difficult to discern exactly the condition in microsaurs. Although little is known of the dorsal surface of gymnarthrid braincase, it does not appear to be roofed in the otic occipital region. Rhynchonkos bears a very small supraoccipital (Carroll and Gaskill 1978), but a roofing element uniting the otic capsules is not evident. The microsaurs are tentatively identified as lacking a synotic

tectum. The synotic tectum is present as the sole remaining chondrocranial roofing element in urodeles. In anurans it is present as one of a suite of roofing elements. There is no mention of the presence or absence of this element in dissorophids (Carroll 1964). Presence of a synotic tectum is here considered primitive, its absence derived. It should be noted here however, that the colosteid braincase possesses no posterior roofing elements (Smithson 1982). The braincase of Eryops is completely roofed dorsally (Sawin 1942).

The occipital arch of primitive temnospondyls is devoid of a supraoccipital element (4) (Smithson 1982), as is probably the case in primtive anthracosaurs (Clack and Holmes in press). Lack of a supraoccipital is inferred on this basis to be the primitive condition among tetrapods, its possession is apomorphic. The braincase of Alstopods, being completely roofed, is considered to possess a supraoccipital (4') (and a synotic tectum). The supraocciptal is absent among urodeles, anurans, cacilians. It is present in lysorophoids as a large element extending anteriorly between the postparietals (Wellstead 1985). It is variably represented within the tuditanomorph microsaurs. It is absent in gymnarthrids (Schultze and Foreman 1981), but present in Rhynchonkos. The dissorophid condition varies. Although it is absent in Tersomius and Doleserpeton, it is presumed to be present in Dissorophus (Carroll 1964; Bolt 1969)

A neomorphic element, the operculum (5), is present in the fenestra ovale of many anurans and salamanders, onto which attach variously the M. cucullaris minor or the M.

Levator scapulae (Monath 1965). Although its presence is variable between and within families of anurans, it appears to be plesiomorphic to that order (Monath 1965). It has been suggested as an synapomorphy of the lissamphibia (Parsons and Williams 1963), but its presence in caecilians is equivocal. It was cited by Els (1963) as being fused to the footplate of the stapes of gymnophionans early in ontogeny. In no adult caecilian is there a known operculum. It is presumed here to be absent in caecilians. Carroll and Holmes (1980), and Carroll and Gaskill (1978) restore the otic region of Goniorhynchus and some other microsaurs (e.g. Pantylus) as having an opening between the footplate of the stapes and the opisthotic border of the fenestra ovale (fig). It is suggested by Carroll and Holmes (1980) that this perhaps housed an operculum similar to that of frogs and some salamanders, but there is no evidence of this. No such structure is found in lysorophoids or nectrideans. Among primitive salamanders, some hynobiids and all cryptobranchids lack an ossified operculum. Its presence is here designated as derived.

Primitively in tetrapods, cranial nerve X (vagus) exits between the exoccipital and the opisthotic (Smithson 1982) (6), the configuration found in nectrideans (Beerbower 1963) lysorophoids (Wellstead 1984) and dissorophids (Carroll 1964). In gymnarthrid and goniorhynchid microsaurs, the foramen is completely surrounded by the exoccipital. It is particularly evident in Rhynchonkos (Carroll and Gaskill 1978). Although a number of groups display extensive co-ossification of the

chondrocranium, the position of this foramen is extremely close to, or is on the ridge forming the craniovertebral joint. Topographically, it is taken to be within the exoccipital. The foramen is located on this ridge in Aïstopods, and immediately anterior to it in caecilians. Its position in anurans and urodeles, although close to the condyle in many forms, is difficult to determine. I have tentatively coded it as within the fused exoccipital/opisthotic (6'). The craniovertebral joint (7) itself exhibits a considerable variety of forms. Primitively, in tetrapods above the level of the ichthyostegalians, it is a single convex unit encompassing the exoccipitals and the basiocciptal. In anurans, urodeles, nectrideans, gymnarthrid microsaurs and some ichthyophiid caecilians it consists of two distinct paired comdyles, lateral or ventrolateral to the foramen magnum (7'''). In some ichthyophiid caecilians, and goniorhynchid microsaurs the two condyles are joined medially by a small isthmus (7"). Uniquely, the aïstopod craniovertebral joint (7') is a single medial parabolic concavity with a raised rim (Gregory 1948). Primitive microsaurs and lysorophoids share a condition in which there is a single strap-shaped element spanning the basioccipital and exoccipitals (Wellstead 1985), approximating the primitive condition.

The structure of the stapes (8) varies between groups. In frogs (8'), the stapes has a long, slender style and acts, in conjunction with the plectrum, as an impedence matching element (Bolt and Lombard 1985). This is very similar to the

dissorophid condition (Bolt and Lombard 1985). The gross structure of the stapes in lysorophoids, caecilians, and urodeles is similar. It consists of a large footplate with a short style directed towards the suspensorium (8"). The nectridean stapes is unknown. The stapes of Phlegethontia was restored as having an extremely long, slender style by Turnbull and Turnbull (1955) Although the style of the aïstopod stapes is unknown, the morphology of the footplate is unique in its ventral location on the braincase, and its roughly polygonal shape (8''')(Gregory 1948). Stapedial morphology is highly variable in the microsaurs, but in the families Gymnarthridae and Goniorhynchidae it conforms to the urodele -lysorophoid-caecilian type. Gregory et al 1956 assert that the stapes of gymnarthrids caecilians aïstopods and urodeles share the same gross morphology.

The primitive condition of the tetrapod stapes has been discussed by Smithson (1982) and Smithson and Thompson (1982). Primitively the stapes was a large heavy structure, with a small footplate relative to its overall size, and a long, ventrally directed quadrate process. Additionally, the primitive tetrapod stapes bore a stapedial foramen (9) that permitted the passage of the stapedial artery (Smithson 1982; Godfrey et al 1987). The primitive condition is present in lysorophoids, gymnarthrid and goniorhynchid microsaurs with the exception of Cardiocephalus sternbergi dissorophids (Bolt and Lombard 1985) and primitive caecilians. The stapedial foramen is absent in anurans, and urodeles (Kingsley

and Reid 1942). There is a single exception in the urodeles. In approximately 40% of specimens of Ranodon, the stapes is fenestrated for the passage of the orbital artery, according to Schmalhausen (1968).

In primitive tetrapods, a relatively short paraoccipital process extends dorsolaterally from the otic capsule to brace against the skull roof (Smithson 1982) (10). In keraterpetontid nectrideans that have tabular horns, the otic capsule is considerably extended laterally (10'). Similarly in anurans, the crista parotica of the prootic is extended laterally and joins the squamosal. A similar arrangement is found in urodeles such as Cryptobranchus, although the otic capsule is less drastically laterally expanded. The otic capsule of caecilians, microsaurs, lysorophoids, aïstopods bears no significant lateral extension toward the skull roof (10").

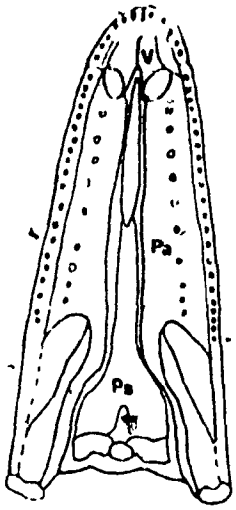
Goniorhynchid microsaurs and caecilians uniquely share an ossified pleurosphenoid element (11) between the oticoccipital and ethmoid moieties of the braincase (Carroll and Currie 1975). The dermal parasphenoid is distinct from the endochondral braincase in primitive tetrapods, frogs, salamanders, microsaurs, dissorophids and lysorophoids (12), although in some of these it may incorporate the basisphenoid. In caecilians the parasphenoid is fused to the braincase (Marcus et al 1935). The aïstopods exhibit a variable condition in which the parasphenoid is either distinct from the braincase (Gregory 1948) or indistinguishaby fused to it (Turnbull and Turnbull 1955). Parasphenoid fusion is derived.

The cultriform process of the parasphenoid (13) of primitive amphibians is a long, slender, tapering structure (Carroll 1982). A number of derived conditions are found within the groups under consideration. The cultriform process is a parallel-sided, strut-like structure in frogs and salamanders that terminates far anteriorly in a wide transverse suture with the vomers (Parsons and Williams 1963). In addition, much of the anteroventral surface of the braincase is formed not by the cultriform process of the parasphenoid but by a mesial extension of the ethmoid unit (13'). In lysorophoids, the cultriform process narrows slightly anterior to the basipterygoid processes, joining the vomers at an oblique apex (Wellstead 1985) (13"). The cultriform process of microsaurs (Carroll and Gaskill 1978) and primitive caecilians is broad posteriorly and narrows rapidly anteriorly (13"'). Both the Aïstopods and the nectridians exhibit the primitive condition of a long slender cultriform process. Primitively in amphibians, and in all groups considered here, there is a distinct sphenethmoid (14). The anterior portion of the braincase, the Os sphenethmoidale in caecilians, and the orbitosphenoid in urodeles is a single, fused endochondral element.

Palate (Fig. 25)

The interpterygoid vacuities (15) are variable in primitive tetrapods, ranging from closed or very narrow in the primitve colosteid temnospondyls ichthyostegalians and anthracosaurs, to extremely wide in later temnospondyls (Bolt

Figure 25 Various skulls in palatal view. Top: Ophiderpeton, an Aïstopod. Ptyonius, a nectridean. Middle: Brachydectes, a lysorophoid, Cardiocephalus, a gymnarthrid microsaur, Doleserpeton, a dissorophid. Bottom: Rana, a frog, Ambystoma, a salamander. (not to scale).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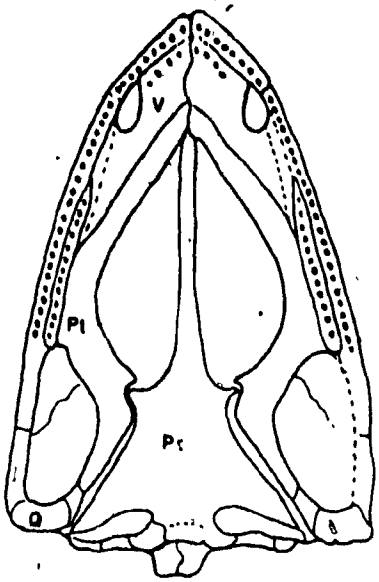
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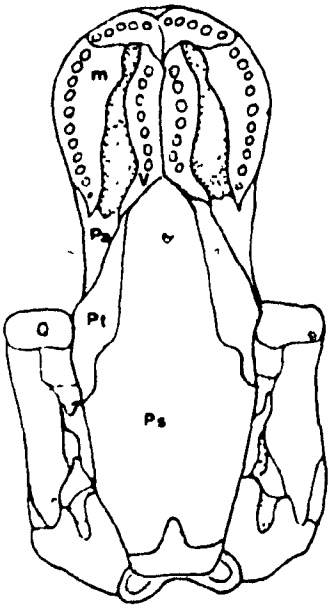
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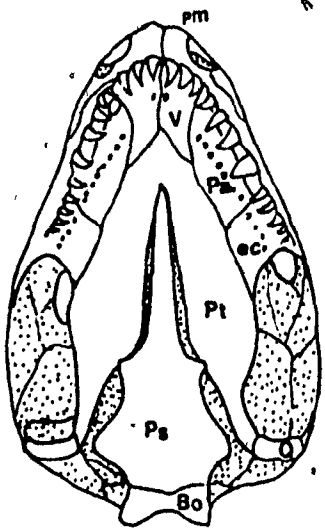
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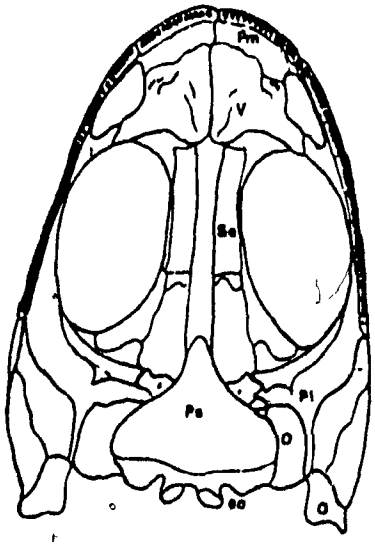
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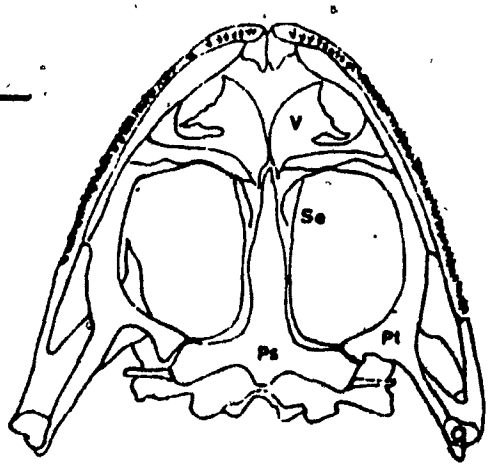
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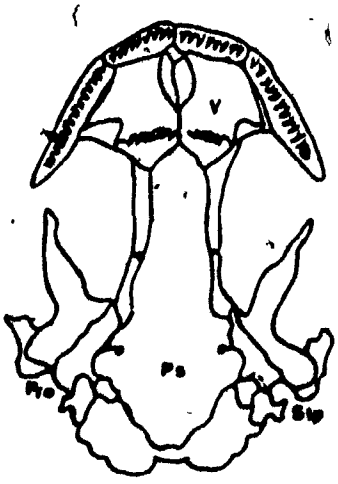
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1977). The primitive condition is probably closed or with a very narrow space between the pterygoids or the pterygoids and the cultriform process. The interpterygoid vacuities of anurans, dissorophids and urodeles are extremely wide (15'). reaching maximum width at the midlength of the cultriform process. In contrast those of microsaurs and caecilians are somewhat constricted (15"). The pterygoids are widely divergent from one another posteriorly, such that the point of widest divergence of the pterygoids, anterior to the otic capsule, is at or near the basicranial articulation. In lysorophoids the interpterygoid vacuity is almost entirely occupied by the parasphenoid and may have been joined to it by cartilage (Bolt and Wassersug 1975). Although the pterygoids are widely divergent, the lack of an interpterygoid vacuity approximates the primitive condition. The pterygoids of aistopods are long narrow structures running parallel and closely appressed to the long slender cultriform process (Lund 1972). Nectrideans exhibit all three states. It is closed in Batrachiderpeton, divergent posteriorly in Sauropleura and extremely wide in Ptyonius and the keraterpetontids. The pterygoids in addition contact their bilateral counterparts anterior to the parasphenoid, thus excluding the vomers from the margin of the interpterygoid vacuity, if present (16). In the advanced form the vomers contribute to the margin of the interpterygoid vacuity. This character is present in all groups considered here except, as mentioned above, certain urocordylid nectrideans.

The general tetrapod condition for the basicranial articulation, above the level of the ichthyostegalians, is that of the pterygoid contacting an eminence formed by the parasphenoid or parasphenoid and epipterygoid (17). That condition is found throughout most of the groups considered except anurans, urodeles, and keraterpetontid nectrideans. In the anurans and urodeles, the basal ramus of the pterygoid, when present, contacts or apposes, the otic capsule (Trueb 1973; Duellman and Trueb 1986) (17'). The pterygoid is fused to the parasphenoid in the nectridean Diploceraspis (Beerbower 1963) (17"). The anterior ramus of the pterygoid contacts the maxillary arch, usually indirectly through the palatine and, when present, the ectopterygoid (18). The pterygoid does not contact the maxillary arch in urodeles, aïstopods, and lysorophoids, the derived condition. The three modern orders generally have no epipterygoid (Romer 1970 ; Goodrich 1986). An epipterygoid element may, however, be present in the hynobiid salamander Batrachupeurus. All other groups have an epipterygoid. Possession of an epipterygoid is the primitive tetrapod condition (19).

An ectopterygoid is present in the palate primitively (20), and in microsaurs and most nectrideans. Most dissorophids, except Doleserpeton, possess an ectopterygoid (Carroll 1964; Bolt 1969). It is absent in all the modern orders, lysorophoids, and advanced nectrideans (Beerbower (1963) makes reference to an ectopterygoid in Diploceraspis but none was found by Milner (1978)).

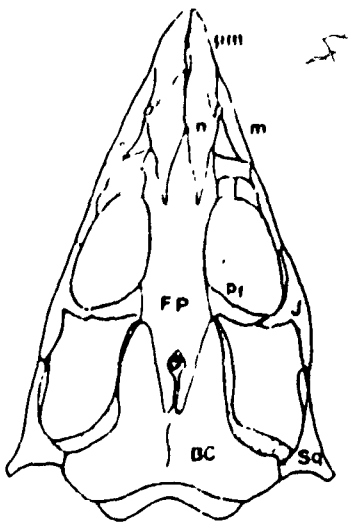
Caecilians are noted for possession of a row of highly

specialized palatal teeth paralleling the marginal row (21'). This is the advanced condition and was thought to be shared with the goniorhynchid microsaurs (Carroll and Currie 1975). A battery of palatal teeth on the vomer palatine and ectopterygoid, such as is found in Rhynchonkos, gymnarthrids and nectridians, however, is probably a retention of the primitive tetrapod condition. The lysorophoids have a well developed row of teeth on the vomers (21"), and none on the palatine (Wellstead 1985). A similar condition is found in most urodeles (including such primitive genera as Hynobius and Cryptobranchus), and a number of anurans. Aïstopods, some anurans, nectrideans (e.g. Scincosaurus, Urocordylus) do not have a well developed row of teeth on the palate (21'''). Generally, dissorophids retain the primitive labyrinthodont palatal dentition. Fangs are present on the palatine and ectopterygoid (Tersomius, Carroll 1965). Small clusters of vomerine fangs are present in Doleserpeton (Bolt 1969). Pedicellate teeth (22) have been noted for frogs, salamanders, Doleserpeton, and caecilians, their presence is universal only in the caecilians (see Estes 1964, 1965,1969,1981; Duellman and Trueb 1986). Possession of pedicellate teeth is an apomorphy (Parsons and Williams 1962).

Dermatocranium and Suspensorium (Figure 26).

Primitively in tetrapods a number of dermal skull roof elements are located posterior to the parietals, including the tabulars, postparitals, and (if posterior) the supratemporals

Figure 26 Various Skulls in Dorsal view. As in fig. 25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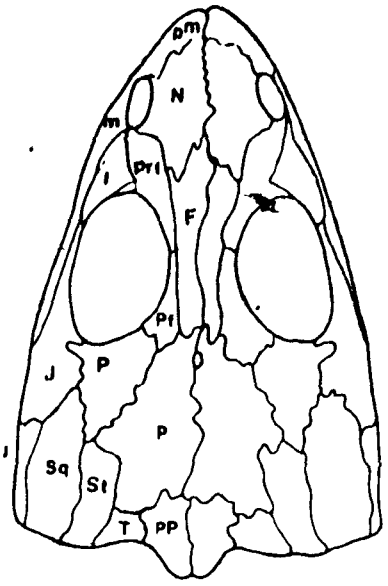
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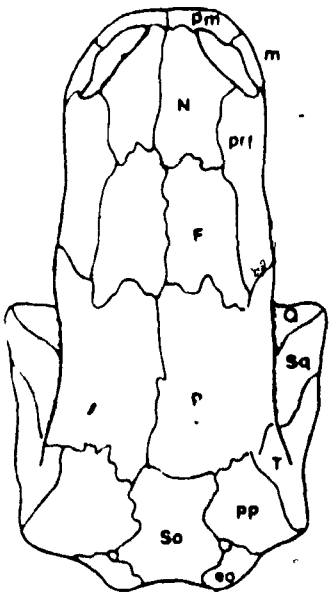
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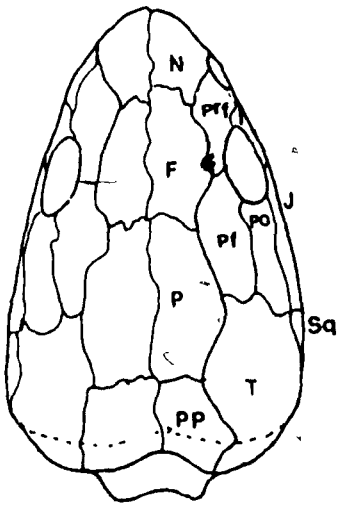
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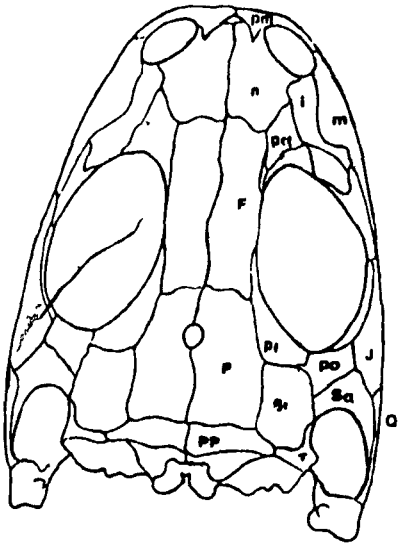
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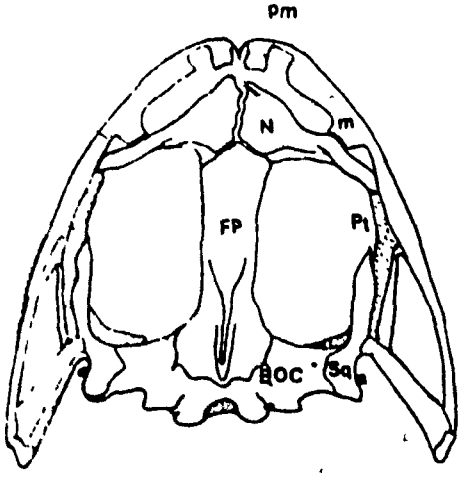
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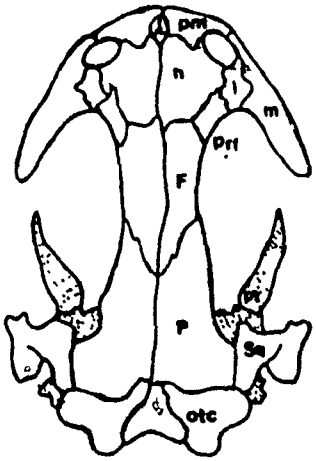
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(23). These undergo reduction in number in a great variety of lineages. The homologies of post-parietal elements is often difficult and has been a cause of much debate. For that reason I treat these units as a whole. There are no dermal skull roof bones posterior to the parietals in any of the members of the modern orders. This is taken to be the derived condition. Postparietal elements are lost in phlegethontiid aïstopods but are retained in ophiderpetontids (Bossy 1976) and Lethiscus (Wellstead 1982). Nectrideans retain postparietal elements. In lysorophoids two separate postparietals lie at the posterior extremity of the skull table. The parietals and frontals are usually, and primitively, distinct from one another (24). A fused frontoparietal is present in anurans, and in phlegethontiid aïstopods. Gregory (1948) has an alternate interpretation of the bones composing the skull roof of Phlegethontia). A parietal foramen (pineal foramen) is located along the mid-parietal suture in primitive tetrapods (25). There is no parietal foramen in the modern amphibian orders or in lysorophoids. A parietal foramen is retained in dissorophids, nectrideans and most aïstopods. Some later aïstopods, Phlegethontia (McGinnis 1967) and Aornerpeton (Lund 1972), exhibit no pineal foramen. Its presence is variable in the gymnarthrid microsaurs, being absent in Cardiocephalus (Broili 1904; Gregory et al 1956) and Euryodus (Schultze and Foreman 1981).

