A PHYLETIC ANALYSIS OF VIPERINE SNAKES

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ABSTRACT

The intention of the present study is to investigate the problem of cladistic relationships among snakes currently assigned to the subfamily Viperinae, using characters drawn from the internal and external anatomy of preserved museum specimens, and elements of the methodology known as cladistic or phyletic analysis.

Introductory sections outline methodology, evidence for viperid monophyly, current concepts of relationships among viperid snakes, and ecogeographical features of viperines.

All but two of the approximately 48 species of Viperinae have been examined. Whenever feasible between two and 15 specimens of each species have been examined. Features of cranial osteology and myology, visceral anatomy, hemipenial morphology, and scalation (including gross arrangement of scales and scale surface micro-ornament), have provided 55 characters of potential cladistic significance. Certain characters appear to be of significance throughout the group, whereas others are of lesser importance and apply only within lineages established on other evidence. Numerous other features have proved impossible to interpret in a cladistic context.

No evidence has emerged that *Causus* is closely related to other viperines, but the derived course of the facial carotid artery in the latter distinguish them as a monophyletic group (Viperinae *sensu stricto*). *Azemiops* may be the sister group of other vipers, within the latter *Causus* may be the sister group of Crotalinae and Viperinae.

Four major monophyletic lineages can be proposed among Viperinae *s.s.* (1) The Eurasian group (*Vipera*, *Pseudocerastes*, *Eristicophis*). (2) *Echis* - *Cerastes*. (3) *Bitis*. (4) The *Atheris* group (arboreal *Atheris*, the terrestrial forms *'Atheris' hindii* and *'Atheris' superciliaris*, *Adenorhinos*).

It has proved impossible to arrive at a single hypothesis of the cladistic interrelations of these four lineages, but on balance, it appears more likely that *Echis* - *Cerastes* are more closely related to the advanced African forms *Bitis* and the *Atheris* group, in particular the latter, than to the Eurasian group.

A PHYLETIC ANALYSIS OF VIPERINE SNAKES

A. INTRODUCTION

B. CHARACTERS EXAMINED

C. DISCUSSION

3. Cladistic relationships within the Viperinae

A. INTRODUCTION

1. Objectives

The major purpose of this study is to investigate the cladistic relationships between species and groups of species currently assigned to the viperid subfamily Viperinae, using characters drawn from the internal and external anatomy of preserved museum specimens, and the methods of analysis developed by Maslin (1952), Hennig (1966), and several subsequent workers (see section 2 of Introduction).

Cladistic analysis is concerned with reconstruction of the branching sequence of lineages of organisms - a major parameter of phylogeny; "cladistic relationship" means relationship in terms of this branching pattern.

An initial enquiry into the problem of relationships among viperines has been made by Marx and Rabb (1965), these workers examined certain elements of cranial osteology in viperines and were thus the first to make any significant use of characters other than those derived from gross external features such as scalation and body proportions; it is the intention here to pursue the problem using a considerably wider range of morphological evidence, a somewhat different methodology, and to rather lower taxonomic levels (whereas Marx & Rabb were concerned mainly with genera, the present study extends to the species and species-group level).

The primary focus of this study was originally intended to be the genus Vipera, but in attempting to determine the strict monophyly or otherwise of Vipera, the cladistic affinities of apparently - or supposedly-related species, and the primitive-to-derived polarity of character state transformation, it became necessary to examine all viperines and also selected crotalines and Azemiops (representing all of the 3 viperid subfamilies currently recognised, Viperinae, Crotalinae, and the monotypic

Azemiopinae, - Liem, Marx, and Rabb, 1970). The scope of the present study was then widened to include all the viperine snakes (except for 2 species not available, neither of which are of key cladistic importance judging by published accounts, see section 4 of Introduction).

Particular attention has been given to the following subjects:-

(1) Relationships within the Eurasian group of species (*Vipera*, and the 2 monotypic genera *Pseudocerastes* and *Eristicophis*). Special interest attached to the cladistic relationship between the 2 south-west Asian arid-zone forms *P.persicus* and *E.macmahonii* (sand desert), and between these species and the morphologically and ecologically more conservative species included in *Vipera*. *E.macmahonii* has recently been synonymised with *Pseudocerastes* (Anderson, 1963:472), while Marx & Rabb (1965:169) preferred to retain *Eristicophis*, but synonymised *Pseudocerastes* with *Vipera*.

(2) The relationships between the Eurasian species and the arid-zone forms *Echis* and *Cerastes* centred in north Africa and Arabia (with *E.carinatus* extending through south-west Asia to India and Sri Lanka). Marx & Rabb (1965:165) considered *Echis* and *Cerastes* to be closely related (in fact, 1965:Fig.46, to form a strictly monophyletic group), and together to be closely related to *Vipera* (including *Pseudocerastes*) and *Eristicophis*; these genera were treated as a "Palaearctic stock", in contrast to an "Ethiopian stock" comprising the sub-Saharan viperines except *Causus*.

(3) The question of the cladistic affinities of the east African forms *hindii* and *superciliaris*, formerly regarded as the only sub-Saharan representatives of the essentially Palaearctic genus *Vipera*, but recently both assigned to the African genera *Bitis* (Kramer, 1961) or *Atheris* (Marx & Rabb, 1965). This is one specific question in the general problem of the relationship between

the Eurasian species, Echis - Cerastes, and the sub-Saharan species.

(4) The problem of the cladistic position of the genus Causus; this group of species has always been associated with the other Afro-Eurasian vipers lacking facial sensory pits. Recently Liem, Marx, & Rabb (1970) erected the monotypic subfamily Azemiopinae for the pit-less Azemiops, and maintained the subfamily Viperinae for the remaining vipers (including Causus) without sensory pits, and the Crotalinae for the pit-vipers. It has emerged during the course of this study that Causus is very distinct from other 'viperines', and while there is good evidence that the latter group (ie., viperines other than Causus, or Viperinae *sensu stricto*) are very probably monophyletic, it is by no means clear that the Viperinae as currently defined are monophyletic. Investigation of the cladistic position of Causus has made it necessary to examine Azemiops and sufficient crotaline material to make possible an estimate of the cladistics of the major lineages within the Viperidae.

To briefly characterise the situation at the completion of the present study, it has been possible to elucidate many of the 'twigs' of the viperine evolutionary tree, but the pattern of many of the primary 'branches' remains imperfectly resolved. Relatively robust hypotheses can now be proposed concerning the relationship of Pseudocerastes and Eristicophis to each other and to Vipera, and the relationship of the east African forms hindii and superciliaris to each other and to their putative relatives Atheris and Bitis. The major overall problem among viperines (*s.s.*) is:- how closely related are Echis and Cerastes (are they a strictly monophyletic group?), and how do they relate to the Eurasian species (Vipera, Pseudocerastes, Eristicophis) on one hand, and to the sub-Saharan African species (Adenorhinos, Atheris, Bitis) on the other.

An unambiguous solution to this problem has remained elusive, and this is the major obstacle to the complete resolution of the cladistic pattern of viperines.

2. Cladistic analysis - terms and methods

This section is intended to provide a brief outline of some basic theoretical and procedural aspects of the approach to cladistic analysis employed herein. It is not intended as a comparative critique of such methods.

Phylogeny may be broadly characterised as the pattern and process of descent through time and space of lineages or organisms, resulting from speciation, evolution, and extinction. The term 'phyletic (or phylogenetic) relationship' is here understood to mean the relations of organisms with reference to all aspects of this pattern of descent.

The phylogeny of a given group of taxa may be described in terms of three basic components:-

(1) Cladistic; pertaining to cladogenesis, or the generation of new lineages (clades) as a consequence of speciation. The study of cladistics is concerned with the number and branching sequence of lineages, forming a hierarchy of strictly monophyletic groups. Taxon A is said to be more closely related to taxon B than to taxon C, if A and B share an immediate common ancestor not also shared with C.

(2) Phenetic; concerned with the relative distinctness of taxa, or the morphological (or biochemical) 'distance' between them. Such differences between taxa may arise during speciation (cladogenesis), or by the accumulation of changes in a lineage during phyletic evolution (anagenesis).

(3) Chronistic; concerned with the events of phylogeny in relation to a time-scale.

The cladistic parameter is surely the most fundamental of the above, but it may be emphasised that cladistic relationship is only a subset of the entire spectrum of phyletic relationships. A hypothesis of the branching sequence of a group of taxa provides the optimum framework for further evolutionary studies (eg., of historical biogeography, convergent or parallel evolution in given characters, rates and magnitude of phenetic changes in different lineages, and the ecological correlates of such changes). Insofar as organisms can be similar to each other in some of the characters studied without being very closely related, a measure of phenetic resemblance alone will be deficient as an estimate of phyletic relationships.

Despite the great theoretical importance of cladistic studies, many difficulties are encountered with the interpretation and restricted availability of the relevant evidence. Some workers, particularly the numerical taxonomists, regard the entire process of cladistic inference as prohibitively unreliable (eg. Sneath & Sokal, 1973:40-52), and consider (1973:60) that classifications should be purely phenetic (ie. based on some measure of general similarity between taxa, regardless of the origin of that similarity). Many other systematists (eg. Bock, 1977; Hecht & Edwards, 1977; Hennig, 1966; Maslin, 1952; Szalay, 1977a), consider that if adequate attention is given to character analysis, in particular, to the primitive-to-derived sequence of character state transformations, it may be possible to construct a valid hypothesis of cladistic relationships. This latter view is fundamental to the present study.

The approach to cladistic analysis adopted here employs many of the concepts introduced by Maslin (1952) and Hennig (1965, 1966, 1975), as developed and modified by several subsequent workers (eg. Hecht & Edwards, 1977; and others cited below).

A cladistic hypothesis can be visually represented by a <u>cladogram</u>, such as the following:-

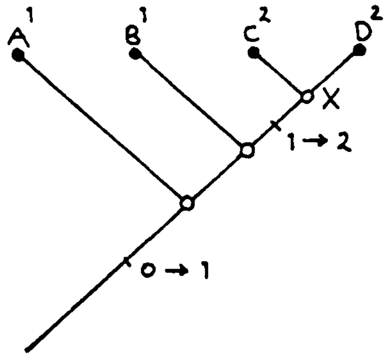


Fig. 1a

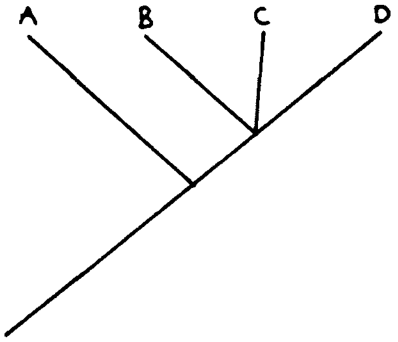


Fig. 1b

The dots in Fig. 1a represent known taxa, the circles represent hypothetical ancestral morphotypes. These symbols may be omitted, as in Fig. 1b. Each ancestral morphotype is basically a composite of the character states uniquely shared by the taxa arising from that node. A crossbar on an internode indicates a character transformation from a primitive to a derived state, present (perhaps with further modifications) in all taxa distal to that internode (eg. in Fig. 1a state 1, retained by taxa A and B, transforms to a derived state 2, present in the hypothetical ancestral morphotype X and its descendants C and D).

The information conveyed in Fig. 1a for example, is that a hypothesis exists that C and D are more closely related to each other than either is to B or A because C and D share a uniquely derived feature (a synapomorphy, see below) not also shared by B or A; given a dichotomous model of evolution it is proposed that C and D share an immediate common ancestor (X, in which the derived state first appeared) not also shared by B or A. Thus in a cladistic analysis 'relationship' is genealogical relationship, the most closely related forms are those sharing the most recent common ancestor.

In Fig. 1b the information is that B, C and D are more closely related to each other than either is to A, but available evidence does not allow resolution of the B-C-D trichotomy, ie., no uniquely derived feature shared by only 2 of the 3 taxa can be found.

The emphasis is on recency of common ancestry because it is only a strictly monophyletic group, composed of an ancestral form and <u>all</u> its descendants (a clade or single complete lineage), that has its own unique origin and phyletic history, its own individuality. Since Hennig (1966:73) workers in cladistic systematics have restricted the term <u>monophyletic</u> to such groups. A group of taxa is monophyletic if the included forms are hypothesised to share a common ancestor not also shared with any other taxa. Other workers, particularly in 'evolutionary systematics' (Mayr, 1974), have retained a broader and less precise traditional definition (eg. "monophyly is the derivation of a taxon through one or more lineages.... from one immediate ancestral taxon of the same or lower rank", Simpson, 1961:124), and following Ashlock (1971, 1974), have used the term 'holophyletic' in place of Hennigs' 'monophyletic'. For the sake of consistency with the cladistic approach adopted here, although unfortunately contrary to the interests of conservatism, the term 'monophyletic' is used throughout in the sense of Hennig.

An important difference between the 2 concepts of monophyly noted above is that in the traditional usage a 'monophyletic' taxon does not necessarily include <u>all</u> the descendants of a stem form. Species or higher taxa that are morphologically and/or ecologically highly divergent from the rest of the group are frequently not included taxonomically with that group, but may be placed in another taxon of similar or equal rank.

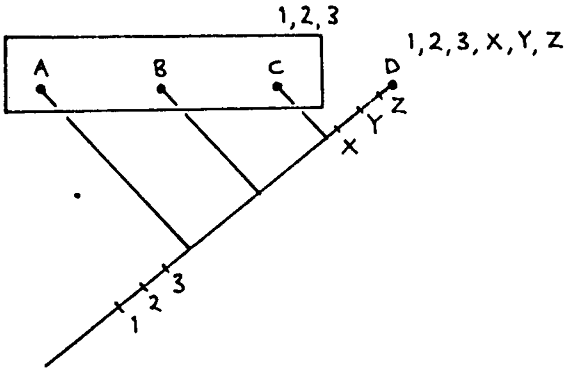


Fig. 2

For example, in Fig.2, taxon D is highly divergent and distinguished by unique features X, Y and Z, and may be ranked taxonomically equal with A, B and C combined. A taxon composed of the residual forms A, B and C is not marked by any unique features of its own, but shares only those states (1, 2 and 3) shared by the entire monophyletic group A-B-C-D. These states are primitive for any taxon within the group A-B-C-D. A group such as A-B-C, marked only by primitive states, is termed paraphyletic by Hennig (1966).

The taxa in a paraphyletic group generally represent a 'grade' of morphological organisation. The Reptilia is a frequently-cited example of a paraphyletic group, from which the highly divergent mammals and birds have emerged, leaving a diverse group of taxa that resemble each other only in the retention of certain basal amniote features.

The crucial point about a paraphyletic taxon is that, unlike a monophyletic taxon, it does not have its own unique phyletic history. While a monophyletic group has its own objective existence in nature, a paraphyletic group is a construct of taxonomy. Although it is clearly desirable to distinguish in principle between mono- and paraphyletic groups, the case is frequently argued (eg.Cartmill, 1975: 348-350; Mayr,1974; Michener,1977:52, 1978; Szalay,1977) that paraphyletic groups may also be recognised taxonomically , particularly where the cladistic evidence is subject to alternative interpretations.

Nelson (1971:472) defined a paraphyletic group more precisely as a monophyletic group minus one species or monophyletic species-group. Nelson also precisely defined a 'polyphyletic' group as a monophyletic group minus two or more species or monophyletic species-groups. These definitions are certainly unambiguous, but do not always correspond to Hennigs' usage; for example the taxon Reptilia, being based on shared primitive character states, is paraphyletic by Hennigs' definition but polyphyletic by Nelsons'. Hennig (1966) distinguished a polyphyletic taxon as one based on convergent character states shared by two separate lineages. Further redefinitions of para- and polyphyly have been provided by Farris (1974), and recommended by Platnick (1977b); while these are entirely logical, they are rather difficult to apply in practice. In the present study the terms 'paraphyly' and 'polyphyly' are used in the sense of Hennig. Thus, in two types of non-monophyly, a paraphyletic group is one based on possession of shared primitive states, a polyphyletic group is one based on shared convergent states.

It must be acknowledged at the outset of any phyletic study that it is not possible to reconstruct a phylogeny of a group of organisms that, in empirical terms, is demonstrably true. Many systematists (Bock, 1973, 1977; Wiley, 1975) have followed a philosophy of scientific activity developed by Popper (eg. 1968), entailing the view that the essence of a truly scientific hypothesis is its ability to be falsified. The bolder, more inclusive, and more precisely stated is a given hypothesis, the more susceptible it is to falsification, and the more it is preferred. The value of a hypothesis is seen as directly proportional to the number and severity of tests that have been applied to it, without falsification of the hypothesis. It has been argued (eg. Wiley, 1975; Engelmann & Wiley, 1977) that Hennigian cladistic analysis satisfies the criterion of testability in Poppers' definition of science. There is much debate whether this approach to systematics is strictly to be regarded as 'scientific' (in Poppers' terms) or not (contrast the views of Kitts, 1977, with Platnick & Gaffney, 1977, 1978). However, regardless of this particular point, this approach at the very least tends to promote clarity of argument, and has considerable heuristic value in stimulating the search for new evidence and new interpretations.

The primary data input of a systematic study must be phenetic in nature, based on perceived patterns of similarity and difference, and containing an element of hypothesis only to the extent that any observation is made in the light of certain preconceptions. In a cladistic analysis it is necessary to add further levels of hypothesis.

One initial hypothesis is that a similar structural, topographical, or developmental, pattern shown by an array of features in different organisms is a result of their being homologous. Such features are termed homologous if they are hypothesised to be evolutionary transformations of one and the same condition that was present in the immediate common ancestor of the taxa in question. An essentially similar definition of homology has been used by both 'cladistic' (Hennig, 1966:93; Wiley, 1975:235) and 'evolutionary' (Bock, 1977:881) systematists. The value of a hypothesis of homology is directly proportional to the closeness and complexity of the pattern of resemblance. Frequently, relevant ontogenetic information is lacking, and, as in the present study, the extent of the structural or topographical similarity in adult morphology is the sole source of evidence.

As Bock has pointed out (1963:269; 1977:881), in the interests of precision it may be necessary to specify the frame of reference of a particular hypothesis of homology. For example, in many snakes the dorsal wall of the trachea is expanded and the alveoli of the true lung extend along it, forming a 'tracheal lung'. A tracheal lung "has undoubtedly been developed several times in snakes" (Underwood, 1967:5). In any 2 snake taxa in which a tracheal lung has evolved independently, these structures are non-homologous as tracheal lungs, although on a higher (more inclusive) level they remain homologous as tetrapod tracheae.

For the present purposes (alternative formulations are possible, Bock, 1973:387; Platnick, 1978:366; Gaffney, 1979), a character is regarded as a homologous feature that varies from one organism to another, and that cannot be reasonably further subdivided for the purpose at hand; a character state is the condition of that feature in any given organism, or a similar condition shared by a group or organisms. For example, 'pupil round' and 'pupil vertical' are states of the character 'condition of pupil'.

A sequence of homologous character states possessed by a group of organisms, postulated to be congruent with the actual evolutionary transformations within the character, although the direction of change may not yet be suggested, is termed a transformation series by Hennig (1966). This term is approximately synonymous with morphocline (Maslin, 1952), although this latter has the merit of brevity it perhaps implies continual unidirectional evolution.

A fundamental proposition of cladistic analysis is that it is in some cases possible to postulate the primitive-to-derived direction of evolution, or polarity, of the character states forming a transformation series. Such a sequenced set of character states is termed a character state tree by Marx & Rabb (1972).

The problem of the estimation of the polarity of character state transformations has been discussed by many systematists (eg. Hennig, 1966; Kluge & Farris, 1969: 5-6; Kluge, 1976:21-25; Marx & Rabb, 1970:530-533; Maslin, 1952;

Voris, 1977:92-93). Kluge (1976) has concisely stated what appear to be the most reliable criteria for estimating which of several conditions of a character is the primitive extreme. The primitive state is:-

(1) Frequently observed among the groups (out-group or secondary group) hypothesised to be related to the one being studied.

(2) Frequently observed within the group chosen for study (primary group).

(3) Exhibited by taxa estimated to possess primtive states of other characters on the basis of rules 1 and 2.

These rules are founded on the principle of parsimony. It is initially presumed that a widespread state, present in taxa that are otherwise diverse, has arisen once during the early history of a group and has persisted in all or several lineages of that group. To suggest that that state is a derived one is to postulate multiple parallel origins in all those lineages. The latter may actually be the case, and may be suggested after analysis of other characters, but is unwarranted as an a priori assumption.

Conversely, the more recently a state has evolved (ie. the closer it is to the derived extreme of the transformation series), the more restricted is its distribution likely to be. This concept requires very careful evaluation however, since many states with restricted distributions may be primitive (on the basis of other evidence), and derived states may be numerically widespread in highly speciose lineages.

The above rules are listed in descending order of priority. For example, among snakes currently assigned to the Viperinae, only the 6 species of Causus possess the standard caenophidian pattern of 9 large head shields, these shields are fragmented in the great majority of viperines. Initial application of rule 2 would lead to the unreasonable conclusion that the state 'head shields fragmented' is primitive for viperines and the state'9 large head shields' is derived; rule 1 indicates, congruent with all other evidence, that the state '9 large head shields' is actually primitive for viperines. In applying rule 1, priority should be given to the out-groups that are, on the basis of other evidence, most closely related to the primary group.

Given the probable primitive extreme of the transformation series, the remaining states are ordered in a logical morphological sequence (again guided by the principle of parsimony). For 2-state characters there is only one possible sequence, but sequencing can be a problem for characters with several states, and it may be impossible for those with very many states. The resulting character state tree may be uni- or multidirectional (eg. Marx & Rabb, 1972:10).

As a working principle, Hennig (1966) proposes that speciation events are typically dichotomous. The 2 descendant species of a common ancestor are termed <u>sister species</u>, two groups of species descended from a common ancestor are termed <u>sister groups</u>. Although in theory sister groups are those that exclusively share an ancestral species, in practice, hypothesised sister groups are only those two taxa, among all those actually known, that are cladistically most closely related (ie. they may in fact be 'aunt' and 'niece' or even 'mother' and 'daughter', rather than true sisters).

Hennig suggests that, following speciation, the state of a given character possessed by the ancestral <u>stem species</u> (the primitive or <u>plesiomorphous</u> state) may be retained by one of the descendant sister species (this species may also retain the primitive state of a majority of other characters). On the other hand, that character may undergo an evolutionary transformation in the second sister species, in which a derived or <u>apomorphous</u> state appears.

A plesiomorphy shared by a group of taxa is termed a symplesiomorphy, an apomorphy shared by a group of taxa is termed a synapomorphy. An autapomorphy is a derived state unique to a single species or single clade whose internal relationships are not currently under study.

All synapomorphies are shared derived states, but the converse if not true. That all shared derived states are not synapomorphies is evident from Hennigs' stipulation (1966:89) that apomorphous states compared in different species must "belong to one and the same transformation series" in order to constitute a synapomorphy; in other words, they must be homologous. The more general term 'shared derived' remains useful for states whose status as synapomorphies or parallelisms is unclear at a given stage of analysis.

Within any sister group pair, a symplesiomorphy is 'primitive' only in relation to the 'derived' synapomorphy of the other member of the pair. The plesiomorphous state is itself a synapomorphy of the larger monophyletic group to which the sister group pair and their ancestral species (and its sister group, and so on) belong. In Fig. 3, state 2 is a synapomorphy of D and E, state 1 is the corresponding symplesiomorphy of C (the sister group of D + E), A, and B; but at a more inclusive level state 1 is a synapomorphy of the entire group A - E. For example, the presence of feathered wings is a symplesiomorphy of any two sub-groups of birds, but is rather certainly a synapomorphy of Aves as a whole.