A number of elements intervene between the squamosal and the parietal in the skull roof of primitive tetrapods (26). Squamosal-parietal (26') contact was adduced as evidence of

lissamphibian ancestry by Nussbaum (1979a). All three modern orders do possess this trait, but in adddition in urodeles and anurans, it commonly occurs that the paroccipital process of the otic capsule is exposed dorsally between the squamosal and parietal, or frontoparietal in anurans (26"). The crista parotica of anurans is the site of connection of the squamosal (Griffiths 1963) Squamosal-parietal contact is present in lysorophoids (Wellstead 1985). The diminutive squamosal of phlegethontiids contacts the otic capsule (26"). Dissorophids maintain the primitive condition.

An otic notch (27) is absent in primitive labyrinthodonts. Although the cheek is embayed, it does not hold a tympanum (Godfrey et al 1987). The only groups under consideration in this study that possess an otic notch are the Anura and the Dissorophidae.

A battery of six bones surrounds the orbit in primitive tetrapods. The configuration of postorbital bones (28) exhibits considerable variation. The postorbital elements are lost completely in lysorophoids (Wellstead 1985), urodeles, and anurans (Trueb 1973) (28"). A single element is present surrounding the orbit in caecilians (28'). This has been called the postfrontal (alternatively called the ocular (Taylor 1969a)) but its homology to that element in early tetrapods is equivocal. The full complement of bones around the orbit is retained in the microsaurs, dissorophids and the nectrideans and is here considered primitive. The orbit is enclosed by bone posteriorly in aïstopods, although

authorities disagree over whether a postorbital is present in the highly derived phlegethontiids. (cf. McGinnis 1967 and Lund 1972).

A septomaxilla (29) is variously absent (e.g. Greererpeton) or present (e.g. Pholidogaster, Panchen (1976)) in the most primitive known temnospondyls. It is manifest as a separate element in batrachosaurs. Its presumed homologue, the lateral rostral is present as a separate element in ichthyostegalians (Schultze 1985). It is considered to be present as a distinct element primitively in tetrapods. It is present as a separate element in members of all the living amphibian orders and the microsaurs. It is absent in aïstopods, nectrideans, and lysorophoids. Carroll (1964) illustrates a septomaxilla in Tersomius. It is evidently missing in Broiliellus (Carroll 1964) and Doleserpeton (Bolt 1969).

The structure of the cheek and suspensorium exhibits a wide array of forms among the groups studied. The quadratojugal (30), present primitively, is absent in lysorophoids, some urodeles, and some anurans (30"). A distinct quadratojugal may be present in a few primitive urodeles (R. Cloutier pers. comm.). The anlage of the quadratojugal is apparently fused to the squamosal unit early in the development of caecilians (30') (Hanken and Wake 1982; Marcus et al 1935 Hypogeophis). It is present in aïstopods, nectrideans and microsaurs.

Urodeles and gymnophionans are both thought to exhibit kinesis (31) associated with the suspensorium (DeVilliers 1938

Carroll and Holmes 1980) (31). The quadrate and squamosal form a vertical bar in salamanders, the fulcrum occuring at the squamosal-parietal or squamosal-oticocciptal suture (Carroll and Holmes 1980) (31'). Caecilian kinesis involves mediolateral movement of the entire cheek region (Straub 1985). The fulcrum is usually located anteriorly between the frontal and maxillopalatine. The kinetic unit articulates with the braincase at the basipterygoid process, and via the stapes-pterygoquadrate joint (Marcus et al 1935; deJager 1939c) (31"). Lund (1972) reconstructed the cheek of Aornerpeton as being highly motile but this interpretation requires further corroberation. The skull roof of nectrideans is thought to have been kinetic, but not to have a mobile suspensorium (Milner 1980). The quadrate of lysorophoids, anurans, and microsaurs is akinetic, the primitive condition (Romer 1950). The cheek of labyrinthodonts is occluded by dermal bone (32), as is that of nectrideans, gymnarthrid and goniorhynchid microsaurs, dissorophids and primitive caecilians. It is fenestrated in anurans, urodeles, aïstopods, and lysorophoids, the derived condition. The ventral cheek margin is complete primitively (33), but is incomplete in lysorophoids and urodeles. The craniomandidular joint is located at the level of, or posterior to the level of the occipital condyles in primitive labyrinthodonts (34). It is clearly anterior to the occiput in gymnarthrid and goniorhynchid microsaurs, urodeles, some anurans, caecilians, and lysorophoids. In fact in the last of these, as Wellstead

(1985) points out, the craniomandibular joint is anterior to the basal articulation. The condition in anurans is variable. Alstopods retain the primitive configuration.

Lower Jaw and Hyobranchium

The lower jaw is terminal primitively in tetrapods (35). In primitive caecilians, gymnarthrid and goniorhynchid microsaurs, the lower jaw is subterminal. The jaw is terminal in all other groups studied here.

Primitively in tetrapods the lower jaw comprises a battery of dermal bones surrounding Meckel's cartilage, including the dentary, angular, surangular, coronoids, splenials, prearticular, as well as the endochondral articular (36). A number of modifications are found in the groups studied here. The lower jaws of the microsaurs, lysorophoids, dissorophids and nectrideans are essentially primitive, apart from the loss or fusion of one or two minor elements. The lower jaw of phlegethontiids, caecilians, anurans, and urodeles all consist of two dermal elements. The distinctive caecilian lower jaw comprises a pseudodentary and a pseudoangular which incorporates the articular. The two elements are joined by a long squamous joint passing from posteromesial to anterolateral (36'). A similar arrangement is found in Phlegethontia (Turnbull and Turnbull 1958). The anuran lower jaw comprises a dentary and an angulosplenial (36"). The urodele jaw is made up of a dentary and prearticular with a separate articular in some forms) (36'''). Anurans and urodeles possess an ossification of Meckel's

cartilage at the mandibular symphysis, known as the mentomeckelian (37). It is an advanced character. It is not present in all frogs but appears to be characteristic of primitive members.

Carroll and Currie (1975) point to the possession of a mesial row of teeth on the lower jaw (38) in Rhynchonkos and in caecilians. This condition is not found universally in caecilians, but is found in the primitive members. It is also evident in gymnarthrid microsaurs, and certain nectrideans (e.g. Sauropleura).

An elongate retroarticular (39") is one of the most distinctive caecilian features. Retroarticular processes of intermediate length are found in microsaurs with the possible exception of Euryodus primus (Schultze and Foreman 1981) and some keraterpetontid nectrideans. In caecilians, it is inflected dorsally. A similar arrangement is seen in Keraterpeton (Milner 1980). Flexion of the retroarticular process however is not amenable to polarization as their is no primitive tetrapod retroarticular process for comparison.

The hyoid apparatus (40) varies widely between groups. The primitive condition of the hyoid is unknown for adult temnospondyls. It has been discussed for Dvinosaurus (Bystrov 1938) Trimerorhachis (Olson 1979), and Kourerpeton (Olson and Lammers 1976). In Trimerorachis, there are five ceratobranchials, in Dvinosaurus and Kourerpeton four. All of these forms are presumed to have been perrenibranchiate, and although Trimerorachis and Kourerpeton are fully ossified and

appear to be adult in other aspects of their anatomy, the retention of the ce atobranchials is inferred to be paedomorphic. Godfrey (1986) reports what he interprets to be the first ceratobranchial in the colosteid temnospondyl Greererpeton. This is the condition found in phlegethontiid aïstopods and is inferred to be primitive. Primitive caecilians have four ceratobranchials (3 and 4 fused). Four ceratobranchials were reported for the microsaur Pantylus by Romer (1969) (40'). Pantylus is a tuditanomrph microsaur but not considered a goniorhynchid/gymnarthrid. Salamanders exhibit an array of hyoid morphology; the primitive hynobiids (Edgeworth 1923, Fox 1959, Hecht and Edwards 1976), proteids, and the neotenic cryptobranchids, retain four ceratobranchials (40'). Wellstead (1985) also figures four ceratobranchials (his epibranchials) for the lysorophoid Brachydectes. The condition is significantly altered in anurans (Trueb 1973), where in adults the hyoglossal skeleton is fused into a large plate-like structure (40").

The outgroup characters and the character state distributions are listed in Tables 4 and 5.

III. The Prevalence of Homoplasy

It is often conjectured that convergence and parallelism, the independent attainment of apomorphies not present in the most recent common ancestor, are quite common among tetrapods. Convergence and parallelism are indistinguishable in cladistic analysis. They are referred to collectively by the term homoplasy. The characters that unite the lepospondyls, for

instance unipartite vertebral centra, have been thought by many workers to have been independently derived (Romer 1950; Baird 1964; Thomson and Bossy 1970). It has further been suggested (Sober 1986), that conservative characters, those less susceptible to undergoing homplasy, would be more reliable indicators of relationship, as it would be less likely that a homoplasy would be misconstrued as a synapomorphy. Of course such characters can only be discerned a posteriori, that is, after the cladogram has been constructed. Nevertheless, it can be quite instructive to determine what types of characters show a propensity for homoplasy. Hypotheses of the interrelationships of tetrapods are often built on the evidence of only a few characters. For this reason it is important to know the a priori likelihood of any single similar apomorphy between any two groups being a homoplasy. It is possible to estimate the minimum likelihood of a homoplasy, but as synapomorphy and homoplasy are not mutually exclusive concepts (Farris 1983; Sober 1983), a portion of the recognized synapomorphies may also be homoplasies. In discussing the assumptions of cladistic analysis, I made the point that it is imperative that if one is to infer certain properties from a cladistic analysis, that no contingent statements about these properties be made in the set of assumptions. Farris (1983) discusses how the minimal assumptions of cladistic analysis, adopted here, are free of assumptions about the frequency of homoplasy.

I have attempted to develop an index of the overall

TABLE 6

PAIRWISE SYNAPOMORPHIES

PAIRWISE HOMOPLASIES

	NECTRIDEA	DISSOROPHIDAE	LYSOROPHIA	AÏSTOPODA	ANURA	CAUDATA	MICROSAURIA	GYMNOPHIONA	TOTAL
NECTRIDEA		8	4	5	8	8	6	7	46
DISSOROPHIDAE	3		2	3	7	5	1	4	30
LYSOROPHIA	3	2		8	7	10	6	8	45
AÏSTOPODA	4	4	0		9	8	6	11	50
ANURA	4	6	1	5		22	4	9	66
CAUDATA	3	4	2	4	3(?)		7	13	73
MICROSAURIA	3	1	1	1	0	1		15	45
GYMNOPHIONA	4	3	1	4	2	3	1		67
TOTAL	24	23	9	21	20	18	10	18	211 / 73

34.6%

prevalence of homplasy for the outgroup analysis. It is shown in Table 6 . The numbers above the main diagonal represent the total number of apomorphic features shared between all groups. These are calculated from Table 2 by counting all pair-wise combinations of the same apomorphic state for all characters. The numbers below the main diagonal represent the number of homoplasies between each group. This quantity is calculated by counting all pair-wise (apparent) homoplasies between groups from the resultant cladogram, including those characters, listed above, that change within terminal taxa The total of all cells below the main diagonal is the proportion of raw apomorphic similarities between groups that is the result of apparent homolasy. The total number of pairwise shared apomorphies is 211. The total number of pairwise homoplasies is 73. The index of homoplasy is 34.6%. The implication is that any shared apomorphy of any of the two groups in this study, chosen at random, has a 34.6% chance of being a homoplasy. This is an alarmingly high statistic, which supports the long-held suspicion that homoplasy is quite a common occurence in the phylogeny of lower tetrapods at least.

The nectrideans and dissorophids show the highest number of homoplasies, 24 and 23 respectively. With the removal of these two groups the index of homoplasy diminishes (26.3%). One can deduce that the characters used are better indicators of the interrelationships of anurans, urodeles, lysorophoids, aistopods, microsaurs and gymnophionans, than of all groups combined. The upshot of the prevalence of homoplasy is that a

simple enumeration of similarites between groups (whether or not they be apomorphies) is not sufficient grounds for hypothesizing close relationships. The prevalence of homoplasy requires of a systematic analysis that it adhere to a well formulated system for arriving at the most parsimonious possible combination for the characters employed.

It is also informative to determine the prevalence of homoplasies between characters. The number of homoplasies in a character is the number of its independent derivations, minus 1. Out of the total of forty characters used, twenty five (62.5%) undergo at least two independent derivations of the apomorphic state (or states). Twenty undergo only one homoplasy. Four undergo two homoplasies (three independent derivations of the advanced state); and one undergoes three homoplasies, for a total of thirty one character homoplasies.

The types of cranial characters vary only slightly in their propensity for homoplasy. Nine characters of the braincase, including the dermal parasphenoid (1-14) (64.3%) undergo a total of ten homoplasies. Six of eight (75.0%) characters of the palate (characters number 15-22 including the epipterygoid) exhibit seven homoplasies. Characters of the dermal skull roof (23-33) are not significantly more labile than the overall average. Eight of eleven (72.7%) converge, a total of twelve homoplasies. Two of the seven (28.6%) characters of the lower jaw and hyoid apparatus undergo a total of two homoplasies. (Combined total, 31).

It was suggested by Hecht (1976) and Hecht and

Edwards (1976) that characters whose apomorphic conditions involve the loss or fusion of distinct elements are particularly susceptible to homoplasy. Thus they are more likely to lead the investigator to misinterpret homoplasies as evidence of common ancestry. Seventeen of the forty characters (42.5%) are of this type. Together they account for 15 (48.4%) of the total number of homoplasies (31). Twelve of the seventeen are homoplastic, (70.6%) not substantially higher than the overall average. Chi-squared analysis does not show any of the differences between the propensities of different types of characters to undergo homoplasy to be significant at the 0.05 level.

In summary, as has long been suspected, homoplasy is prevalent. The index of homoplasy for all groups presented is 34.6%. This number is significantly reduced if hectrideans and alstopods are deleted (28.6%). Hence the probability of any apomorphy shared between any pair of terminal taxa being a homoplasy is 34.6%. Characters involving loss and fusion are not more labile than other types of characters, and thus are equally valid as indicators of phylogenetic relatedness.

IV Previous Hypotheses

Among the previous hypotheses considered, the studies of Gregory et al (1956), Schmalhausen (1968) and Carroll and Holmes (1980) agree with these results as regards the sister

group of the gymnophionans. None of the hypotheses is isomorphic with the phylogeny presented here but that of Schmalhausen (1968) is the closest fit. Schmalhausen's phylogeny and this concur in placing the microsaurs as the primitive sister group (ancestor) of caecilians, and lysorophoids as a primitive sister group (in part at least) of urodeles. They diverge on the placement of the anura and dissorophidae. None of the previous hypotheses encompasses as wide a range of groups as this study however, so direct comparisons may not be appropriate.

CONCLUSIONS

Two main conclusions may be drawn from the results. Firstly, the F. Ichthypohiidae (Ichthyophis and Caudacaecilia) represent the most primitive living assemblage of caecilians. Secondly, based on the designation of ichthyophiids as the most primitive group, the most plausible sister group among those discussed is the tuditanomorph microsaur complex of the Gymnarthridae and Goniorhynchidae. Contrary to the commonly held view, the caecilians would not be included in a monophyletic group with anurans and urodeles that did not also include microsaurs, lysorophoids, and perhaps nectridians.

I Temporal fenestration

The condition of the skull roof, whether fenestrated or not, is not considered as a character in the ingroup cladogram. However, the ingroup analysis suggests that the essentially closed skull roof as found in most ichthyophiids is primitive for the caecilians. The closed skull roof is also seen in microsaurs, nectrideans, and primitive temnospondyls. It cannot be used to denote phylogenetic relationships between any of these groups as suggested by Gregory et al (1956), Schmalhausen (1968) and Carroll and Currie (1975) as it is a tetrapod plesiomorphy. The condition of the skull roof ,

whether open or closed was disqualified as an outgroup character in the analysis of relationships within the caecilians. It is shown to be extremely labile within the group and so even if it were used it might not permit confident phylogenetic inference. However to question the utility of skull fenestration as a taxonomic character is not to deny it its functional significance for the caecilians. The outgroup analysis does incorporate skull fenestration as a characteristic. In the major tetrapod groups studied here, skull fenestration is much less labile than in the caecilians. The ingroup and outgroup results permit a discussion of the functional and phylogenetic significance of temporal fenestration in caecilians, and in amphibians in general.

Ingroup

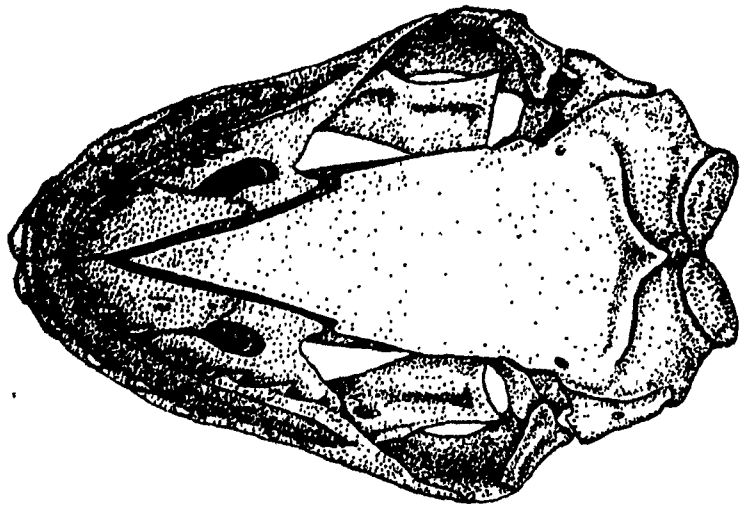
That caecilian stegokrotaphy is structurally different from the closed skull condition in stegocephalian amphibians is often cited in support of the contention that it is a secondary acquisition within the order (Nussbaum 1977; Wake and Hanken 1982). The contention is that as the dermal elements that intervene between the squamosal and parietal (intertemporal and supratemporal) in primitive tetrapods are absent in gymnophionans, the contact of the squamosal and parietal in caecilians represents the expansion of one or both of these elements into a gap created by the loss of the intervening bones. There is good evidence for this within the Scolecomorphidae (Nussabaum 1985 and pers. comm.) The

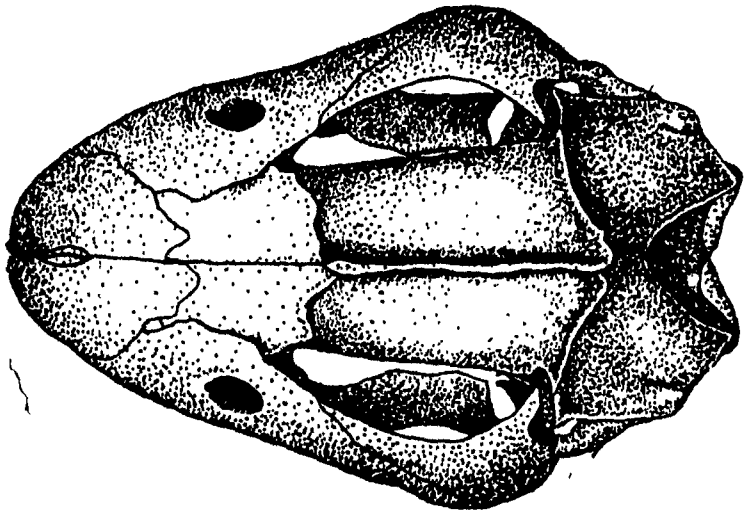
cladograms of figures 21 and 22 however, demonstrate clearly that squamosal-parietal contact is independent of the open or closed nature of the skull roof. Squamosal-parietal contact is attained independently in the open-skulled lysorophoid-aïstopod + anuran-urodele assemblage and within the closed-skulled nectridians and caecilians. It appears to have been acquired numerous times in a variety of tetrapod lineages: the adelogyrinids (Carroll 1967), primitive captorhinomorphs (Carroll 1967; Clark and Carroll 1973), diadectomorphs (Heaton 1980) and others, without the prior existence, phyletically, of a temporal fenestra. The absence of dermal elements between the squamosal and parietal, then, does not preclude stegokrotaphy from being primitive. One should be wary of interpreting too literally the homologies between similarly named bones of caecilians and other groups. Marcus et al (1935) identify separate areas of ossification in the squamosal, and suggest that the cheek unit is a compound element formed by the fusion of a number of separate bones.

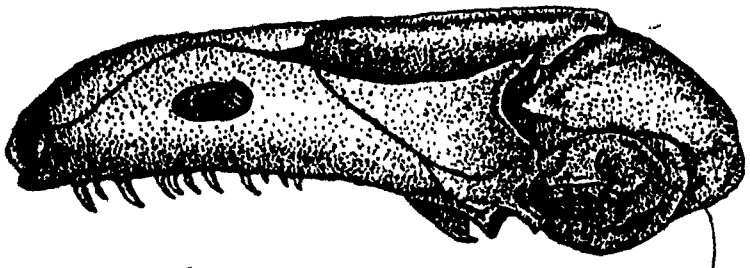
Zygokrotaphy occurs mainly in three families, the Rhinatrematidae (both genera), the Scolecomorphidae (one of two genera), and the Typhlonectidae. There are three reasonably distinct morphologies of the open skull condition corresponding with each (fig. 27). In addition, there are minor openings in some dermophids, ichthyophiids, and in Uraeotyphlus.

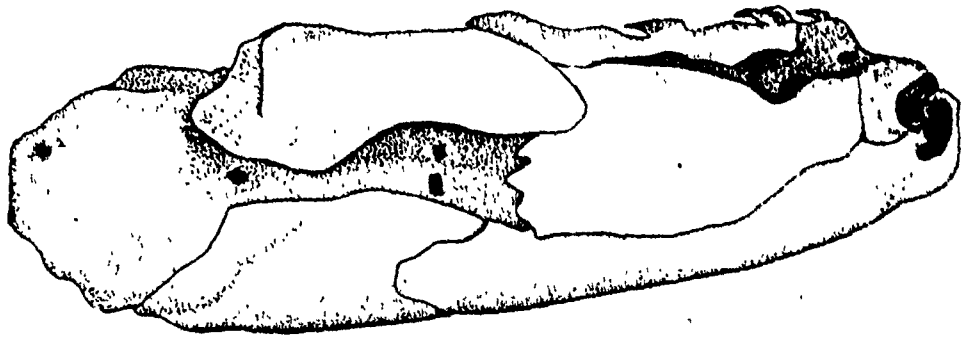
In the rhinatrematids, the fenestrae are elongate anterodorsally. No portion of the parietal is in contact with the cheek. Uniquely in this family, a process of the

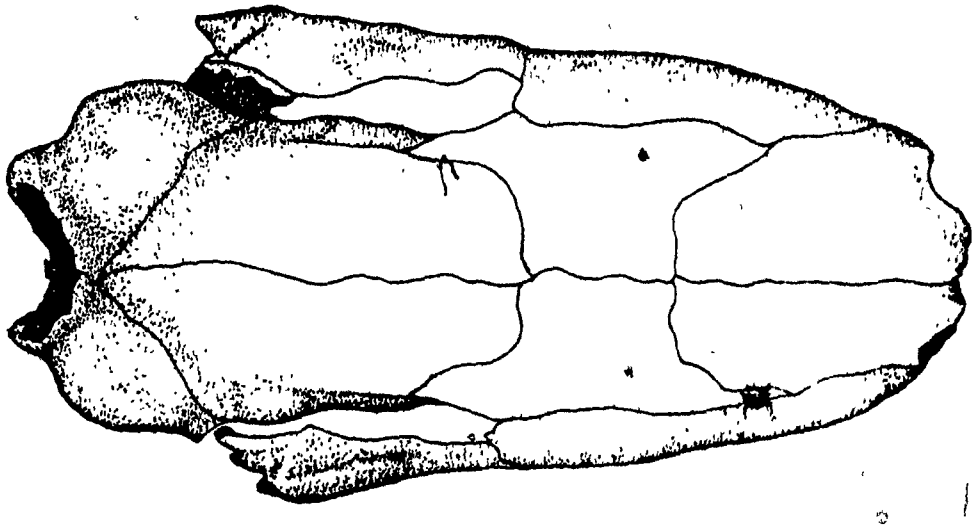
Figure 27 A comparison of zygokrotaphic caecilian skulls. A Epicrionops, a rhinatrematid. (Redrawn from Nussbaum 1977). B.Scolecomorphus, a scolecomorphid. C. Typhlonectes, a typhlonectid. (B and C redrawn from Taylor 1969a)

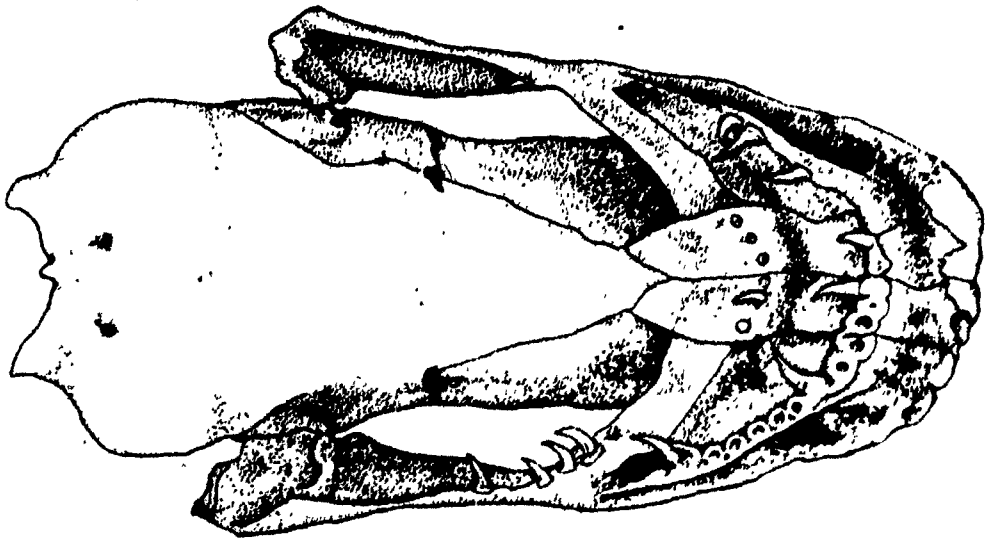


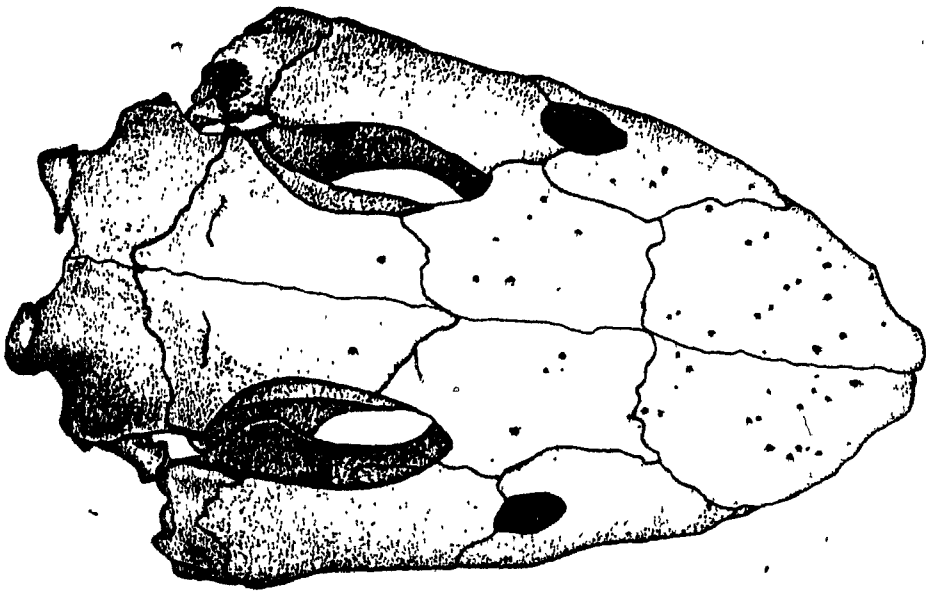


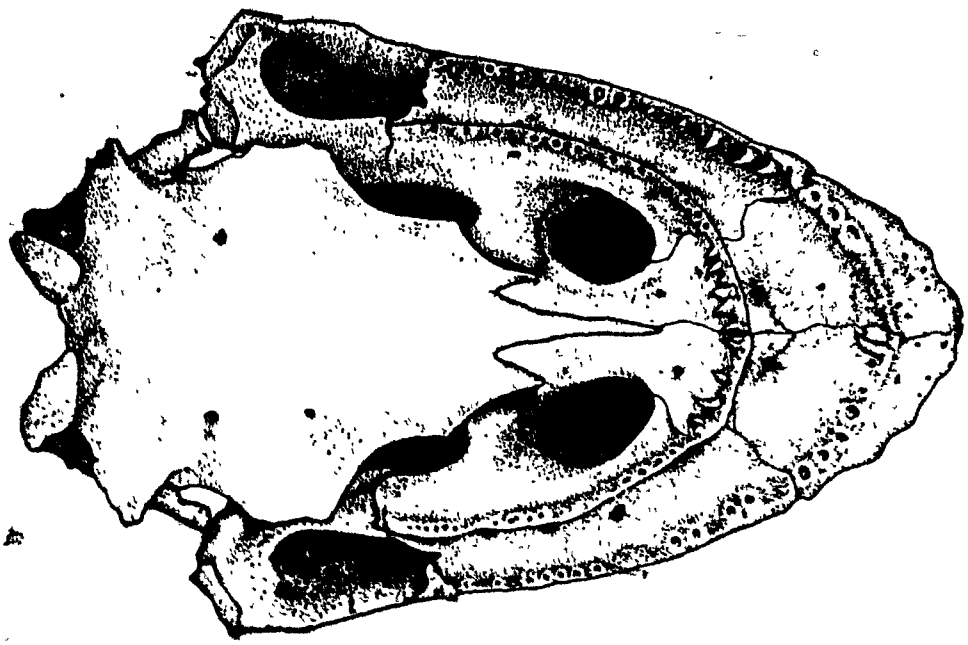












dorsolateral portion of the os basale fits into a notch in the squamosal (Nussbaum 1977). The pterygoid is a distinct unit that occupies some of the volume of the adductor chamber. The structure of the typhlonectid fenestra differs in possessing a frontal-squamosal suture at its anterior extremity and a closely apposed, or sutured quadrate and parietal posteriorly. The pterygoid is fused to the quadrate. The scolecomorphid condition differs from both of the rhinatrematid and the typhlonectid configuration, in that the maxillopalatine contributes a substantial portion to the anterior border. There is no discernible quadrate or pterygoid, the suspensorium being represented by a diminutive cartilagenous element. In some zygokrotaphic forms, there is no posterior connection between the cheek unit and the skull roof or os basale. Nussbaum (1985) tentatively identified an element as the pterygoid in one specimen of Scolecomorphus kirkii. The three main types of caecilian zygokrotaphy are sufficiently different that it is probable that all three types are independently derived.

Most of the conjecture concerning the functional significance of zygokrotaphy surrounds the specialized fossorial, or semifossorial nature of most caecilians. The majority of authors claim that zygokrotaphy is primitive and attribute the evolution of secondary stegokrotaphy to selection for improved fossoriality. As Gans (1969) points out, a small, strong and terete head is the most efficient form for locomotion beneath the surface of the soil. It is

argued that selection for fossoriality in caecilians would act to modify a primitively weak skull configuration (zygokrotaphic) into a strong one (stegokrotaphic) (deJager 1939c; Nussbaum 1977; Wake and Hanken 1982). Despite the paucity of natural history information, there does seem to be a correlation between possession of stegokrotaphy and the degree of fossoriality. The zygokrotaphic typhlonectids are aquatic (Taylor 1969b). The rhinatrematids and the weakly stegokrotaphic ichthyophiids are found most commonly in surface vegetation, in or under rotting logs, or under rocks (Ramaswami 1936; Nussbaum and Hoogmoed 1979), whereas strongly stegokrotaphic forms are usually found in the topsoil layer under the soil surface. The rough correlation however does not suffice to ascribe polarity to the condition of the skull roof.

Bearing in mind the potential pitfalls of the argument by analogy in evolution, it is still quite illuminating to compare the hypothesis that selection for fossoriality leads to closure of a fenestrate skull to the strategies found in other burrowing tetrapods. Amphisbaenid lizards are small, limbless, fossorial forms that superficially resemble caecilians. The head is highly specialized as a digging structure. The skull has undergone extensive consolidation and compaction over the condition seen in most lizards (Gans 1960, 1969, 1974). As a result of the compaction, the temporal fenestrae are greatly enlarged at the expense of the intervening arches such that the adductor muscle mass is uncovered and has expanded laterally and dorsally. The jaw

adductor musculature originates on the braincase wall (Gans 1960, 1969; Taylor 1969; Berman 1977).

Snakes are thought to have arisen from a fossorial squamate ancestor. As in amphisbaenians, the skull of snakes is small and consolidated. Fossorial adaptations are most strikingly expressed in the family Uropeltidae (Gans 1973). In a specialization analogous to that of amphisbaenids, the adductor musculature is greatly expanded, and the bony coverings of the primitive adductor chamber are lost. Similar trends are apparent in burrowing scincomorph lizards (e.g. Acontias Rieppel 1980).

In each of the above instances, specialized burrowers have evolved independently from ancestors with fenestrate skulls not by closure of the existing fenestrae, as has been suggested for caecilians, but by their enlargement. As a consequence of the compaction of the skull necessitated by fossorial existence, the jaw adductor musculature has undergone relative expansion beyond the confines of the primitive adductor chamber. The only caecilians in which the adductor musculature extrudes through the skull roof are the rhinatrematids. As the opposite strategy has occurred in the skull roof of caecilians to that seen in other burrowing tetrapods, it is not unreasonable to postulate that the caecilian condition, unlike that of amphisbaenids and uropeltids, is derived from an ancestor that lacked temporal fenestration. The relative expansion of the jaw adductor musculature, necessitated by the reduction in skull size,

appears not to have been effected by the M. Adductor Mandibulae mass, a physical impossibility if the adductor chambre is occluded by bone. Instead, the action of the adductor mass was augmented by the elaboration of a novel jaw levator system, the M. Interhyoideus Posterior (Nussbaum 1983). This scenario, like its contenders, cannot be tested. However, it is the one that is most compatible with the results of the ingroup analysis for this study.

Outgroup

Above the level of dissorophids in the outgroup cladogram (fig. 22), there is a major bifurcation that apparently occurred early in tetrapod history. One of the rami is made up of the lysorophoids, aïstopods, anurans and urodeles (group 5). The other contains the microsaurs and gymnophionans (group 8). The two groups can be distinguished from one another by the condition of the skull roof. The skull roof of group 8 members is fenestrated; the skull roof of group 5 members is stegocephalian. Temporal fenestration is the derived condition.

In three of the groups, anurans, urodeles and lysorophoids, the temporal fenestration is extensive. Hanken and Wake (1982) suggested that parietal-squamosal contact (26') was associated with the developement of temporal fenestration in amphibians. Squamosal-parietal contact occurs at the internode uniting these groups, but not uniquely.

Squamosal contact with the parietal also characterizes the caecilians, who do not appear to have been derived from open-skulled predecessor. The only character that transforms uniquely at the node subtending group 3 is the loss of postorbital elements (0 -> 28"). It is tempting to conjecture that the fenestration seen in anurans, urodeles, and lysorophoids is associated with, and has been attained through, the loss of the dermal elements posterior to the orbit. The nature of the fenestration of the skull, and how it has been attained is of great significance for the argument of lissamphibian monophyly. It has been shown here that the open skull condition was derived within the caecilians and is an essentially different structure.

Lissamphibian Monophyly

Reviews of extant ampihibians or amphibians in general have tended to view the modern orders as constituting a monophyletic assemblage. The trend has been particularly pronounced in recent years (Noble 1931; Parsons and Williams 1963; Estes 1965; Cox 1967; Duellman and Trueb 1986). Among the characters that allegedly unite the three living groups are the presence of pedicellate teeth (Parsons and Williams 1962), cutaneous respiration (Cox 1967), a prominent parasphenoid, green bodies in the retina (Parsons and Williams

1963) and a larval stage. The life history, thermal regime, respiratory physiology (Cox 1967), and sensory structures of the eye and inner ear (Lombard and Bolt 1979), delimit the modern amphibians as a biologically distinct group among the living tetrapods but as there is no extant plesiomorphic sister group within the Tetrapoda, and as paleontological evidence of soft tissue other than muscle scarring is rare and at best equivocal, it cannot be determined whether these similarities are synapomorphies or are symplesiomorphies of the tetrapods.

The most thorough recent analysis of lissamphibian monophyly remains that of Parsons and Williams (1963). Their consideration of the Lissamphibia unfortunately, largely ignores the caecilians. Hanken (1986) emphasizes that caecilian anatomy and development is comparatively poorly known. As Gregory et al (1956) point out, it has often been assumed that if a plausible argument can be made for anuran-urodele affinities, the caecilians would automatically be included in that assemblage, perhaps a consequence of the propensity of earlier workers to ally the caecilians with the urodeles. As is evident from the skull roof structure, fenestration, one of the most frequently cited characters uniting the modern groups (Dunn 1942; Taylor 1968a) is fundamentally different in caecilians. Rather than being the result of loss of the postorbitals, caecilian temporal fenestration is formed by a failure of the cheek and skull roof ossification centres to occlude; it is probably a paedomorphic trait. Tooth pedicelly is probably independently derived in all living orders (see

fig. 22 and Table 5) or perhaps a synapomorphy of anurans and urodeles. The two interpretations are equally likely. The cladogram in figure 22 suggests that there are no apomorphies shared by the three modern orders that are not also shared by lysorophoids and microsaurs. It is highly improbable that the Lissamphibia, as commonly conceived, is a natural assemblage. Anurans and urodeles are shown to share 26 (perhaps 29) apomorphic features, 13 of which are also shared with the lysorophoids. Anurans and urodeles do share 13 (perhaps 16) synapomorphies exclusively. A compelling case can be made for a monophyletic Lissamphibia if the caecilians are removed. It was not the objective of this study to consider in depth the interrelationships of the caudates and anurans beyond the context of the caecilians. However, as a contingent result of this analysis, a rather unusual hypothesis of anuran/urodele sister group relationship can be formulated. In light of this, a minor divagation would not be inappropriate.

The anuran-urodele synapomorphies are discussed above. They are primarily features of the braincase and palatal region, mostly involving reduction of the number of discrete elements by loss or fusion (fig. 22 and Table 5). I shall concentrate the following discussion on three characters that do not emerge at the internode immediately proximal to the anuran-urodele divergence; these are the presence or absence of postorbital elements (28"), the relationship of the pterygoid to the maxillary arch (18), and the emargination of the cheek (33).

It has been recognised in a number of lineages that severe reduction in the size of the skull, as has taken place in most living amphibians, carries with it a number of predictable morphological correlates. Among these are the loss and fusion of elements (Hanken 1983, 1984) and an increase in the relative size of sensory structures. The size of an image forming eye has a restricted minimum related to the maximum number of retinal cells per unit area (Walls 1942: 170-1). Likewise, in order that the function of the inner ear be maintained, there is a minimum diameter of the semicircular canals determined by the viscosity of the endolymphatic fluid (Jones and Spells 1963). Minimum size of the brain is also constrained. Hanken (1983) has shown the effects of phyletic decrease of skull size on the crowding of sensory structures in the very small plethodontid salamanders (genus Thorius). The force of a muscle is also size related; its contractile strength is proportional to its crossectional area (Gans 1966). Its excursion is dependent upon its length. The distance through which a muscle can contract is an additive function of the number of linearly arranged myofibrils (Gans and Bock 1965). Its contractile strength also decays as a function of the distance of contraction, so a longer muscle mass will have a wider range for effective contraction (Gans 1966). Rieppel (1984) has characterized the tetrapod skull as being essentially a bony tube within a tube. As the size of the inner tube (braincase and otic capsule) grows relative to the outer (dermal skull roof), with decreased head size, the space between them, occupied by the jaw adductor muscles

becomes progressively constricted. In order that the M. Adductor Mandibulae mass (MAM) maintains its function, it must expand beyond the adductor chamber. One can postulate that this has been the selective pressure for the fenestration of the skull in anurans and urodeles. Caecilians augment the adductor mass in an entirely different way, by elaborating the gular adductors.

Carroll and Holmes (1980) have recently countered the standard view of lissamphibian monophyly by arguing that the strategies followed by anurans and urodeles in fenestration of the skull roof and the increase of the jaw adductor mass are essentially different (see fig. #-10). In urodeles the ventral margin of the skull is incomplete, and fenestration, they claim, is formed by the emargination of the cheek region, similar to the condition in hapsidopareiontid microsaurs. This permits the considerable expansion of the MAM Externus and MAM Internus divisions of the adductor musculature. In contrast, the fenestration of anuran skulls is formed by a posterior extension of the orbit, and the MAM Posterior is greatly expanded. In developing their argument Carroll and Holmes interpret the similiarities as simply correlates of small size, and therefore not indicative of common ancestry. It is highly probable that the cranial similarities of skull structure between these groups are attributable to small size. The exigencies of small skull size are quite stringent, but identifying the efficient cause of the similarity, small size, does not inform us about the formal cause, patristic

relationship or independent acquisition.

As discussed above, the open skull of anurans and urodeles corresponds with the absence of postorbital elements (28"). Figure 22 and Table 5 reveal that skull fenestration attained by loss of the postorbital elements in lysorophoids, urodeles and anurans, and emargination of the cheek are not two distinct, mutually exclusive strategies as suggested by Carroll and Holmes (1980). The cladograms suggest that gymnokrotaphy emerged before the divergence of anurans and urodeles. The latest common ancestor of urodeles and anurans probably had a gymnokrotaphic skull with the adductor musculature bulging through or passing through the fenestra. The loss of the ventral cheek margin appears to have occurred subsequently in urodeles, perhaps permitting the enlargement of the MAM Externus seen in many salamanders as a secondary modification. Analogously, the ventral margin of the cheek appears to have been lost a number of times within the lepidosauromorphs (Carroll 1987), thought to be a correlate of the expansion of the MAM Externus superficialis head laterally, and dorsally (Rieppel and Gronowski 1981).

Anurans and urodeles share a distinct morphology of the pterygoid. It is reduced in size and closely associated with the supensorium. The pterygoid is usually associated with the otic capsule rather than the parasphenoid. The anterior ramus is much reduced in both orders but the similarity does not occur as a synapomorphy in the cladograms. The major difference between the two states for this character is that in anurans the pterygoid reaches the maxillary arch,

connecting with the maxilla at the ventral margin of the skull, whereas in urodeles it does not. There is no ventral margin with which to connect. If the emargination of the cheek is a recent acquisition of urodeles, it is plausible that the disconnection of the pterygoid and the maxillary arch is also. The similarity in the structure of the anterior ramus of the pterygoid may also be a synapomorphy of the two groups.