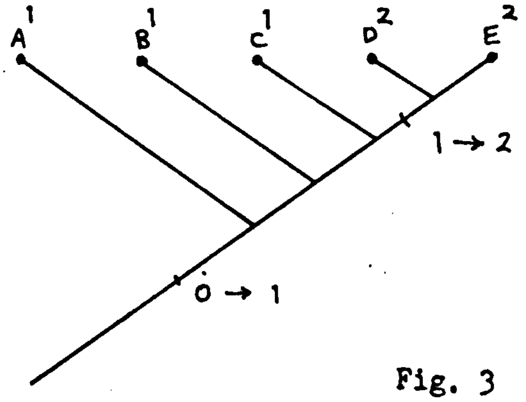


Fig. 3

The crucial point about synapomorphies is that they indicate the strict monophyly of the taxa possessing that particular state (in Fig.3, state 2 is a synapomorphy shared by D and E indicating that they share an immediate common ancestry, it is less parsimonious to suggest _a priori_ that state 2 is non-homologous and evolved in parallel in D and E). A nested hierarchy of synapomorphies implies a nested hierarchy of monophyletic groups and thus the cladistic relationships among the taxa under study.

Symplesiomorphies simply indicate non-evolution in that particular character from a more remote ancestral condition, they may thus be retained as phenetic similarities by taxa that are not especially closely related , and they become significant for determining cladistic relationship only at the higher (more inclusive) level at which they exist as synapomorphies (eg. as noted above, state 1 in Fig. 3 is a synapomorphy of the entire groups A - E).

Similarity between organisms can thus be seen to have three components:-

(1) Homologous states newly and uniquely derived in the immediate common ancestor of a group, thus constituting a synapomorphy of the included taxa.

(2) Homologous states retained from a genealogically more remote common ancestor, thus constituting a symplesiomorphy of any sub-group of taxa, but a synapomorphy of the more inclusive group (descended from the remote common ancestor.

(3) Non-homologous (or Homoplasious) states.

The criterion of homology between a set of character states possessed by a group of organisms is transformation from a single state in the immediate common ancestor of the taxa in question. Homology can therefore _only_ be established at the level at which it is distinguished as a synapomorphy (case 1, above) and the terms 'homology' and 'synapomorphy' are seen to refer to one and the same relation between character states and taxa.

The parallel concepts of homology and synapomorphy constitute the basic units of a cladistic hypotheses. Each hypothesis of synapomorphy will indicate a certain arrangement of taxa, namely, that those taxa sharing the apomorph state are monophyletic. Among a group of taxa, each such hypothesis can be regarded as a subset of the more inclusive hypothesis of cladistic relationships that can be constructed from them. To the extent that they are independent of each other, one hypothesis of synapomorphy can be used to 'test' another, and the cladistic sequence that it implies. The criterion is congruence with the stated cladistic arrangement.

As an example of cladogram construction, a basic 3-taxon problem may be considered. There are four possible ways in which three taxa can be related cladistically (Fig.4).

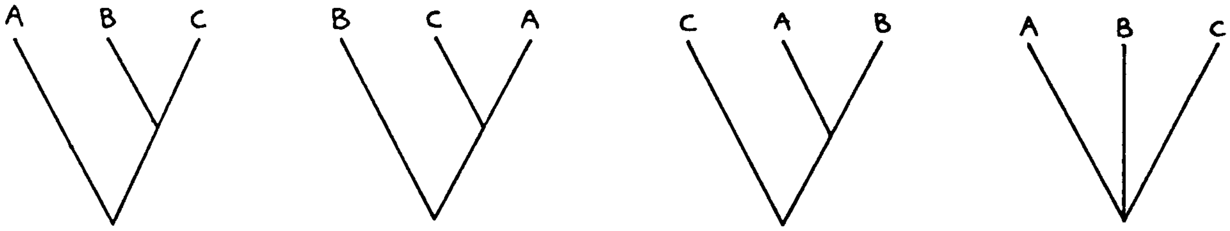


Fig. 4

These hypotheses can be tested by the distribution of character states. A state found in all three taxa (a symplesiomorphy of any sub-group), or in one taxon alone (autapomorphy), could be consistent with all four possible cladograms. The only test is provided by a synapomorphy indicating the joint monophyly of two out of the three taxa, for it is only such a distribution that is consistent with only one of the three cladograms, indicating that two of the taxa are more closely related to each other than either is to the third. In order to provide a basis for a hypothesis of synapomorphy comparisons must be made within an outgroup in addition to the three primary taxa.

Suppose that a synapomorphy linking B and C can be proposed, suggesting that B and C are monophyletic (state 1a, Fig. 5a). This hypothesis can be tested with a second synapomorphy, if this state is also shared by B and C the initial cladistic hypothesis (Fig. 5a) is not falsified and remains the preferred current hypothesis. However, it may be that the second supposed synapomorphy is shared by A and B, suggesting that they are monophyletic (state 2a, Fig.5b). The two cladistic patterns (Figs.5a & 5b) are seen to be incongruent with each other.

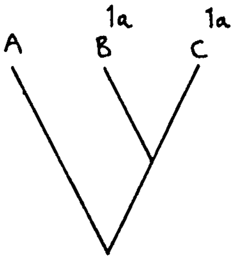


Fig. 5a

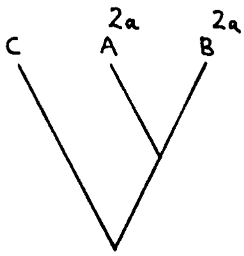


Fig. 5b

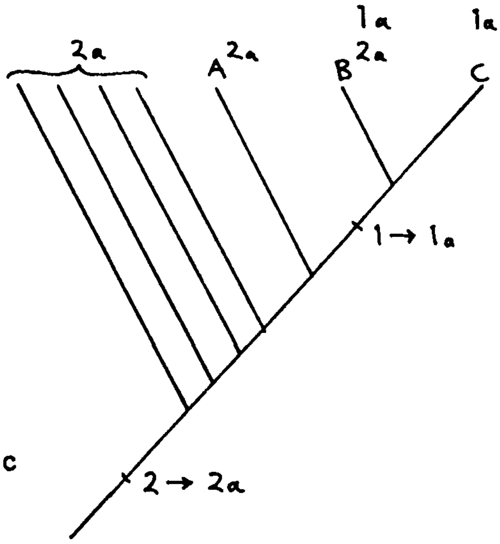


Fig. 5c

This incongruence can be due to at least one supposed synapomorphy (perhaps both) being incorrectly identified, and actually either a symplesiomorphy or a non-homology. A further complication is added by the possibility of regarding a state resulting from evolutionary reversal as primitive instead of derived (or 'secondarily primitive').

Further investigation is required to establish which is the most likely of these possible sources of incongruence. More detailed dissection of a structure may reveal sufficient morphological differences to suggest that one 'synapomorphy' is based on non-homologous states (ie. convergence or parallelism). Perhaps by raising the level of generality of the analysis (ie. by making comparisons among a larger and more diverse outgroup), it may become more parsimonious within the context of the enlarged problem to suggest that one 'synapomorphy' is actually a symplesiomorphy if the state in question is also shared by the added taxa (eg. state 2a in Fig. 5c; in this case the cladogram of Fig. 5a would remain unfalsified). Further hypotheses of synapomorphy may be congruent with only one of the two already existing, and thus lead to a suspicion that the second of these is incorrectly interpreted as a synapomorphy.

The cladistic arrangement congruent with the greatest number of unfalsified synapomorphies may be regarded as the current preferred hypothesis, if one character is given no more 'weight' than another.

Although a set of perfectly congruent synapomorphies can be translated into a single unique pattern of cladistic relationships, it is frequently the case that <u>in</u>congruence is found. This incongruity may persist after reanalysis of the data (as outlined above), and most frequently appears to be due to parallel evolution of similar derived states in different lineages. It has often been suggested (eg. Bock, 1963) that parallelism is likely to be most common in 'genetically similar' groups, having a similar gene pool and similar developmental constraints on which possibly similar forces of mutation and natural selection can act to produce similar phenotypic results. If parallelism is indeed common among closely related taxa, a cladistic analysis attempted at low taxonomic levels (ie. around the species-level) will frequently encounter a major limit to its depth of resolution.

It may be that a simple 'count of votes' (ie. of supposed synapomorphies) will not allow the clear choice of a preferred cladistic hypothesis. Some workers have attempted to overcome this problem by assigning weighting values to their characters, so that in cases of incongruence due to parallelism or reversal the higher weight character has priority over the lower. This will result in an apparently non-parsimonious hypothesis for the evolutionary transformations of the lower-weight character. The basis of such weighting, and the validity of any form of <u>a priori</u> weighting at all (apart from that involved in the selection and definition of characters), is subject to some dispute.

For example, Bonde (1977:751, in the context of 'cladistic systematics') states that a cladistic hypothesis should involve "...as few changes and as small changes as possible" in character states, ie. that maximum parsimony is the only criterion for making a choice among competing cladistic hypotheses, and that no weighting system is legitimate. He further states that functional studies are irrelevant to the construction of cladistic hypotheses. By contrast, Bock (1977:889. in the context of 'evolutionary systematics') states that the testing of supposed synapomorphies in cases of incongruity"...is based upon the different probabilities of certain evolutionary changes occurring independently two or more times". States with a high probability of parallel evolution are correspondingly unlikely to be true synapomorphies, but merely shared and derived states, and are to be given low weight or discarded entirely. Bock further suggests that functional studies should play a major part in assessing these probabilities.

Hecht and Edwards (1976,1977) have recently proposed a weighting system in which character states are rated according to the amount of information contained in each, by means of which parallelism may potentially be detected.

Thus, derived states involving the loss of a feature, and which lack ontogenetic evidence of possible different pathways of loss, are given the lowest weight. At the opposite extreme are states that are complex, innovative, and apparently unique. The probability of parallelism is regarded as inversely proportional to the complexity of the character state. Possible clues as to parallel evolutionary pathways may be more frequent in the more complex character states. Such states are given the highest weight. The Hecht and Edwards weighting system (1976:655-656, 1977:15-16) includes five categories. They note that the categories are artificially clearly defined, and that more or fewer categories could be used, depending on the study in hand. The categories are as follows, in ascending order of significance:-

I. states involving loss of a structure, with absence of ontogenetic evidence regarding unique or parallel loss.

II. states involving simplification or reduction of a complex feature, possibly with ontogenetic or structural evidence of parallelism, eg. fusion of ossification centres.

III, states resulting from differential growth, including phenomena of allometry and neoteny, eg. form of muscle attachments.

IV, states contributing to an integrated functional complex.

V, states that are complex, innovative, and apparently unique; extreme examples are, the amniote egg, the artiodactyl astragalus, the gekkonid cochlea.

Hecht and Edwards (1977:17) suggest that states belonging to groups IV and V"...should be the primary data used in phylogeny reconstruction". They rightly point out that theoretically only one reliable character is necessary to indicate lineage, and that the mere multiplication of ambiguous, poorly-analysed, or low-weight, characters may not resolve areas of doubt.

Although an analysis at a low taxonomic level will suffer from a distinct scarcity of character states in Hecht and Edward's high-weight categories, I have attempted to use a rather similar approach to character-weighting in the present study.

A situation in which possible synapomorphies are lacking, or one combining a high frequency of incongruent supposed synapomorphies with a low frequency of high-weight characters will persistently defy analysis. There are several such problem areas remaining in the present study, and whatever the optimum theoretical basis for a classification (cladistics or phenetics, or both), purely phenetic evidence must be considered if a classification is to be produced, which will inevitably contain paraphyletic taxa.

3. The family Viperidae

a. Introduction

The family Viperidae currently contains approximately 170 described species of caenophidian (colubroid) snakes, characterised by a highly developed venom production and injection system.

Most species are terrestrial, occurring in a wide spectrum of habitats, including various types of forest, scrub and grassland, heathland, and with several species penetrating to high altitudes or into desert regions. Many other species are arboreal, in forest regions of southeast Asia, India, tropical Africa, and the Americas. A few species of the pit-viper genus Agkistrodon (eg. A.piscivorus, the Water Moccasin or Cottonmouth) are largely aquatic. Most species prey primarily on a variety of small vertebrates, including mammals, birds, and lizards.

The majority of species occur in tropical regions, rather fewer in temperate areas, and only Vipera berus (Common Adder) extends beyond the Arctic Circle (in Scandinavia). Of the numerous South American crotalines, Bothrops ammodytoides reaches furthest south, extending well into Patagonia. The family is almost worldwide in distribution, but is not represented in the Australian region.

b. The venom injection system -evidence for viperid monophyly

Various components of the viperid venom system have been described in numerous works (eg. Boltt & Ewer, 1964; Dullemeijer, 1956, 1958; Kardong, 1973, 1974, 1977; Kochva, 1958, 1962, 1979; Kochva & Gans, 1965, 1970; Liem, Marx & Rabb, 1971; Schaefer, 1976). The basic features of the system are briefly outlined in the following paragraphs.

In contrast to other snakes, the maxilla is very much shortened, instead of elongated, in an antero-posterior direction. The proximal tip has a highly mobile articulation with the prefrontal, which itself (except in Azemiops and Causus) is highly mobile on the frontal. The distal tip bears a large tubular (solenoglyphous) fang, with apertures proximally and distally for the entry into the fang, and exit into the prey, respectively, of venom. The functional fang is accompanied by a series of non-ankylosed developing fangs. Of the two fang sockets, one medial and one lateral, typically only one is occupied at any given time. Schaefer (1976) has described how the structure of the soft tissues of the fang sheath, surrounding the basal portions of the fang and the maxilla, facilitate transfer of venom from the venom duct to the fang lumen. The posterior face of the distal portion of the maxilla articulates with the anterior edge of the ectopterygoid. Movement of the pterygoid and palatine, produced by muscles of the constrictor internus dorsalis (CId) group, is transmitted via the ectopterygoid to the maxilla. During protraction of the palato-maxillary arch, the distal fang-bearing portion of the maxilla, pushed by the ectopterygoid, is rotated in a para-sagittal plane from a rest position directed posteriorly along the roof of the mouth, to a strike position directed antero-ventrally in the open mouth. Retraction is accomplished by other CId muscles and the M.pterygoideus.

The large venom gland, and its associated compressor muscles, occupies much of the temporal region, and is responsible (with the distal tip of the quadrate) for the distinctly triangular plan of the head in most viperids. The large central lumen of the main gland is surrounded by branching secretory tubules. The primary venom duct connects the main gland with the accessory gland (secreting mucins), the secondary venom duct connects the accessory gland with the fang sheath, and thus with the fang lumen. Kochva (eg. 1979;150) has emphasised the distinctive musculature, developmental pattern, and adult structure, of the viperid venom gland system.

The ability to retract the fangs to a horizontal position along the roof of the mouth means that relatively very large fangs can occur, without interfering with mouth closure. This contrasts with the situation in the other front-fanged snakes (elapines and hydropiines) that lack such a highly-kinetic maxilla, where the fangs are much shorter. The shock associated with the penetration of long fangs, and the depth to which the venom may be injected, probably contribute (with the venom itself) to increased efficiency in the killing of prey animals.

The pattern of kinesis and the efficiency of the entire fang protraction-retraction system is influenced by very many elements of cranial anatomy. Among these elements, there is a variation among viperids particularly in the area of origin and line of action of the *M.levator pterygoidei* (of the CId group), and in the form of the ectopterygoid, maxilla, and prefrontal, and their articulations and associated ligamentous ties. Some of these features are discussed in part B (Character Analysis) of this report.

Despite differences in detail, the entire venom production/injection character complex is of a fundamentally similar pattern in all viperids (not including *Atractaspis*, these forms are not vipers, see below). There is no evidence within the complex to suggest that it has evolved more than once, nor is this suggested by other known characters. It is certainly to be regarded as derived or advanced in relation to the unmodified condition typical of other snakes. In accordance with the principles outlined in section A.2, it may therefore be proposed that the venom system constitutes a high-weight synapomorphous complex, indicating the strict monophyly of the Viperidae.

c. *Major divisions of the Viperidae, as currently conceived.*

The fullest and most recent significant discussion of systematic divisions within the Viperidae appears in the study of Liem, Marx, & Rabb (1971), in the context of an account of the cephalic anatomy of Azemiops, a rare and generally primitive monotypic form occurring in southeast Asia. In their classification (1971:120-121) Liem, Marx & Rabb divided the Viperidae into 3 subfamilies:-

(1) Azemiopinae (Azemiops, a single species)
(2) Crotalinae (pit-vipers, about 122 species)
(3) Viperinae (all other vipers, about 48 species).

This arrangement was designed to reflect "in some measure" (p.118) the suggested phylogenetic relations among viperids. Liem et al proposed that Azemiops shows few derived character states, but combines several primitive states that may also occur in the more conservative viperines and crotalines; they concluded (p.118) that "Azemiops arose as an early offshoot of the main line of vipers near the evolutionary paths to the crotalines and viperines". In cladistic terms, their discussion and phyletic diagram (1971:118) can be translated only into a trichotomous cladogram (Fig. 6).

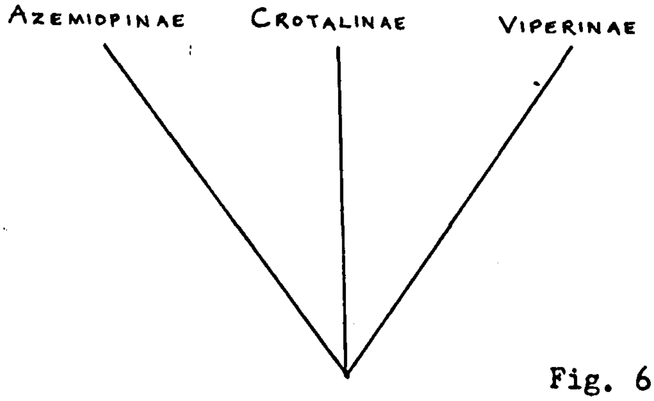


Fig. 6

As noted in a previous section of this study (A.1), no evidence has emerged that the Viperinae (of Liem et al, 1971) is a monophyletic taxon; furthermore, there are indications that the Crotalinae and viperines other than Causus may together form a monophyletic group, with Azemiops and Causus as two separate more conservative lineages; the taxon 'Viperinae' would thus be paraphyletic.

It should be understood that the term 'viperine' used herein, until more definite systematic conclusions are reached (pp.). refers to a group that is not necessarily strictly monophyletic (unless qualified, eg., 'viperinae *sensu stricto*', i.e., viperines other than *Causus*).

More recently than that of Liem *et al* (1971), an alternative arrangement of viperid taxa has appeared, as part of a "Summary of Snake Classification" (Smith, Smith, & Sawin, 1977). This work is indeed summary, since it comprises little more than a list of taxa, unaccompanied either by any morphological information, or by any discussion of the methodological basis on which the classification was constructed. Such a list of taxa is, in itself, of minimal interest or significance; however, it may be relevant to note their treatment of viperids. Smith *et al* (1977:119) divide the family into two sub-families instead of the three used by Liem *et al*. The Azemiopinae of the latter is reduced to the level of a tribe within the Viperinae, *Causus* is removed from the remaining viperines (*sensu* Liem *et al*) and these two groups constitute the second and third tribes of the Viperinae (*sensu* Smith *et al*). Their overall arrangement is as follows:-

(1) Subfamily: Viperinae (vipers without facial sensory pits)
    Tribe: Viperini (Viperinae of Liem et al, except *Causus*)
    " Azemiopini (*Azemiops*)
    " Causini (*Causus*)
(2) Subfamily: Crotalinae (pit-vipers)
    Tribe: Lachesini (Bushmasters)
    " Crotalini (viviparous pit-vipers)

Two workers primarily concerned with pit-vipers, Brattstrom (1964), and Burger (1971), have preferred to treat the pit-vipers as a full family, Crotalidae, with the remaining vipers as a second family, Viperidae. These authors do not provide any significant discussion of relationships within the vipers.

The name 'Viperinae' is used herein in the sense of Liem _et al_, with the reservations noted above. The question of relationships within the Viperidae is discussed in section C.

Until quite recently the many species of the genus _Atractaspis_ were included in the Viperidae. The genus _Atractaspis_ comprises a group of venomous fossorial caenophidian snakes (Mole 'Vipers'), with hollow fangs and a fang protraction-retraction system superficially similar in some respects to those of true viperids (see Fig.27, in Parker & Grandison, 1977, for skull of _A.aterrima_). They occur through most of sub-Saharan Africa, and into Israel and the southwest of the Arabian Peninsula. Recent anatomical, chromosomal, and serological, evidence has indicated beyond reasonable doubt that this group is not at all closely related to viperids, but probably has much greater affinity to the aparallactines (Caenophidia), (Bourgeois, 1961, 1965; Branch, 1975; Kochva, Shayer-Wollberg & Sobol, 1967; McDowell, 1968:570); Minton, 1968; Underwood, 1967:103). Kochva & Wollberg (1970:222) were uncertain as to the affinities of _Atractaspis_. _Atractaspis_ is not treated in the present study.

d. Geographical distribution

Although the Viperidae as a whole have an almost worldwide distribution, being absent most notably from the Australian region, the 2 major subfamilies have almost completely exclusive complementary distributions. The Crotalinae are predominantly New World, being most numerous in terms of species and morphologically most diverse in the Americas, but with many species also in eastern Eurasia (the latter group including some of the most conservative forms). The Viperinae (s.l.) are entirely Old World, primarily in Africa and western Eurasia. On a small-scale map the ranges of these two subfamilies overlap in only a few areas, and actual sympatry between crotaline and viperine species appears to be even more restricted.

The third subfamily, comprising only Azemiops feae, occurs in southeast Asia; the few known specimens originating from extreme northern Burma (the type specimen only), extreme northern Vietnam, and parts of China, including Szechwan.

4. The subfamily Viperinae

a. List of viperine species

The following is a list of currently-described species presently assigned to the Viperinae (*sensu* Liem, Marx & Rabb, 1971). It has been compiled, with the additions and changes noted below, from the standard checklists of Klemmer (1963, world venomous snakes; 1968, west Palaearctic), Broadley (1968, sub-Saharan Africa), Leviton (1968, Afghanistan, Pakistan, India, east Asia), Leviton & Anderson (1970, Afghanistan), Minton (1966, Pakistan), and Saint-Girons (1978, European *Vipera*). I have listed *Vipera seoanei* as a full species, after Saint-Girons & Duguy (1976) and Duguy & Saint-Girons (1976). Following Underwood (1968) *Bitis inornata* is regarded as a subspecies of *B.cornuta.* I have followed Marx & Rabb (1965) in treating *Pseudocerastes bicornis* and *P.fieldi* as conspecific with *P.persicus*, but not in assigning *persicus* to the genus Vipera. Additions to the cited checklists are: *Atheris desaixi* (Ashe, 1968); *Bitis parviocula* (Böhme, 1977); *Bitis xeropaga* (Haacke, 1975); *Echis leucogaster* (Roman, 1975) and *Echis ocellatus* (Hughes, 1976); *Vipera bornmuelleri* (Mertens, 1967) and *Vipera latifii* (Mertens, Darevsky & Klemmer, 1967).

Adenorhinos barbouri (Loveridge) 1930
Atheris ceratophorus Werner 1895
Atheris desaixi Ashe 1968
Atheris chloroechis (Schlegel) 1855
Atheris hindii (Boulenger) 1910
Atheris hispidus Laurent 1955
Atheris katangensis de Witte 1953
Atheris nitschei Tornier 1902
Atheris squamiger (Hallowell) 1854
Atheris superciliaris (Peters) 1854
Bitis arietans (Merrem) 1820
Bitis atropos (Linnaeus) 1758

Bitis caudalis	(Smith) 1839
Bitis cornuta	(Daudin) 1803
Bitis gabonica	(Duméril & Bibron) 1854
Bitis heraldica	(Bocage) 1889
Bitis nasicornis	(Shaw) 1802
Bitis parviocula	Böhme 1977
Bitis peringueyi	(Boulenger)1888
Bitis schneideri	(Boettger) 1886, (formerly *B.paucisquamata*-see Haacke, 1975)
Bitis worthingtoni	Parker 1932
Bitis xeropaga	Haacke 1975
Causus bilineatus	Boulenger 1905
Causus defilippii	(Jan) 1862
Causus lichtensteini	(Jan) 1859
Causus maculatus	(Hallowell) 1842
Causus resimus	(Peters) 1862
Causus rhombeatus	(Lichtenstein) 1823
Cerastes cerastes	(Linnaeus) 1758
Cerastes vipera	(Linnaeus) 1758
Echis carinatus	(Schneider) 1801
Echis leucogaster	Roman 1972
Echis ocellatus	Stemmler 1970
Echis coloratus	Günther 1878
Eristicophis macmahonii	Alcock & Finn 1896
Pseudocerastes persicus	(Duméril, Bibron & Duméril) 1854
Vipera ammodytes	(Linnaeus) 1758
Vipera aspis	(Linnaeus) 1758
Vipera berus	(Linnaeus) 1758
Vipera bornmuelleri	Werner 1898
Vipera kaznakovi	Nikolsky 1909
Vipera latastei	Bosca 1878
Vipera latifii	Mertens,Darevsky & Klemmer 1967
Vipera lebetina	(Linnaeus) 1758
Vipera russelli	(Shaw) 1802
Vipera seoanei	Lataste 1879
Vipera ursinii	(Bonaparte)1835
Vipera xanthina	(Gray) 1849

The species of viperine snakes can be divided, in purely geographic terms, into 3 fairly distinct groups; whether any of these are also monophyletic groups will be discussed subsequently.

One group is virtually restricted to Africa south of the Sahara (the Ethiopian zoogeographic region). The one exception within the group is Bitis arietans, whose range extends northwards into the southwestern periphery of the Arabian Peninsula, and in parts of northwestern Africa to extreme southwest Morocco. This group, here referred to as the 'African group', includes the monotypic Adenorhinos, 7 arboreal species of Atheris plus the terrestrial species hindii and superciliaris recently assigned to Atheris (Marx & Rabb, 1965), 12 species of Bitis, and the 6 species of Causus.

The second group comprises 2 species of Cerastes and about 4 species of Echis (E.coloratus and members of the carinatus-complex), occurring mainly in the arid zone intermediate between the Ethiopian and Palaearctic regions (chiefly in the Sahara and its extensions, including Arabia, but with E.carinatus spreading further east into Iran, Turkestan, Afghanistan, Pakistan, India, and Sri Lanka). This group may be referred to as the 'Saharo-Arabian group'.

The third group includes about 12 species of Vipera plus the monotypic Pseudocerastes and Eristicophis, and is almost entirely restricted to the Palaearctic zoogeographic region. The major exception is V.russelli, occurring in Pakistan, India, Sri Lanka, and parts of southeastern Asia (ie. within the Oriental zoogeographic region). Two species V.latastei and V.lebetina, extend into parts of North Africa, in an area usually included within the Palaearctic region. This group is here referred to as the 'Eurasian group'.

The informal group names used here are simply for convenience in the brief characterisation of the many species involved given in the following part of this section. No implication is intended that these are monophyletic groups. At all times during this study morphological comparisons have been freely made between all species, an effort was made to avoid an a priori division, on a geographical basis, of the species to be investigated, since this could be expected to obscure the sought-after phyletic patterns within the group. A previous study of viperine phylogeny (Marx & Rabb, 1965), initially divided the viperines into Palaearctic and Ethiopian groups that were then treated almost completely separately. The 'Saharo-Arabian' group (Echis and Cerastes) with the 'Eurasian group', above, is equivalent to the 'Palaearctic stock' of Marx & Rabb (1965).

To briefly preview some results of the present study, it has emerged that the 'Eurasian group' form a phenetically coherent assemblage and may well be strictly monophyletic. The 'African group', however, includes at least 2 separate groups of species, with those of the genus Causus being phenetically and cladistically distinct from all other viperines. The 'Saharo-Arabian group' is not only geographically intermediate between the Eurasian and African groups, but is intermediate in several aspects of morphology between the Eurasian species and the African group of 'true Viperines' (ie. all except Causus).

b. Sample examined

Of the 48 species in the above list, all but *Atheris katangensis* (specimens unavailable) and *Bitis parviocula* (known only from the type specimen) have been examined.

Features of external, visceral, and hemipenial, anatomy have been examined in at least 2 specimens of virtually all species; in addition, external features alone have been examined in all or a majority of further specimens available (ca. 3 - 15) of most species. Most of the viscera had been removed from the 2 specimens of *Adenorhinos* (but the anterior portion of the trachea remained so it was possible to determine that a tracheal lung is present). Jaw muscles and cranial osteology have been examined in at least one specimen of each species; in many cases, and in all critical species (where more than 1 specimen was available for dissection), I have prepared or examined from 2 to 5 skulls. In a few cases (including certain rare species) where information on a particular feature of head anatomy was required, I have examined the relevant portion of second or further specimens by reflecting part or all of the skin of the head without dissecting the jaw muscles fully, or fully preparing the skull.

For comparative purposes, where published information was lacking, it has been necessary to examine *Azemiops*, several crotalines, and several non-viperid snakes.

c. Viperine snakes - introductory notes.

(i) African group

Adenorhinos barbouri, a poorly-known form occurring in the Ukinga and Uzungwe regions of the southern highlands of Tanzania, was originally described as a member of the genus *Atheris* by Loveridge (1930, 1933). *Adenorhinos* is a relatively short-bodied snake, with the head not strongly triangular in plan, and appears to be of secretive terrestrial habits. Marx & Rabb (1965:182,184) noted that *barbouri* differs from the true arboreal *Atheris* in several anatomical characters (particularly in the unique form of the nasal scale and the ectopterygoid, and other features of head scalation and cranial osteology), and apparently also in ecology. In recognition of these differences they removed *barbouri* to the new monotypic genus *Adenorhinos*. Marx & Rabb (1965:184) also believed that *Adenorhinos* was unique among viperines in possessing a "compound mucus secreting nasal gland", however, Taub (1966:532) has re-interpreted this structure as a portion of the supralabial gland (Taub also quotes Rabb as agreeing that it is not a nasal gland). Although this re-interpretation removes one point of difference between *Adenorhinos* and *Atheris*, numerous other differences remain.

Marx & Rabb (1965:184) proposed that *Adenorhinos* may represent "a radiation....toward a subterrestrial life", and that it is "apparently adapted for feeding on soft-bodied animals". These inferences are quite likely to be correct, although published information is a little ambiguous. Their statement (1965:184) that Loveridge "found an earthworm in the gut of one *barbouri* among several that were "dug up" when hoeing for planting", is misleading. Loveridge actually says (1933:278) that an earthworm was found in a young *barbouri* caught while crossing a road. The diet of adults remains unknown (the gut and most other viscera have been removed from the two specimens I have been able to examine), and the young of many viperines are known to feed on a variety of invertebrates, including earthworms. Loveridge also suggests that a pair "dug up" when hoeing may actually have been "concealed among sods such as litter the gardens", this does not necessarily indicate subterrestrial habits since many viperines are similarly secretive. While Loveridges' information is strongly suggestive of radical differences in ecology as compared with other viperines, it would be most valuable to have some new field observations. It is certainly true that Adenorhinos differs from arboreal Atheris, and other viperines, in several features of head and body proportions, head scalation and cranial osteology.

Marx & Rabb (1965:Fig.40) appear to believe that Adenorhinos is not at all closely related to Atheris, but that the genera Adenorhinos, Atheris, and Bitis, form 3 entirely separate lineages descended from a common African ancestry. Böhme (1977:66) further suggests that such an ancestral group may have been centred in the east African mountains. However, clear evidence has emerged in the present study (pp.) that Adenorhinos and Atheris are more closely related to each other than either is to Bitis.

The 7 arboreal species of Atheris (Tree or Bush-Vipers) occur in forest regions at various altitudes, and upland swamps (A.nitschei), from West Africa across to East Africa. Although primarily arboreal, hunting may take place mainly on the ground. They are moderately or very slender in body porportions, with a short triangular head, a wide gape, and a strongly prehensile tail. They are cryptically camouflaged in various combinations of green, yellow, and black (with a tendency to melanism in some forms). The scales of A.squamiger, and particularly A.hispidus, themselves have a 'leafy' appearance, with the apex and median keel of each scale being much extended. In some Atheris species the flank scale keels are serrated, as in *Echis* and *Cerastes*, and *A.desaixi* (Ashe, 1968:56) and *A.nitschei* (Goetz, 1975: 198) have been reported to show a similar warning display, in which the snake coils upon itself and rubs the flank scales together. Certain species are superficially very similar to some arboreal crotalines of the genera *Bothrops* and *Trimeresurus.* Pitman (1974) provides valuable ecological data for 3 species.

Atheris chloroechis and *A.squamiger* are widely distributed in West and Central Africa; *A.katangensis*, *A.hispidus*, and *A.nitschei* occur in the Congo region and adjacent areas; *A.desaixi* is restricted to the region of Mr.Kenya and a locality in the Nyambeni Hills (Rilling, 1972), while *A.ceratophorus* is restricted to the Usambara area of Tanzania.

Ashe (1968:56) suggested that, on the basis of snout scalation, the species of *Atheris* may be arranged in two groups (*ceratophorus*, *chloroechis*, *desaixi*, and the remainder in a second group), perhaps to be ranked as subgenera. Marx & Rabb (1965:Fig.40) suggested only that the arboreal *Atheris* (not including *hindii* and *superciliaris*) share an immediate common ancestor (*A.desaixi* was described subsequently to their paper).

The 2 problematical terrestrial species, *hindii* and *superciliaris* were both originally described as species of *Vipera.* In general body proportions and in certain details of scalation, they do indeed resemble *Vipera*. They each have a restricted range in East Africa; *hindii* in montane moorland in the Aberdares range of Kenya and a locality on Mt.Kenya, *superciliaris* primarily in swampy lowlands to the south of Lake Malawi in Malawi and Mozambique), specimens are also known from near the north end of Lake Malawi (in Tanzania) and from northeast Mozambique (type specimen from Cape Delgado). Some biological information on *hindii* is given in Ionides & Pitman (1965), Pitman (1965), and Andren (1976), and on *superciliaris* in Stevens (1973).

It would be of considerable zoogeographic interest if these two forms were truly closely related to Vipera, essentially all species of which are Palaearctic in distribution. However, it seems quite clear after Kramer (1961a), Marx & Rabb (1965), and the present study, that hindii and superciliaris are not actually closely related to Vipera. In an analogous situation among lacertid lizards, Arnold (1973) has shown that African 'Algyroides' and 'Lacerta' are not closely related to the supposedly congeneric Palaearctic forms. Kramer (1961a) assigned hindii and superciliaris to the African genus Bitis (suggesting an especially close affinity to B.atropos, cornuta, and worthingtoni), primarily on the basis of shared resemblance in the shape of the postorbital bone and in colour pattern. Marx & Rabb (1965:182) removed the 2 species to the African genus Atheris on the basis of shared resemblances in 3 characters, "... the type of ectopterygoid, absence of a supranasal sac, and a narrow postorbital...". In cladistic terms these latter 3 characters are certainly primitive (plesiomorph) resemblances that in themselves give no basis for suggesting recent common ancestry. It may be recalled (section A.2) that the existence of a distinct monophyletic evolutionary lineage may be hypothesised on the basis of shared uniquely derived features; shared primitive features simply indicate non-evolution in those particular features, and as such may be retained as phenetic similarities by relatively unrelated forms. However, it does appear from evidence collected in the present study that hindii and superciliaris are more closely related to Adenorhinos and the true arboreal Atheris (Atheris sensu stricto) than to other viperine species. The 2 species differ from each other in many characters, and it seems quite probable that they do not form a monophyletic pair. Marx & Rabb (1965:Fig.40) suggest that they do form a monophyletic group that itself is monophyletic with a group formed of the arboreal Atheris (Atheris s.s.);

these workers assigned all these species to the genus *Atheris* (ie. *Atheris sensu lato*).

The genus *Bitis* includes 12 terrestrial species virtually restricted to sub-Saharan Africa. Although the species show a considerable range of morphology, they share certain distinctive derived features, in particular, a crescentic supranasal scale and a supranasal sac (Boulenger, 1896:493; Parker, 1963), a flanged ectopterygoid, and a broad postorbital (Marx & Rabb, 1965:181). In terms of body size, they can readily be divided into two groups. One group of dangerously venomous species (*B.arietans*, *gabonica*, *nasicornis*) may attain a very large size, with a broad flat triangular head, very stout trunk, and a very short tail. FitzSimons (1962) and Pitman (1974) include much valuable ecological data. *Bitis arietans* (Puff Adder) is the most widely distributed species, occurring throughout the non-forested regions of Africa, chiefly south of the Sahara, but also extending as far as southwest Morocco and southwest Arabia. *Bitis gabonica* (Gaboon Viper) and *B.nasicornis* have a distribution complementary to that of *arietans*, occurring in forest regions of West and Central Africa, and with B.gabonica extending southeast into Natal. Both *gabonica* and *nasicornis* have a complex multicoloured pattern which probably has a disruptive camouflage effect in a leafy forest floor environment. *Bitis gabonica* in particular may reach a very large size, occasionally exceeding 6 feet in length and 1 foot in girth.

Bitis parviocula, from the forested highlands of southwest Ethiopia, is a recently described addition (Böhme, 1977) to the 'big *Bitis*' group. This species is known only from the single type specimen, which I have not seen. Dr. Böhme was kind enough to send some excellent colour transparencies for examination. The specimen seems to combine pattern and head shape features of both *B.arietans* and *B.nasicornis*, and at first sight looks like a possible arietans x nasicornis hybrid individual. Böhme (1977:64) considers and discounts, this possibility, and rightly points out that only arietans has previously been found in Ethiopia. Probable hybrids of arietans x gabonica (Broadley & Parker, 1976), gabonica x nasicornis (Hughes, 1968), and nasicornis x arietans (Hughes, pers. comm. 1978), are known; this represents all three possible combinations among the big Bitis species (excluding B.parviocula). Böhme suggests that parviocula may be of subterranean habits, largely on the basis of head proportions and reduced eye and nostril size.

The second group of Bitis includes 8 small-size species ('dwarf Bitis'), each with a relatively restricted distribution. All but B.worthingtoni are restricted to southern Africa. Bitis worthingtoni is a very poorly-known form occurring chiefly in the Gilgil and Naivasha regions of Kenya, immediately to the west of the Aberdares range; it also occurs north of the Rift at Eldoret and a little way south at Kijabe. It favours higher ground and has not been found below 1500m (Spawls, 1978:12). An equally poorly-known species is Bitis heraldica from the upland regions of west-central Angola (Mertens, 1958). The remaining 6 species are relatively better-known; Branch (1977), FitzSimons (1962, 1970), Haacke (1975), and Robinson and Hughes (1978), include valuable ecological data. They occur in a variety of non-forest habitats. Bitis atropos (whose venom has a predominantly neurotoxic effect, unusual for a viperid venom) has several isolated populations scattered through the eastern uplands from the Inyanga Mountains of Rhodesia, south through the east Transvaal and the Drakensbergs, and down to sea level in eastern Cape Province. The last 5 species are restricted to relatively lower altitude, more or less arid regions in the west and south of southern Africa (only B.caudalis extends eastward through the Kalahari to southwest Rhodesia and the Transvaal). Bitis cornuta, and more especially B.xeropaga, occur on rocky outcrops or hills. Bitis caudalis, peringueyi, and schneideri, are found in flatter sandy areas. The latter 2 species are strictly sand-desert forms, peringueyi being restricted to the Namib sand dunes, and schneideri occurring in more vegetated sand areas immediately to the south. The sand-living species typically use sidewinding locomotion, and are able to sink vertically under the surface of the sand. The eyes of B.peringueyi are dorsal in position, so that vision may be little impaired while the snake is thus concealed (a similar condition occurs in some other sand-sinkers such as Cerastes vipera and the boid Eryx jayakari).

While the 'big Bitis' and 'dwarf Bitis' differ conspicuously in size and in colour pattern, Underwood (1968:83) has reported a major internal difference between Bitis species. The small Bitis (including B.peringueyi and xeropaga, not seen by Underwood) except B.worthingtoni, lack a well-developed tracheal lung; a tracheal lung is present in almost all other viperids, including Bitis worthingtoni and the big Bitis (this character is not known for B.parviocula).

The 6 species of Causus (Night Adders) occur in Africa south of the Sahara. Causus rhombeatus is the most widely distributed, in savanna regions from Sudan to Cape Province. Causus defilippii and C. resimus are found through much of eastern Africa, with the latter extending in the west to northern Nigeria. Causus bilineatus, lichtensteini, and maculatus, are more western in distribution; lichtensteini is widespread in rain forest regions, maculatus is a forest form in Zaire but also occurs in savanna in West Africa (Hughes, 1977). They are all chiefly nocturnal, and feed almost exclusively on frogs and toads. Pitman (1974:201) notes that prey is often swallowed alive, without use of the fangs, but FitzSimons (1970:186) observes that larger prey may be held in the mouth until dead, and also (1962: 328) that frogs and toads are extremely susceptible to

Causus venom. Causus differs from other viperids in having a round pupil and large head shields, both being features characteristic of most caenophidian snakes, and the latter, in particular, probably primitive within viperids. There are also differences from other viperids in many other characters of external and internal anatomy. Four species (C.resimus, rhombeatus, bilineatus, and maculatus) are unique among viperids in having the venom glands much elongated posteriorly, extending into the neck region. As noted elsewhere in this report, species of Causus may not be the closest relatives of the remaining snakes currently assigned to Viperinae.

(ii). Saharo-Arabian group

The 2 species of Cerastes, C.cerastes and C.vipera, occur through the Sahara desert and its margins. While C.cerastes also extends further eastwards throughout the Arabian Peninsula, C.vipera appears to reach its eastern limit in the Negev. They both use sidewinding locomotion, are able to sink vertically into the sand, and are sandy in general colouration, with patterning frequently reduced or absent. Some individuals of some populations of C.cerastes (Horned Viper) have large supraocular 'horns' formed of a single elongate scale. Cerastes vipera is usually smaller in size than C.cerastes, the eyes are dorsal in position, and there is a strong superficial resemblance to Bitis peringueyi of the Namib Desert. Although C.vipera is largely restricted to loose sand areas, C.cerastes is frequently found in sandy areas with scattered rocks and vegetation (data for Libya; Schnurrenberger, 1959).

The genus Echis (Carpet Vipers) until very recently contained only 2 described species; coloratus in the Arabian Peninsula, Sokotra, Israel, and eastern Egypt, and carinatus with a much wider range, from West Africa through most of the Sahara region, including North Africa, south into northern Kenya, then into much of Arabia (but absent from Sinai and Israel), and from Iran into Turkestan and east to India and Sri Lanka. *Echis carinatus* is both highly abundant in some areas, and highly venomous. It has frequently been cited as the world's most dangerous snake, in terms both of morbidity and mortality (Warrell & Arnett, 1976).

It has recently been demonstrated (Roman, 1975) that '*carinatus*' is represented by two good species in West Africa. Roman separated specimens from the sahel zone as a new species, *Echis leucogaster* (previously regarded a subspecies of *carinatus*; Roman, 1972) Hughes (1976) was uncertain whether *leucogaster*, or the second West African form *E.carinatus ocellatus* (Stemmler, 1970), should be treated as specifically distinct from typical *carinatus*. In the absence of specimens from critical areas, Hughes preferred to regard both *leucogaster* and *ocellatus* as full species of *Echis*. Several differences have emerged in the course of the present study between eastern and western populations of *Echis carinatus*, and it seems likely that further study could resolve the present confused picture. It is sometimes convenient to refer to this population group as the 'carinatus-complex', or as *carinatus* (*sensu lato*).

All forms of *Echis* inhabit arid regions; while *E.carinatus* (s.l.) is typically found on sandy substrates *E.coloratus* frequently occurs in more rocky habitats, sometimes at rather higher altitudes. Ionides & Orme Smith (1965:126) record that *E.coloratus* and *Cerastes cerastes* occur "side by side" in a mixed sand and rock habitat in South Yemen. Biological information on *E.carinatus* can be found in several works including, Deoras & Vad (1965-66a), Duff-Mackay (1965), Minton (1966), and Pitman (1973); Mendelssohn (1965) includes much valuable detail on *E. coloratus* (and notes, p.201, habitat separation of *coloratus*, *Cerastes cerastes*, and *Pseudocerastes persicus fieldi* in the Yotvata region of Israel).

A striking and almost unique external feature shared by *Echis and Cerastes* is that the flank scales are set at an angle to the long axis of the body, and the keels of these scales are prominently serrated. When alarmed the snake can produce a prolonged hissing noise by moving the body in multiple loops and rubbing the comb-like serrations together. It has been suggested (Mendelssohn, 1963:146-7) that this system may be of adaptive value to these desert species, perhaps serving to minimise respiratory water loss, since it is unnecessary to ventilate the respiratory tract in sound production (in contrast to the 'vocal' hissing of other snakes).

(iii) Eurasian group

The approximately 12 species of *Vipera* occur in relatively mesic habitats across Eurasia. In contrast, the other 2 members of this group, the monotypic *Pseudocerastes* and *Eristicophis*, are found in more arid regions of the Mid-East and southwest Asia, the latter being restricted to sand deserts in Baluchistan and Seistan.

All the species are primarily terrestrial. The trunk is moderately stout in form, with a short tail. There is neither the extreme slenderness of some of the arboreal *Atheris*, nor the extreme stoutness of the large *Bitis* (both the latter being African genera). The head may be either moderately or very distinct from the neck, and in the latter case is prominently triangular in plan.

When adult they feed chiefly on small vertebrates, frequently small mammals, birds or lizards rather less frequently. A notable exception is *Vipera ursinii*, whose diet includes a high proportion of Orthoptera and other insects. *Pseudocerastes persicus fieldi* has been reported to readily take carrion (Mendelssohn,1965). Numerous works provide information on the biology and systematics of various Eurasian viperines, including; Arnold & Burton (1978), Bruno (1977), Darevsky (1966), Duguy (1972), Eiselt & Baran (1970), Kramer (1961b), Kretz (1972), Mendelssohn (1963), Minton(1966), Saint Girons (1973, 1975a, 1975b, 1976, 1977a, 1977b), Smith (1943, 1973), Steward (1971), Street (1979). Valuable data on *Pseudocerastes* and *Eristicophis* may be found in Mertens (1965), Minton (1966), Smith (1943); on *Pseudocerastes* also in Mendelssohn (1965); and on *Eristicophis* in McMahon (1897a, 1897b), Guibe (1957:141, under the synonym *Pseudocerastes latirostris*), and the original description of Alcock & Finn (1896).