There are a number of problems facing an hypothesis of exclusive anuran-urodele monophyly. They are morphologically quite distinct groups, despite the large number of synapomorphies. The most striking differences in cranial anatomy occur in the region of middle ear and suspensorium, probably in part related to the presence of impedence matching in anurans. The possibility of close anuran-urodele affinities exclusive of the caecilians warrants further consideration

III Jaw Adductor Apparatus of Caecilians

The major point of departure of this classification of caecilians from most other recent schemes is simply the inversion of the relative primitiveness of the families Ichthyophiidae and Rhinatrematidae. While this is only a minor difference, its functional implications are immense. As there are no apomorphic features shared between rhinatrematids and all other families, it appears that two quite distinct groups

emerge from an ichthyophiid or ichthyophiid-like ancestor very early in caecilian history. The rhinatrematids are distinguished by twelve autapomorphies, five of which are components of the skull roof and jaw apparatus. These are cheek attachment (20), recessed lower jaw (24), retroarticular process inflection (25), extension of the M. Adductor Mandibulae Internus mass through the temporal fenstra (28) and a single M. Interhyoideus Posterior (27), oriented transversely between the jaw rami. In the lineage comprising all other families except ichthyophiids, despite a high degree of variation of all characters within and between groups, the same state for each of the five jaw apparatus characters is shared by all families (fig. 21, Tables 2 and 3). The inference can be made from this that these characters compose a functional suite of features associated with closing the jaw and that two relatively distinct patterns of the jaw and jaw musculature are present in the caecilians. Given that the rhinatrematids bear the apomorphic condition all of these five characters, they are considered here to have the more highly derived pattern. The other families elaborate the primitive arrangement to varying degrees.

The unique jaw apparatus of caecilians was described by Nussbaum (1983). The suite of features associated with rhinatrematids, as discussed by Nussbaum, include a large MAM Internus mass that expands beyond the adductor chamber to originate on the dorsal surface of the skull roof and a sagittal crest is present. The M Adductor Mandibulae muscle mass dominates but a significant M. Interhyoideus is present.

The mouth is terminal. The retroarticular process is comparatively short and not reflected dorsally. The suite of features exhibited by all other caecilians includes a small MAM mass, that does not originate beyond the primitive adductor chamber irrespective of the condition of the skull roof, a dominant, obliquely oriented M. Interhyoideus posterior, a variably deflected retroarticular process, and a subterminal mouth. Whichever way polarity is drawn, those characters listed by Nussbaum (1983) as features of the unique jaw closing apparatus of caeciians are also those that distinguish the two major lineages above the ichthyophiids in the results of this study. There appears to be compelling evidence that two distinct strategies of jaw adduction have evolved in two separate lineages of caecilians. One, found in rhinatrematids, has deemphasized the 'novel' jaw adductor mass (MIp) and expanded the MAM mass, concomitantly, the mandibular rami have been lengthened over the primitive condition, the retroarticular process shortened and straightened. The other, characteristic of all groups except the ichthyophiids, and to some extent the ichthyophiids themselves, has emphasized the 'novel' jaw adductor mass to varying degrees, decreased the length of the jaw rami, and increased the length and angle of inflection of the retroarticular process.

The question of the jaw apparatus composing a functional suite of features and the question of its significance in the evolution of the unique caecilian cranial are addressed in more detail in the following chapter.

CHAPTER IV.

CRANIAL MORPHOMETRICS

INTRODUCTION

The previous section suggests, based on the characters as polarized, that the most probable plesiomorphic sister group of caecilians is the microsaur complex of the Goniorhynchidae and Gymnarthridae. It further resolves the ingroup relationships, taking the family Ichthyophiidae as the most plesiomorphic living member. In this section I supplement the systematic analysis of the ingroup by quantifying the relationships of the characters used. In this way it is hoped that further inferences can be made about the function and evolution of the highly derived caecilian skull.

An early bifurcation within the caecilians is evident from the ingroup cladogram. One branch contains the rhinatrematids, the other is made up of all families except the ichthyophiids (fig 21). The two major groups above the level of the ichthyophiid-like stem group are differentiated largely by elements of the jaw and jaw musculature. The rhinatrematids possess an open skull roof, through which the musculature extrudes, and a comparatively short and straight retroarticular process. The other major assemblage elaborates the primitive condition of the jaw to varying degrees.

The cladistic analysis treats the characters of the jaw apparatus as independent entities and as a result cannot illustrate any higher order interactions that might occur

between them.

The interdependence of morphological features is of considerable biological interest. The jaw and jaw musculature of caecilians amply illustrate this point. Not only do the characters exhibit close correspondence, they also seem to define two quite distinct groups of caecilians. At a more general level, the jaw structure establishes caecilians as a highly distinctive tetrapod assemblage. This suggests that the structure of the jaw apparatus is of fundamental significance to the evolution of the group.

Functional Suites of Features

In the previous chapter, I surmised that the jaw apparatus constitutes a functional suite of features because of their correspondence in the ingroup cladogram. The actual recognition of functional suites is not that straight forward. Although it is necessary that elements of a functional complex are correlated in some way, the simple correspondence of character states in a cladogram is not a sufficiently strong basis for the conclusion that they do indeed constitute a functional suite. Characters can be associated by chance or by necessity and their simple distribution in a cladogram does not allow one to tell the difference. It must also be shown that the correspondence is obligatory. If features of an organism conjointly perform some function then their rates of phylogenetic change will be coupled in some way. This presumes that a change in one element necessitates a concomitant change in the others if optimal function is to be maintained. There

is a common causal structure between elements of a functional suite of features that accounts for the correspondence between them and that is presumed not to exist between other characters. If that causal structure can be revealed, then there is ample reason to conclude that the features under investigation are part of a functional suite.

In tetrapods, rates of change of morphological features generally show high correlations in both ontogeny and phylogeny (Gould 1966). This is attributable to the existence of general growth factors (Jolicoeur 1963; Jolicoeur and Mossiman 1959), i.e. as an organism grows, so do its constituent parts, or to the physical requirements that overall size imposes on structure (Thompson 1942; Gould 1966). In recognising functional suites, the covariances between individual characters are of more interest than the uniform effects of general size on all characters. Interdependence of characters over and above that caused by general growth or size must be demonstrated.

I take the conclusions of the last chapter as the hypotheses of this chapter. These are that the jaw apparatus of caecilians constitutes a closely related functional suite of features and that the rate and direction of change of these characters show evidence of common cause additional to the factors that account for the general correlations between all cranial features. In addition, the structure of the jaw apparatus should account for a large proportion of the quantitative morphological differences between the two major branches of caecilians (see fig 21). Differences in jaw

structure between the major groups are predicted to be larger than those within the major groups.

Miniaturization and Fossoriality

Generally, caecilian skulls are small. The smallest adults in this sample have total skull lengths similar to those of plethodontid salamanders (Idiocranium observation #73 = 4.15 mm, Siphonops #132 = 6.38 mm, Afrocaecilia #122 = 6.60 mm). Additionally, the structure of the skull is thought to be well adapted for burrowing (Dunn 1942; Taylor 1969; Wake and Hanken 1982). The advantage of small skull size to fossorial animals is intuitively quite obvious. A small skull is easier to push through the soil than a large skull of similar shape. The cranial specializations required for burrowing are not those usually seen in small-skulled tetrapods. Miniaturization of the caecilian skull must meet concurrently the often conflicting requirements of small skull size and burrowing habit. A greater knowledge of the functional significance of the caecilian cranial anatomy may permit some understanding of the ways in which the unique caecilian solution to miniaturization has been attained.

METHODS AND MATERIALS

Observations

Twenty cranial characters were measured from cleared and stained specimens and dried skulls. Measurements taken were: Length of the skull roof (LSKRF), Width of the skull roof at jaw joint (WSKRF), Width of the skull table (WSKT), Length of the Os Basale (LOB), Width of the Os Basale at the otic capsules (WOB), Distance between tooth rows (DTR), Number of teeth in the outer arcade (TOA), Number of teeth in the inner arcade (TIA), Area of the adductor chamber (ArAC), Depth of the skull at the jaw joint (DSKJJ), Length of upper jaw (LUJ), Length of the skull anterior to the jaw joint (LSKAJ), Distance from the occipital condyle to the jaw joint (OCTJJ), Distance from the orbit to the tentacle (OTT), Length of the preorbital portion of the skull (LPO), Length of the lower jaw anterior to the jaw joint (LLJPM), Length of the retroarticular process - upper margin (LRAPU), Length of the retroarticular process - lower margin (LRAPL), Angle of inflection of the retroarticular process mesially (ARAPM) and, Angle of inflection of the retroarticular process dorsally (ARAPD). Two composite measurements were also used in various analyses. These are Total skull length (TSL= LSKAJ + OCTJJ),

and the amount of overhang of the upper jaw (LSKAJ - LUJ).

Measurements for the dried skulls and some of the cleared and stained specimens were taken from drawings made at 6X and 12X through a camera lucida attached to Wild M5 and M6 binocular microscopes. Values were recorded using a Jandel Scientific digitising pad and the SigmaScan (Jandel Scientific) program for IBM PC. Measurements of most of the remaining cleared and stained specimens are from photomicrographs taken with a Wild binocular microscope and camera attachment. The negative images were projected onto the same digitising pad, and measurements were taken as for the drawn specimens. The scales of the drawn and photographed specimens were calibrated by matching the scale of a stage micrometer image (Bausch and Lomb 2mm) with that of the drawn specimens.

All linear measurements were taken in mm. The area of the adductor chamber was measured in mm^2. The angles were measured in degrees, where a retroarticular process with no inflection has a value of 180°. Dorsally and mesially directed retroarticular processes have values less than 180°. All continuous measurements were log transformed. In addition to log transformation, in successive analyses, angles were treated in their raw form, as their value subtracted from 180, or as the sine of their divergence from 180° in radians. Measurements are listed in Appendix 2.

A total of 148 observations was compiled encompassing 28 genera and 37 species. Among these, two extensive ontogenetic sequences were observed. One of these was of

Epicrionops sp. (14 specimens), a rhinatrematid; the other was of Dermophis mexicanus (38 specimens), a member of the other major subgroup. There are other ontogenetic sequences in the data set but none encompasses such a complete range of developmental stages as those of Epicrionops and Dermophis

A subsample of presumed adults was taken from the data set. An adult was defined as any individual whose WSKRF value fell within 20% of the largest WOB value for that genus. There were 63 individuals in this subsample.

For comparison with caecilians, values of LSKAJ, WOB, and ArAC were taken from reconstructions of stegocephalian (closed-skulled) amphibians. The measurements were also taken on the digitizer, and log transformed. Sources are listed in Table 22.

Statistical Analysis

Three types of statistical tests were used, two multivariate and one bivariate. Factor analysis was employed to infer the existence of functional suites of features. Canonical discriminant analysis determined the morphological distinctness of families and the extent to which the structure of the jaw apparatus contributes to the differences between groups. Reduced major axis analysis was applied to the ontogenetic sequences in order to quantify the relative rates of change of cranial characters during development and to compare developmental rates between Epicrionops and Dermophis. Bivariate analysis was also used to describe the

size relationships of cranial elements between adult caecilians, and adult stegocephalian amphibians.

Not all of the variables were employed in any one analysis. Those with a large number of missing values or exhibiting linear dependence or partial linear dependence with others were unused. Despite their potential importance, angles of inflection of the retroarticular process (ARAPD, ARAPM) were omitted from the final analyses for both factor and canonical discriminant procedures. They showed extrememly low correlations with other factors (Rho > .5) and there is no indication that their distribution is either log-normal or linear-normal.

Factor analysis

Factor analysis reduces the variation of values within a set of variables to a linear combination of the variation ascribable to common factors, plus a unique factor for each variable. The number of common factors is usually taken to be much smaller than the number of variables (Harman 1967 Ch1.; Kim and Mueller 1984, 1985). The assumption of factor analysis is that there is an underlying causal structure to the variables. Common causal factors account for the covariances between variables. This is the same form of causal structure postulated for the recognition of functional suites and so the application of factor analysis is appropriate to this type of question.

The analysis was performed using the FACTOR procedure of SAS statistical package version 2.8 for IBM PC. Factors

for IBM PC. Factors were extracted by the maximum likelihood method as recommended by Kim and Mueller (1985). Promax oblique rotation was chosen because of the high correlations between variables and yielded the final factor structure. All factors with eigenvalues less than 1 were discounted. The entire data set was used.

Canonical discriminant analysis

Canonical discriminant analysis is a commonly used morphometric technique that is akin to Principal Component Analysis (Albrecht[4] 1980; Klecka 1980; Shaffer 1984). It identifies orthogonal factors that account for the maximum variance between specified groups of observations.

The between groups canonical structure indicates the correlation coefficients of each variable on the factors that best discriminate between groups. The values can also be seen as direction cosines. If a factor and a variable are perfectly correlated (1.00), the angle of which that correlation is the cosine (0°) indicates that the factor and the variable are coincident. This is a useful measure of the contribution of each variable to the information in each factor.

The CANDISC procedure of SAS version 5.16 (SAS Institute 1985b) from McGill University Computing Services was used to perform the canonical discriminant analysis. All canonical variates with eigenvalues greater than one were plotted against one another. The classes defined were: A) Dermophis, (42 specimens) B) Caecilia (17 specimens), C)

Typhlonectes (11 specimens), D) Ichthyophiids (Ichthyophis plus Caudacaecilia) (11 specimens), E) Geotrypetes (11 specimens) and, F) Epicrionops (14 specimens). These genera represent the largest number of samples for each of their respective families. Five of the seven families recognised in the ingroup cladogram (fig 21) are represented. Canonical discriminants results are affected by grossly unequal group sample sizes (Klecka 1980). For this reason specimens of uraeotyphlines and scolecomorphids, for which small numbers of specimens were available, were omitted.

Reduced major axis analysis

Among the available methods of linear bivariate analysis, reduced major axis is the most highly recommended for morphometrics (Kidwell and Chase 1967). Its advantages are that it does not assume that either of the variables is independent, the slope of Y versus X is the reciprocal of X versus Y (Imbrie 1956) and the result of the analysis is not largely affected by differences in the scale of the measurements (Kermack and Haldane 1950).

The analyses were all performed on a hand calculator following the formulae given by Kermack and Haldane (1950) and Imbrie (1956). The Correlation matrices and descriptive statistics of the variance-covariance matrices generated by various analyses on SAS PC were used in the calculations. The values of Z are taken from Steel and Torrie (1960).

RESULTS

Factor Analysis

The results for the factor analysis are given Tables 7 through 10 and are summarized in Table 11. Table 7 is the target matrix for the oblique rotation. It takes as its reference axes the most widely divergent variables (characters). Table 8 shows the correlations between factors. When factors are orthogonal their correlations are zero. The elements of Table 9 are correlation coefficients between each variable and each factor. Table 10 displays the standardized regression coefficients. These are the r^2 values for the coregressions (Van Valen 1974), or codeterminations of each variable with each factor.

The target matrix consists of four factors. From the loadings of each factor on the variables, an intuitive idea of its general meaning can be gleaned. The loadings and factor descriptions are as follows:

Factor 1:

LUJ	1.0000 (r^2=.8068),	Length of upper jaw
LLJPM	.7581 (r^2=.6503),	Length of lower jaw -anterior
LSKAJ	.7116 (r^2=.6314),	Length of skull ant. to jaw

These are all elements of the jaw anterior to the jaw joint.

Factor 2:

LRAPL 1.0000 (r^2=.8669), retroarticular process -lower
LRAPU .8520 (r^2=.7498), retroarticular process -upper

These are both measurements of the length of the retroarticular process.

Factor 3:

OCTJJ 1.0000 (r^2=.7185), Occipital condyle to jaw joint
WSKT .9273 (r^2=.7051), Width of skull table
WOB .8804 (r^2=.7495), Width of os basale

These are elements of the breadth of the braincase, or the size of that portion of the braincase at the level of the jaw joint or behind it. The edge of the skull table is coincident with the dorsolateral margin of the braincase.

Factor 4:

LSKRF 1.0000 (r^2=.46408), Length of skull roof
LOB .8177 (r^2=.39392), Length of os basale

These are measurements of the overall length of the skull.

The four factors combined account for over 99% of the variance in the entire sample. Factor 1, 'length of the jaw anterior to the craniomandibular joint' accounts for the largest amount of the variance (total variance explained 98.157). Factor 2, 'length of the retroarticular process' explains the next largest amount of the variance (80.245), followed by factor 3, 'width of the os basale' (76.552), and then by Factor 4, 'length of the skull' (60.832). The coefficients of codetermination for Factor 4 are all rather small.

The correlations between factors are extremely large. This is particularly apparent between Factor 1 and Factor 2 (correlation=.7213). Rather than being orthogonal, in Euclidean space these factors would be deployed at an angle of

RESULTS OF FACTOR ANALYSIS

TABLE 7

Target Matrix

VARIABLE	Factor 1	Factor 2	Factor 3	Factor 4
LSKRF	.30863	.20809	.22841	1.0000
WSKT	.05852	.09376	.92732	.19918
LOB	.41314	.09059	.32085	.81768
WOB	.14660	.07944	.88035	.06551
ArAC	.53477	.10088	.47087	.01617
DSKJJ	.22122	.34123	.42561	.06305
LUJ	1.00000	.15773	.11815	.03882
LSKAJ	.71158	.22881	.15498	.13279
OCTJJ	.11414	.07582	1.00000	.00309
LLJPM	.75812	.28684	.12373	.03521
LRAPU	.17690	.85196	.11833	.03509
LRAPL	.12177	1.00000	.08725	.04786

TABLE 8

Correlations Between Factors

	Factor 1	Factor 2	Factor 3	Factor 4
Factor 1	1.00000	.72126	.69085	.63849
Factor 2		1.00000	.63986	.61314
Factor 3			1.00000	.63925
Factor 4				1.00000

RESULTS OF FACTOR ANALYSIS

TABLE 9

Factor Structure (Correlations)

VARIABLE	Factor 1	Factor 2	Factor 3	Factor 4
LSKRF	.86999	.83021	.81728	.89953
WSKT	.63932	.63936	.85964	.66620
LOB	.82018	.69733	.78469	.81180
WOB	.76738	.70134	.94510	.69031
ArAC	.84943	.69945	.82633	.62441
DSKJJ	.69414	.71315	.72338	.58872
LUJ	.96694	.77495	.72694	.66857
LSKAJ	.95582	.83482	.77500	.74603
OCTJJ	.61813	.57112	.79802	.50351
LLJPM	.92099	.81691	.71933	.65539
LRAPU	.79675	.95065	.71594	.64671
LRAPL	.78310	.99397	.70250	.66142

TABLE 10

Coefficients of Codetermination:

VARIABLE	Factor 1	Factor 2	Factor 3	Factor 4
LSKRF	.29071	.22223	.17759	.46408
WSKT	-.03579	.10875	.70505	.17164
LOB	.37440	.01725	.26319	.39392
WOB	.15787	.06440	.74953	.07087
ArAC	.51346	.05585	.45350	-.02760
DSKJJ	.18422	.32260	.36365	.04074
LUJ	.80675	.13268	.06531	.03034
LSKAJ	.63137	.22884	.10640	.13452
OCTJJ	.11717	.07317	.71851	-.07549
LLJPM	.65031	.29181	.07482	.01335
LRAPU	.17689	.74980	.11290	.00166
LRAPL	.09629	.86691	.06374	.02743

TABLE 11. SUMMARY OF FACTOR ANALYSIS

FACTOR 1. The jaw anterior to the jaw joint

VARIABLE	CORRELATION	r^2	COMMUNALITY
LUJ	0.96994	0.80675	0.95065
LLJPM	0.92099	0.65031	0.89987
LSKAJ	0.95582	0.63137	0.97730
(ArAC	0.84943	0.51346	0.83272)

FACTOR II. Retroarticular process length.

VARIABLE	CORRELATION	r^2	COMMUNALITY
LRAPL	0.99397	0.86691	1.00000
LRAPL	0.95065	0.74980	0.93564

FACTOR III. Braincase, otic capsule size.

VARIABLE	CORRELATION	r^2	COMMUNALITY
OCTJJ	0.79802	0.71851	0.64958
WSKT	0.85956	0.70505	0.76708
WOB	0.94510	0.71851	0.92361
(ArAC	0.82633	0.45350	0.83272)

FACTOR IV. Skull length

VARIABLE	CORRELATION	r^2	COMMUNALITY
LSKRF	0.89953	0.46408	1.00000
LOB	0.81180	0.39392	0.84541

43.84°.

The proportion of the variance in each variable explained by the common factors (communalities) ranges from .65 to 1.00. The lowest of these are DSKJJ, OCTJJ and WSKT. All components of 'jaw factors', 1 and 2, have communalities of .90 or higher.

Although 83% (communality=.83) of the total variance of the area of the adductor chamber (ArAC) is explained by the the common factors, it does not have a high coefficient of determination with any single factor. ArAC has a 'degree of complexity' of 2.0 (Harman 1967), meaning that it is determined jointly by two factors. The coefficient of determination of ArAC on Factor 1 is .5135. Its value on factor 3 is .4535 (Table 10). Therefore, the area of the adductor chambre is a function of the length of the jaw anterior to the jaw joint and the width of the os basale.

Canonical Discriminant Analysis

Three canonical variates had eigenvalues greater than or equal to one. Together they describe 87.77% of the total variation. Canonical variate 1 describes 45.46%, variate 2 24.25%, and variate 3 18.06%. These are the only significant variates ($P < .05$).

Table 12 shows the between-factor canonical structure. The variables with the highest loadings on variate 1 are: LRAPL (.6122) and LRAPU (.4175). Those on variate 2 are: OCTJJ

(.8582), DSKJJ (.7801), WOB (.7774) and, WSKT (.7689). The highest coefficients on variate 3 are LUJ (.8118) and LSKAJ (-.8105), followed by LOB (-.7855), LLJPM (-.7540), ArAC (-.7532) and, LSKRF (-.7254). Unfortunately SAS does not calculate F-to-remove values, which would determine how much information each variable contributes uniquely to each variate.

Mahalonobis distances are listed in table 13. These are straight-line Cartesian distances between each of the group centroids (Albrecht 1980; Klecka 1980; Van Valen 1974). The values above the main diagonal are the actual distances. Below the diagonal are P values associated with the null hypotheses that the distance between each pair of group centroids is zero. The largest distances are all associated with the Rhinatrematid genus Epicrionops (Group F). These are all highly significant ($P < .005$). There are only three other significant distances: Dermophis - Caecilia ($P = .0075$), Geotrypetes -Typhlonectes ($P = .0055$) and, Geotrypetes - ichthyophiines ($P = .0060$).