Within the Eurasian group, *Vipera berus* (Common Adder) has the most extensive distribution.It is found in a variety of habitats (marshland, grassland, deciduous or coniferous forest margins, heathland) from France in the west across the entire continent to Sakhalin in the east. It also occurs at higher latitudes than any other viperine, extending inside the Artic Circle in Scandinavia. *Vipera seoanei*, in the north of the Iberian Peninsula (and just across the border into France; Duguy, 1975), was until recently (Saint Girons & Duguy, 1976) usually treated as a sub-species of *V.berus*. A third species *V.ursinii*, overlaps in a few parts of the northern edge of its range with *V.berus*. *V.ursinii* has several isolated populations; in highlands in southeast France, central Italy, and Yugoslavia (*V.u.ursinii*); in lowlands of Central Europe *V.u.rakosiensis*); in grasslands of the USSR (*V.u.renardi*, sometimes treated as a full species); in southwest Turkey (*V.u.anatolica* ; now synonymised with *V.u.ursinii*,St. Girons, 1978:581), and in highlands in the region of the Caucasus, eastern Turkey, and the Elburz Mountains of Iran. The status of the Caucasian/east Turkish form, and its relation to the Elburz form (Wettstein, 1953; named *V.u.ebneri* by Knoepffler & Sochurek, 1955) requires investigation (both are grouped in *V.u.ebneri* by St. Girons 1978). *Vipera kaznakovi*, formerly confused with both *V.Berus* and *V.ursinii* occurs in the western Caucasus region and in extreme northeast Turkey (Kramer, 1961; Kretz, 1972). These four species are phenetically quite similar. Compared with other Vipera they are typically relatively slender in build, with the head not prominently triangular, smaller in size, the large head shields (characteristic of caenophidian snakes, and the viperids Azemiops and Causus)are not so fragmented, and they lack any specialisation of the snout (the latter being characteristic only of the following 3 Vipera species).

Three species of Vipera are largely restricted to southern Europe, with a different species being widespread in each of the 3 mediterranean peninsulas. Vipera ammodytes occurs in the Balkan Peninsula, north to northeast Italy and southern Austria, east to Rumania and European Turkey, parts of southwestern Asian Turkey, and with an apparently isolated population (V.a.transcaucasiana) in the Armenian region of the USSR and northeast Turkey. Vipera aspis is found in Italy, south and central France, extreme northern Spain, and in parts of Switzerland and Germany. Viper latastei (two sub-species) occurs over most of the Iberian Peninsula, and in certain Mediterranean regions of Morocco and Algeria, with an isolated dwarf montane form in the high Atlas,(the third sub-species, V.l.monticola). These 3 species are phenetically quite similar. The snout in V.aspis is distinctly upturned, in V.ammodytes and V.latastei it forms a prominent 'nose horn'. V.aspis and V.ammodytes possess a derived karyotype pattern (2n = 42; 2n = 36 in other viperids; Saint Girons, (1977a), Saint Girons (1977a:47) considers that this has evolved in parallel in these two species. Vipera seoanei and some populations of V.aspis tend to bridge the phenetic gap between these 3 species and the 4 noted in the previous paragraph. There are few areas where any of these species are sympatric; a valuable study of one such area has been been made by Saint Girons (1975a), other instances of near or definite sympatry are noted by Duguy & Saint Girons

(1978), Duguy et al (1979), Bruno (1965), and Lorenzo (1977). The distributions of what may be termed the '*berus*-group' and the '*aspis*-group' are largely complementary, the former occurring at higher latitudes and the latter at lower latitudes.

There is a quite clearly defined phenetic gap between the mainly European group of *Vipera* noted above, and the remainder of the Eurasian group of viperines, which are restricted to Asia. A conspicuous external difference lies in the scalation of the nasal region (further modified in *Pseudocerastes* and *Eristicophis*), there is also increased fragmentation of the head shields, and in most forms, a distinct increase in body size.

There is a group of allopatric forms (here termed the '*xanthina*-complex') in Israel, the Levant, Turkey, the Armenian region of the USSR, and northwest Iran, all of which have at some time been treated as conspecific with the Turkish *Vipera x.xanthina*. Both *V.x.palaestinae* of Israel, adjacent Jordan and Lebanon, and probably Syria, and *V.x.raddei* of the Armenian regions of USSR and Turkey, were originally described as full species (by Werner, 1938, and Boettger, 1890, respectively). They were subsequently treated as subspecies of *V.xanthina* by Mertens (1951, 1952), without any significant discussion to justify the change in status. This treatment was then followed in the standard checklists of Mertens & Wermuth (1960), and Klemmer (1963,1968). Some Israeli workers (eg.Kochva, 1958,1962; Frankel & Kochva, 1970) have treated *palaestinae* as a full species again, but without discussion of the matter (their papers cited are concerned with anatomy, not taxonomy). A form similar to the Turkish *V.xanthina* occurring in the mountains of north Lebanon, and later found by Israeli workers on Mt. Hermon (Syria), was treated as a full species, *Vipera bornmuelleri* by Mertens (1967). Another form, *Vipera latifii*, most similar to *V.x.raddei* in particular, among this complex, was newly described in 1967 (Mertens, Darevsky & Klemmer).

Whether some or all of the 5 forms noted above should be regarded as full species or as subspecies of V.xanthina is a rather finely-balanced question, and one that is insoluble by the criterion of reproductive isolation in sympatry, since all the forms are allopatric. A close approach to sympatry is made by bornmuelleri and palaestinae in Lebanon; here palaestinae occurs in the lowlands (Zinner, 1967) and bornmuelleri occurs in the northern highlands (where it is possibly in sympatry with Vipera lebetina - specimens in the BMNH). A similar altitudinal separation probably occurs in the Mt. Hermon area (see map in Kochva, 1974). In such a situation it becomes necessary to assess degrees of morphological difference; because it has become evident that each form is rather distinct, I have treated them separately in this study. Through the extreme generosity of Dr. M. Latifi, I have also been able to examine specimens of a presently undescribed form occurring in northwest Iran that is very similar to raddei.

Vipera lebetina has sometimes been included with the xanthina-complex outlined in the previous 2 paragraphs. This species, or species-complex is present in 2 geographical regions, north Africa, and west/central Asia. The desert forms southeast of the Atlas Mountains (Vl.deserti) and the remaining north African populations (V.l.mauritanica Morocco, Algeria, Tunisia, western Libya), have recently been combined into a single full species, Vipera mauritanica (Kramer & Schnurrenberger, 1959, 1963). Other workers have disagreed with this arrangement (eg. Pasteur & Bons, 1960; Klemmer, 1968). Examination of material in the BMNH has suggested that there may be 3 fairly distinct forms in North Africa, but field observations and more material would be necessary to pursue the matter. I have not attempted to investigate the detailed systematics of the 'lebetina-comclex', but have examined specimens from both the North African and the Asian portions of the range.

Eastward of the North African range, there is a gap in distribution covering most of Libya, Egypt, Israel, the Arabian Peninsula, and most of Iraq and Syria, until the Asian range of *Vipera lebetina* begins. This species may have been present in the Palestine region until quite recently; there is a BMNH specimen collected by Tristram, supposedly in Galilee (see Tristram, 1888:146, under '*V.euphratica*'), but no specimens have subsequently been reported from Israel (Mendelssohn, 1963:150). In Asia *lebetina* extends from northern Lebanon and Syria, eastern Turkey, northeast Iraq, and the east Caucasian region, through Iran to Turkestan, Afghanistan, Pakistan, and Kashmir. The central Asian forms have been assigned to *V.l.turanica*, the remaining Asian forms to *V.l.obtusa* (*V.l. euphratica*, type specimen from Birecik in southeast Turkey, is synonymous with *V.l. obtusa*, Eiselt & Baran, 1970:367). There are also 2 isolated island populations of *lebetina*, on Cyprus (*V.l.lebetina*) and in the Cyclades (*V.l.schweizeri*).

The region immediately to the west of the Indus River forms the eastern boundary of the range of *lebetina* and the western boundary of that of *Vipera russelli*. *V.russelli* is a very distinct large species occurring in grassland, scrubland, and forest margins, through the Indian subcontinent from the Himalayan foothills to Sri Lanka, and eastward through Burma to northwest Thailand. There is a probable gap in the range, and a further population in Taiwan and the Kwangtung region of China, and certainly isolated populations in eastern Java, Komodo, Flores and Lomblen (Brongersma, 1958). *V.russelli* is phenetically highly divergent from the other *Vipera*, particularly in features of the internal anatomy, but shares certain characters with *palaestinae* among the more conservative *Vipera* (indeed it is easy to see why Tristram, 1888, assigned the form now known as *V.x.palaestinae* to the genus *Daboia*, erected by Gray, 1842 (and see Gray, 1849).

for V.russelli; Daboia also included, less justifiably, V.x.xanthina).

The remaining 2 genera are monotypic and restricted to southwest Asia. They are together distinct from Vipera in several, probably derived characters (eg. presence of a supranasal sac), but also differ from each other in certain features (Pseudocerastes has prominent supraocular horns, Eristicophis has several unique characters, notably in scalation). Marx & Rabb (1965) synonymised Pseudocerastes with Vipera because they believed the differences between these two genera were less than those distinguishing them from Eristicophis, they appear to suggest that Eristicophis is not especially closely related to Vipera/Pseudocerastes (1965:46). Because of the derived features shared by Pseudocerastes and Eristicophis, I suggest, contrary to Marx & Rabb, that these 2 genera form a strictly monophyletic group.

Pseudocerastes occurs in Pakistan and Iran (P.p.persicus), and in Sinai, Israel, Jordan, extreme northern Saudi Arabia, and western Iraq (P.p.fieldi). Specimens have recently been found in Jebel Akhdar region of Oman (Arnold & Gallagher, 1977), and in the Ruus al Jibaal (highlands of the Musandam Peninsula; BMNH specimen). The recently-discovered Oman localities are in broken rocky country at relatively high altitudes (1860,2130m), but P.p.fieldi in Israel occurs on more or less level sandy ground, at lower altitude, often with scattered rocks and shrubs (Mendelssohn, 1965). Localities reported for P.p.persicus in Iran and Pakistan seem to combine elements of both these extremes.

Eristicophis macmahonii is restricted to areas of loose sand in the northern Baluchistan desert region, comprising the Chagai district of Pakistan from Nushki westwards, and there is a single record from the Seistan region of Iran (Guibe, 1957; 'Pseudocerastes latirostris'= Eristicophis, Marx & Rabb, 1965:170).

Because it was discovered by members of the 1896 Afghan-Baluch Boundary Commission, Eristicophis is virtually certain to occur in Afghanistan also, although definite records are lacking. It has also been reported both from the Cholistan desert region of Pakistan (Mountford, 1969: 261, and in litt), and from the Rajasthan desert region of India (Krishna & Dave, 1956). Both these localities are east of Indus, within the Thar or Great Indian Desert, and would thus be of some zoogeographic interest(since Eristicophis is restricted to sand desert). However, both reports are unconfirmed. Mr. Tom Roberts, a prominent naturalist with almost 30 years experience in Pakistan, has kindly informed me (in litt.) that Eristicophis "definitely doesn't occur" in Cholistan. Also, although Krishna & Dave reported the presence of Eristicophis in Rajasthan in their 1956 paper, it was not included in the list of Rajasthan snakes in their later paper of 1960. It therefore seems unlikely, on present evidence that Eristicophis is to be found east of the Indus River (although the existence of 2 apparently independent reports from adjacent areas of the Great Indian Desert remains intriguing).

Eristicophis appears to be strictly nocturnal. Although it resembles Pseudocerastes in being able to use sidewinding locomotion, it differs in being able to sink vertically into the sand by lateral body movements (as can Cerastes and desert species of Bitis). McMahon (1897b:410) reports that Eristicophis "lies during the day with only its head showing above the sand, and it is almost impossible to distinguish it from the sand. At night, however, it used to sit up and hiss loudly whenever anyone approached it". Minton (1966: 159) reports, of a captive specimen,"that it fed readily on mice. Prey was seized as it approached the snake, lying buried in the sand. The snake usually retained its grip until the animal was dead or nearly so". Maynard (in Alcock & Finn, 1896:565) states that captive specimens fed freely on lizards, and Roberts (*in litt.*) suggests that lizards may form a major part of the natural diet. Most authors have noted the general pugnacity of *Eristicophis*, and the loudness of its hissing when aroused; Alcock (in McMahon, 1897b:421) reports that the new generic name (Alcock & Finn, 1896:564) was derived from the Greek for 'lover of fighting'.

B. CHARACTERS EXAMINED

Head scalation

There are several features involving the scalation of the head that show variation among viperine species. The probable primitive condition within vipers is outlined in the following paragraph, and the several separate characters treating this region are discussed subsequently.

Comparison with numerous and diverse non-viperid caenophidians, and among *Azemiops*, crotalines and viperines, make it possible to suggest the primitive form of scalation in the head region of vipers with considerable confidence.

The primitive condition, shown by the vast majority of Caenophidia, and fully retained by *Azemiops* (on other grounds the most primitive viper, see pp.198-205), and largely retained by *Causus* (also generally primitive) and partly by some crotalines, has the following features. The nostril is located more or less centrally in an elongate nasal scale, or the nasal scale may be partially or entirely divided dorsal and ventral to the naris, to form an anterior and posterior nasal scale. The nasal contacts the supralabials ventrally, the rostral anteriorly, and the internasal dorsally (and other scales posteriorly). The rostral is subtriangular or squarish in shape. The internasals are large, and contact the rostral anteriorly and each other in the midline (when, as in the majority of vipers, the scales of the head are more or less fragmented, the portion of the internasal remaining in contact with the nasal scale(s) is frequently termed the supranasal). On the dorsal surface of the head the standard 'colubroid' pattern of 9 unkeeled head shields is present; a pair each of internasals, prefrontals, supraoculars, parietals, and the unpaired frontal. There is an elaboration of spines or horns in the nasal or supraocular region. The ventral margin of the eye contacts the dorsal margin of one or more supralabial scales. The dorsal margin of the eye contacts the supraocular. There is not a high number of supra - and sublabial scales, or of rows of gular scales. All head scales, including gulars, are without keels.

Departures from the general pattern noted above are regarded as derived. Variations in this area within viperines may be divided into the following separate characters (numbers 1 - 10). It has long been recognised that there is a general trend in vipers toward fragmentation of the primitive large head shields, and other scales, which become replaced by smaller and more numerous scales in parallel in more than one lineage. The probable adaptive significance is that skin mobility, required by the fang erection system, would presumably be increased.

1.

Divisions of rostral scale (Figs 16-18)

In 'Atheris' hindii, true Atheris, and Adenorhinos there are two scales(further divided in certain Atheris) together having the same positional relationships as the single rostral scale of most other viperines and other out-group taxa. It appears that, in the former three taxa, the rostral has become divided by a horizontal suture into two scales. The lower of the two scales, since it is the median anterior-most scale bordering the mouth, is frequently termed the rostral scale although it apparently represents only the ventral segment of the primitive rostral. In hindii, Atheris and Adenorhinos the 'rostral' scale thus forms a transversely elongate rectangle, rather than the sub-triangular shape seen in most other viperids (the rostral is elongate in Cerastes, Bitis and Eristicophis, but in the latter this is associated with other unique modifications of the snout, and in the former two genera it is surmounted by irregular small scales and without any suggestion of a hindii-like mode of formation; other characters make it very probable that these represent three independent derivations).

A further derived condition is seen in certain species of Atheris (ceratophorus, chloroechis, desaixi), where the upper of the two rostral derivatives is divided into two scales by a median near-vertical suture. This feature was noted, in slightly different terms, by Ashe (1968:56) in the course of his description of A.desaixi. In one specimen of A.squamiger out of 15 examined the upper rostral was median in position as usual, but accompanied on the right side by an additional small scale. This was also the case in two out of 20 A.nitschei, where in three specimens there was also an additional scale on the left side. In one of 10 A.chloroechis the rostral scalation was very irregular, and difficult to assign to one state or the other.

A - primitive

B - horizontal division

hindii, *Adenorhinos*, *Atheris* *ss*.

C - upper 'rostral' with vertical division

Atheris ceratophorus, *A.chloroechis*, *A.desaixi*

D, E, F - parallel elongation of rostral

Bitis, *Cerastes*, *Eristicophis*

$$\begin{tikzcd}
 & A \arrow[r] \arrow[dl] \arrow[d] \arrow[dr] & B \arrow[r] & C \\
D & E & F &
\end{tikzcd}$$

An initial hypothesis, that states B & C are synapomorphies of *hindii*, *Adenorhinos*, *Atheris* *ss*., and of *Atheris ceratophorus*, *chloroechis* and *desaixi*, respectively, is not contradicted by other characters.

2.

Nasal-rostral separation (Figs 19 - 24)

Primitively the nasal (or anterior segment of a divided nasal) contacts both the rostral and the first supralabial (frequently the second also). This condition is retained among viperids by *Azemiops*, *Causus* and virtually all crotalines. Among the very many crotalines examined, only *Bothrops nummifer* was found to have the nasal partly or entirely separated from the rostral by small scales. The primitive condition is modified to various derived states in the great majority of viperines (except *Causus*), but an apparently primitive condition is retained by *Echis carinatus* and *'Atheris' superciliaris* (this fact, combined with overall differences in snout scalation among viperines, suggest a certain amount of parallelism in the trend towards an increased number of relatively smaller scales in the head region).

In the smaller species of Eurasian *Vipera* and in the sub-Saharan forms *hindii*, *Adenorhinos* and *Atheris* (s.s.), the nasal is entirely separated from the rostral by a single large 'naso-rostral' scale. The rostral, naso-rostral, and nasal arrangement in the East African *hindii* rather resembles that of the small *Vipera* (but the snout scalation and proportions are much modified in *Adenorhinos* and *Atheris*, probable close relatives of *hindii*). However, there are no other shared derived states shared by *hindii* and *Vipera*, and coupled with the evidence linking *hindii* (and *Adenorhinos*, *Atheris*) to other taxa (*superciliaris*, and possibly *Echis*, *Cerastes*), it seems most probable that the vertical suture resulting in the formation of a naso-rostral has appeared separately in these two groups, thus the naso-rostral in *hindii* is non-homologous with that in *Vipera*.

In the larger *Vipera* there is a single nasal of rather complex form that does contact the rostral. These (mainly southwest Asian) species are more derived in many characters than the smaller (mainly European) *Vipera* species.

There is also a clear indication of a partial suture in the position of that separating the nasal and naso-rostral in the small _Vipera_. Because of concordance with trends in other characters, I suggest that the large _Vipera_ are derived (secondarily 'primitive') in showing nasal-rostral contact, and that this contact is due to secondary fusion of the nasal with the naso-rostral. It is of course possible to interpret the partial suture as indicating incipient formation of a naso-rostral, ie., that the polarity is opposite to that suggested above, but this would run counter to the polarity of the several features in respect of which the larger _Vipera_ show derived states. In a few specimens of _V.lebetina mauritanica_, two (or three) small scales, not a single naso-rostral, separate the nasal and rostral. This would seem to be an autapomorphy of certain populations of North African _lebetina_, but insufficient material has been examined for further comment.

In _Pseudocerastes_ and _Eristicophis_, close relatives of the larger _Vipera_, the nasal scale is much modified in form, correlated with the presence of a supranasal sac (character 3). It is possible to derive the _Pseudocerastes_ snout pattern in which there is either two rows of small scales separating the nasal and rostral, or with two of these scales replaced by a single larger naso-rostral-like scale, from either a small _Vipera_ or large _Vipera_-like ancestry. Other characters suggest the latter is most probable, for example the close similarity with the atypical condition in some _V.lebetina_ (noted above) in which two small scales separate the nasal and rostral. The snout scalation of _Eristicophis_ is somewhat similar, but the nasal and rostral are separated by a large scale which, however, faces anteriorly instead of laterally and is surmounted by a large 'anterior supranasal', forming the "butterfly scaled" snout region noted by Marx & Rabb (1965:179). There can be no doubt, on the basis of nasal scale and supranasal sac morphology, that _Pseudocerastes_ and _Eristicophis_ form a monophyletic pair of species, and the snout scalation of the latter is readily derivable from a more *Pseuodcerastes*-like ancestor (*Eristicophis* is more derived than its sister species in several other characters; p.223).

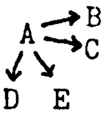
Overall within the Eurasian group of species it is possible to distinguish four derived states; state 1 - naso-rostral present (European 'small' *Vipera*); state 2 - naso-rostral largely fused with nasal (the 'large' *Vipera* ie. *xanthina* and *lebetina* groups, *russelli*); state 3 - presence of one large and a few small scale, or a few small scales only, between nasal and rostral (*Pseudocerastes* and *Eristicophis*); state 4 - "butterfly scaled" snout region (*Eristicophis*). In cladistic terms these are interpreted as a nested sequence of synapomorphies, state 1 delimiting the Eurasian group, and the remaining states delimiting progressively more exclusive groups.

The species of *Bitis* form a monophyletic group (p.209), and within this lineage only *worthingtoni* retains nasal-rostral contact. At least partly because of scalation modifications in association with the presence of the *Bitis* pattern supranasal sac (character 3), the nasal is not precisely similar to that of the taxa, such as *Causus*, that more certainly retain the primitive nasal-rostral contact. However, *worthingtoni* is also primitive to other *Bitis* in other characters (especially of cranial osteology, characters p.209), and there is no evidence that the nasal-rostral contact in *B.worthingtoni* is other than primitive. Parker (1932:221) suggests that the nasal-rostral contact is derived in *worthingtoni*, but the weak indication of a suture noted by Parker can be read in either evolutionary direction; the evidence noted above suggests that any trace of a suture is 'incipient' rather than 'vestigial'. In most *Bitis* two small scales separate the nasal and rostral, but *nasicornis* and *gabonica* are further modified (also in other characters p.210) in having 4-6 scales in this position.

In the two species of *Cerastes* the nasal and rostral are separated by one or a few rows of scales, but this resemblance to some *Bitis* is only superficial and other characters do not suggest any special relationship between the two genera. It is possible that *Cerastes* is closely related to *Echis* (p.226). *Echis carinatus* and *leucogaster* retain an apparently primitive nasal-rostral arrangement, but in some populations of *coloratus* a naso-rostral scale is divided off from the nasal. If *Echis* and *Cerastes* form a monophyletic group, this would seem to be yet another lineage in which modification of the primitive snout scalation has occurred, with a general trend toward increasing fragmentation of the scales of the head.

It has been necessary to take other cladistic characters, and overall phenetic resemblance, into account in interpreting this character, which is thus not of the highest cladistic significance.

A - primitive
B - naso-rostral present
Vipera (further modified in *Pseudocerastes*, *Eristicophis*)
C - naso-rostral present (parallelism)
hindii, *Adenorhinos*, *Atheris* *ss*.
D - several small scales separate nasal and rostral
Bitis (except *worthingtoni*)
E - several small scales separate nasal and rostral (parallelism)
Cerastes



3.

Supranasal sac (Figs 25-29)

In species of 4 genera of viperids (Bitis, Causus, Eristicophis, and Pseudocerastes) a form of cavity or invagination is present deep to the supranasal (internasal) or a portion thereof. This 'supranasal sac' was discussed by Schmidt (1930:229) in his description of Pseudocerastes fieldi (now Ps. persicus fieldi), and by Parker (1932:222) in his description of Bitis worthingtoni, but had been noted earlier by Boulenger (1896:492-3) in his generic diagnosis of Bitis. Lynn (1935:10) stated that a similar structure is present in Causus. Smith (1943:19,492) noted the presence of a supranasal sac similar to that of Pseudocerastes in Eristicophis.

Lynn (1935) has provided the only major discussion of the supranasal sac, with emphasis on Bitis, but a thorough anatomical-physiological study remains to be done. Lynn noted that although the region of the sac in Bitis is innervated by twigs of a latero-dorsal branch of the ophthalmic division of the trigeminal, this same general region around the nostril receives similar innervation in snakes such as Coluber constrictor that lack a supranasal sac. Auen and Langebartel (1977:210) state that this branch, the lateral nasal nerve, in Elaphe and Thamnophis "presumably distributes general sensoryfibres to the lining of the sac "(nb., 'sac' here refers to the nasal capsule, not a supranasal sac)" and perhaps secretomotor fibres as well as to the many small, simple acinar glands that are common to the sac's specialized olfactory epithelium. The principal part of the lateral nasal nerve continues inferiorly and anteriorly, lateral to both the nasal capsule and the nasal gland. The nerve terminates by cutaneous branches to the skin at the posterior rim of the external naris, and, more substantially, by a set of fibres that innervates the external nasal gland". A rather similar nerve distribution is also seen in viperines, including Bitis, Causus, Eristicophis and Pseudocerastes.