The discriminant function analysis reveals that the structure of the retroarticular process is the best discriminant between groups. The group mean of rhinatrematids Epicrionops on this variable (3.4536) is considerably different from that of other genera (Dermophis -.2162, Caecilia -1.023, Typhlonectes -1.7771, ichthyophiines -.7131, and, Geotrypetes .4218). This variate corresponds with Factor 2 of the factor analysis. Factor 3 of the factor analysis, plus the depth of the skull at the jaw joint is the second

CANONICAL DISCRIMINANT ANALYSIS

TABLE 12

Between-Groups Structure:

VARIABLE	Variate 1	Variate 2	Variate 3
LSKRF	-.2795	.5367	-.7254
WSKT	-.3168	.7689	-.5363
LOB	.3387	.4343	-.7855
WOB	-.0094	.7774	-.3235
ArAC	.0220	.5713	-.7532
LUJ	.0405	.5406	-.8118
LSKAJ	-.1204	.5036	-.8105
DSKJJ	-.3394	.7801	-.3450
OCTJJ	-.0020	.8582	-.4614
LLJPM	-.0005	.6373	-.7540
LRAPU	-.4175	.6722	-.5492
LRAPL	.6122	.4895	-.5719

TABLE 13

Mahalonobis Distances:

CLASS	A	B	C	D	E	F
A	-	3.0972	3.2228	2.6569	2.6868	4.2257
B	0.0075	-	3.4706	3.3187	3.0059	4.8921
C	0.3631	0.1272	-	2.4957	3.9464	5.4753
D	0.4655	0.0660	0.1700	-	4.0851	4.4986
E	0.6574	0.3068	0.0055	0.0060	-	4.1011
F	0.0036	0.0001	0.0001	0.0001	0.0001	-

best discriminant between groups. The jaw anterior to the jaw joint is only the third best discriminant between groups. The inclusion of the length of the skull roof (LSKRF) and the length of the os basale (LOB) into this factor, plus the fact that all coefficients have the same sign suggest that this variate incorporates a factor of overall size (Jolicoeur 1963; Pimentel 1980). This being the case then, it is not surprising that when the groups include growth series, the length of the jaw does not discriminate between them strongly. An adequately large sample of adults should also be analysed in this way.

Reduced Major Axis

Bivariate plots of the relationship between elements of factors 1, 2 and 3, with one another, and with the area of the adductor chamber are shown in figure 28. The relevant statistics are listed in tables 14 through 22. The equation is given in the form of $y = mx + \ln b$, where m is the slope and $\ln b$ is the natural logarithm of the intercept (Gould 1966). Unless otherwise stated, the significance values given are for the slope of the reduced major axis. Missing values for the adductor chamber and length of the retroarticular process of Epicrionops unfortunately make some sample sizes quite small.

Adductor Chamber vs Factor 1: The rate of change in ontogeny between the area of the adductor chamber (ArAC) and the length lower jaw anterior to the jaw joint (LLJPM) is not significantly different between Epicrionops and Dermophis

Table 14-1 The same is true for ArAc versus LUJ. The latter however shows a strong trend toward significance (P= .057). Values of ArAC versus LSKAJ for Epicrionops, Dermophis, adult caecilians, and adult stegokrotaphic amphibians are given in Table 21. The values for adult caecilians and adult amphibians in general do not differ (P> .05). The Y intercepts are not significantly different. The difference in growth rate of ArAC versus LSKAJ between Epicrionops and Dermophis is not significant at .05. It does however show a strong trend (P= .066).

Adductor Chamber vs Factor 2: The rate of developmental change between ArAC and the retroarticular process (LRAPL) is significantly different between Epicrionops and Dermophis (Table 15).

Adductor Chamber vs Factor 3 : Neither the slopes nor the Y intercepts are significantly different between genera for ArAC vs WOB (Table 16).

Factor 1 vs Factor 2: The slope of LRAPL vs LLJRM are not significantly different between the two genera; their y intercepts however show a highly significant difference (P<< .05). The difference in slope between the length of the retroarticular process and the upper jaw are borderline significant (P= .051). Y intercepts are also calculated for this relationship. They are significantly different (P<< .05) (Table 17).

Factor 3 vs Factor 1 : There is no significant difference in either slope or intercept between Epicrionops and Dermophis for WOB vs LUJ (Table 18).

Factor 2 vs Factor 3: The slopes of LRAPL vs WOB are not different between genera, nor are the Y intercepts (Table 19).

Within Factor 1: The growth rate of the upper jaw versus the lower jaw is significantly different between the two genera (Table 20).

Adults and Stegocephalian Amphibians:

The allometric relationship between length of skull anterior to the jaw and the area of the adductor chamber is plotted in figure 28. The slope is 2.084; the Y-intercept is -3.043. Allometric relationships of braincase dimensions(WOB, LOB, OCTJJ) versus skull length (LSKAJ and TSL) are shown in table 22.

REDUCED MAJOR AXIS -RESULTS

TABLE 14. Adductor chamber and Factor 1

Group	lnb	m	r^2	S_a	N	Z	P
1. ArAC vs LUJ							
Epicrionops	-3.748	2.215	.858	.252	10	1.90	.057
Dermophis	-3.0119	1.716	.927	.0806	30		
*Y-intercepts Z_b= 4.11 P<< .05							
2. ArAC vs LLJPM							
Epicrionops	-3.074	1.910	.813	.275	9	1.09	>.05
Dermophis	-2.550	1.585	.859	.0744	28		
*Y-intercepts Z_b=2.59 P< .05							
3. Arac vs LSKAJ							
Epicrionops	-4.139	2.305	.849	.283	10	1.82	.066
Dermophis	-3.330	1.761	.916	.0931	30		
* Y-intercept Z_b=1.63 P> .05							

REDUCED MAJOR AXIS-RESULTS

TABLE 15. Adductor chamber and Factor 2.

Group	lnb	m	r^2	S_a	N	Z	P
ArAC vs LRAPL							
Epicrionops	-1.027	1.634	.874	.193	10	2.66	<.05
Dermophis	-1.219	1.109	.859	.0744	28		

TABLE 16. Adductor Chamber and Factor 3

Group	lnb	m	r^2	S_a	N	Z	P
ArAC vs WOB							
Epicrionops	-4.098	2.992	.955	.179	12	1.86	.063
Dermophis	-3.742	2.456	.832	.175	33		
* Y-intercepts Z_b= 1.06 P>.05							

REDUCED MAJOR AXIS - RESULTS

TABLE 17. Factor 2 and Factor 1

A.

Group	lnb	m	r^2	S_a	N	Z	P
1. LRAPL vs LUJ							
Epicrionops	-1.692	1.356	.937	.107	10	1.94	.051
Dermophis	1.503	1.468	.878	.0904	32		
* Y-intercepts				Z_b= 16.2		P<< .05	
2. LRAPL vs LLJPM							
Epicrionops	-.772	.856	.895	.0923	9	1.14	>.05
Dermophis	-.314	.783	.865	.0463	34		
* Y-intercepts				Z_b= 5.32		P<< .05	

B.

Group	lnb	m	r^2	S_a	N	Z	P
1. LSKAJ vs LRAPL							
Epicrionops	1.354	.709	.855	.0853	10	.49	>.05
Dermophis	1.158	.664	.913	.0337	34		
* Y-intercept				Z_b= 3.77		P< .05	

REDUCED MAJOR AXIS - RESULTS

TABLE 18. Factor 3 and Factor 1

Group	lnb	m	r^2	S_a	N	Z	P
WOB vs LUJ							
Epicrionops	.108	.758	.807	.0133	11	1.44	>.05
Dermophis	.300	.697	.877	.0402	33		
* Y-intercepts				Z_b= 0.11	P>.05		

TABLE 19. Factor 2 and Factor 3

Group	lnb	m	r^2	S_a	N	Z	P
LRAPL vs WOB							
Epicrionops	-1.884	1.788	.854	.216	10	1.18	>.05
Dermophis	-2.125	2.1007	.881	.154	35		
* Y-intercepts				Z_b= 0.70	P> .05		

REDUCED MAJOR AXIS - RESULTS

TABLE 20. Within Factor 1

Group	lnb	m	r^2	S_a	N	Z	P
1. LUJ vs LLJPM							
Epicrionops	.321	.861	.072	.0438	10	5.18	<.05
Dermophis	-.597	1.134	.976	.0289	34		
2. LSKAJ vs LUJ							
Epicrionops	.651	.961	.978	.0427	11	.27	>.05
Dermophis	.162	.974	.986	.0289	37		

* Y-intercept Z_b= 6.45 P<< .05

REDUCED MAJOR AXIS -RESULTS

TABLE 21. Adult Caecilians; Adult Amphibians

Group	lnb	m	r^2	S_a	N	Z	P
1. ArAc vs LSKAJ							
Adults	-4.186	2.134	.820	.120	63	0.19	>.05
Amphibians	-3.043	2.084	.766	.291	12		
* Y-intercept Z_b= 2.49 P< .05							
2. LSKAJ vs. LRAPL							
Adults	.779	1.02	.755	.0707	53	0.30	>.05*
* slope is not significantly different from 1.00							
3. WOB vs. LSKAJ							
Adults	1.09	.62	.747	.0724	63	1.21	>.05*
* slope is not significantly different from 1.00							

REDUCED MAJOR AXIS - RESULTS

TABLE 22. Braincase versus Skull Length: Adult Caecilians

Group	lnb	m	r^2	S_a	N	Z	P
WOB vs TSL	-0.758	.983	.797	.0609	53	0.26	>.05
OCTJJ vs TSL	-1.254	.979	.721	.0678	58	0.32	>.05
LOB vs TSL	-0.407	.979	.846	.05286	53	0.37	>.05
OCTJJ vs LSKAJ	-0.828	.931	.546	.0809	53	1.06	>.05

No slope is statistically different from 1.00.

DISCUSSION

The Jaw as a Functional Suite

The factor analysis reveals that the elements of the jaw apparatus covary in the manner expected of a functional suite of features. Two separate factors are found that explain the variation in the jaws. One corresponds to the retroarticular process; the other is associated with the jaw anterior to the jaw joint. These two factors in turn are closely interrelated, having a correlation coefficient of .72. The associated variables are Factor 1 LUJ, LLJPM, LSKAJ, and Factor 2 LRAPL and LRAPU. The area of the adductor chamber is determined partially by the length of the jaw anterior to the jaw joint and partially by the size of the posterior portion of the braincase and so does not appear to be fully a part of this suite of features.

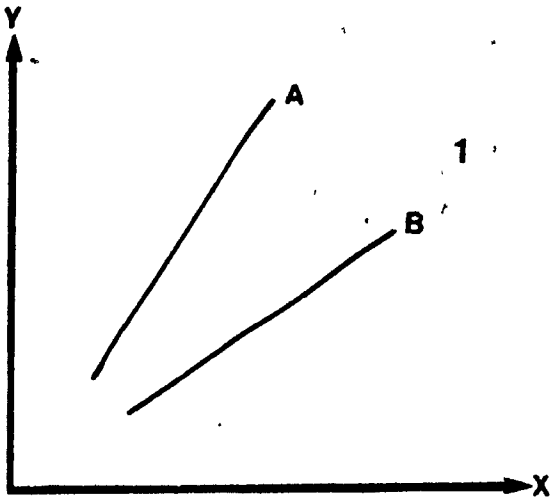
The structure of the jaw apparatus accounts for most of the measured morphological differences within the caecilians. Although the first factor, that of the jaw anterior to the jaw joint (LUJ, LLJPM, LSKAJ), describes the largest portion of the total variance of the sample, the length of the retroarticular process accounts best for the morphological differences between families.

There is a striking concordance between the cladogram of caecilians and the morphometric differences between families. The cladistic analysis showing the number of apomorphies, and the canonical discriminant analysis showing the degree of their morphological divergence, both suggest that the rhinatrematids are a highly distinctive assemblage and share only distant common ancestry with most other caecilians. In both analyses the rhinatrematids are the best differentiated family. The largest Mahalonobis distance occurs between Epicrionops and Typhlonectes. The respective families are separated by the largest number of character transformations (27) in the ingroup cladogram (fig. 21). The significant morphological distance between Dermophis and Caecilia (3.097 P= .0075) supports the reclassification of subfamilies Caeciliinae and Dermophiinae as distinct families suggested in chapter III.

Ontogeny of the Jaw Apparatus

Garstang (1922) and others have pointed out that adult morphologies are the result of development and therefore, variation in adult morphologies must also be the result of developmental variations. There are a number of ways in which this variation can manifest itself. They have been characterized by Alberch et al (1979). For the purposes of this study, where only differences in proportions of morphological units are of interest, the schema can be simplified (fig. 28). The bivariate analysis can discern three

Figure 28. Bivariate plots of changes in allometric relationships between the ontogeny of two elements (X and Y) in two organisms A and B. 1. the rate of change (slope) varies between species. 2. neither slope nor intercept changes, the adult of A has the same proportions of X:Y as does the juvenile of B. 3. rate of change (slope) remains the same, timing of onset of development (Y-intercept) changes.



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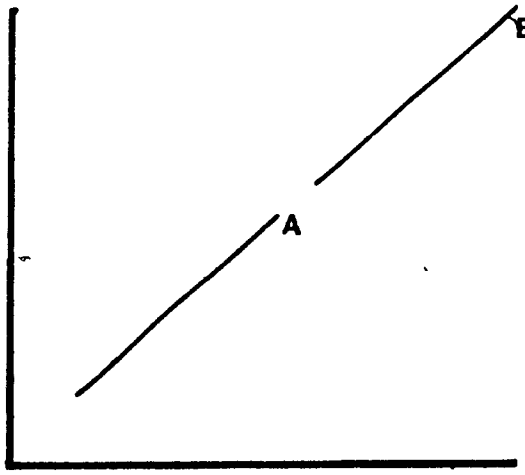

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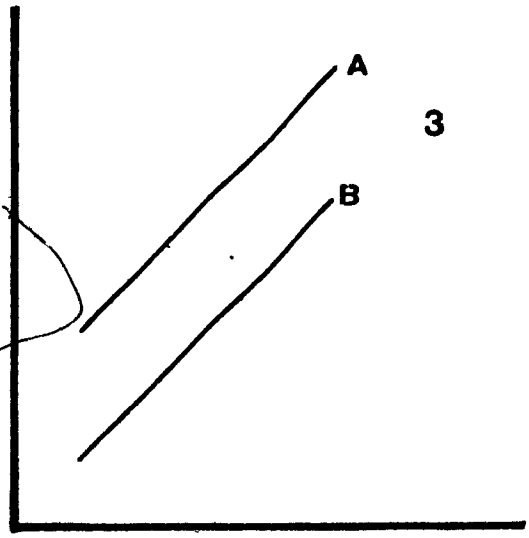


3

heterochronic effects in the growth of one feature relative to another (Shea 1985). Firstly, between any two organisms, the rate of change of one element relative to another can be altered during growth. When this occurs the bivariate plots will have different slopes. If the rate change is constant, the proportions can be altered by extending or truncating the developmental process (or altering the absolute rate of change of the elements coincidentally). In this instance both slope and intercept of the respective plots will coincide. One individual will resemble an earlier ontogentic stage of the other (Wayne 1986). Alternatively, if both relative and absolute rates of development are constant, alterations in proportion can be brought about by changing the time of onset or offset of the development of one element relative to another (Gould 1977; Løvtrup 1974). In this case, the respective bivariate plots should have similar slopes but differing intercepts (White and Gould 1965) (fig. 28). Combinations of these processes are less amenable to study by bivariate analysis than their occurences alone.

In comparing the growth rates of elements of each of the factors with one another, some differences in the developmental trajectories of the jaw apparatus can be seen. The relative rate of growth of the adductor chamber versus Factor 1 (the jaw anterior to the jaw joint) generally exhibits differences in scaling. The Y intercept of Epicrionops is significantly higher for the adductor chamber versus the length of the upper jaw ($P << .05$), and the adductor chamber versus the length of the lower jaw. Although the

slopes of these lines are not significantly different, two of them show strong tendencies toward signicance (ArAC vs LUJ P=.057, ArAC vs LSKAJ P=.066). The slope of the adductor chamber versus Factor 2 (the length of the retroarticular process) is significantly different between the two genera. Neither the slope nor the intercept of the adductor chamber vs Factor 3, here represented by WOB, is different between genera, although again there is a tendency toward differing slopes (P=.063).

The relationships of the growth of the adductor chamber to the size of each of the factors suggest that there is a difference in timing of development between the jaw and adductor chamber. The rate of growth of the adductor chamber relative to the jaw is similar between the two genera, certainly for the lower jaw and probably for the upper. In Epicrionops however, the ossification of the dermal cheek is much delayed by comparison with that seen in Dermophis (Wake pers. comm. Wake and Hanken 1982). In Dermophis the squamosal-parietal space is the last gap to close between dermal roofing bones. The gap does not occlude in rhinatrematids, leaving the open-skulled condition. Its delayed development in Epicrionops probably permits the growth of the M. Adductor Mandibularis mass through the cheek fenestra. Thus early onset of growth of the adductor muscle mass relative to the cheek and, as suggested by Table I, relative to the jaw, produces a larger muscle mass in the rhinatrematids. The ratio of length of the lower jaw to the adductor chamber area in adult Epicrionops is

TABLE 23

SKULL LENGTHS AND ADDUCTOR CHAMBER AREAS

OF STEGOCEPHALIAN AMPHIBIANS

Genus	ln LSKAJ (mm)	ln ArAC (mm^2)	Source
Eryops	6.075	9.056	Sawin 1942
Greererpeton	2.904	7.369	Smithson 1982
Sauropleura	3.074	1.758	Bossy 1978
Dendrerpeton	4.161	5.254	Godfrey et al 1987
Cardiocephalus	2.413	1.589	Carrolland Gaskill 1978
Rhynchonkos	2.713	2.041	"
Microbrachis	2.654	2.653	"
Odonterpeton	1.627	0.916	"
Proterogyrinus	4.992	8.733	Holmes 1985
Anthracosaurus	5.997	8.774	Panchen 1977
Eogyrinus	5.973	8.285	Panchen 1972
Gephyrostegas	4.119	3.939	Carroll 1970

approximately 3.52:1, whereas it is 4.15:1 in Dermophis. The area of the adductor chamber grows at a distinctly faster rate as a function of the growth of the retroarticular in Epicrionops as compared to Dermophis.

It is more difficult to interpret the developmental rates of Factor 1 (the jaw in front of the jaw joint) as a function of Factor 2 (the length of the jaw behind the jaw joint) (Table IV). Neither of the slopes, LRAPL versus LUJ or LRAPL versus LLJPM differs significantly between the two genera but in the case of LRAPL vs LUJ this may be an artefact of sample size ($N=10$ $P=.051$). Further observations may establish this difference as significant. Although the slopes are not significantly different, the intercepts certainly are. Care must be taken in attributing biological meaning to differences in intercept when slopes are not the same. The difference between the Y-intercepts of the LRAPL versus LUJ plots are not interpretable. However LRAPL versus LLJPM (length of the lower jaw posterior versus anterior) shows a very strong effect of scaling ($P<<.05$). It appears that the portions of the lower jaw are constrained to grow at similar rates. In photographs of developmental stages, the retroarticular process appears much earlier in Dermophis than in Epicrionops.

There are distinct differences in the growth of elements within Factor 1. The lower jaw grows at a higher rate than the upper in Epicrionops (slope=0.861). The converse is true for Dermophis (slope=1.134) (Table VII). Not only are these values significantly different from one another ($Z=5.81$, $P<.05$), but each is significantly different from 1.0, the

slope of the isometric rate (Z= 3.48 Epicrionops, Z=4.63 Dermophis). This in part accounts for the recessed jaw of dermophids. The relationship of the skull anterior to the jaw and the length of the upper jaw is a measure of the degree to which the skull extends beyond the upper jaw. In the rhinatrematids it is near zero. The rate of growth of LSKAJ and LUJ are extremely similar between these genera (Z=.273). The Y intercepts are significantly different however. While the upper and lower jaws may grow at different rates, the upper jaw and skull seem constrained to grow at the same rate. The upper jaw is slightly subterminal in the smallest Dermophis observed. That the slope of this relationship is not different from 1.0 in either case, indicates that the amount that the jaw is recessed remains constant throughout growth in both genera.

The developmental trajectories of Factor 1 and Factor 2 on Factor 3 do not differentiate the two genera. Neither slopes nor intercepts of the lines show any significant differences.

The major differences in the development of the jaw in rhinatrematids and dermophids can be summarized as follows. The delayed ossification of the cheek in Epicrionops appears to permit the expansion of the adductor chamber. It is not clear whether early onset of development of the adductor chamber alone accounts for the striking difference in the adductor mass, or whether the adductor mass also grows faster in Epicrionops than in Dermophis. The retroarticular process

developes significantly earlier in Dermophis but the relative growth rates of the anterior and posterior parts of the lower jaw are the same. The lower jaw grows faster than the upper jaw in Epicironops, but the converse is true of Dermophis. In neither does the relative amount of extension of the skull beyond the upper jaw change in ontogeny, but it is significantly different between the two genera.

Jaw Mechanics and Jaw Function

Nussbaum (1983) explored the comparative anatomy of the interhyoideus musculature, showing that it augments the M. adductor mandibulae mass by pulling down on the retroarticular process in the manner of a third order lever. Bemis et al (1983) demonstrated its activity during jaw adduction. It is less apparent to what extent this musculature assists or replaces the adductor, or what the selective pressures for its evolution may have been. In order to understand caecilian jaw musculature as such a radical departure from the standard tetrapod type, it is first necessary to understand something of the standard tetrapod condition. Table 23 shows log transformed measurements for area of the adductor chamber and the length of the skull anterior to the jaw joint for a variety of stegocephalian amphibians. Amphibians with closed skull roofs were chosen for a number of reasons. This is the presumed primitive condition for caecilians. All of the M. adductor mass of stegocephalian amphibians is contained within the adductor chamber and so its area can be estimated

accurately by measuring the adductor chamber. None of these members is presumed to have masticated food, or to have been durophagus feeders, so jaw function between them is probably similar. They are all kinetic inertial feeders, presumably the condition in caecilians. Amniotes were not used because of the extensive pterygoideus musculature found largely beneath the adductor chamber.

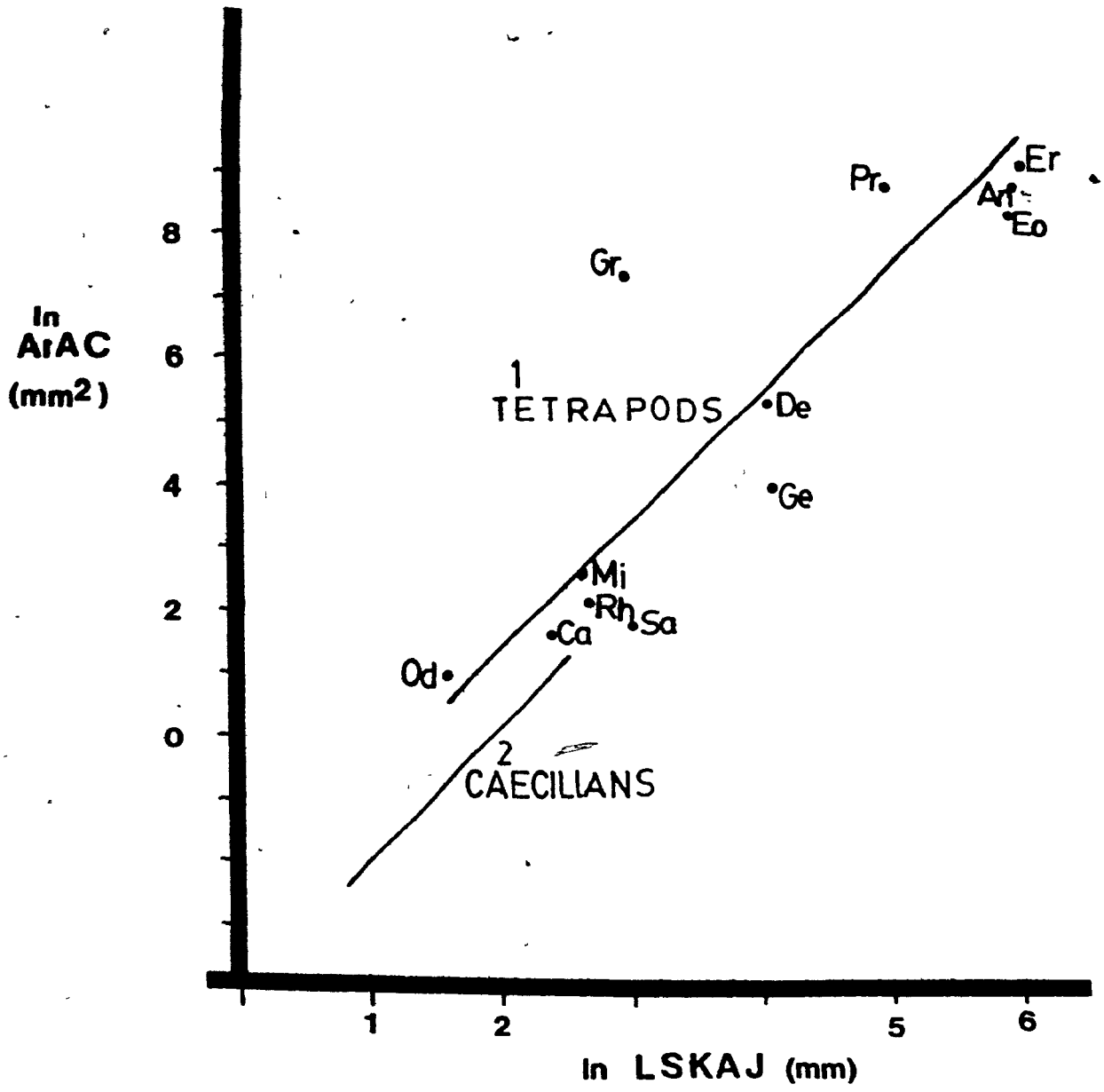
The relationship of ArAC versus LSKAJ has a number of implications. The contractile strength of a muscle has a 1:1 correlation with its cross sectional area (Gans and Bock 1965). The slope of the relationship shown is extremely close to 2.0 ($Z=0.39$, $P>>.05$). Assuming similar relative jaw muscle capacity of these individuals, this suggests that in order to maintain function, the power of the jaw muscles must increase at a rate equivalent to the increase in skull length, squared. Furthermore, if the length of the skull anterior to the palate is a good measure of the size of the skull, as it is in these animals, then the adductor chamber area occupies a roughly equal proportion of the area of the skull in palatal, irrespective of overall skull size (Fig 29).

If the function of the caecilian jaw apparatus is fundamentally different from that of other tetrapods, then one would predict a different relationship between adult caecilians than that outlined above. The reduced major axis of ArAC vs LSKAJ is plotted for adult caecilians and for closed-skulled amphibians in figure 29. Measurements for the plots are in the same units and so their relationships can be compared. The allometric equations are compared in Table 21-1.

Like the slope of ArAC versus LSKAJ for all amphibians, the slope for this relationship in adult caecilians does not deviate significantly from 2.0 ($Z=1.12$, $P > .05$). The slopes are not significantly different between caecilians and other amphibians ($Z=.19$ $P > .05$), but the intercepts are ($Z=2.49$, $P < .05$). In the development of Epicrionops, the slope of ArAC versus LSKAJ is not significantly different from 2.0. However, in the development of Dermophis the slope of ArAC versus LSKAJ is significant ($Z=4.43$ $P < .05$) (Table I-3), suggesting that the M. adductor mass diminishes in relative strength during the growth of Dermophis , but not Epicrionops.

Differences in the Y-intercept of the caecilian adult and general amphibian curves for ArAC versus LSKAJ give some idea of the relative strength of the adductor mass. White and Gould (1965) argue that, where slope is equivalent, differences in intercept are scaling values. In geometrically similar systems, the scaling value is represented as $(b_2/b_1)^{(1/1-a)}$, where b_1 and b_2 are the respective Y-intercept values (the antilog of the value given in Table 21 -1), and a is the common slope. It is a measure of the ratio of values of X between organisms for a given value of Y. Taking the theoretical value 2.0 as the common slope, the 'scaling ratio' is 3.14. This means that for the area of the adductor chamber to be equivalent between a caecilian and a stegocephalian amphibian, the caecilian skull (anterior to the jaw joint) would have to be approximately three times as long. No pair of observations exactly meets this condition, but the scaling

Figure 29. Graph of Adductor Chamber area versus length of skull for caecilian adults and closed-skulled amphibians see table 23. An=*Anthracosaurus* Ca=*Cardiocephalus* De=*Dendrerpeton* Eo=*Eogyrinus* Er=*Eryops* Ge=*Gephyrostegas* Gr=*Greererpeton* Mi=*Microbrachis* Rh=*Rhynchonkos* Od=*Odonterpeton*


ln
ArAC
(mm2)
8
6
4
2
0
1
2
5
6
ln LSKAJ (mm)
1
TETRAPODS
2
CAECILIANS
Er
Pr.
Ar
Eo
Gr.
De
Ge
Mi
Rh
Sa
Ca
Od

ratio of 3.14 appears roughly to fit the observations. The largest LSKAJ for caecilians is 12.606 mm (Typhlonectes compressicauda); the smallest for amphibians is 5.09 mm (Odonterpeton)- a ratio of 2.47. The adductor chamber sizes are roughly equal (Typhlonectes=2.58 mm^2, Odonterpeton=2.50). That of Typhlonectes is only slightly larger than would be expected.

Another, perhaps more important scaling ratio can be deduced. If the ratio of skull length of stegocephalian amphibians and caecilians of equal adductor chamber size is 1:3.14, and the adductor chamber area varies as the second power of the skull length, then ratio of the area of the adductor chamber between tetrapods and caecilians of comparable size is roughly $1:(1/3.14)^{1/2}$, or 1:0.56. (Actual values found are 1:0.59 and 1:0.54 for Cardiocephalus cf. Dermophis, but 1:0.17 for Odonterpeton cf Schistometopum). Assuming comparable power of the jaw mass relative to size, this implies that between 40% and 50% of the total power of the jaw adductor musculature in caecilians is assumed by the M. interhyoideus complex.

The adductor chamber in adult caecilians has the area:skull length allometric coefficient seen in adult closed-skull amphibians but for skulls of equal length, the caecilian adductor chamber is smaller by a factor of roughly one half. Therefore, the gular musculature augments the adductor musculature to equal degrees in adult caecilians, irrespective of size. One can predict from this that, with the area of insertion of the interhyoideus being linear, the

retroarticular process length would display isometry with LSKAJ and with LUJ among adults. The slope of the first line is 1.02, not significantly different from the predicted isometry (Z=.304, P"" .05). Likewise slope of LRAPL versus LUJ for adult caecilians coincides with the predicted isometry (slope=1.10 Z=1.13 P".05)

The developmental allometric relationship for these elements (LSKAJ versus LRAPL) is not the same as that between adults. The curve for Epicrionops has a slope of .709 and an intercept at 1.354. That of Dermophis has a slope of .664 and an intercept at 1.158. The slopes are not statistically different (Z=.492). This indicates that the retroarticular process changes more quickly relative to overall changes in skull size in ontogeny than it does between adults. The ratio of LSKAJ vs LRAPL of a small adult is not equivalent to that of an earlier ontogenetic stage of a large adult.

The intercepts of LSKAJ vs LRAPL in ontogeny are significantly different between Epicrionops and Dermophis. The scaling ratio is 1.63. The length of the retroarticular process for comparably sized skull is predicted to be 1.63 times longer for dermophids than rhinatrematids. This is exactly the size ratio observed from adult specimens. One can infer from this that the gular musculature augments the adductor musculature to a much lesser degree in rhinatrematids than adult caecilians in general.

Although the adductor musculature was not investigated directly, two predictions can be made concerning the its

structure and function in caecilians. 1) The M. interhyoideus of most adult caecilians will contribute 40% - 50% of the adduction power of the combined jaw musculature. 2) The development of the gular musculature will proceed at similar rates between genera. Differences in mass of this muscle will be the result of varying time of developmental onset.

Miniaturization

The description of the allometric relationship between jaw and skull elements both in ontogeny and between adults allows an understanding the miniaturization of the caecilian skull. A comparison of the trends found in miniaturization in other tetrapods with those of caecilians is also informative.

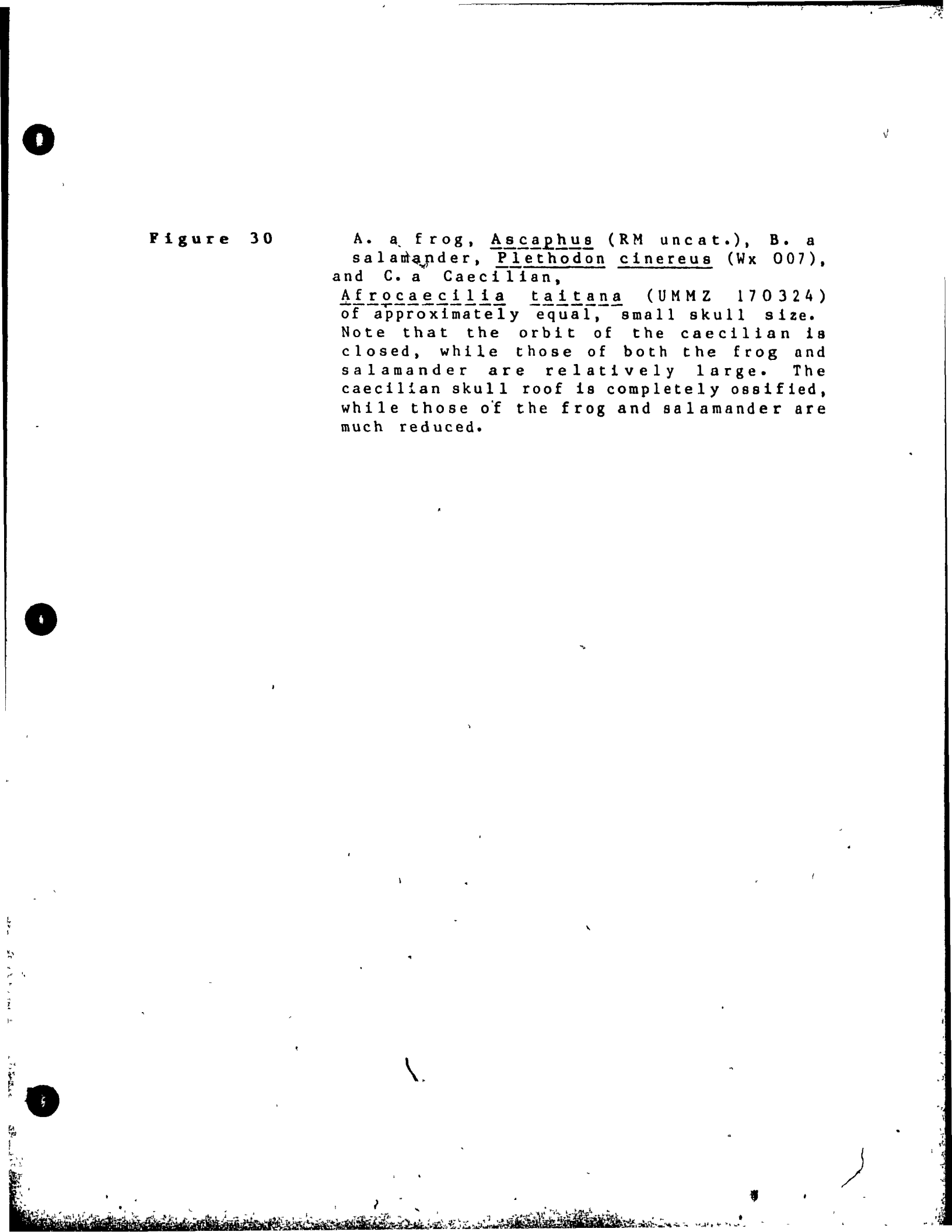
Gans (1974) points out that the maintenance of adequate sensory function is a limiting factor in the miniaturization of a tetrapod skull. The size of a functional eye is limited by the number of retinal cells required for adequate image formation (Walls 1942; Thompson 1942). Eye size is known to exhibit negative allometry with overall skull size in most tetrapods. The eyes of small animals are relatively larger than those of large animals with comparable visual acuity. Likewise, the function of the inner ear is size-dependent (Bernaczek and Carroll 1977). The minimum size of the otic capsule is determined by the viscosity of the endolymphatic fluid in relationship to the diameter of the semicircular canals (Jones and Spells 1973). The size of the otic capsule, and the braincase are both negatively allometric

relative to skull length in tetrapods (Hanken 1983).

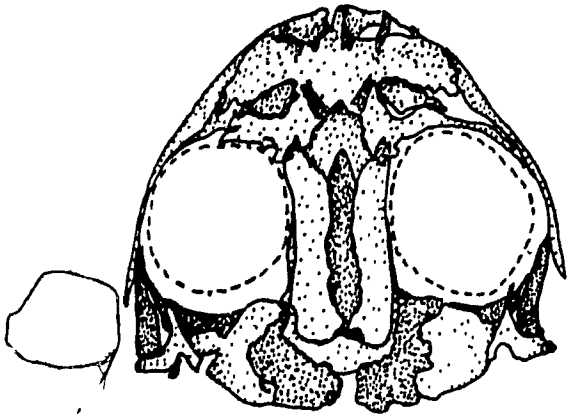
Given the strong negative allometry of the brain, the eye and the otic capsules relative to overall length, there is an absolute minimum size for a functional tetrapod skull. Hanken (1984) suggests that the theoretical minimum skull size is approached in the small plethodontid salamander Thorius. As the sensory capsules become relatively larger, there is less space available for jaw musculature in a closed tetrapod skull (Rieppel 1984). In compensation, the dermal covering of the skull of many small tetrapods is much reduced allowing the expansion of the jaw musculature beyond the confines of the skull. Hanken (1983) outlines the effects that relative enlargement of the sensory capsules exerts on the skull structure of Thorius. The size of the orbits produce appreciable constriction of the anterior portion of the braincase. The relative size of the otic capsule induces a reorientation of the suspensorium. From these observations he presents a model, or a null hypothesis, for the miniaturization of the vertebrate skull in general stating that small tetrapod skulls are characterized by a loss of ossification, structural variation and, morphological novelty. The modifications of the skull are brought about primarily through paedomorphosis (Hanken 1984).

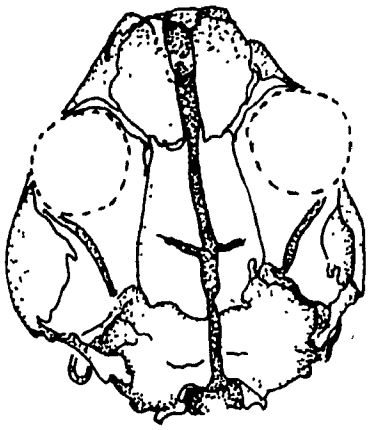
Hanken's model predicts quite accurately the changes observed in small frogs (Trueb and Alberch 1985) and salamanders as well as some fishes (Hanken 1984). Based on my data, caecilians do not appear to conform (figs.30 and 31). There is little evidence of paedomorphosis in the skull of

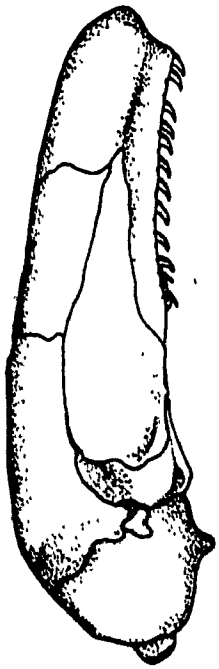
Figure 30

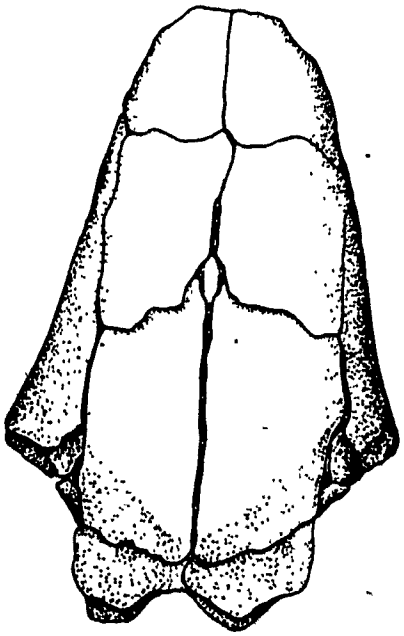


A. a frog, Ascaphus (RM uncat.), B. a salamander, Plethodon cinereus (Wx 007), and C. a Caecilian, Afrocaecilia taitana (UMMZ 170324) of approximately equal, small skull size. Note that the orbit of the caecilian is closed, while those of both the frog and salamander are relatively large. The caecilian skull roof is completely ossified, while those of the frog and salamander are much reduced.









small adults. Small adult caecilians have well ossified skull roofs (see Fig.30 Afrocaecilia). One possible example is the persistence of a large dorsal exposure of the mesethmoid in Idiocranium (Wake 1986). The morphometric relationships between the jaw apparatus do not evidence the early truncation of development. If this were so, the line of allometry for the jaw apparatus between adults would be coincident with that of the ontogeny of large individuals such as Dermophis. There appears to be little variation in adults from the allometric relationships of the jaw and skull length.

The caecilian solution has emphasized the retention of the highly ossified skull roof. This is probably a necessary feature for diggers (Gans 1974 :Ch.4). The M. adductor manibulae muscle of caecilians is roughly half of the size that would be predicted for a tetrapod of similar skull size. Most caecilians have functional eyes, but there is a definite trend toward the de-emphasis of vision (Wake 1985). Vision is not so crucial a faculty for fossorial animals. In many caecilians the orbit is completely occluded by dermal bone. The eye is diminutive making accurate measurements difficult but the change in shape of the braincase induced by eye size in other small tetrapods is not seen in caecilians. Braincase of small and large members of the same family show the same braincase shape. The major structure occupying the anterior portion of the skull is the nasal capsule, which changes isometrically with skull length in other tetrapods. It is closely associated with the tentacle in caecilians (Badenhorst