The concentration and relative thickness of these twigs of the lateral nasal nerve in viperines possessing a supranasal sac is only slightly increased in comparison to other viperines and other caenophidians, but it may be significant that many of the nerve twigs are seen (by gross dissection under a binocular microscope) to terminate specifically in the immediate region of the supranasal sac. Lynn (1935) demonstrated that the viperine sac is not homologous to the crotaline facial sensory pit, and also suggested that the supranasal sac does have a sensory function. The former is certainly acceptable, and the latter seems quite possible, although there is no relevant experimental evidence (Barrett, 1970:297).

Smith (1943:19) was the first to raise the possibility that the supranasal sac may not be a strictly homologous structure in all the groups possessing it. Marx & Rabb (1965: 175) suggest that "presence of such structures in groups as diverse as *Causus*, *Bitis*, and *Vipera* "(in which they include *Pseudocerastes*)" strongly implies an ancient shared genetic capacity in the viperine line or completely independent origin in each of these stocks".

In the present study, examination of the supranasal sac has revealed 3 distinctly different types, in terms of gross structure and pattern of innervation.

In *Causus* the sac is weakly developed (*C.bilineatus*, *defilippii*, *maculatus*, *resimus*, *rhombeatus*), or virtually absent (*lichtensteini*), and lies beneath a short postero-ventral extension of the supranasal. The supranasal is otherwise of unmodified standard caenophidian form. The posterior portion of the sac receives a few thin twigs of the lateral nasal nerve.

In *Bitis* the supranasal scale has a specialised form and relation to the nasal; it is prominently semicircular in shape and imbricates the nasal, the sac is formed by the overlap of the supranasal over the nasal. As stated by Lynn (1935:11) twigs of the lateral nasal nerve terminate in the floor of the sac. The third form of sac occurs in Eristicophis and Pseudocerastes. The relatively large external naris lies in the postero-dorsal corner of the large plate-like semicircular nasal scale, the well-developed nasal pad (Smith, 1943:19) is prominent within it. The antero-ventral portion of the naris leads to the vestibulum nasi while the postero-dorsal portion leads into a large supranasal sac lying beneath 3-5 scales on the dorsal side of the snout (which may include a moderately-developed supranasal scale). Unlike Bitis, the sac is not formed entirely by the supranasal, is not limited by it, and is independent of the nasal scale. Dissection has revealed that in both Eristicophis and Pseudocerastes it is the dorsal portion of the sac that is innervated, in contrast to Bitis where it is the ventral portion.

Although Smith (1943:19) is correct in his statement that the supranasal sac is entirely different in Bitis than in Eristicophis and Pseudocerastes, the suggestion that in the latter two forms the sac serves no special purpose but has merely been isolated in the hypertrophy of the nasal pad to act as a valve against sand (Pseudocerastes is found in sandy and rocky area, Eristicophis is restricted to areas of loose sand) is a little difficult to accept in view of the distinct innervation of the sac, and the fact that a valve-like development of the nasal pad has occurred in other arid zone snakes (eg. Cerastes, Malpolon without formation of a supranasal sac.

Marx & Rabb (1965:169) suggest that a "proto-sac" is present in Vipera lebetina, V.xanthina, and V.russelli (and is seen fully developed in Pseudocerastes persicus, which they assign to Vipera). While the interstitial skin between the supranasal and nasal may be slightly creased inwards in the former 3 taxa, this same slight crease is also present beneath the supranasal scale in specimens of those populations of Pseudocerastes that retain a large supranasal, but the true supranasal sac is also present in its typical location, It is therefore totally erroneous to suggest that *V.lebetina*, *V.xanthina*, and *V.russelli* possess a "proto-sac", homologous to the supranasal sac and to thus imply that a supranasal sac is a feature shared by *Vipera* and *Pseudocerastes* (Marx & Rabb, 1965, Table 5).

There can be no doubt that absence of a supranasal sac is the primitive state for viperines; it is absent in *Azemiops*, crotalines, most viperines, and all other snakes. In view of the considerable differences between the 3 types of supranasal sac in gross structure, location, and innervation, I conclude that the supranasal sac is non-homologous and developed in parallel in *Bitis*, in *Causus*, and in *Eristicophis* plus *Pseudocerastes* (there is no evidence to the contrary from other characters). The sac is somewhat variably developed in *Causus*, but of characteristic form and constantly present in all *Bitis*, where it constitutes a striking synapomorphy of the *Bitis* species, and of entirely different but equally characteristic form in the group *Eristicophis* - *Pseudocerastes*, where it constitutes a strong synapomorphy of *E.macmahonii* and *Pc.persicus* (contrary to Marx & Rabb, 1965:175;198, Fig.47).

A - primitive
B - *Causus*-type sac
    Causus (small in *lichtensteini*)
C - *Bitis*-type sac
    Bitis
D - *Pseudocerastes*-type sac
    Pseudocerastes, *Eristicophis*

$$\begin{tikzcd}
C & A \arrow[l] \arrow[r] \arrow[d] & B \\
 & D &
\end{tikzcd}$$

4.
Adenorhinos-type nasal (Figs 30-31)

As noted by Marx & Rabb (1965:182) the posterior portion of the nasal in Adenorhinos barbouri has a broad but shallow semi-circular excavation, around which the margins of the nasal form a more superficially-placed rim. This excavation is not associated with the supranasal (as is the supranasal sac of certain other viperines, Character 3), and the area does not appear to receive an increased innervation. The functional significance, if any, of the excavation is unknown.

This form of nasal is not seen elsewhere among viperids, and does not resemble the nasal of those advanced Vipera in which the nasal is somewhat concave posteriorly. The Adenorhinos form of nasal is here interpreted as an autapomorphy of A.barbouri, and as such simply indicates evolutionary change in a single lineage without giving any information on the cladistic affinities of that lineage.

In the original generic diagnosis of Adenorhinos Marx & Rabb (1965:186) associated a "subcutaneous nasal gland" with this unique form of nasal, and also stated (1965:184) that the presence of "a subcutaneous compound mucus secreting nasal gland in this species is unique in the viperines". However, on histological evidence Taub (1966:532) reinterpreted the gland in question as "a supralabial gland, most probably a pre-maxillary gland". Although, if correct, this reinterpretation significantly reduces the morphological distinctness of Adenorhinos in relation to other viperines (supralabial glands being present in all snakes), this genus does remain peculiar in several respects.

5.

Vipera russelli-type nasal scalation (Figs 32-34)

In most Vipera the naso-rostral scale (or the naso-rostral portion of the nasal, where the former is fused with the latter, Character 2) has a vertical or near vertical orientation. The supranasal scale (or scales) surmounts both the nasal and at least the posterior half of the dorsal margin of the naso-rostral. The snout, in dorsal view, may be rather blunt (eg.lebetina) or somewhat pointed (eg. ammodytes).

Unique to Vipera russelli and V.xanthina palaestinae, the slender naso-rostral portion of the nasal is prominently inclined forward, and the narrow supranasal, now exposed laterally more than dorsally, appears to wedge downwards between the naso-rostral section and the main portion of the nasal; the snout, especially dorsally, is distinctly narrowed. All these features are rather more developed in russelli than in palaestinae (noted for russelli by Smith 1943:483).

There is a clear and constant difference in snout morphology between palaestinae and its supposedly conspecific relatives. I propose that the russelli-type snout morphology noted above is a synapomorphy of palaestinae and russelli; this is concordant with shared derived resemblance in dorsal head patterning (and in general size and scale count increase, also shared with V.lebetina, Pseudocerastes and Eristicophis). A corollary of this proposal is that palaestinae should be regarded, not as a subspecies of V.xanthina (Mertens, 1951, 1952), but as a full species (as originally described by Werner, 1938). As noted above the form now usually known as V.x.palaestinae was previously (Tristram, 1888) assigned to the genus Daboia, which included russelli (and, with less justification, the Turkish form of xanthina).

A - primitive

B - Vipera russelli-type snout scalation

V.palaestinae, V.russelli

A→B

6.

Nasal horns (Figs 35-40)

In almost all snakes there is no elaboration of the snout region, and this would seem to be the primitive condition in viperines, but two distinct types of nasal 'horn' are developed in two viperine lineages.

Among the large *Bitis* group, *arietans* and the recently-described *parviocula* (Böhme, 1977) retain the primitive state, while in *gabonica* and *nasicornis* one or more pairs of scales at the tip of the snout, postero-dorsal to the rostral and between the nasals, are enlarged to form erect horns. Typically in *gabonica* there is one variably-developed pair of horns, whereas in *nasicornis* up to three pairs of scales are enlarged into horns, with the pair corresponding in position to that in *gabonica* being most strongly enlarged.

Among the smaller European *Vipera*, the top of the head, including the snout, is flat in *ursinii*, *berus*, *kaznakovi* and *seoanei* (occasionally the dorsal tip of the snout weakly raised), whereas in *aspis* the tip of the snout is distinctly upturned (very occasionally not prominently so), and in *latastei* and *ammodytes* the tip of the snout is extended dorsally into a distinct 'nose-horn'. Winokur (1977:251) has recorded the presence of cavernous tissue at the base of the nose-horn in *ammodytes*, that is "presumably capable of erection of the appendage". In *latastei* the rostral is typically drawn out dorsally to extend onto the anterior face of the nose-horn, which is covered by less than nine scales; in *ammodytes* the rostral does not extend up the nose-horn, which is usually covered by more than nine scales. These differences probably represent divergence from a shared ancestral condition. Regarding the polarity of these states in *Vipera*, it seems reasonable to suggest that the upturned snout is a synapomorphy of *aspis*, *latastei* and *ammodytes*, with the latter two species sharing a further modification, the full nose-horn.

A - primitive

B - double or multiple snout horn

Bitis gabonica, *B.nasicornis*

C - snout tip upturned

Vipera aspis

D - apical nose-horn

Vipera latastei, *V.ammodytes*

$$\begin{tikzcd}
A \arrow[r] \arrow[d] & C \arrow[r] & D \\
B & &
\end{tikzcd}$$

7.

Circumocular scales (Figs 41-42)

In almost all vipers the eye is separated from the supralabials by small scales (one or a few rows), that, with fragmented pre- and postoculars scales, form a ring of small scales around the eye, only broken dorsally by the supraocular (as in Caenophidia generally).

Unique to Vipera latifii, V.'x'.raddei, and a raddei-like form from N.W. Iran, the pre- and postocular scales meet dorsally above the eye, thus forming a complete circumocular ring, and isolating the supraocular from the eye (Boettger, 1890; Mertens et al,1967). This is proposed as a synapomorphy of the taxa noted above (and is one piece of evidence suggesting that raddei should be treated as a full species, as originally described by Boettger, 1890, not as a subspecies of xanthina, as stated by Mertens, 1951, 1952).

A - primitive

B - complete circumocular ring

Vipera latifii, V.raddei

A→B

8.
Supraocular shape (Figs 43-44)

Among the viperines retaining a discrete supraocular, its shape may vary from rather squarish to distinctly elongate, the outer margin is typically nearly straight or gently convex (outwards). Unique to V.latifii, V.'x' raddei, and a raddei-like form from N.W. Iran, the supraocular is distinctly triangular in plan, with the outer margin forming one apex. This is proposed as a synapomorphy of these taxa (see also Character 7).

A - primitive
B - triangular supraocular
Vipera latifii, V.raddei

A→B

9.

Supraocular horns

Supraocular horns have been developed, apparently independently, in several viperid species, eg. the crotaline Bothrops schlegeli, and in the viperines Pseudocerastes persicus (short triangular horn, several scales contributing to its base, apex formed of one or two adpressed tapering scales), Cerastes cerastes (single erect elongate scale, variably present or absent in same population), Atheris ceratophorus (two or three separate erect elongate scales), Bitis cornuta (nominate subspecies only, similar to A.ceratophorus), Bitis caudalis and worthingtoni (single scale), Bitis schneideri (like caudalis, but very weak).

The erratic taxonomic distribution of this feature, and differences in construction, make cladistic interpretations insubstantial.

10.
Head shield fragmentation

As noted above, all viperines except Causus show a derived condition in which the typical nine dorsal head shields of most Caenophidia are fragmented to some degree. There is good evidence that this shift has occurred in parallel several times in crotalines (Brattstrom, 1964; Burger, 1971), and this, coupled with wide intraspecific variation in some Vipera, tends to diminish the cladistic significance of this feature.

However, within the Eurasian group, when considered with other characters, this feature is of some importance. The four small European Vipera (ursinii, berus, seoanei, kaznakovi) all typically retain well-formed parietals and a frontal shield. In V.aspis there is a spectrum of variation from a berus-like pattern to a pattern, seen in the majority of specimens (eg. Bruno & Maugeri, 1977:151), where these three scales are almost unrecognisable. In ammodytes the frontal may be barely indicated, while there is complete fragmentation in all the mid-east and far east species of Vipera, eg. V.xanthina; this is accompanied by prominent carination of the head scales. In most lebetina, and in Pseudocerastes and Eristicophis, the supraoculars, retained by the above forms, are also fragmented, and there is an increased tendency to reduction of head scale carination.

A - primitive
B - frontal and parietals well-formed
Vipera ursinii, berus, seoanei, kaznakovi
C - frontal and parietals more or less fragmented, carination weak or absent
Vipera latastei, aspis, ammodytes
D - frontal and parietals fully fragmented, strong carination
Vipera xanthina, raddei, bornmuelleri, latifii, palaestinae, russelli
E - as 'D' but supraoculars also fragmented (except a few lebetina 'deserti')
and carination moderate or weak
Vipera lebetina, Pseudocerastes, Eristicophis

$A \rightarrow B \rightarrow C \rightarrow D \rightarrow E$

Head shield are fragmented in other viperines (except Causus), but taking other characters into account, this seems unlikely to be a homologous fragmentation.

11.

Keeling of gular scales. (Figs 45-46)

In almost all viperids, and in Caenophidia generally, there is no keeling of the gular scales. In three viperine lineages the gular scales are weakly to strongly keeled. In Eristicophis there is weak keeling; in Cerastes, keeling is weak in C.vipera, but moderately developed in C.cerastes; in most 'true' Atheris, (but not A.nitschei, and not the related forms hindii, superciliaris, Adenorhinos), gular keeling is strongly developed. It is most prominent in A.chloroechis, hispidus, and squamiger, but more similar to C.cerastes in A.ceratophorus and desaixi.

This feature has rather certainly evolved in parallel in these three groups (in Eristicophis and Cerastes very probably associated with sand-sinking behaviour, although this feature is not developed in the sand desert Bitis peringueyi), and is thus not of primary cladistic significance. However, it is important in suggesting that Atheris nitschei (keeling weak) is more primitive in this respect than the remaining 'true' Atheris (keeling present); given the other evidence relating Atheris species to one another, and the phenetic similarity among the group, there can be little doubt that this gular keeling is homologous in Atheris and thus a synapomorphy of Atheris other than nitschei.

A - primitive

B - gular carination strongly developed
Atheris (except nitschei)

A → B

12.

Scale surface microornament (Figs 179-189)

Variation in the microornament of the exposed surface (Oberhautchen) of the outerlayer of the squamate epidermis have been known for a considerable time (Leydig, 1873; Picado, 1931), but have only received significant attention following the advent of the Scanning Electron Microscope (eg. Burstein et al, 1974; Stewart & Daniel, 1975; Gans & Baic, 1974).

The morphology of the squamate epidermis has been the subject of much recent research (eg. Bryant et al, 1967; Maderson et al, 1978). The stratum corneum (the more superficial horny layer) forms by proliferation and keratinisation of the stratum germinativum; α-keratin in the deeper layers, β-keratin in the outer layers. The Oberhautchen is the exposed patterned surface of the β-keratin layer. Before sloughing, a new inner horny layer is formed under the existing outer layer. A cleavage zone appears immediately superficial to the newly-differentiated Oberhautchen of the inner generation, which becomes the new outer layer when the original outer generation is shed.

Most preserved museum specimens, unless freshly sloughed when preserved, retain both inner and outer cell generations of the stratum corneum. Usually, depending on the actual stage of the slough cycle, the outer layer (next to be sloughed) can be readily removed with forceps. Following washing (in alcohol or acetone, and one minute in an ultrasound bath, to assist in removing surface debris and bacteria), and drying in air, the 'scales' were glued to specimen stubs, coated in gold, and examined in a Cambridge 600 Scanning Electron Microscope.

As a preliminary partial check on the degree of within-individual and within-species variation, 'scales' from the lateral and dorsal levels of the anterior, mid and posterior trunk region of Vipera berus were examined; two specimens were used, one V.b.berus from France, and one

V.b.sachalinensis from Sakhalin Island, about 7,000 km away at the other end of Eurasia. In all cases an essentially identical Oberhautchen pattern was found. Significant intraspecific variation may well occur in other taxa, or between other V.berus populations, but it was not possible to check all viperines for this. Thomas & Dixon (1977) report that Philodryas and Tropidodryas species show a consistent patternin various stages of the slough cycle.

In most of the relatively conservative species of the Eurasian group, the small scale surface texture consists of ridges and intervening grooves, oriented approximately along the long axis of the scale. Frequently these are superimposed on a larger scale relief, consisting of more widely spaced larger ridges. Quite similar conditions are present in Azemiops (but with features unique among vipers), and in the few other snakes examined (Xenodon merremii, Dispholidus, Amphiesma, Python sebae), and in Philodryas (Thomas & Dixon, 1977), and the crotaline Crotalus viridis (Stewart & Daniel, 1975). On the grounds of this wide distribution, and correlation with other primitive features within viperines, this would seem to be a generally primitive morphology (State A). It would be desirable to investigate a much wider range of non-viperines to assist in estimating the polarity of this character.

Although the β-layer is densely keratinised with cell walls not apparent or poorly-defined in microscope sections, what appear to be cell boundaries are frequently apparent in the Oberhautchen. In most state A taxa, these junctions are rather obscured because they run partly parallel with the longitudinal ridges noted, the boundary section running transverse to these ridges are more prominent. In most cases the cells are seen to be rectangular, with the long axis parallel to the long axis of the scale. The distal margins of each cell (ie. nearest the scale apex) tend to be rather jagged, as if stretched out distally, and may be raised up somewhat (eg. Vipera *ursinii*). There is a trend, first apparent in the *V.xanthina* complex but more prominent in *V.lebetina* and *V.russelli* (and continued in *Pseudocerastes* and *Eristicophis*), for the cells to become more nearly square in shape or even rectangular but oriented transverse to the scale axis, and for the patterning to change from longitudinal ridges to an irregular reticulate 'honeycomb' pattern. *Pseudocerastes* and *Eristicophis* are assigned to a separate state (state B) in view of the distinct gap between them and *Vipera*. This trend parallels those evident in many other features (p.218). In *Pseudocerastes* the underlying relief has changed from widely-spaced longitudinal ridges, as in most *Vipera*, to irregular low undulations, superimposed on this is an open network formed of raised cell boundaries, enclosing the irregular reticulate microornament. Unique to *Pseudocerastes* are larger-scale 'wrinkles' of the scale surface, converging distally toward a slight swelling of the keel (see Smith, 1943, Fig.155C). In *Eristicophis* the overall degree of relief is very low, possibly associated with the arid sand environment (a similar reduction in relief occurs in the desert form *Bitis peringueyi*), but at the level of discrimination employed here I have assigned these two advanced Eurasian species to the same character state.

Uniquely to *Bitis* (state C), the scale surface is raised up into a dense array of erect blade- or plate-like projecting laminae, about 20-25μm long and of slightly less height. At the extreme proximal end of the scale these are reduced in height to form a series of humps. *Bitis peringueyi* (state D) differs from other *Bitis* in the entire scale is covered with these low humps, this would seem to be a probable secondary reduction, associated with its strict sand environment. In *peringueyi* a dense and regular honeycomb pattern of microornament is apparent, albeit in a reduced (or possibly worn) condition. In other *Bitis* these reticulations become 'stretched' up the sides of the laminae, and are thus linear rather than reticulate.

In *Echis*, *Cerastes*, *hindii*, *superciliaris*, *Adenorhinos*, and *Atheris*, the microornament consists of a reticulate honeycomb pattern, more dense and more regular than that seen in the advanced Eurasian vipers, but very similar to that in *Bitis* (in *B.peringueyi* and between the laminae in other *Bitis*). This could perhaps be regarded as a synapomorphy of the true viperines other than the Eurasian group, but this is a rather slender piece of evidence.

In *Echis* and *Cerastes* (state E), the scale surface relief is virtually identical. This feature, and the serrated keels and orientation of the flank scales, constitute the only possible synapomorphies of the two genera. The underlying large-scale relief consists of regular close-packed humps. Superimposed on this is a very open but quite regular network of cell boundary lines, enclosing the dense reticulate microsculpture noted above. This morphology cannot, however, be regarded as an unambiguous synapomorphy because of the rather close similarity to the humps seen in the anterior end of *Bitis* scales, and the overall close resemblance to *B.peringueyi*, and the somewhat lesser resemblance to *Pseudocerastes* (with its irregular undulations). Possibly *Echis*, *Cerastes*, and *Bitis* (and possibly other taxa) share a common ancestor that had an *Echis*-like scale surface pattern, subsequently elaborated into laminae in *Bitis*, and then secondarily reduced in the desert-adapted *B.peringueyi*. In this interpretation the similar scale pattern in *Echis* and *Cerastes* would be a symplesiomorphy not a synapomorphy. As a further possibility, the various elements of similarity between *Echis*, *Cerastes*, *B.peringueyi*, *Pseudocerastes* and *Eristicophis* may all be parallelisms adaptively related to a hot desert environment, including sand-sinking behaviour (not *Pseudocerastes*).

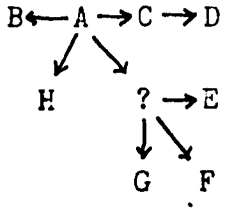
In '*Atheris*' *superciliaris*, true *Atheris* and *Adenorhinos* (state F), the cell boundary lines, forming a low-relief open network in *Echis*, *Cerastes*, *Pseudocerastes*, and *Bitis* (where visible, as especially in *peringueyi*), are raised up to form a fairly regular large-scale reticulate pattern, each reticulation encloses the dense reticulate microsculpture noted above. Frequently, especially in Adenorhinos, the cell margins are markedly imbricate.

A unique pattern is present in 'Atheris' hindii (state G), there is a partial resemblance to Bitis in that the scale surface is raised up into numerous erect laminae, but in hindii these are much longer (some may extend for nearly one quarter the length of the scale, the majority are shorter). Between the laminae can be seen a dense reticulate microornament, as in Bitis these reticulations become linear as they ascend the flanks of the laminae. Possibly the laminae are adaptively involved in some aspect of radiation flux through the skin, perhaps increasing heat energy absorbance; hindii is a tropical zone montane grassland species.

A further pattern unique among viperines (s.l.) is present in Causus (state H). The large-scale relief consists of low, irregularly spaced, elongate humps. The microornament is a dense covering of erect finger-like processes; at 2,000 times magnification the scale has a very striking velvet-like texture (at a macroscopic level the exterior of Causus species is often also very velvet-like, with notable interference colours). Cell boundaries are not readily visible. This pattern is present in rain forest forms (lichtensteini) and those from drier, more mesic and more open habitats (eg. defilippii), and would thus appear to be a strong indication of the monophyly of the genus. A rather similar microornament has been reported for Tropidodryas (Thomas & Dixon, 1977), and for the lizard Coleonyx variegatus (Stewart & Daniel, 1975).

It would seem probable that the Oberhautchen cells possess only a limited spectrum of potential surface morphologies, limited by the nature of keratin and by parameters related to locomotion and general wear at the body surface, among other possible factors. Within this range there may be a partly random fluctuation from one extreme to another, directed at times by particular adaptive requirements in particular lineages. A given similarity in scale pattern may thus be due either to parallel evolution in more than one lineage, or to a real phyletic proximity. Overall, characters of the scale surface ornament have generally been most useful in viperines in linking species at about the generic level, but has provided little unequivocal evidence for grouping these genera or species groups into larger monophyletic groups. Bitis and Causus, both very distinct and certainly monophyletic genera on other evidence, each also have a unique and distinctive scale surface pattern. There is a suggestion that Echis and Cerastes may share a synapomorphy in scale surface pattern, and may possibly be related to Bitis and to Atheris s.l., there is also an intriguing lesser resemblance to Pseudocerastes (recalling the phenetic similarity in the parietal postorbital process between Cerastes in particular, and Pseudocerastes). As in many other characters (p.218) a gradual progressive trend in scale surface modification is apparent through the Eurasian group of species.

A - primitive (Vipera)
B - Pseudocerates, Eristicophis
C - Bitis (except peringueyi)
D - B.peringueyi
E - Echis, Cerastes
F - superciliaris, Adenorhinos, Atheris ss.
G - hindii
H - Causus



13.
Flank scales: orientation and keel serration (Figs 47-50)

In both *Echis* and *Cerastes* longitudinal scale rows 1 and 2 are more or less longitudinally oriented (long axis parallel with that of the trunk), row 3 is slightly to strongly inclined, the next few rows are strongly inclined (long axis of scale about 40° from horizontal), then there is a fairly sudden return at row 8 or 9 to a longitudinal orientation. All trunk scales are strongly keeled except row 1 (slight trace of keeling in *Echis*) and 2 (very weak keel, especially in *Echis*). The keels of the array of inclined scales are serrated for essentially their entire length, with up to 8 to 10 teeth (in *Echis* each tooth is slightly widened basally, and the keel on row 2 typically takes the form of 1 or 2 incipient teeth, rather than a simple ridge keel).

In warning display, the snakes body is formed into mobile loops, which, moving past each other, produce a sustained stridulation as the serrated oblique flank keels are rubbed past each other. The sound may be augmented by inflation of the lung-airsac system. Mendelssohn (1963:146, 7) suggested, but could not demonstrate experimentally, that this type of display may assist in water conservation in these desert snakes, water loss may be expected to be greater in the hissing behaviour of other snakes, involving ventilation of the moist buccal and respiratory tissues.

At first sight this most unusual morphology-behaviour complex would seem to be a good synapomorphy of *Echis* and *Cerastes*, indeed, the only synapomorphy other than the scale surface pattern (Character 12). However, trunk scales with serrated keels are also present in *Tropidodryas serra* (Thomas & Dixon, 1977) and in *Dasypeltis* (Gans, 1974) among non-vipers, and in certain *Atheris* species among vipers. These examples complicate interpretation of this character.

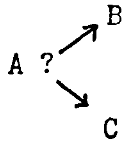
Serrated flank scale keels are present in *Atheris ceratophorus*, *A.nitschei*, *A.desaixi*, and slight serration is present on some scales of *A.chloroechis*. In these species, and other *Atheris*, there is not a relatively sharply delimited array of oblique scales as in *Echis* and *Cerastes*; row 1 is slightly or moderately oblique, the next rows are more so, and then after row 6 to 8 there is a more gradual change to longitudinal orientation. A further difference from *Echis* and *Cerastes* is that serrations are restricted to the posterior ½ or ¼ of the keel. Although *Atheris* species are primarily arboreal, hunting may frequently occur on the ground, and both *A.nitschei* (Goetz,1975:198) and *A.desaixi* (Ashe, 1968:56) have been reported to show the same 'rasping' warning behaviour as *Echis* and *Cerastes* (it is unclear if this can take place in bushes etc. in *Atheris*).

A multitude of characters permit the conclusion that serrations have been developed in parallel in *Tropidodryas*, in *Dasypeltis*, and in vipers. The fact that *Dasypeltis* shows the same aposematic display as *Echis* and *Cerastes* can be reasonably interpreted as an example of Batesian mimicry (Gans, 1974:68). This assumes that the same predator population will encounter both *Echis-Cerastes* and *Dasypeltis*, currently there is only minimal geographic overlap between these groups, and none at all between the former and *Atheris*, this may cast a little doubt on the mimicry hypothesis. The phenetic similarity between *Echis*, *Cerastes* and *Dasypeltis*, in the size and extent of keel serrations, in the quite precise array of inclined scales, and in behaviour is astonishing, and immediately raises the problem that the same degree of similarity may also have arisen in parallel in *Echis* and *Cerastes*, and further in *Atheris* in parallel. In any event, if it is accepted that *A.nitschei* is the sister taxon of other *Atheris* (p.213), either dual origin within *Atheris*, or presence in the common ancestor of *Atheris* and subsequent loss of serrations, is indicated. The concept that parallelism may be expected to be more frequent in closely related groups, presumably with a broad genotypic similarity, may apply to *Echis*, *Cerastes* and *Atheris*. I am inclined to accept that the presence of serrated flank scale keels in these groups is indicative of a real phyletic affinity, but it is not possible to provide a rigorous explanation; however, this arrangement is congruent with the evidence of certain other characters (p.228). Possibly the common ancestry of this group developed the genetic coding capacity for serrations, which subsequently became 'switched on' in different lineages within the group.

A - primitive

B - serrations apical only, flank scales not in precise oblique array
Atheris nitschei, *ceratophorus*, *desaixi*, (*chloroechis*)

C - entire keel serrated, flank scales in quite precise oblique array
Echis, *Cerastes*



14. Orientation of transverse scale rows

As in most snakes the ventral surface of the skin of the trunk in vipers forms transversely enlarged scales (gastrosteges), while the flanks and dorsum bear smaller scales. These scales reflect the segmental organisation of the body, thus there is one large ventral scale corresponding to each vertebra, and one row of dorsal scales abutting each ventral. The dorsal scales form a fairly regular lattice-like pattern; it is possible to visualise a path traversing the dorsal scales from one end of a ventral, around the trunk, and back to the other end of the same ventral, either as a zig-zag or as an oblique row inclined either anteriorly or (highly oblique) posteriorly.

Only in the monotypic Eristicophis among all the vipers, a different pattern is found, in which the dorsal trunk scales form a series of prominent transverse 'rings' (noted in the original description of the species by Alcock & Finn, 1896:565, and by Marx & Rabb, 1965:175). This ring-like arrangement of the dorsal trunk scales is accentuated by transverse folds in the soft and unusually well-exposed interstitial skin.

This condition is interpreted as an autapomorphy of Eristicophis macmahonii, that as such gives no information on the cladistic affinities of the species, but contributes to the phenetic distance between it and its sister species (Pseudocerastes persicus) and other relatives.

A somewhat Echis-like condition is present in Causus lichtensteini, and is occasionally suggested in some Cerastes individuals (contrary to Marx & Rabb, 1965:167, Table 2, not in all Cerastes); the latter suggests a parallelism related to the sand-desert habitat and sand-sinking behaviour.

15.
Duplication or fusion of transverse scale rows

The general arrangement of the dorsal scales in the majority of snakes, including vipers, has been noted in Character 14. Although the orientation of transverse scale rows is similar in all vipers except Eristicophis, several species are unusual in that duplication or fusion occurs in transverse scale rows (the observations below refer specifically to the mid-trunk region but frequently apply for most of the trunk length).

The widespread caenophidian pattern of single obliquely-transverse scale rows is maintained in Vipera, Pseudocerastes Echis, most Cerastes, superciliaris, Adenorhinos, and most Bitis.

In the most heavy-bodied Bitis (B.gabonica and B.nasicornis), transverse scale rows are frequently and regularly duplicated after the first or second scale in each row. Thus for much of the trunk there may be about 18 vertebral scales corresponding to each stretch of 10 ventral scales. Occasionally rows double and then fuse again. All other Bitis retain the primitive state, except B.schneideri, in which both duplications and fusions may occur irregularly, but the latter outnumber the former, so that there may be only 8 or 9 vertebral scales corresponding to each stretch of 10 ventrals.

In all Atheris (s.s.) (and very occasionally in Cerastes) except A.hispidus only the lower flank scales of each transverse row (typically scales 2-5) are frequently doubled, and whole transverse rows are only occasionally duplicated. The related terrestrial form hindii is similar, but superciliaris (only a single duplicated row found in 2 examined specimens) and Adenorhinos (both the latter being probable close relatives of Atheris s.s.) possess the usual caenophidian pattern. Atheris hispidus shows an opposing tendency in that there are frequent and regular fusions of transverse rows (occurring at scales 2-5), thus 7 vertebral scales may correspond to a section of 10 ventrals (this seems to be related to the hyperdevelopment of the scale apices and keels in this species).

Unlike all other Eurasian species, *Eristicophis* resembles the large two *Bitis* noted above in that there is frequent duplication of transverse scale rows; 15 vertebrals may correspond to 10 ventrals. The overall arrangement of scales is more irregular than in the large *Bitis*, and the increase in *Eristicophis* is accompanied by the 'ring' orientation of the transverse scale rows (Character 14). There is no evidence to suggest that *Eristicophis* and *Bitis* are closely related, and I conclude that duplication has occurred independently in these forms (and in *Atheris*).

State B is proposed as a synapomorphy of *Bitis gabonica* and *B.nasicornis*, it is congruent with several other characters suggesting the monophyly of these 2 species. State C is an autapomorphy of *B.schneideri*. State D would seem to be a synapomorphy of *hindii* and *Atheris* (*s.s.*); state E, an autapomorphy of *A.hispidus*, is presumably a further modification, while the primitive state A, as shown by *Adenorhinos*, is possibly a reversal because other evidence strongly suggests that *hindii*, *Atheris* (*s.s.*), and *Adenorhinos* are closely related and probably monophyletic, with *hindii* possibly the sister group of the remainder. The fact that *superciliaris* retains the primitive state is consistent with other evidence suggesting that *superciliaris* may be the sister group of the *hindii-Atheris-Adenorhinos* group. State F, shown by *Eristicophis*, is but one of several autapomorphies of this unique and interesting form that make if phenetically quite distinct from *Pseudocerastes* and related Eurasian species.

A - primitive

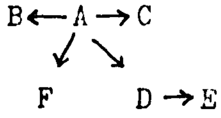
B - transverse scale rows regularly duplicated
Bitis gabonica, *nasicornis*

C - duplications and fusions
Bitis schneideri

D - lower scales of row frequently duplicated
hindii, *Atheris* (except *hispidus*)

E - transverse scale rows frequently fuse
Atheris hispidus

F - transverse scale rows regularly duplicated (parallelism)
Eristicophis



16.
Body size and proportions

There is quite a wide range of body forms to be found among vipers, and no doubt there has been a degree of oscillation between one extreme or another in different lineages. However, three conditions stand out from the mean or generalised morphology, these are recognised as derived states.

On one hand, Bitis arietans, nasicornis and gabonica (and parviocula) are marked by their relatively very large adult body size, with widely triangular heads and thick trunks; this is most accentuated in nasicornis and gabonica, where relative trunk diameter is increased over that seen in arietans (which typically appears as a 'scaled-up' small Bitis). On the other hand, species of Atheris.s.s. are distinguished by their combination of high ventral count, high subcaudal count, and slender, attenuated body form, with short, broad heads. Although a very few other taxa (eg. large Vipera and Echis coloratus) may have similar combined ventral and subcaudal counts, the actual body form is relatively unmodified. Echis most closely approaches Atheris, and A.nitschei is the least extreme form of the genus.

The slender body form of Atheris, including a strongly-prehensile tail, is presumably adaptively associated with both ease of mobility and cryptic behaviour in their arboreal habitat. The large size of the 'big Bitis' is possibly associated with the availability of a wider range of prey sizes than exploited by their congeners and other potential competitors. Head and trunk width, not length, would seem to set an upper limit on prey size, hence a wide head and short but broad trunk would allow an increase in prey size. This body form is limited by mechanical constraints to use of rectilinear locomotion on most occasions, which is relatively slow and hence allows greater exposure to predators; this would tend to favour a 'sit and wait' feeding strategy, as reported for these vipers (eg. Cansdale, 1973:60, Visser, 1979:No.35), and also effective cryptic colouration. Body form, feeding strategy, and colour pattern, appear to mutually reinforce one another. A drive to increasing size, partly to deter ground predators, is probably counter-balanced by limits on muscle volume and attachment areas set by allometric functions.

Within the Eurasian group of species, *Vipera lebetina* *V.'x' pal'estinae*, *V.russelli*, *Pseudocerastes* and *Eristicophis*, (state D), are distinguished by a greater adult size than other *Vipera*.

Body size and form were assessed by ventral and subcaudal scale counts, transverse scale row counts, the ratio of snout-vent length (cms) to ventral scale width (mm), and by simple inspection.

A - primitive ('mean condition')

B - gross body form

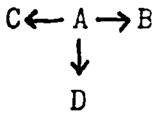
Bitis arietans, *nasicornis*, *gabonica*, *parviocula*

C - attenuated body form

Atheris ss.

D - moderately enlarged adult body size (this state applies only within the Eurasian group)

Vipera lebetina, *palaestinae*, *russelli*, *Pseudocerastes*, *Eristicophis*



17.
Superficial palate (Figs 51-59)

The superficial palate comprises the expanse of soft tissue lying between the bony palate and the oral cavity (Bellairs, 1949:117). Although this region may be variously elaborated in most Henophidia, in the vast majority of Caenophidia the surface of the superficial palate is relatively simple (Groombridge, 1979a). Its posterior extremity, the choanal arc, forms a simple semicircular rim immediately ventral to the palatal openings of the nasopharyngeal ducts into the orbitonasal trough, see eg. Parsons, 1970, Fig.15D; Parker & Grandison, 1977, Fig.9C). In most viperids the continuity of the choanal arc is interrupted by a median projection, the choanal papilla or tongue, extending posteriorly from the region of the nasal septum and the superficial palate into the anterior of the orbitonasal trough. Because any elaboration of the palate is absent in almost all other Caenophidia, and where present it is unlike the condition in viperids, it appears very probable that a simple superficial palate is the primitive state within Caenophidia and the presence of a choanal papilla is a derived state.

In Azemiops and Causus, taxa that are primitive viperids on the evidence of other characters, there is no choanal papilla; this appears to be retention of a primitive Caenophidian state. In the case of Azemiops, there is a very small element of doubt. I have been fortunate to be able to examine four specimens of this poorly-collected form, in one of these the skull has been removed, in another (a juvenile) the soft tissues are somewhat shrunken by preservative and damaged in places, a third has been partially dissected but the remaining portion of the superficial palate (including its posterior extremity) appears to show no evidence of a papilla, this specimen (FMNH 152987) forms the basis for the statement that Azemiops retains the primitive state. I had unfortunately examined the fourth specimen, the holotype located in Genoa, before discovering this character.

In all specimens of all species of *Causus* there was no trace of a papilla.

In all crotalines examined (*Agkistrodon*, 4 specimens; *Bothrops*, 3; *Crotalus*, 1; *Hypnale*, 1; *Lachesis* ; *Sistrurus*,1; *Trimeresurus*, 2) there is a well-developed choanal structure, typically spatulate in form andthus more tongue-like than papilla-like. In some cases it is weakly bilobed or bifurcate posteriorly, but overall is of essentially similar form in all the diverse crotalines examined.

With few exceptions a somewhat similar structure is present in viperines other than *Causus*, but is typically less tongue-like and more papilla-like in form. In most cases it is moderately or very strongly bifurcate posteriorly, and in the latter situation is more aptly described as a pair of papillae. The exceptions noted are among the species of *Vipera*, all other viperine taxa (except *Causus*) have a prominent choanal papilla. In *Vipera ursinii* (16 specimens, including *V.u.macrops*, *V.u.renardi*, and *V.u.rakosiensis*)there is either no papilla (11 specimens) or a very tiny papilla (this sample of 16 includes 12 *V.u. rakosiensis* from a single locality in which 9 lack a papilla). In *V.berus* (12 specimens) there is a small papilla that is typically very slightly bilobed. *V.seoanei* (6) is rather similar, but the papilla is a little wider and more prominent. The papilla in one specimen of *V.kaznakovi* (2) is somewhat similar to that of crotalines although not so elongate, like crotalines it is distinctly spatulate and weakly bilobed distally (Fig. 58); it is more elongate but otherwise similar in a second specimen. Most of the remaining *Vipera* (*aspis*, *ammodytes*, *latastei*, *latifii*, *bornmuelleri*, *raddei*, *xanthina*, *palaestinae*, and *lebetina*) have a papilla like that of *berus* and *seoanei* but yet more prominent and distinctly bilobed or bifurcate (Fig.54).

The papilla is further developed in *Pseudocerastes* and *Eristicophis*; the forks of the papilla are modified into two flat lobes that lie flush with the surface of the superficial palate (Figs.55,56) In Eristicophis the lateral and anterior margins of each lobe is convex. The condition in *Pseudocerastes* is intermediate between that of typical *Vipera* and *Eristicophis*;the papilla in *palaestinae* (3 specimens) is rather similar to that of 2 *Pseudocerastes* (7 examined) in which the papilla is less modified toward the *Eristicophis* condition.

There is significant intraspecific variation in *Vipera russelli*. In 6 specimens there is a small single papilla exactly resembling that of some *V.ursinii*, in 2 specimens there is a larger bilobed papilla as in *V.berus*, and in 4 specimens there is a long single papilla (with a trace of bifurcation in 2 of these). These specimens are from Pakistan, India, Sri Lanka, and Thailand; there is no evident geographical pattern in the variation. Because on other evidence there is little doubt that *russelli* shares an ancestry with some member of the large *Vipera* group (and is probably monophyletic with *palaestinae*), and it has evolved several unique states in other characters, I interpret the condition of the superficial palate in *russelli* as the result of a secondary reduction of the choanal papilla. This appears to be the case also in the single *V.lebetina schweizeri* examined which has an elongate weakly bifurcate papilla, apparently resulting from fusion (as in certain *russelli*) of the strongly bifurcate papilla present in other *lebetina* and most *Vipera*.

The choanal papilla in the remaining viperines (*Echis*, *Cerastes*, *Atheris*, *Adenorhinos*, *superciliaris*, *hindii*, *Bitis*) is well-developed, typically strongly bifurcate, and is essentially similar to that present in most *Vipera*. There is some variation within these taxa. In most *Bitis*, in particular, the papilla is almost completely divided into two, but in two of the large *Bitis*, *nasicornis* and *gabonica* (that on other evidence appear to be a monophyletic pair), a majority of specimens have the two papillae apparently secondarily fused into a single elongate papilla that may or may not be bifurcate just at the tip. This reduction is paralleled by Vipera russelli and V.lebetina schweizeri among the Eurasian species. The palate in some Echis and Atheris has some resemblance to that of Pseudocerastes.

I had initially assumed that a choanal papilla is primitively absent in viperines; it is absent in virtually all Caenophidia, and in Azemiops and Causus among viperids. The morphological sequence shown by Vipera ursinii (papilla absent or tiny)-- V.berus (papilla small, weakly bilobed)-- larger Vipera (papilla prominent, strongly bilobed), is exactly parallel to the trends apparent in many other characters (of head scalation, trunk scale rows, scale surface sculpture, cranial osteology and myology) in which V.ursinii in particular shows apparently primitive states whereas the larger Vipera show derived states. However, a majority of V.russelli specimens precisely resemble V.ursinii and V.berus, but in the case of V.russelli this must almost certainly be due to a secondary reduction of the papilla. So if reduction can occur once, the possibility must be considered that V.ursinii and berus are secondarily primitive also. Also a well-developed papilla is present in V.kaznakovi, closely related to ursinii and berus on other evidence. Because the apparent sequence in development of the papilla, starting with V.ursinii is so neatly congruent with trends in other characters it does seem a priori likely that V.ursinii and berus are truly primitive, not secondarily so. A major difficulty of this hypothesis is that Echis, Cerastes, and the African viperines (except Causus) have a palate essentially similar to that of most Vipera. If V.ursinii and V.berus are truly primitive to other Vipera then this character would suggest either (1) that the advanced African forms, Echis, and Cerastes, and the advanced Vipera share a common ancestry subsequent to that shared by V.ursinii and berus, or (2) that an identical form of choanal papilla was derived in parallel in Echis, Cerastes, and advanced African taxa, and in advanced Vipera. Neither of these latter possiblities is readily acceptable, the former is not suggested by other characters, the latter is unparsimonious and likewise is not suggested by other characters. If these corollaries are rejected, then the initial hypothesis, that Vipera ursinii and berus are truly primitive in respect of the palate, must be rejected also.

A second hypothesis is that the choanal papilla is actually a synapomorphy of all viperids other than Azemiops and Causus, and that the papilla has undergone secondary reduction in Vipera ursinii and V.berus, V.russelli, and partial reduction in Bitis nasicornis and B.gabonica.

The different form of choanal papilla in crotalines could have been derived from the primitive state, shown by Azemiops and Causus, in which no elaboration is present, or from an initial stage of partial development shared with viperines other than Causus; the latter is most parsimonious and is also suggested by the state of the M.hyotrachealis insertion in crotalines and viperines other than Causus.

It may be that the clefts in the posterior margin of the superficial palate on either side of the choanal papilla or tongue are of functional significance, and not the median choanal papilla itself. Possibly the clefts serve to mechanically isolate the median region of the palate from the highly kinetic palato-maxillary arch on each side, and thus generally reduce stress in this area during uni- or bilateral fang protraction. This may be the source of a selective force guiding parallel evolution of a choanal papilla in crotalines and in viperines other than Causus.

A - primitive (papilla absent)
B - choanal papilla present
    homologous in viperines and crotalines ?
C - papilla small/absent
    reduced ? (Vipera ursinii, V.russelli - intraspecifically variable)

$A \rightarrow B \rightarrow C$

18.

Hyoid: lingual process (Figs 60-64)

In the "parallel type" hyoid (Langebartel, 1968) present in all Caenophidia (also *Tropidophis*, *Trachyboa*, and acrochordids, see addendum in Groombridge, 1979a), the hyoid has the form of a hairpin loop with the long parallel cornua joined anteriorly. A lingual process may or may not be present, extending anteriorly from the junction loop of the cornua. This process may form a barely defineable convexity, a broad and sometimes truncated triangular projection, or an elongate spike. The process and the rest of the hyoid are entirely cartilaginous, as in all snakes except some typhlopids where ossification may occur (List, 1966). The precise embryonic derivation of the components of the different forms of snake hyoid (Langebartel, 1968) has been the subject of some dispute, but the arguments of McDowell (1972:232-4). that the cornua are composed of first branchial arch derivatives in all snakes, is most persuasive. The lingual process may be homologous with the lingual process (*processus entoglossus*) of the lizard hyoid, usually considered to be of basihyal derivation.

Some form of lingual process is present in the hyoid of *Azemiops* (pers.obs.), in crotalines, and a majority of other Caenophidia (Langebartel, 1968); this is probably the primitive state for viperids, and the absence or extreme reduction of a process is derived. Within viperines, certain species entirely lack a lingual process and the anterior of the hyoid forms a simple unornamented semicircle, certain species have a long spike-like process, while other species are intermediate.

The lingual process is entirely or virtually absent in most *Bitis*, all *Causus*, *Atheris*, *Adenorhinos*, and one of two specimens of *superciliaris*. While usually being of consistent form there is wide interspecific variation in certain taxa. In two *Bitis worthingtoni* examined the process is entirely absent in one specimen but a long spatulate process is present in the second. A minute process is present in one

Bitis cornuta but a long process in a second (Langebartel, 1968, recorded a short process in his specimen). A similar situation occurs in two *superciliaris*. In *hindii* the anterior point of junction of the cornua is somewhat thickened, forming a slight process in one specimen and a rather stronger process in a second, but not exactly of the spike-like form of *Vipera*, for example.