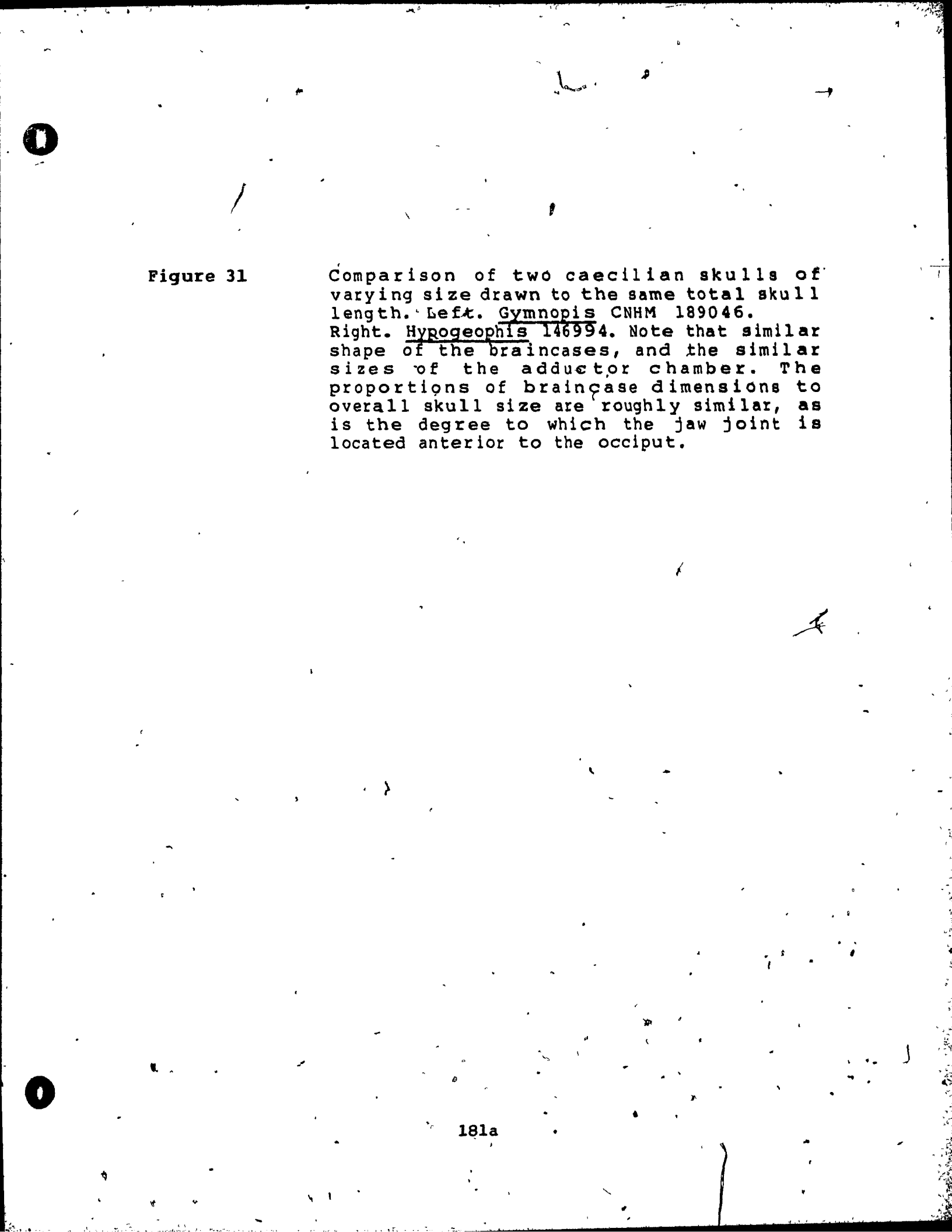
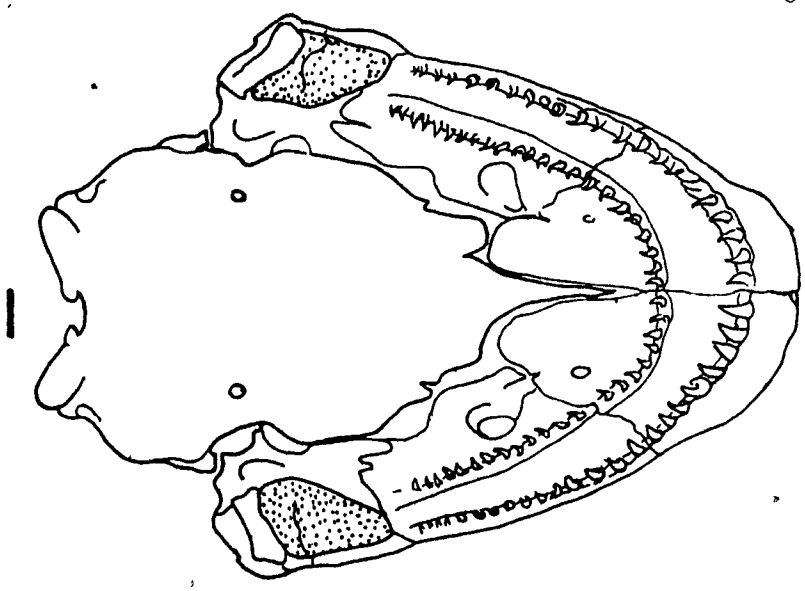
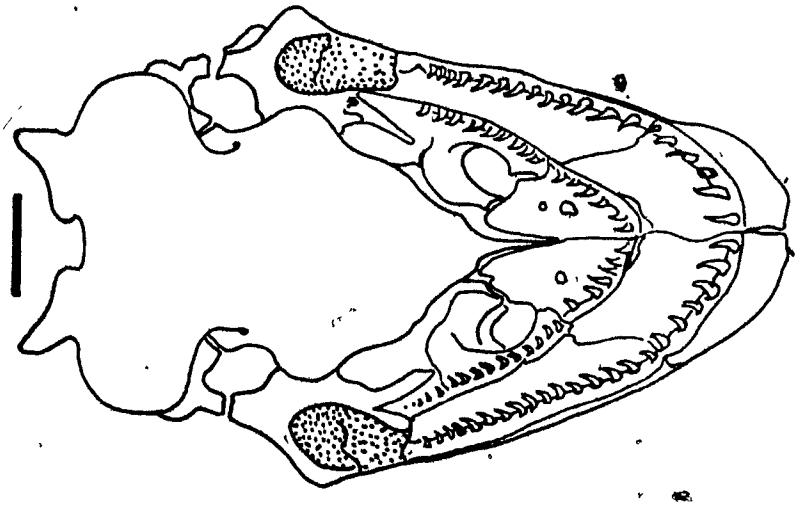


Figure 31 Comparison of two caecilian skulls of varying size drawn to the same total skull length. Left. Gymnopis CNHM 189046. Right. Hypogeophis 146994. Note that similar shape of the braincases, and the similar sizes of the adductor chamber. The proportions of braincase dimensions to overall skull size are roughly similar, as is the degree to which the jaw joint is located anterior to the occiput.





1978; Wake 1985).

The negative allometric relationship of the braincase and otic capsule with skull length seen in most tetrapods (Hanken 1984) is not evident in caecilians. All curves for the dimensions of the braincase and otic capsule versus total skull length are isometric for adults (Table22). In small tetrapods, the jaw joint is usually located anterior to the otic capsule. The relative distance of the jaw anterior to the occitpital condyle increases with decreasing overall size. While the jaw joint in caecilians is anterior to the jaw, the distance from the occipital condyle to the jaw joint (OCTJJ) versus the length of the skull anterior to the jaw joint (LSKAJ) is isometric for adults (slope=0.91 Z=1.06 P".05) and in development of both genera analyzed here (Table 22).

A small and solid skull is essential for a burrowing animal. It has been attained in caecilians by the removal of approximately half of the required jaw adductor mass from the skull, the severe diminution of the eye, and the location of the jaw joint anterior to the largest portion of the braincase. This unique solution to the antagonistic requirements of having both a small and a solid skull has permitted caecilians to circumvent the usual changes that small size imposes on skull structure.

CONCLUSIONS

The elements of the jaw show coupling of their rates and directions of change, both developmentally and phylogenetically. This would be expected of a functional suite of features.

The rhinatrematid condition of the skull is quite atypical of caecilians in general in its adult morphology, and probably in its development. In the growth and proportions of the the jaw and jaw musculature rhinatrematids more closely approximate the standard tetrapod condition than do other caecilians. While other authors have taken this to be evidence of the primitiveness of rhinatrematids, it appears from the ingroup cladogram to be a secondary reversion, primarily associated with a trend away from fossoriality. Phylogenetically, this family seems to have separated early from the main caecilian stock.

Miniaturization of the caecilian skull appears not to have been attained in the manner usual for small-skulled tetrapods. There is little evidence of paedomorphosis, either in the proportions of the jaw structure or in the degree of ossification of the dermal skull. Three factors seem to contribute to the unique caecilian solution to small skull size. These are the location of roughly half of the required jaw adduction musculature behind the head, the location of the jaw joint and suspensorium fully anterior to

the otic capsules, and the severe diminution of the eyes. These specializations probably facilitate miniaturization of the caecilian skull, while concurrently maintaining the strength of the jaw musculature and the solidity of the skull roof.

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APPENDIX 1

SPECIMENS OBSERVED

A. Gymnophionans.

I. Family Caeciliidae

#	Genus	Species	Condition
UMMZ 170324	Afrocaecilia	taitana	C & S
UMMZ 182013	"	"	"
UMMZ 171947	"	"	"
* 2003	"	"	"
MCZ 20003	Boulengerula	titanus	"
MCZ 25002	"	boulengeri	"
KU 119394	Caecilia	tentaculata	D
KU 104438	"	"	"
KU 94377	"	nigricans	"
* 898	"	sp.	"
* uncat.	"	occidentalis	"
MCZ 14829	"	ochrecephala	C & S
* uncat. (14 specimens)	"	occidentalis	"
539	"	sp.	C & S
UMMZ 171947	Dermophis	mexicanus	D
UF 42887	"	"	"
* uncat.	"	"	"
MHW 890	"	"	"
MHW 892	"	"	"
MHW 893	"	"	"
MHW 894	"	"	"
MHW 895	"	"	"
MHW 896	"	"	"
MHW 899	"	"	"
I 62746	"	"	C & S
D 1035	"	"	"
* 959c	"	"	"
* 9302	"	"	"
* 9581	"	"	"
* 939	"	"	"
* 10079	"	"	"
* 1348	"	sp.	C & S
D 1037	"	"	"
* 971c	"	"	"
D 1062	"	"	"
D 1078	"	"	"
* 958g	"	"	"
* 730a	"	"	"
* 789b	"	"	"
* 930a	"	"	"
* 772c	"	"	"
* 730b	"	"	"
* 869a	"	"	"
* 789a	"	"	"

SPECIMENS OBSERVED

A. Gymnophionans.

I. Family Caeciliidae

	#	Genus	Species	Condition
*	923b	Dermophis	mexicanus	C & S
*	772d	"	"	"
*	772c	"	"	"
*	772b	"	"	"
*	813	"	"	"
*	790	"	"	"
*	923a	"	"	"
*	869a	"	"	"
*	4132	"	"	"
*	792a	"	"	"
*	783a	"	"	"
*	869b	"	"	"
*	783b	"	"	"
*	779a	"	"	"
*	779a	"	"	"
*	897	"	"	"
*	891	"	"	"
*	1380	"	"	"
*	uncat	"	"	"
UMMZ	172068	Gegeneophis	ramaswamii	C & S
UMMZ	182014	"	"	"
BM	1131	Geotrypetes	grandisnoae	C & S
*	514	"	seraphini	"
*	516	"	"	"
*	uncat. (3 specimens)	"	"	"
MCZ	22408	"	"	"
*	530	"	"	"
*	515	"	"	"
*	501	"	"	"
*	502	"	"	"
*	539	"	"	"
*	1304	"	"	D
UMMZ	145047	Grandisonia	alternans	C & S
UMMZ	182012	"	"	"
CNHM	189046	Gymnopis	Multiplicata	C & S
MCZ	8	"	"	W
MCZ	?	"	"	"
*	uncat. (2 specimens)	"	"	C & S
CNHM	166830	Herpele	Squalostoma	C & S
UMMZ	169935	Hypogeophis	rostratus	C & S
UMMZ	146994	"	"	"
UMMZ	174032	"	"	"
UMMZ	174037	"	"	"

I. Family Caeciliidae

#	Genus	Species	Condition
UMMZ 174040	Hypogeophis	rostratus	C & S
* 1946	Idiocranium	russeli	C & S
UMMZ uncat.	Indotyphlus	battersbyi	W
UIMNH 96671	Microcaecilia	albiceps	EtOH
UIMNH 57303	"	"	"
CNHM 75753	Schistometopum	thomensis	C & S
MCZ 20912	"	gregorii	"
ZNK R0239	Siphonops	sp.	D
ZNK R0276	"	annulatus	D

II. Family Ichthyophiidae

#	Genus	Species	Condition
CNHM 189165	Caudacaecilia	asplenia	D
CNHM 189167	"	larutensis	D
CNHM 189245	"	nigroflava	D
UMMZ 181759	"	weberii	C & S
UMMZ 154884	Ichthyophis	kohtaoensis	D
UMMZ 154071	"	"	"
CNHM 189242	"	"	"
CNHM 189229	"	beddomei	"
* uncat.	"	sp.	"
* uncat	"	"	C & S
UCMVZ 179663	Uraeotyphlus	narayani	C & S
UCMVZ 179716	"	"	C & S chck

III. Family Rhinatrematidae

#	Genus	Species	Condition
LSUMZ 27266	Epicrionops	bicolor	C & S
LSUMZ 27245	"	"	"
LSUMZ 27291	"	"	"
LSUMZ 27265	"	"	"
LSUMZ 27272	"	"	"
LSUMZ 27289	"	"	"
LSUMZ 27267	"	"	"
LSUMZ 27283	"	"	"
LSUMZ 27243	"	"	"
LSUMZ 27317	"	petersi	"
LSUMZ 27306	"	"	"
LSUMZ 27300	"	"	"
LSUMZ uncat. (2 specimens)	"	"	"

IV. Family Scolecomorphidae

#	Genus	Species	Condition
* 12226	Scolecomorphus	uluguruensis	C & S
MCZ 12216	"	"	C & S
MCZ 27103	"	kirkii	"
MCZ 5	"	"	W
MCZ 25010	"	vittatus	C & S

V. Family Typhlonectidae

#	Genus	Species	Condition
MCZ	Chthonerpeton	indistinctum	W
MCZ	"	viviparum	W
UMMZ 154071	Typhlonectes	compressicauda	D
UMMZ 82854 (2 more)	"	"	W
UCMVZ 179716	"	natans	C & S
* 146	"	natans	C & S
UMMZ 150625	"	"	D
MCZ 89471	"	obessus	C & S
MCZ 24524	"	sp.	"
* uncat. (8 specimens)	"	"	"

10 undientified specimens.

B. Fossil groups

I. Alstopods

#	Genus	Species	description
AMNH 6912	Ophiderpeton	amphiumium	lower jaw cast
AMNH 6908	"	"	skull cast
AMNH 6857	"	"	skull cast
AMNH 6908	"	"	skull cast
BM(NH) R2673	"	"	skull cast
BM(NH) R26579	"	"	skull cast
AMNH 6966	Phlegethontia	linearis	whole specim. cast
USNM 4484	"	"	"
UCMP 62580	"	cf. linearis	braincase

II. Lysorophoids

#	Genus	Species	description
BM(NH) R2544	Cocytinus	gyrinoides	cast, skull and vertebral column
AMNH 4698	"Lysorophus"	sp.	skull
AMNH 4699	"	"	skull
AMNH 6172	"	"	"
AMNH 7558	"	"	"
AMNH 4884	"	"	"
AMNH 4701	"	"	"
AMNH 4696	"	"	"
AMNH 4762a	"	"	"
AMNH 4700	"	"	"

III. Nectridéans

#	Genus	Species	description
RM 14.514	Ptyonius	mummifer	cast, skull and partial postcranium
RM 14.510a	"	"	cast, entire skeleton
HM M339	Urocordylus	scalaris	cast, skull and postcranium
RM. 14.502	Partial postcranium unidentified		

IV. Microsaurs

uncatalogued Euryodus sp. dentary and poscranial elements
uncatalogued partial maxilla. unidentified.

V. Dissorophids

#	Genus	Species	description
AMNH 6841	Amphibamus	lyelli	cast, entire specimen

VI. Primitive tetrapods

#	Genus	Species	description
	Ichthyostega		cast skull, palatal view
CMNH 11090	Greererpeton	burkemorani	skull.

Abbreviations:

AMNH	American Museum of Natural History
BM(NH)	British Museum (Natural History)
CMNH	Cleveland Museum of Natural History
CNMH	Chicago Natural History Museum.
KU	Kansas University
MCZ	Museum of Comparitive Zoology Harvard
LSUMZ	Los Angeles University, Museum of Zoology
MHW	Collection of Dr. Marvalee Wake Berekeley
RM	Redpath Museum McGill University
UCMP	University of California Museum of Paleontology
UCMVZ	University of California, Museum of Vertebrate Zoology
UF	University of Florida
UIMNH	University of Illinois Museum of Natural History

APPENDIX II

Untransformed measurements for caecilians. Values are (in order) LSKRF, WSKRF, WSKT, ARAPM, LOB, WOB, DTR, TOA, TIA, ArAC, DSKJJ, LUJ, LSKAJ, OCTJJ, OTT, LPO, LLJPM, LRAPU, LRAPL, ARAPD. ArAC measured in mm^2. ARAPD and ARAPM in degrees. All other measurements are in mm.

1	Caecilia	occid	7.936	6.826	3.205	132.410	5.971	4.143	1.338	8	.	1.180	2.375	5.682	6.762	2.506	.	.	4.673	2.408	2.446	127.298
2	Geotrypet	serap	5.679	4.707	2.379	.	5.143	3.247	0.876	.	.	0.823	1.461	3.150	4.357	1.923	.	.	2.926	.	.	.
3	Typhlonec	obes	5.666	6.985	3.935	135.189	4.652	4.283	0.994	.	.	2.006	2.977	3.617	4.181	2.703	.	.	3.579	1.845	2.074	143.138
4	Typhlonec	natan	9.716	9.414	5.136	154.223	.	.	.	.	.	1.166	.	.	8.575	3.928	.	3.899	.	2.879	.	.
5	Gymnopis	multi	4.635	4.116	2.291	165.780	.	.	.	.	.	0.383	2.635	2.539	3.129	2.111	1.196	.	6.847	1.024		152.141
6	Geotrypet	grand	4.473	.	1.369	.	3.457	2.247	0.655	.	.	0.249	3.238	1.552	3.522	1.117	.	.	2.411	0.978	1.015	154.693
7	Afrocaeci	taita	5.687	3.762	2.438	154.681	4.003	2.208	0.909	.	.	0.441	2.053	.	3.474	1.419	.	.	3.487	1.480	.	.
8	Geotrypet	serap	5.384	3.818	2.034	158.953	4.199	3.002	0.684	.	.	0.301	1.411	4.519	5.086	.	.	.	3.645	1.242	1.765	136.391
9	Dermophis	mexic	7.117	5.704	3.498	148.639	5.827	4.120	.	.	.	0.537	2.993	3.130	4.562	1.430	2.813	.	2.782	3.188	3.489	142.435
11	Geotrypet	serap	6.978	4.773	2.512	167.990	5.741	3.796	0.930	.	.	0.576	2.174	4.366	5.302	1.682	.	3.153	3.508	1.551	1.682	150.406
12	Geotrypet	serap	7.725	6.294	2.679	156.416	5.339	4.023	1.173	.	.	0.598	2.967	4.964	5.990	.	.	3.515	4.002	1.698	2.540	121.699
13	Caecilia	ochre	6.264	5.688	3.259	146.486	.	3.105	.	.	.	.	3.231	4.239	5.731	1.373	.	.	3.764	2.491	2.420	125.539
14	Boulenger	boule	4.973	3.475	2.197	170.577	3.083	2.620	0.746	.	.	0.353	1.951	3.625	4.044	1.293	.	.	3.421	1.172	1.278	156.108
15	Boulenger	taita	5.603	3.598	1.978	141.785	3.473	.	0.752	.	.	0.167	1.812	3.992	4.380	2.065	.	.	3.473	1.496	1.814	132.705
16	Geotrypet	serap	8.846	7.008	4.276	154.597	6.055	9.878	.	.	.	0.948	2.281	4.358	5.642	3.576	.	3.160	2.946	2.157	2.371	149.160
17	Typhlonec	sp.	8.229	7.246	4.552	151.087	4.819	5.399	.	.	.	0.712	1.908	4.566	4.500	2.066	1.717	2.434	3.659	1.478	1.822	148.943
18	Unident	sp.	4.663	3.121	1.940	.	3.201	2.561	1.118	.	.	0.190	1.255	3.416	3.664	.	.	.	2.747	.	.	.
19	Geotrypet	serap	4.985	.	2.279	156.108	3.771	2.698	0.767	.	.	0.213	1.826	3.535	4.539	1.592	0.691	2.411	2.685	1.366	1.498	139.503
20	Unident	sp.	4.288	3.028	1.959	153.343	3.096	2.256	0.681	.	.	0.157	1.791	1.888	2.442	1.390	.	.	1.733	0.901	1.197	128.413
21	Geotrypet	serap	5.367	3.790	2.351	169.166	4.021	2.937	0.786	.	.	0.252	1.142	3.684	4.250	1.636	.	2.931	2.719	1.505	1.431	143.605
22	Dermophis	mexic	7.197	5.395	2.939	152.485	5.615	4.268	.	.	.	0.566	1.705	4.505	5.773	0.886	1.311	3.422	4.405	2.484	2.753	.
24	Typhlonec	sp.	9.238	7.606	4.749	147.030	6.136	4.912	.	.	.	0.714	.	5.848	7.543	2.786	.	.	.	.	.	.
25	Geotrypet	sera	8.459	6.858	2.744	145.771	6.707	4.094	.	.	.	1.172	.	6.261	6.711	2.295	.	.	5.555	.	.	.
26	Epicriono	peter	9.023	6.981	3.533	172.731	8.437	4.768	.	.	.	1.682	4.026	6.632	6.761	3.865	.	2.240	6.005	2.389	2.530	166.270
27	Epicriono	bicol	9.699	7.793	4.173	.	8.906	4.846	.	.	.	1.671	2.403	7.601	8.058	3.074	.	3.248	7.757	2.751	3.205	171.334
28	Epicriono	peter	8.595	7.763	3.418	140.586	7.775	5.131	.	.	.	1.863	2.812	7.671	8.303	2.523	.	.	7.630	2.382	2.349	169.709
29	Epicriono	bicol	4.458	3.587	2.170	178.625	3.756	2.599	0.767	.	.	0.295	1.839	3.832	4.547	1.352	.	.	3.499	1.079	0.843	184.697
30	Epicriono	bicol	9.942	8.797	4.140	163.061	9.103	5.854	.	.	.	3.080	3.616	7.986	8.426	2.764	.	3.150	7.130	2.979	3.270	155.598
31	Epicriono	bicol	4.219	3.024	1.955	173.403	3.357	2.417	.	.	.	0.264	1.728	3.054	3.065	1.841	.	.	2.421	0.823	0.789	177.986

32	Epicriono	peter	5.095	4.044	2.554	166.202	4.858	3.423	.	. .	0.411	1.777	4.422	4.840	1.982	.	2.826	4.321	1.414	1.275	186.415
33	Epicriono	bicol	7.267	6.353	3.240	171.295	7.183	3.700	.	. .	0.939	3.510	5.901	6.372	2.625	.	2.949	.	1.780	1.897	179.592
34	Epicriono	bicol	5.363	4.867	2.640	164.288	4.547	3.302	.	. .	0.726	.	.	.	.	.	.	.	.	.	.
35	Epicriono	bicol	7.343	6.847	3.071	174.537	7.623	5.249	.	. .	1.932	3.527	6.300	7.163	3.227	.	2.681	5.613	1.991	1.766	168.104
36	Epicriono	bicol	7.370	6.777	3.447	176.425	6.985	4.782	.	.	1.662	.	.	.	.	.	.	.	.	.	174.271
37	Epicriono	bicol	6.465	5.375	2.887	162.175	5.352	3.453	.	. .	.	2.337	4.985	5.766	.	.	2.771	4.051	1.594	1.451	176.700
38	Epicriono	peter	3.385	2.529	1.083	.	.	.	.	. .	0.496	.	.	.	.	.	.	.	.	.	.
39	Epicriono	peter	4.108	3.916	2.684	176.113	3.737	3.179	0.781	. .	0.412	1.970	2.788	3.272	1.989	.	.	2.561	.	.	.
40	Scolecono	ulugu	5.242	3.947	2.109	127.526	3.802	2.231	0.924	. .	0.292	2.379	3.709	4.305	0.995	.	2.032	2.490	1.317	1.766	120.750
41	Schistone	thone	6.803	5.175	2.589	142.341	5.116	3.179	.	. .	0.432	2.910	4.389	5.087	2.212	.	.	4.203	2.766	3.134	147.745
42	Schistone	grego	5.595	4.883	2.057	130.413	.	.	.	. .	0.359	.	.	.	.	.	.	.	.	.	.
43	Ichthyoph	sp.	.	.	.	.	.	.	.	. .	.	2.465	4.576	5.401	2.652	.	2.981	4.944	2.364	2.870	119.058
44	Geotrypet	serap	7.529	6.234	2.789	159.047	6.250	3.773	.	. .	1.182	2.986	5.653	6.261	2.603	2.360	3.452	5.350	3.228	3.743	127.204
46	Unident	sp.	7.974	7.529	3.720	153.617	5.686	3.916	.	. .	0.962	3.660	5.789	6.443	.	.	.	5.141	2.961	3.652	142.803
47	Caecilia	occid	6.647	4.682	2.763	129.169	4.816	3.195	1.199	. .	0.463	2.677	4.366	5.266	1.312	.	2.673	2.997	1.361	1.712	139.372
48	Geotrypet	serap	7.412	5.839	2.735	154.553	6.032	3.979	.	. .	0.670	2.459	5.812	6.175	1.678	.	2.964	5.290	.	.	.
49	Unident	sp.	6.233	6.034	3.423	123.190	4.315	4.317	.	. .	0.455	2.663	5.196	7.131	.	.	.	5.161	2.344	2.846	134.051
50	Dermophis	mexic	8.368	7.765	4.130	162.996	7.423	4.830	.	. .	1.510	2.682	6.671	7.364	2.136	1.891	4.680	6.298	2.521	3.192	140.188
51	Typhlone	sp.	9.108	7.972	4.482	140.653	5.724	5.385	1.168	. .	1.233	4.103	6.923	8.546	3.052	3.170	4.217	6.347	2.096	3.139	139.406
52	Uraeotyph	naray	5.463	4.656	2.816	137.195	3.074	3.096	.	. .	0.723	1.676	4.029	4.639	.	.	.	.	1.927	1.864	144.950
53	Typhlone	natan	6.950	5.625	2.522	145.567	5.029	3.521	.	. .	1.316	4.184	2.857	4.332	.	0.985	2.014	3.580	1.890	2.040	129.729
56	Caecilia	occid	7.786	4.847	2.870	143.523	5.218	3.354	.	. .	0.575	2.238	4.887	5.646	2.686	.	3.229	3.791	1.780	2.378	138.705
55	Caecilia	occid	7.910	5.292	3.061	144.600	5.761	3.527	.	. .	0.624	2.132	4.332	5.639	1.755	.	3.503	3.935	2.556	2.637	136.122
57	Caecilia	occid	4.964	3.254	2.090	161.889	3.464	2.370	.	. .	0.286	1.587	3.281	3.714	1.635	.	2.190	2.600	1.382	1.353	142.333
58	Caecilia	occid	4.396	3.032	2.099	137.281	3.709	2.250	0.722	. .	0.212	1.508	3.160	3.636	1.397	.	.	2.771	1.423	1.652	136.229
59	Caecilia	occid	5.866	.	2.118	142.965	4.139	2.729	1.017	. .	0.281	.	.	.	.	.	.	.	.	.	.
60	Caecilia	occid	6.035	4.019	2.636	148.754	4.225	2.727	.	. .	0.329	2.045	3.991	4.482	2.303	.	2.159	2.881	1.565	1.873	127.416
61	Caecilia	occid	5.579	3.802	2.454	119.981	4.473	2.657	.	. .	0.602	2.134	3.813	4.598	1.866	.	2.191	2.783	1.325	1.756	141.232
62	Caecilia	occid	7.222	4.844	2.484	160.220	4.590	3.175	.	. .	.	.	.	.	.	.	.	.	.	.	.