A long spike-like process is present in *Cerastes*, *Echis coloratus*, and is somewhat reduced in some *Echis carinatus*. In the European *Vipera*, that appear relatively more primitive in other characters than the larger *Vipera*, a long process is also present, but there is an apparent tendency for this to be much reduced in the larger *Vipera* such as *palaestinae*, some *lebetina*, and *russelli*. A moderate lingual process is retained by the two *Pseudocerastes p.persicus* examined, but no process was reported in *Ps.p.fieldi* by Langebartel (1968). In two specimens of *Eristicophis*, a minute process is present in one, but entirely absent in the second. This apparent trend is but one of several lines of evidence suggesting that *Pseudocerastes* and *Eristicophis* are a monophyletic group whose ancestry is shared with advanced *Vipera*, with *Eristicophis* possessing more derived states overall.

While *Vipera*, *Pseudocerastes*, *Echis*, and *Cerastes* retain the primitive state in which a distinct lingual process is present, *Causus*, *Atheris*, *Adenorhinos*, *hindii*, *superciliaris*, *Bitis* and *Eristicophis* share the derived state (except in the cases noted of interspecific variation). It may initially be proposed that this shared derived state provides good evidence on which to associate *Atheris*, *Bitis*, *Causus*, and the listed taxa, however there is strong evidence (pp. 192-205) indicating that *Causus* forms an entirely separate lineage, and similarly that *Eristicophis* is very closely related to *Pseudocerastes* and the larger *Vipera*. These indisputable examples of parallelism in the reduction of a lingual process make it correspondingly less probable that the derived state shared by *Atheris*, *Adenorhinos*, *hindii*, *superciliaris*, and *Bitis* is a true synapomorphy indicating the joint monophyly of these taxa. The reservations that must be held about this character are reinforced by the striking interspecific variation found in *Bitis worthingtoni*, *B.cornuta*, and *superciliaris*. The evidence of other characters must be brought to bear on the problem of the cladistic interrelations of this group of African taxa.

19.

Hemipenis (Figs 65-70)

As in all Squamata, the male external genitalia in viperids comprises a pair of eversible hemipenes. The retracted hemipenis forms a hollow tube located in the base of the tail, the lumen of the organ opens proximally at the cloaca and is closed off distally. Eversion is affected by the filling of blood and lymph sinuses within the wall of the organ, and by the action of propulsor muscles. During eversion the organ is turned inside out so that the inner surface of the retracted organ becomes the outer surface of the everted organ. Sperm is carried to the tip of the organ in a narrow channel, the sulcus spermaticus. There is considerable variation within snakes in the gross form of the hemipenis, in the course of the sulcus, and in the pattern and distribution of surface ornament on the everted organ. Basic anatomy and some taxonomic variations are summarised by Dowling & Savage (1960).

Many aspects of gross form and surface detail (especially of the apical region) that are readily visible on an everted hemipenis are not so apparent in a dissected retracted organ of the same species, and the everted hemipenis is much more similar to the "true" morphology of the organ during coitus (although in the latter case its form is presumably more or less constrained by enclosure within the female cloaca). It would clearly be preferable for systematic purposes to study the everted organ, but as in the present study, it is usually not possible to obtain everted hemipenes of all species of a large group using routinely-preserved museum specimens. The use of retracted hemipenes alone enforces a coarse level of discrimination in the definition of characters.

I have examined retracted hemipenes of Azemiops, selected crotalines and all but 2 of the described species of viperines (s.l.). In nearly all viperines the hemipenis of one side of 2 or 3 specimens of each species have been examined, much larger samples (10-12 hemipenes) have been examined in a few species, for a very few species only 1 hemipenis has been available (this includes Adenorhinos and Eristicophis, for both of which only single male specimens have been available, both with the hemipenis of one side largely everted). For one or a few species of most genera (Atheris, Bitis, Causus, Echis, Vipera) it has been possible to compare features seen in the retracted organ with the same feature on a fully everted organ (I am indepted to Dr.W.R.Branch for the loan of everted preparations of hemipenes of most Bitis species). Figures of everted hemipenes of various viperines are provided by, among others, Branch & Wade (1976), Deoras & Vad (1965-66b), Domergue (1954 ,1962), Doucet (1963), Gasc (1968), and Volsøe (1944).

A major disadvantage of using the retracted hemipenis as a source of taxonomic characters is that its length and proportions can be expected to be affected by varying methods of preservation and by the state of associated muscles (eg. the M.retractor penis magnus)and the degree of engorgement of the soft tissues of the wall of the organ at the time of preservation. Details of ornamentation are subject to appreciable intraspecific variation in some cases, and parallel modification of features (eg. the terminal awn) in different groups seems not uncommon. These factors lead to difficulty in selecting characters for use in a cladistic analysis. In the present study, hemipenial characters have been found most useful at the genus or species-group level, but have not been found useful in relating genera to one another (except in the case of the hindii-Adenorhinos-Atheris s.s.group). This limitation would probably not apply were a comprehensive collection of everted hemipenes available.

The hemipenis in all viperids is highly bifurcate, as is the sulcus spermaticus, which continues semi-centrifugally to the tip of each lobe. Surface ornament consists of a dense carpet of spines, usually diminishing in size distally, where they frequently grade into reticulate calyces.

Frequently the most proximal spines, near the level of the fork in the *sulcus*, are enlarged to form basal hooks. Sometimes a terminal awn is present at the apex of each lobe, this is often (eg. in Vipera) highly variable intraspecifically. A rather generalised viperid hemipenis is shown by *Vipera berus* (Fig. 66), although this particular species lacks prominent distal calyces. A similar morphology is also shown by other Vipera (except russelli), *Pseudocerastes*, *Eristicophis*, some *Bitis*, *superciliaris*, *Echis coloratus*, and quite similar conditions are found in Azemiops and among crotalines. Because of its wide distribution among diverse viperids I have regarded this general kind of morphology as primitive for viperines (state A), and major deviations from this form as derived states. The following are the derived states recognised.

State B, *Causus* (everted - *C.maculatus*, *C.rhombeatus*)

In the retracted hemipenis of *Causus*, dissected open, the *sulcus spermaticus* from its bifurcation to the apex of each lobe is surrounded by a zone of shallow calyces. This calyculate zone is bordered on each side by a prominent ridge of tissue, and the remainder of each lobe is densely spined. In the everted organ, the calyculate zone occupies most of the sulcate face of the organ, all the medial aspect of each lobe, and extends onto the asulcate face. Spines are restricted to the lateral aspect of each lobe, the spined zone being narrowest at the apex and widening proximally. There is a very prominent spinose ridge or wall, not so evident in the retracted organ, demarcating the calyculate and spined zones from each other. This wall begins near the distal end of the *sulcus spermaticus*, extends over the apex of each lobe, and converges proximally with that of the opposite lobe on the asulcate face. The calyces present on the medial face of each lobe are much reduced or absent adjacent to the ridge, thus accentuating the difference between the two zones, particularly on the asulcate side. In *C.defilippii* the calyculate zone was partly replaced by minute papillae or highly-dissected calyces.

The non-spined or naked zone in Causus differs in position from the similar but very probably non-homologous naked zone in Atheris s.s., Adenorhinos, hindii, and a few Bitis, in that it is not restricted to the medial face of each lobe and in the extent and location of the demarcating ridge. There is no terminal awn, nor enlarged basal hooks.

State C, Cerastes (retracted only)

The hemipenis in both species of Cerastes is distinguished by the dense even carpet of very small spines, extending from the region of the sulcus fork nearly to the apex of each lobe, where there is a short area of flounces and calyces. There is no terminal awn, nor basal hooks.

State D, 'Atheris' hindii (retracted only)

The region almost opposite the sulcus spermaticus, that will form the medial face of each lobe in the everted organ (ie. facing the medial face of the opposite lobe), is devoid of spines or other ornament. This naked zone extends from the fork of the organ up each lobe to the apical region, where there is a short calyculate zone. The rest of each lobe is covered with relatively short spines, starting proximal to the sulcus fork and, unusually for viperids, reaching maximum length halfway up each lobe. There is no terminal awn, nor basal hooks.

State E, Atheris s.s., Adenorhinos (everted - Atheris nitschei, A.squamiger; part everted only - Adenorhinos)

The same as State D (hindii) except that the spines are largest proximally as in other viperines, and the naked zone is accentuated by being surrounded dorsally (everted) and on each side by a spinose ridge of tissue. Distally, in the retracted organ, this ridge usually forms a conspicuous pocket at the distal tip of the naked zone. In the everted organ this ridge is seen to be most prominent on the asulcate side of the organ (the opposite condition in *Causus*), and the naked zone is much narrower than in *Causus* so that the *sulcus* is still well within the spined region (as in *hindii* also).

Because of the other evidence (pp. 215) indicating that *hindii*, *Adenorhinos*, and *Atheris s.s*. form a monophyletic group, I have accepted that the naked zone is homologous in each case and forms a synapomorphy of these taxa, and that the development of a surrounding ridge is a further synapomorphy of *Adenorhinos* and *Atheris* s.s. It may be noted that the hemipenis of *superciliaris*, assigned to *Atheris* by Marx & Rabb (1965), retains a more or less primitive morphology (state A). There is a somewhat *hindii*-like naked zone in *Bitis atropos*, and to a lesser degree in *B.cornuta* and *B.xeropaga*; because *Bitis* undoubtedly form a monophyletic group, with *B.worthingtoni* (with no naked zone) very probably primitive to other *Bitis*, I have regarded the naked zone in *Bitis* as a parallelism. Differences from *Causus* have been noted above.

State F, *Vipera russelli*, (retracted only)

The hemipenis of V.russelli is generally similar to that of other members of the Eurasian group of species *Vipera*, *Pseudocerastes*, *Eristicophis*, all state A), but differs in the lack of a terminal awn (also very much reduced in *Eristicophis* and somewhat so in *Pseudocerastes*), in having a relatively short base and relatively long and slender lobes, and in the spines being relatively shorter (especially noticeable proximally, where there are large basal hooks in *Vipera*).

State G, Bitis nasicornis, B.gabonica (retracted only)

In these two large Bitis species the base of the organ is short and the lobes are relatively long and slender. Spines are absent, ornamentation consisting of oblique partly calyculate flounces proximally (but distal to the sulcus fork) and wide shallow calyces distally. No terminal awn is present.

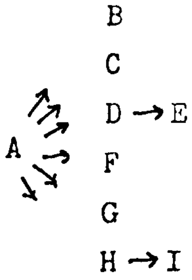
State H, Bitis atropos, B.cornuta, B.xeropaga (retracted and everted)

These species show a moderate length (atropos) or short naked zone, similar to that in State D ("Atheris" hindii); see discussion of State E for proposal that the naked zone in these Bitis species is non-homologous to that in the other genera noted. There is no terminal awn or basal hooks. The everted organ is relatively stumpy in form, particularly in atropos, with short base and lobes. The spines are rather short, especially distally, and particularly in atropos are interspersed with small papillae.

State I, Bitis heraldica (retracted only).

The organ differs from that of other Bitis in being without prominent ornament. There is no terminal awn nor enlarged basal hooks. I suggest that this may be a further development of an atropos-like condition (state H) in which there is a moderately-developed naked zone, and the spines are very short. Presence of some very small papillae on the hemipenis of heraldica may indicate reduction from an atropos-like condition.

This interpretation is somewhat compromised by the observation of distinct intraspecific variation in B.caudalis (assuming "caudalis" is a single species). One specimen (TM 41336, Rosh Pinah Mine) has moderate-length lobes and normal-size spines, while two other specimens (TM46898, Vivo area; and TM 46986, Messina) have much elongate lobes and spines entirely replaced by small papillae. Also, FitzSimons (1962:342) reported absence of spines and calyces from *B.peringueyi*,whereas the specimen I examined possessed both.



20.

Facial carotid artery (Figs 71-72)

In caenophidian snakes typically only the left common carotid artery is present (Underwood, 1967:32-33). In certain viperids a very thin right common carotid is present (crotalines, Van Bourgondien & Bothner, 1969; most specimens of Vipera palaestinae, Frenkel & Kochva, 1970; a few specimens V.aspis, Lecuru-Renous & Platel; 1970:48) Although the right common carotid may be absent, the cranial components of the carotid circulation persist on the right side, sometimes in a reduced form, and are supplied via an anastomosis in the neck region (Underwood, 1967:33; O'Donoghue, 1912) from the carotid system on the left side of the head (there are also intracranial anastomoses).

At the back of the head the left common carotid divides into the internal carotid artery supplying blood to the brain and other structures of the head, and the external carotid artery supplying the throat region and lower jaw. Passing anteriorly medial to the quadrate and close to the braincase the internal carotid itself divides ventral to the stapes to form the cerebral carotid artery and the facial carotid artery. The cerebral carotid artery turns ventrally to enter the posterior opening of the Vidian canal (for passage of the palatine branch of the facial nerve) lying within the sphenoid. The cerebral artery finally enters the braincase via the cerebral foramen, which typically opens within the Vidian canal. In most viperids (Underwood, 1967;18) the cerebral foramen does not open within the Vidian canal but is entirely separate, the former located immediately postero-medial to the posterior opening of the latter (see Character 52).

The facial carotid artery passes anteriorly and its subsequent divisions supply the lateral jaw muscles, the venom gland, the Harderian gland, the eye, and other structures. In its forward passage along the temporal region of the braincase the facial carotid artery crosses first the mandibular branch (V_3) and then the maxillary branch (V_2) of the trigeminal nerve (V)as they exit from the prootic. Within viperids two different patterns have been described with respect to the positional relationships of the facial carotid artery of these two branches of the trigeminal.

In *Agkistrodon* (7 species examined), *Bothrops* (2 species), *Crotalus* (3 species), *Lachesis* mutus, *Sistrurus* (2 species), and *Trimeresurus* (1 species), the facial carotid passes dorsal to both the mandibular and the maxillary branches of the trigeminal (Liem, Marx & Rabb, 1971; Rathke, 1856:10; Van Bourgondien & Bothner, 1969). This pattern is also present in *Azemiops* (Liem, Marx & Rabb, 1971), and in the supposed viperine *Causus*, both these taxa are primitive among viperids in other characters. Liem, Marx & Rabb (1971:107) reported not this pattern but the one characteristic of true viperines in the single specimen of *Causus* they examined (listed as *C.defilippii* on page 123, but given as *C.rhombeatus* in the main text, page 107). I have not found the viperine pattern in any *Causus* (6 each specimens of *rhombeatus*, *defilippii*, and *lichtensteini*, 1 each of *bilineatus*, *maculatus*, and *resimus*).

By contrast, viperines except *Causus* show a second pattern in which the facial carotid passes anteriorly ventral to the mandibular branch and dorsal to the maxillary branch of the trigeminal. This pattern was reported in *Vipera berus* by Rathke (1856); in *Atheris* (4 species comprising 3 arboreal 'true' *Atheris*, and *hindii*), *Bitis* (2 species), *Cerastes cerastes*, *Echis carinatus*, *Eristicophis macmahonii*, *Pseudocerastes persicus*, and *Vipera* (3 species) by Liem, Marx, and Rabb (1971:107); and has been found, with the following few exceptions, in all viperines except *Causus* examined in the present study. In one of three *Echis coloratus* and one of two *hindii* dissected, the facial artery runs dorsal to both the mandibular and maxillary branches of the trigeminal on one side of the head only. This situation was also reported by Liem, Marx, and Rabb (1971) in one specimen each of *Atheris squamiger* and *Pseudocerastes* persicus. Since the carotid system on the right side is modified in virtually all Caenophidia, including most viperines, the condition shown by that of the left side may be more significant; in the Echis coloratus specimen noted above the facial carotid has the typical viperine course on the left side (only one side recorded in hindii). Liem, Marx and Rabb do not state which side has the viperine course in their asymmetrical specimens.

I suggest, in agreement with Liem, Marx and Rabb (1970: 113), that the 'crotaline pattern' (facial carotid dorsal to trigeminal) is the primitive state within viperids. This state is not only most widespread within the Viperidae, being present in Azemiops, Causus, and crotalines (the former two genera also retaining primitive states of certain other characters), but is also present in all Caenophidia except viperines examined by Rathke (1856:10, Chironius, Clelia, Natrix, Spilotes); by Liem, Marx & Rabb (1970:108, taxa unspecified); Anthony & Serra (1951, Xenodon merremii); and several boigines (Rasmussen, 1979:143) and in the present study (Calamaria, Coluber, Crotaphopeltis, Denisonia, Miodon, Naja, Pareas, Psammophis, Spalerosophis). This character state distribution leads to the hypothesis that the 'crotaline pattern' is primitive both within viperids and Caenophidia as a whole, and that the 'viperine pattern' is a derived state within viperids. The derived state, in which the facial carotid passes ventral to the mandibular branch but dorsal to the maxillary branch of the trigeminal, appears to be a good synapomorphy of all taxa, other than Causus, currently assigned to the Viperinae. There is no evidence that would conflict with this hypothesis.

Although the 'viperine pattern' is rather certainly a derived state within the Caenophidia, a similar condition with the facial carotid passing ventral to the mandibular branch of the trigeminal has also been found in several Henophidia and in "den engmäuligen Schlangen" (= Scolecophidia and Aniliodea) by Rathke (1856:10). It may thus be primitive for snakes in general. If this is the case then the 'crotaline pattern' would be a derived state shared by Caenophidia and Acrochordidae (the probable sister group of Caenophidia, Groombridge, in prep.), but thereby primitive for any taxon within Caenophidia. The 'viperine pattern' of viperines except Causus would actually be secondarily primitive and a derived state within Caenophidia because the 'crotaline pattern' was present in the immediate common ancestor of Caenophidia, and in the ancestor of the group Caenophidia plus Acrochordidae. That this is indeed an example of character state reversal is supported by the exceptional cases within viperines that retain the pattern shown by crotalines and other examined Caenophidia. The alternative hypothesis, that the 'viperine pattern' is strictly homologous to that of examined lower snakes and not a reversal, would imply that Acrochordidae and all Caenophidia other than viperines (except Causus) share a common ancestry, with the 'crotaline pattern' of facial carotid course, more recently than that shared with viperines except Causus. This can be rejected with considerable confidence; one of the more improbable corollaries would be that the group Acrochoridae plus Caenophidia passed through a viperine grade of evolution, or that the precise viperid venom injection system evolved twice, once in viperines except Causus, and once in other viperids including Causus.

A - primitive (facial carotid dorsal to V_3)

B - facial carotid ventral to V_3

Viperinae, except Causus

A→B

21.

Anterior azygos vein (Figs 73-75)

In what appears to be the typical condition in snakes, venous blood leaving the dorsal portions of the anterior trunk passes into the azygos(or azygous) veins by way of a series of short lateral vessels emerging on the right side close to the vertebral column at irregular intervals of one or several segments (O'Donoghue, 1912:630; Lecuru-Renous & Platel, 1970)Frenkel & Kochva, 1970. Both anterior and posterior azygos veins may be present, but on the right side of the body only. The azygos vein(s) and the right jugular join immediately anterior to the heart.

In all viperids examined the posterior azygos is very short or absent. However, there is significant variation in the condition of the anterior azygos.

The anterior azygos is fully developed in Azemiops and Causus, taxa that retain primitive states of several other characters (pp.198-205); and in most Bitis, some Vipera, and Pseudocerastes and Eristicophis, among 'true' viperines. The vein is also fully developed in certain Agkistrodon examined (the least derived group of crotalines; azygos present in A.halys and A.himalayanus, modified in A.rhodostoma, the latter species sometimes assigned to Calloselasma), and in the other crotalines examined (Bothrops alternatus, Crotalus adamanteus, Trimeresurus monticola). The anterior azygos is also present in the non-viperid Caenophidia and Henophidia examined (Boiga drapiezi, Calliophis macclellandii, Coluber viridiflavus, Natrix natrix, Pareas carinatus, Boa constrictor, Xenopeltis unicolor, Acrochordus javanicus -somewhat modified). Because this condition is widespread in diverse viperids and in other Caenophidia and Henophidia examined, I interpret the presence of an anterior azygos to be the primitive state among viperids (see below for possible exception).

In several viperines the short lateral vessels draining the trunk join the right jugular vein directly, and thus no long separate azygos is present. I interpret this as a derived state, and suggest that it may be the result of fusion during early ontogeny of the precursors of the jugular and the azygos. It appears that this fusion may take place in a posterior-to-anterior direction. For example, in Bitis atropos, although a relatively long anterior azygos is present, it joins the jugular a few ventral scale-lengths anterior to the heart, and the jugular itself receives 1 or 2 lateral vessels in the section between this junction and the heart (Fig. 74). In Atheris and smaller Vipera most of the lateral vessels join the jugular directly, ie., no true anterior azygos is present. However, just posterior to the head is a short or very short longitudinal vessel that receives one or a few lateral vessels before joining the jugular; this short longitudinal vessel appears to be a possible vestige of the anterior azygos, the main course of which has fused with the jugular (Fig. 75). In some cases (eg. Bitis arietans) in which most of the azygos is absent, in addition to anterior vestige, a posterior vestige may also be present, resembling the immediate proximal portion of the azygos. In a few specimens where an anterior azygos is present (eg. Bitis gabonica, Vipera russelli), there may be 1 or 2 points of anastomosis between the azygos and the jugular.

Overall, two major conditions can be recognised among viperines; one in which a long separate anterior azygos is present (ie. all or most lateral vessels empty into the azygos, not directly into the jugular), and a second in which no long separate anterior azygos is present (ie., all or most lateral vessels empty directly into the jugular). In the latter case, a short longitudinal vessel just posterior to the head, and sometimes, a short longitudinal vessel immediately anterior to the heart, appear to represent vestiges of the anterior azygos (most of which have fused with the jugular during ontogeny).

It has been suggested above that the presence of an anterior azygos in diverse viperids (including those retaining the most primitive states in other characters, *Azemiops* and *Causus*), and in other examined Caenophidia and *Henophidia*, strongly indicates that this condition is primitive for viperids (see below for possible exception); this implies that the loss of anterior azygos is a derived state.

Among viperines, the anterior azygos is present in all species of *Causus*, all *Bitis* examined except *B.arietans*, (I cannot confirm Beddard's account of *B.nasicornis*, 1906:37) and the large *Vipera* (*lebetina*, the *xanthina*-group, *russelli*), *Pseudocerastes*, and *Eristicophis*. The azygos, in its typical condition, is absent in *Bitis arietans*, the smaller *Vipera* (*aspis*, *ammodytes*, most *berus* - present in 1 of 6 examined, *kaznakovi*, *latastei*, *seoanei*, *ursinii*), also *Echis*, (see also Deoras & Vad, 1965-66b, Fig. 92) *Cerastes*, *Atheris* (including *hindii* and *superciliaris*). Both specimens of *Adenorhinos* available had been eviscerated.

The interpretation of the distribution of these conditions has raised some problems.