63	Caecilia	occid	6.002	3.897	2.437	.	4.601	2.721	.	.	.	.	1.908	3.750	4.297	.	.	.	3.140	1.305	1.459	126.522
64	Unident	sp.	7.557	5.450	3.028	144.275	.	.	.	.	.	0.387	2.321	4.752	5.801	.	2.428	3.453	4.748	2.872	2.646	147.300
65	Geotryp	mexap	4.110	2.955	1.941	177.558	3.321	2.357	.	.	.	0.264	1.546	3.039	3.368	1.359	.	1.916	2.834	1.211	1.411	140.139
66	Caecilia	occid	6.941	4.801	2.885	143.606	5.326	3.013	.	.	.	0.313	2.562	4.893	6.238	2.246	.	3.455	4.144	1.846	2.243	139.307
67	Herpele	squal	7.536	6.007	3.534	155.982	5.378	3.904	.	.	.	0.478	.	.	.	.	.	.	.	.	.	.
68	Scolecono	ulugu	5.096	3.966	2.124	.	3.519	2.321	.	.	.	0.275	2.125	3.430	4.109	2.096	.	.	2.704	1.098	1.731	138.237
69	Scolecono	kirki	6.692	4.491	2.176	.	4.983	2.324	.	.	.	.	2.331	4.252	5.592	1.947	.	.	3.010	1.601	2.098	132.738
70	Scolecono	vitta	8.150	5.845	4.102	.	.	.	.	.	.	0.980	3.513	5.949	6.838	.	1.337	3.813	5.013	2.354	3.175	136.812
72	Unident	sp.	4.255	2.409	1.512	.	2.758	1.740	.	.	.	0.054	.	.	.	.	.	.	.	.	.	.
71	Unident	sp.	3.675	2.166	1.397	.	3.127	1.949	.	.	.	0.163	1.176	2.862	3.233	1.431	.	.	.	.	.	.
73	Idiocrani	russe	3.286	2.283	1.267	.	2.783	1.976	0.550	.	.	0.103	1.059	1.929	2.473	1.618	.	.	.	.	.	.
76	Dermophis	sp.	10.957	8.962	5.000	135.673	9.029	6.679	.	.	.	.	4.230	7.520	8.966	3.707	.	5.436	7.571	3.287	4.584	143.940
77	Typhlonec	sp.	10.464	9.617	5.323	144.912	8.943	6.780	.	.	.	.	4.322	7.748	10.130	.	3.344	4.809	7.308	3.431	4.214	149.150
78	Typhlone?	sp.	11.637	9.517	5.306	132.340	.	.	.	.	.	.	5.022	9.365	10.871	3.597	4.392	5.302	7.216	4.640	6.126	131.158
79	Unident	sp.	9.148	6.599	3.768	.	6.233	4.926	.	.	.	1.403	3.702	5.036	6.880	2.863	.	3.306	4.803	1.483	1.935	128.736
80	Dermophis	mexic	7.640	4.763	2.728	133.395	4.740	4.320	.	.	.	0.648	3.011	5.061	6.071	2.654	.	3.360	4.410	3.118	3.298	153.663
81	Dermophis	mexic	5.247	4.517	2.723	.	3.892	2.923	.	.	.	0.267	2.223	3.925	4.583	1.228	0.788	1.982	3.598	1.478	1.593	151.755
82	Dermophis	mexic	4.770	3.703	2.574	163.236	3.358	1.972	.	.	.	0.458	2.394	3.288	3.769	1.635	.	.	3.001	1.247	1.452	155.201
83	Dermophis	mexic	5.876	4.444	2.724	.	4.068	3.527	0.763	.	.	0.406	2.283	3.425	4.210	1.648	.	2.552	.	.	.	.
84	Dermophis	mexic	6.677	5.051	3.079	162.238	4.567	3.691	.	.	.	0.427	2.142	4.299	5.347	1.866	.	2.685	3.771	2.558	2.601	142.497
85	Dermophis	mexic	4.871	4.514	2.953	.	3.573	3.262	0.443	.	.	0.289	2.834	2.950	4.014	2.178	0.904	1.683	2.216	1.689	1.849	143.337
86	Dermophis	mexic	6.663	5.271	3.430	164.324	5.033	3.975	0.638	.	.	0.444	2.372	4.208	4.974	2.393	1.123	3.557	.	2.229	2.655	146.325
87	Dermophis	mexic	6.761	5.494	3.452	135.231	5.027	3.436	.	.	.	0.668	.	.	.	.	.	.	.	.	.	.
90	Dermophis	mexic	6.349	4.653	3.162	.	4.535	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
91	Dermophis	mexic	5.904	4.778	2.973	178.595	4.211	3.590	.	.	.	0.323	2.884	3.983	4.587	1.877	.	2.139	3.524	1.841	2.199	144.706
92	Dermophis	mexic	5.230	4.625	3.015	159.430	3.740	3.154	.	.	.	0.373	3.017	3.456	3.981	2.477	.	1.889	3.371	1.277	1.419	155.300
93	Dermophis	mexic	5.394	4.527	2.817	167.028	4.300	3.433	.	.	.	0.250	.	.	.	.	.	.	.	.	.	.
94	Dermophis	mexic	5.181	4.239	2.685	168.626	4.246	3.210	.	.	.	0.264	2.483	3.179	3.879	1.836	0.477	1.929	3.603	1.551	1.773	151.024
95	Dermophis	mexic	5.514	4.555	2.770	169.953	3.976	3.503	.	.	.	.	3.304	3.697	4.106	2.560	0.619	1.994	3.088	1.512	1.534	159.886
96	Dermophis	mexic	4.608	4.120	2.656	163.699	3.945	3.046	.	.	.	0.300	1.790	2.599	3.258	2.356	0.806	1.775	2.491	1.266	1.113	160.339

97	Dermophis mexic	5.252	4.513	2.732	170.496	4.018	3.163	0.793	. .	0.283	1.760	3.762	4.325	1.882	.	2.077	3.130	1.375	1.403	156.473
98	Dermophis mexic	5.496	4.291	2.735	168.790	4.418	3.349	0.506	. .	0.351	2.883	3.394	3.822	2.468	.	1.829	2.887	1.567	1.588	145.739
99	Dermophis mexic	4.443	2.953	3.690	160.161	.	3.117	.	. .	0.161	2.051	2.644	2.938	2.093	0.249	1.678	1.873	0.896	0.824	177.341
100	Dermophis mexic	4.741	3.973	2.776	172.180	3.539	3.148	0.352	. .	0.277	1.945	3.059	3.603	2.017	.	1.839	2.610	1.033	0.901	170.335
101	Dermophis mexic	4.594	4.047	2.829	169.563	2.851	3.160	0.583	. .	0.248	2.488	2.819	3.283	1.983	.	1.825	2.275	.	.	.
102	Dermophis mexic	4.529	3.753	2.470	162.331	3.076	2.814	0.409	. .	0.276	1.862	2.790	3.416	1.807	.	1.568	2.663	0.821	0.869	154.988
103	Dermophis mexic	5.029	3.468	4.383	170.646	3.634	3.264	0.412	. .	0.509	.	3.065	3.519	2.448	0.527	1.824	2.475	0.974	1.005	.
105	Dermophis mexic	4.582	.	3.616	.	.	2.647	.	. .	.	0.962	2.404	2.992	2.047	.	1.798	2.214	.	.	.
106	Dermophis mexic	4.101	2.149	3.073	163.480	.	2.786	.	. .	.	1.154	2.133	2.678	1.829	.	.	1.981	0.656	.	.
107	Dermophis mexic	4.474	3.405	2.523	171.952	.	3.134	0.544	. .	.	1.290	.	3.057	1.908	.	.	1.902	0.593	0.607	167.873
108	Dermophis mexic	.	.	.	.	3.745	3.353	0.427	. .	0.345	1.550	2.984	3.627	1.877	.	1.848	2.334	0.857	0.989	172.655
111	Dermophis mexic	4.623	4.023	2.871	.	3.275	3.324	0.514	. .	0.766	.	.	.	.	.	.	2.435	0.970	1.268	167.105
109	Dermophis mexic	4.087	2.792	1.346	169.959	3.239	1.997	.	. .	.	1.237	2.480	2.888	1.745	.	1.376	2.299	0.717	0.831	171.192
110	Dermophis mexic	3.947	2.476	.	172.757	3.925	1.968	.	. .	.	1.050	2.236	2.236	1.727	.	1.309	1.967	0.713	0.522	168.106
112	Dermophis mexic	4.100	3.120	1.505	176.522	.	2.371	.	. .	.	1.366	.	2.651	1.850	.	1.552	2.277	0.719	0.640	171.350
113	Dermophis mexic	3.641	3.058	1.669	170.236	.	2.125	.	. .	.	0.896	2.344	2.597	1.625	.	1.124	2.280	0.757	0.567	173.348
114	Dermophis mexic	3.698	3.580	2.649	167.269	2.294	3.045	.	. .	.	.	.	.	.	.	.	.	.	.	.
54	Dermophis mexic	11.389	9.727	5.015	154.449	8.539	5.640	.	. .	1.273	3.974	8.072	9.077	2.763	.	5.490	7.929	3.333	4.004	148.229
115	Hypogeoph rostr	6.020	4.141	2.748	157.507	4.401	3.307	0.532	20 18	0.313	2.470	4.056	5.746	1.754	1.447	3.187	3.972	1.905	1.908	147.308
116	Dermophis mexic	6.230	4.590	2.775	169.506	4.476	3.402	0.967	21 23	0.363	2.468	4.484	5.674	2.887	1.810	3.158	4.377	1.758	2.469	141.880
117	Hypogeoph rostr	7.123	5.846	3.067	177.760	5.187	4.037	.	. .	.	.	.	.	.	.	.	.	.	.	.
118	Grandison alter	9.794	7.961	4.008	147.162	7.700	4.749	0.969	29 26	1.088	3.290	5.167	6.818	4.156	2.077	3.036	7.009	3.663	3.923	164.509
119	Gegeneoph ranas	6.482	2.779	5.006	143.124	5.179	3.552	0.944	11 15	0.397	2.133	4.359	5.028	.	.	.	4.073	2.432	2.291	166.586
120	Caudacaec weber	9.270	7.324	5.582	156.093	6.183	4.986	0.653	23 22	1.543	3.065	6.721	6.807	3.270	2.015	4.410	5.889	2.393	3.524	138.718
121	Afrocaeci taita	5.934	3.976	2.537	60.269	4.436	3.027	1.043	14 18	0.450	2.329	4.247	5.179	1.778	0	.	4.089	2.534	2.460	156.782
122	Afrocaeci taita	5.558	4.187	2.397	159.075	4.302	2.811	0.986	13 14	0.276	1.706	3.626	4.395	2.204	.	.	3.809	1.954	2.201	145.434
123	Hypogeoph rostr	5.346	3.695	2.383	162.796	3.802	2.951	.	. .	.	2.241	2.894	3.521	2.417	1.052	1.685	2.140	1.105	1.720	128.551
124	Ichthyoph kohta	7.102	6.170	3.662	160.494	5.509	4.193	0.705	18 17	0.799	2.370	5.495	5.941	2.478	0.816	2.656	5.040	2.202	2.829	152.178
125	Dermophis mexic	12.491	10.176	5.100	153.202	8.205	6.023	1.654	19 19	2.664	4.482	10.546	11.904	3.926	2.385	6.178	10.394	3.843	4.704	149.543
126	Ichthyoph kohta	.	5.675	.	.	5.769	4.470	0.726	. .	0.701	2.497	4.916	5.213	3.564	0.938	3.331	5.973	2.763	3.754	147.900
127	Typhlonec natan	11.718	8.876	4.032	152.725	6.724	6.228	1.367	18 17	2.513	7.453	3.701	9.763	3.795	3.239	5.025	6.810	3.998	4.560	149.502
128	Typhlonec compr	13.458	10.996	5.425	146.075	7.472	6.707	1.346	25 25	2.577	4.053	10.323	12.606	3.325	4.192	6.088	10.607	3.238	4.185	136.959
129	Caecilia tenta	7.614	5.494	3.234	154.357	5.169	3.357	1.791	8 8	1.091	2.518	6.065	7.105	1.946	2.230	3.114	5.867	2.266	2.843	142.005
130	Caecilia nigri	8.368	5.931	3.610	153.339	5.677	3.831	2.169	12 10	0.958	2.915	7.231	7.596	2.138	.	.	6.665	2.285	3.043	139.283

131	Caecilia	tenta	9.120	7.148	3.858	147.542	6.264	4.209	2.401	11	11	1.452	7.584	7.196	8.027	2.969	.	3.872	7.393	2.320	3.217	140.589
132	Siphonops	sp.	5.859	4.369	2.983	146.682	3.360	2.674	.	14	..	.	1.905	3.806	4.235	2.148	0.708	2.418	3.577	2.460	2.651	149.042
133	Siphonops	annul	5.791	5.138	2.649	154.752	4.255	3.037	0.724	12	14	0.658	2.179	4.722	5.552	1.689	0.781	2.944	4.910	1.940	2.209	141.015
134	Typhlonec	sp.	8.488	6.485	2.654	146.250	5.941	3.936	1.362	23	24	1.246	2.847	6.907	7.980	2.064	2.597	3.640	6.956	2.909	3.204	124.534
135	Dermophis	mexic	5.491	4.415	1.893	145.842	4.640	2.967	0.754	16	15	0.435	1.840	4.262	4.791	2.027	1.263	2.693	3.810	2.157	2.396	148.770
136	Ichthyoph	beddo	8.338	6.287	3.841	.	5.582	4.330	0.649	16	13	1.390	2.875	7.169	7.545	2.454	1.207	3.474	.	.	.	.
137	Caudacaec	asple	7.432	5.666	3.132	164.651	5.476	3.943	0.775	19	19	1.120	2.178	6.038	6.601	2.438	.	2.277	6.559	2.405	3.034	154.228
138	Caudacaec	larut	8.763	6.245	3.941	154.522	5.456	4.243	0.931	16	17	1.257	2.500	7.424	7.637	2.462	1.508	4.115	7.281	2.778	3.237	160.706
139	Caudacaec	nigro	10.093	7.396	4.050	154.346	6.618	5.149	0.823	18	20	1.548	3.069	8.642	8.516	2.413	3.328	4.340	8.472	2.622	2.938	165.608
140	Ichthyoph	kohta	10.294	7.812	4.073	158.355	6.268	4.892	0.706	18	20	2.175	3.763	9.332	9.422	2.524	1.372	3.463	8.707	3.717	4.156	156.608
141	Microcaec	albic	6.181	4.377	2.258	150.024	4.634	2.976	0.735	8	14	0.386	2.306	4.330	5.016	2.040	.	.	4.350	1.918	2.331	158.342
142	Microcaec	albic	5.686	2.425	2.379	.	3.896	2.605	0.765	7	14	0.467	1.993	4.361	4.539	2.272	0.878	2.294	4.307	.	.	.
143	Geotrypet	sp.	11.181	8.625	.	161.229	8.500	6.250	.	22	.	.	3.750	9.750	11.250	3.566	3.875	5.141	7.875	4.404	4.657	147.996
144	Dermophis	sp.	9.877	9.500	.	152.605	11.625	6.375	1.375	18	19	2.492	3.875	7.750	8.500	5.276	3.250	4.975	8.375	5.376	5.797	151.218
145	Typhlonec	sp.	.	8.500	.	154.574	7.750	5.875	3.250	19	17	1.372	3.625	8.500	10.750	3.125	4.375	.	6.875	3.931	4.380	142.534
146	Dermophis	sp.	.	12.250	.	.	11.500	7.250	1.375	13	16	2.617	8.375	10.625	12.124	4.625	3.375	.	.	.	.	.
147	Typhlonec	sp.	11.035	7.375	.	.	8.125	6.000	.	13	.	.	2.625	7.500	9.250	3.863	3.125	.	7.500	2.958	3.754	146.107
148	Caecilia	occid	6.458	4.250	.	147.932	.	3.000	.	8	6	.	2.500	6.000	6.375	1.675	2.625	3.015	4.625	1.908	2.256	140.772
149	Ichthyoph	sp.	.	7.750	.	163.032	10.250	5.000	0.875	18	19	1.949	3.250	10.250	10.250	2.055	1.375	.	8.125	3.390	4.530	144.262
150	Caecilia	sp.	10.393	6.875	3.945	161.103	6.500	5.000	.	19	.	.	2.750	7.250	9.000	3.669	3.000	4.070	7.250	2.490	3.393	145.753
151	Caecilia	sp.	.	6.250	.	150.676	6.250	5.500	0.875	13	12	0.908	3.000	5.500	6.500	2.847	1.875	.	5.375	2.870	3.164	150.756
152	Dermophis	mexic	.	10.125	.	147.154	10.125	6.625	1.250	16	16	2.357	3.750	9.625	10.500	4.595	.	2.625	10.125	4.517	4.660	156.801
153	Dermophis	mexic	.	6.375	.	154.384	7.125	4.375	0.875	15	12	0.924	2.625	5.875	6.500	3.175	1.500	.	5.250	3.077	3.503	144.579
154	Dermophis	mexic	.	10.750	.	139.990	10.750	6.250	1.500	17	17	2.875	4.250	9.375	10.750	4.811	2.375	.	8.250	4.757	4.914	151.978
155	Dermophis	mexic	.	11.500	.	145.649	11.800	7.000	1.500	14	14	2.159	4.375	10.875	12.000	4.128	2.500	.	10.125	4.414	5.451	150.344
156	Dermophis	mexic	.	5.800	.	156.873	2.875	6.875	0.750	14	9	0.847	2.875	5.875	6.625	2.618	1.500	.	5.250	2.719	3.331	146.600
157	Dermophis	mexic	.	5.800	.	156.694	2.875	4.375	1.125	14	12	0.889	2.875	6.125	6.875	2.859	1.375	.	6.000	3.112	3.686	145.378
158	Dermophis	mexic	.	10.000	.	147.536	10.375	6.625	1.250	15	15	2.427	4.375	9.750	10.375	3.746	2.500	.	8.750	4.595	5.215	148.181

APPENDIX III

ANATOMICAL ABBREVIATIONS

ba	Basal articulation
bo	Basioccipital
Bc	Braincase
bs	Basisphenoid
cmj	Craniomandibular joint
eo	Exoccipital
EOC	Exoccipital-Opisthotic
F	Frontal
Fp	Frontoparietal
J	Jugal
L	lacrimal
M	Maxilla
MPa	Maxillopalatine
N	Nasal
NPm	Nasopremaxilla
O	Opisthotic
OB	Os Basale
P	Parietal
Pa	Palatine
Pf	Postfrontal
Pls	Pleurosphenoid
Po	Postorbital
PP	Postparietal
Ps	Parasphenoid

APPENDIX III

ANATOMICAL ABBREVIATIONS

Psa	Pseudoangular
Psd	Pseudodentary
Pt	Pterygoid
Ptq	Pterygoquadrate
Q	Quadrate
Qj	Quadratojugal
So	Supraoccipital
St	Supratemporal
Stp	Stapes
T	Tabular
Ta	Tentacular apeture
V	Vomer
X	Tenth nerve foramen