Because *Bitis* is such a highly distinctive genus (synapomorphies in several characters, p209), and *B. arietans* is a relatively derived member of the group, there can be virtually no doubt that *B.arietans* has modified its azygos independently of other viperines. The differences in detail (see above) and the forms of intraspecific variation among species of *Bitis* (not fully given here) are entirely consistent with this view. I have thus recognised a separate character state for *B.arietans*

An apparently primitive state (anterior azygos present) is shown by the larger *Vipera*, *Pseudocerastes*, and *Eristicophis*, although these forms are more undoubtedly derived in several characters (see pp.219-224) than the smaller *Vipera*, in which a derived state (azygos absent) is evident. Taken at face value, this would imply that the small *Vipera* may form a monophyletic group with *Echis*, *Cerastes*, and *Atheris*, all being viperines with the derived state in which the anterior azygos is absent. However, the several characters (p.219) suggesting that the larger *Vipera*, *Pseudocerastes*, and *Eristicophis*, are, loosely speaking, progressively modified '*small Vipera*'; the proposed *Vipera-Pseudocerastes-Eristicophis* synapomorphy (p.217); and the overall phenetic distinctness of the group; the most parsimonious hypothesis is that the presence of an anterior azygos in the large *Vipera*, *Pseudocerastes*, *Eristicophis* sub-group is a reversal to a 'pseudo-primitve' condition. This would constitute a derived state indicating the monophyly of the latter sub-group. The intraspecific variation in *Vipera berus* (azygos present in 1 out of 6 specimens, but typically absent in the small *Vipera*) is consistent with the hypothesis of reversal in the large *Vipera* group.

This character is not of the highest weight since other features have been taken into account in interpreting character transformations.

A - primitive (anterior azygos present)

B - anterior azygos absent

small *Vipera*, *Echis*, *Cerastes*, *superciliaris*, *hindii*, *Adenorhinos*, *Atheris*

C - anterior azygos present, secondarily ?

large *Vipera*, *Pseudocerastes*, *Eristicophis*

D - anterior azygos absent (parallelism)

Bitis arietans

$$\begin{tikzcd}
A \arrow[r] \arrow[d] & B \arrow[r] & C \\
D & &
\end{tikzcd}$$

Lungs and pulmonary arteries (Figs 76-80)

Brongersma (1949, 1951a, 1957a,b,c,), Kardong (1972), and Underwood (1967,197), have described aspects of the lungs and pulmonary vessels in snakes, and given interpretations of the probable primitive condition of these structures in snakes (these works give reference to the older literature). The following features comprise the primitive snake condition. Unlike most reptiles and other tetrapods (except caecilian amphibians) the left lung is variably reduced in snakes and some snake-like lizards, but primitively in snakes the left lung remains relatively large and may be up to 85% the length of the right (Underwood, 1967:35). The pulmonary arterial trunk branches into right and left pulmonary arteries, the former tending to be more dorsal at the point of bifurcation (Brongersma, 1949:63). The entry of the trachea (or of each bronchus, when distinct bronchi are present) into the lung is sub-terminal (Underwood, 1978:346), there is thus a forward pocket of the lung. A tracheal lung is absent. The trachea-lung boundary is well-defined and located near the level of the ventricle of the heart.

The above features are considered primitive in snakes because they resemble conditions typically found in lizards and other reptiles. Retention of the above features in snakes is frequently associated with retention of primitive states in other characters, as in most henophidian groups. A variety of more or less extensive modifications in these features is found in less conservative snakes, including viperids.

Reduction of left lung

Whereas most Henophidia retain a large or moderate-size left lung, in Caenophidia the left lung, if present at all, is usually only 1-2% the length of the right lung (Underwood 1967:35). Complete absence of the left lung, as found in very few Henophidia and many Caenophidia, is undoubtedly a derived condition, but also undoubtedly, complete loss must have occurred in several or many lineages.

Among viperids, a vestigial left lung persists only in several crotalines (summarised in Kardong, 1972:371) and in Azemiops (Fig. 76), it is totally absent from viperines (sensu lato, ie., including Causus). Butler (1895) reports that in Vipera aspis the lung primordium is unpaired from its first appearance during ontogeny, whereas in Natrix natrix and Coluber gemonensis the lung primordium is paired initially, but the left portion fails to develop further.

With reference to viperines (s.l.) the lack of a vestigial left lung is a derived state shared by Causus and 'true' viperines , but it is rather doubtful if this can be regarded as a synapomorphy because of the evidence for multiple loss in other snake lineages. The crotalines (Kardong, 1972:371) provide a relevant example, the genera Agkistrodon, Bothrops, and Crotalus each contain some species possessing a vestigial left lung and other species lacking it, this implies that total loss has occurred in at least 3 separate lineages; similarly, the elapid genera Aspidomorphus and Denisonia contain species with and without a left lung (Brongersma, 1957a:302).

Relationship of trachea and right lung

Primitively the entry of the tracheas (or bronchus, if present) into the lung is sub-terminal, thus leaving an antero-lateral pocket of the lung. This pocket persists in many higher snakes, with or without a vestigial left lung, but seems to be absent from all snakes with a well-developed tracheal lung. When a tracheal lung is present, the lack of an anterior pocket of the right lung is a major feature contributing to the blurring of the morphological distinction between the tracheal lung and the right lung. The entire system tends to form a single elongate sac, with vascularisation largely or entirely restricted to the region anterior to the heart. While the zone of vascularisation may thus transgress anteriorly, in some forms the tracheal cartilages tend to transgress posteriorly, extending into the right lung as a series of weakly-curved bars (the intra-pulmonary bronchus).

Among viperids, I have found an anterior pocket of the lung only in *Azemiops* and *Cerastes* (both species, *C.cerastes* & *C.vipera*). This would seem to be a retained primitive feature. As will be argued below, a tracheal lung seems to have been evolved several times within viperids, in association with this modification the anterior pocket of the lung has apparently been lost several times.

The tracheal cartilages in viperines typically end near the ventricle of the heart or somewhat posterior to it, this is similar to the primitive condition. Two significant modifications are found. In *Causus* except *defilippii* and *lichtensteini* and in *superciliaris*, the tracheal cartilages extend far posteriorly down the right lung, and reach a level equal to near halfway, or further, down the liver. There can be no doubt that this has occurred independently in these taxa, By contrast, in two of the large *Bitis* (*B.gabonica* & *B.nasicornis*), the tracheal cartilages terminate at, or anterior to, the anterior portion of the heart. This condition is a probable synapomorphy of *B.gabonica* & *B.nasicornis*.

Tracheal lung and pulmonary arteries.

Modifications to the pulmonary artery are associated with reduction of the left lung and with development of a tracheal lung. Brongersma (1951:5) has noted that, in contrast to other amniotes, in snakes with two lungs one or more branches of the right pulmonary supply the left lung (eg. *Azemiops*, Fig. 76). In several species there are actual anastomoses between the right and left pulmonary arteries. Brongersma also suggests (1951a:33) that reduction of the left lung, and increasing importance of the right pulmonary as a source of blood supply to it, may both precede the reduction and final loss of the left pulmonary. A small diverticulum from the pulmonary trunk, present in many snakes lacking a complete left pulmonary, may be connected by a ligament (ligamentum arteriosum) to the left aortic arch. The ligament would appear to be a remnant of the embryonic ductus arteriosus (d.Botalli), and the diverticulum a last vestige of the left pulmonary artery (Brongersma, 1949:63). Thus, in snakes in which only the right lung is well-developed, and in which a tracheal lung is absent, the primary pulmonary arterial vessel is the right pulmonary artery running posteriorly.

The right pulmonary artery becomes elaborated when a tracheal lung is developed. In snakes all except the anterior-most cartilaginous supports of the trachea do not form complete rings, but are incomplete dorsally; the dorsal portion is closed by a soft membrane. The free ends of the incomplete tracheal rings on each side of the body tend to interdigitate with one another (see Fig. 10 in Frenkel & Kochva, 1970, with reference to Vipera palaestinae; a henophidian example is noted by Brongersma, 1951b, with ref. to tropidophiines). In very many species this membraneous portion of the trachea is somewhat expanded, and in several unrelated groups this expansion is accentuated and vascularised, forming a 'tracheal lung'. When a tracheal lung is present the vascularisation of the true (right) lung may be much reduced until most or all of the 'lung' forms a simple non-vascular air-sac, and vascularisation is largely or entirely restricted to the tracheal lung. Accordingly the right pulmonary artery bears one or two branches running anteriorly of the heart to supply the tracheal lung, and posterior branches are reduced in calibre, or in a few cases, absent altogether. In a majority of snakes with a tracheal lung there is only a single anterior artery, running along the right-lateral or right-dorsal side of the tracheal lung. The possible functional significance of these modifications are discussed by Brattstrom (1959), McDonald (1959), Kardong (1972), Heatwole & Seymour (1975), and also see Hartline (1971).

Whereas in snakes lacking a tracheal lung there is typically a gap equal to one or more heart-lengths between the posterior tip of the heart and the anterior tip of the liver, this gap is usually reduced or lost, apparently due to a relatively more posterior heart position, in snakes possessing a tracheal lung (Brongersma, 1951b, 1957c:453; Underwood, 1967:38).

Brongersma (1949) and Bourgondien & Bothner (1969) have described conditions in several viperids.

A tracheal lung is absent in *Azemiops*, *Lachesis mutus* (Brongersma, 1949:60). Within viperines (s.l.) it is absent in the small southern African *Bitis* (*atropos*, *caudalis*, *cornuta*, *heraldica*, *schneideri*, Underwood, 1968; *xeropaga*, Haacke, 1975; also absent in *peringueyi*), and in *Cerastes* (*cerastes*, *vipera*). Although the dorsal portion of the trachea is expanded to a greater or lesser degree in *Azemiops* and all viperines, extensive vascularisation does not extend anteriorly past the heart in the species noted above, and there is no prominent anterior pulmonary artery; I have considered a tracheal lung to be absent in such circumstances (after Brongersma, 1957c:453). Accordingly it seems inappropriate to include the presence of a tracheal lung in the familial definition of the Viperidae given by Liem, Marx & Rabb (1970:120).

Underwood (1967:5) concluded that a tracheal lung had undoubtedly been developed several times in snakes. Within several groups of apparently closely related species, e.g., those assigned to *Pareas* (Brongersma, 1957c) and *Laticauda* (McCarthy, pers.comm.), there are some forms lacking a tracheal lung and some with it moderately or extensively-developed.

As noted above, a tracheal lung is absent in diverse viperids, one of these (*Azemiops*) retains a generally primitive viperid morphology, but the other species appear to be members of rather more specialised lineages. If it is assumed that a tracheal lung is indeed primitively absent in these species, and not secondarily lost, one corollary is that a tracheal lung must have been developed in parallel in several or many lineages (depending on the precise cladistic pattern). It would seem to be more parsimonious to suggest that a tracheal lung was developed in the common ancestry of viperids, and has later been lost in a few species. This latter suggestion originally seemed quite plausible because the viperines (s.l.) without a tracheal lung nearly all occur in moderately or very arid regions, and it was thought that the tracheal lung may have been eliminated as an undesireable source of water loss during respiration (however, Dmi'el, 1972, has attributed the low rates of water loss in Cerastes to other factors, and a well-developed tracheal lung is present in the related arid-zone viperid Echis, and in the desert crotaline Crotalus cerastes, Kardong, 1972:371). This ambiguity in interpretation seemed to reduce the cladistic significance of this character; however, a closer examination of the condition in Azemiops, Cerastes, and Bitis, has somewhat clarified the situation.

In Azemiops and Cerastes (both species, C.cerastes & C.vipera) a prominent forward pocket of the right lung is present , i.e., tracheal entry into the lung is sub-terminal, as in other reptiles including almost all lower snakes with two lungs; this is rather certainly a primitive feature. No snake with a well-developed tracheal lung is currently known to retain a forward pocket of the right lung; as noted above when a tracheal lung is present the boundary between the tracheal lung and the true (right) lung is more or less obscured as the two elements blend into a single elongate air-chamber. The retention of a primitive anterior pocket of the true lung in Azemiops and Cerastes thus makes it highly improbable that a tracheal lung has ever been present in the ancestry of these species.

In all viperines with a tracheal lung the heart closely approaches or (usually) contacts or overlaps the anterior tip of the liver. It has been noted above that in snakes lacking a tracheal lung there is typically a more or less extensive gap between the heart and the liver. It appears as if the development of a tracheal lung tends to 'crowd' the heart into a relatively more posterior location. There is a large gap between the heart and the liver in *Azemiops* and *Cerastes*. This gap would have to have been opened up secondarily if a tracheal lung, with correlated heart-liver contact, has actually been lost in these species; it is more parsimonious to assume that a tracheal lung has never been present.

In all snakes with a true tracheal lung there are one or more anterior branches of the pulmonary artery, and the posterior branches may be reduced or lost. In the two specimens of *Azemiops* dissected I could find no trace of any anterior branch of the right pulmonary artery passing forward of the heart. In *Cerastes* there is a short and very thin vessel arising from the pulmonary artery posterior to the heart and running forward along the left side of the dorsal expansion of the trachea. It fades out, with the alveoli of the true lung and its short tracheal extension, at around the anterior level of the heart. This vessel does not arise from the ventro-dorsal curve of the pulmonary trunk across to the right side of the body, as do the anterior tracheal branches of viperids possessing a tracheal lung, and does not appear to represent such an anterior pulmonary vessel in reduced form. The presence of a *Cerastes*-like anterior vessel (not necessarily from the same point of origin) would seem to be a requisite initial step toward development of a full tracheal lung. A similar very thin vessel was found in *Bitis cornuta*, but was not definitely seen in the other small *Bitis* lacking a tracheal lung. The absence of an anterior pulmonary (tracheal) vessel resembling that of viperids with a tracheal lung is consistent with the suggestion that a tracheal lung is primitively absent in *Azemiops*, *Cerastes*, and probably *Bitis*, and not secondarily lost.

Whereas in *Azemiops*, *Cerastes*, and southern African small *Bitis*, the posterior branches of the right pulmonary artery are the only significantly-developed pulmonary arteries, in all viperines with a tracheal lung the posterior branch of the pulmonary artery is much reduced, or absent altogether (Causus), and the anterior branch (or branches) constitute the major or only pulmonary artery. If the ancestors of *Azemiops*, *Cerastes* and small *Bitis* had a tracheal lung, the latter condition would be expected there also, so if a tracheal lung has been lost in these species it would seem that the posterior pulmonary arteries have been re-enlarged and the anterior ones reduced.

Overall, if a tracheal lung was present in the ancestry of *Azemiops* and *Cerastes*, and has subsequently been lost, it is necessary to postulate that these species have: - lost alveoli from the dorsal expansion of the trachea, re-developed a forward pocket of the right lung, re-developed a heart-liver gap, lost anterior branches from the right-side curve of the pulmonary artery, and re-enlarged the posterior arteries. Although some of these features may be developmentally or functionally correlated (e.g., loss of tracheal alveoli and loss of tracheal arteries), the hypothesis of secondary loss seems too complicated and unlikely. The retention of a forward pocket of the lung appears highly significant. I have concluded that a tracheal lung is indeed primitively absent in *Azemiops* and *Cerastes*, not secondarily lost. It may be remembered that *Azemiops* also retains a distinct vestige of the left lung (present elsewhere in viperids only in some crotalines) and primitive states of many other characters. The small *Bitis* without a tracheal lung do not retain a forward pocket of the lung, (although a distinct 'shoulder' is present) but there is typically a more or less extensive heart-liver gap (exceptions are some *B. caudalis* and *B.heraldica*; gap present in B.*atropos*, most *caudalis*, *B.cornuta*, *B.peringuey*, *B.schneideri*, *B.xeropaga*), and no prominent anterior pulmonary arteries. Although the situation is not so clear as for *Azemiops* and *Cerastes*, it seems probable that a tracheal lung is primitively absent in *Bitis* also.

The conclusion that a tracheal lung is primitively absent in *Azemiops*, *Cerastes*, and probably in *Bitis*, carries the implication that a tracheal lung has been evolved in parallel in several viperid lineages. I have accepted this implication, in view of the evidence noted above and the fact that a tracheal lung has developed in parallel in several other groups of snakes. The evidence of other characters must be considered in some detail before the number of parallelisms within viperines can be suggested. For example, *Bitis* forms an undoubtedly monophyletic group, within this group *B.worthingtoni* is primitive and the remaining species are derived, on the basis of skull characters. Within the latter group, a tracheal lung is present in the large species (*B.arietans*, *nasicornis*, *gabonica*); a tracheal lung is also present in *B.worthingtoni*. If a tracheal lung is primitively absent in the genus, it must have been evolved separately in *worthingtoni* and the large *Bitis*. A difference in pulmonary artery pattern (see below) is consistent with this interpretation.

Hartline (1971:363) has demonstrated the importance of the lung complex as a mechanical pathway for the transmission of sound incident on the trunk to the inner ear system in certain snakes. The experimental species of *Crotalus* used by Hartline possess an extensive tracheal lung and the posterior portion of the lung forms a non-vascular air-sac; the role of this advanced form of lung morphology in sound transmission provides a possible adaptive explanation for the multiple evolution of tracheal lungs in snakes (although no direct comparison of hearing abilities in closely related snakes with and without tracheal lungs has yet been reported).

When a tracheal lung develops it seems that the 'easiest' point of origin for the necessary anterior artery is from the right-side ventro-dorsal curve of the right pulmonary artery (the left vessel being absent). The anterior artery passes forward along the right-dorsal or right-lateral side of the tracheal lung, and the posterior vessel is reduced. This pattern is found among crotalines in *Agkistrodon* (the most primitive crotalines on other evidence), *Trimeresurus*, some *Bothrops*, some *Sistrurus*, and in *Atheris*, *hindii*, *superciliaris*, *Echis*, *Bitis worthingtoni*, *Vipera*, *Pseudocerastes*, *Eristicophis*, among viperines. On the grounds of its wide distribution among viperids, and among other snakes in which a tracheal lung is present, this would appear to be the primitive pulmonary artery arrangement for any group possessing a tracheal lung.

In the large *Bitis* (but not *B.worthingtoni*) and in *Causus* (and some crotalines, Brongersma, 1949; Bourgondien & Bothner, 1969), there is an additional anterior pulmonary artery on the left-ventral side of the tracheal lung. This is a derived feature, but because the genus *Bitis* is certainly monophyletic, the left-ventral anterior vessel must have been derived in parallel in the large *Bitis* and in *Causus* (and separately within crotalines). *Causus* shows three further derived states of the pulmonary arteries; the primitive right-dorsal anterior vessel has shifted ventrally, so that there is now a right-ventral and a left-ventral artery running anteriorly alongside the trachea; the posterior branch of the right pulmonary artery has been lost altogether; and there is a moderately-developed posterior artery that supplies the true lung and arises anterior to the heart from the left-ventral anterior vessel (a somewhat similar but very thin posterior vessel is found in the large *Bitis*, but arising either from a point close to the origin of the primitive left pulmonary artery, or well anterior to the heart; a similar vessel is present in *Lachesis*, some *Crotalus* and *Sistrurus*, and some non-viperids).

Overall, seven basic patterns of lung and pulmonary artery morphology can be distinguished among viperids (not including certain patterns apparently derived within crotalines, and not of immediate relevance to the present study - see Bourgondien & Bothner, 1969).

A - primitive
Tracheal lung absent, anterior pulmonary artery (tracheal artery) absent, heart-liver gap present, left lung vestige present, antero-lateral pocket of right lung present,
Azemiops

B - as 'A' but thin and short tracheal artery present, left lung absent,
Cerastes

C - as 'B' but heart-liver gap variably present, antero-lateral pocket of right lung absent,
Bitis atropos, *cornuta*, *caudalis*, *heraldica*, *peringueyi*, *schneideri*, *xeropaga* (all the southern African dwarf *Bitis*)

D - as 'C' but tracheal lung present, anterior pulmonary (tracheal) artery present and in right-dorsal position, posterior pulmonary artery reduced,
Atheris, *Adenorhinos* (probably, p.34), *hindii*, *Bitis worthingtoni*, *Echis*, *Vipera*, *Pseudocerastes*, *Eristicophis*. This pattern is also found in many crotalines.

E - as 'D' but with long intra-pulmonary bronchus, extending to the posterior half of the liver,
superciliaris

F - as 'D' but with addition of a left-ventral anterior pulmonary artery, right posterior pulmonary artery absent,
Causus defilippii, *lichtensteini*

G - as 'F' but with long intra-pulmonary bronchus,
Causus bilineatus, *maculatus*, *resimus*, *rhombeatus*

Certain state transformations, eg., C → D, have almost certainly occurred in parallel, and are thus not of highest cladistic significance.

$$\begin{tikzcd}
A \arrow[r] & B \arrow[r] & C \arrow[r] & D \arrow[r] \arrow[d] & F \arrow[d] \\
 & & & E & G
\end{tikzcd}$$

23.

Maxillo-postorbital ligament (Figs 81-83)

In most snakes (except certain elapids, Kochva, 1962: 262-3) a quadrato-maxillary ligament is present, extending from the ventro-lateral extremity of the quadrate at the quadrato-mandibular articulation, anteriorly to the posterior portion of the maxillar. This ligament appears to have a role in retraction of the palato-maxillary arch, in particular the maxilla (Albright & Nelson, 1959a, b; Frazzetta, 1966), insofar as it connects the maxillar to the M. Cervico-mandibularis (= M.retractor quadrati of Frazzetta, 1966:244; Kochva, 1962) arising from the dorsal cervical region and inserting on the quadrate and/or the quadrato-mandibular articulation. Contraction of the M.cervico-mandibularis will tend to retract the quadrate and thus retract the maxilla when the quadrato-mandibular ligament becomes taut.

In viperids the form and function of the quadrato-maxillary ligament and the maxillar are modified. Typically the mid-section of the ligament is absent, presumably fused indistinguishably to the lateral face of the capsule of the venom gland; there are thus two ligaments present, a posterior one passing between the quadrato-mandibular articulation and the venom gland capsule, and an anterior one passing between the neck of the venom gland and the maxillar. The form of the maxilla is very different in viperids from that in other snakes (pp.23-25), and the ligament inserts on its antero-dorsal portion, partly crossing the maxillo-prefrontal articulation, superficial to other associated ligaments. The point of origin of the anterior portion of the ligament is partly or largely from the distal tip of the postorbital, there is an apparent tendency for this connection to become stronger, until the anterior portion is entirely separate from the venom gland and arises entirely from the distal tip of the postorbital. For example, in the seemingly more conservative small European Vipera (such as V.ursinii, V.berus) there is only a weak partial connection to the postorbital, this connecttion is much more prominent in the intermediate *V.aspis* and *V.ammodytes*, and the origin is entirely from the postorbital in more advanced *Vipera* (such as *V.lebetina*). This division of the ligament is also characteristic of crotalines, and in view of the clear separation in *Agkistrodon piscivorus* Kardong (1974:338) uses the term 'ligamentum maxillo-postorbitale' for the anterior portion. Kardong (1974:347) proposes that the primary function of the ligament in viperids is to resist hyperextension of the maxilla during fang protraction and striking. This proposal seems well-founded, such a role can be readily demonstrated in wet bone-ligament preparations, and it is noteworthy that forms such as *Bitis*, *Cerastes*, most *Echis* and advanced *Vipera*, with a very prominent maxillo-postorbital ligament arising entirely from the postorbital also appear to have reinforced the articulation of the postorbital with the braincase, either by development of a supporting process of the parietal (*Cerastes*, large *Vipera*), or by expansion of the head of the postorbital (*Bitis*). Marx & Rabb (1965:163-4) give very great significance to the nature of the postorbital and its articulation with the parietal; because of the functional association with the fang mechanism I would not be inclined to give overriding cladistic importance to this feature (see character).

Hyperextension of the maxilla is also resisted by lateral and medial maxillo-prefrontal ligaments running between the prefrontal and the maxilla ; in wet bone -ligament preparations these ligaments appear more important in resisting hyperextension of the maxilla than is the maxillo-postorbital ligament, one relevant factor is that the latter acts too close to the maxillo-prefrontal articulation for a high mechanical advantage. These additional means of resisting hyperextension may provide some explanation as to why the maxillo-postorbital ligament has been reduced in certain species and lost in a few.

The maxillo-postorbital ligament is frequently confluent, usually at the tip of the postorbital, with a circum-ocular ligamentous ring, running from the postorbital tip, along the lower margin of the eye, and up the posterior face of the prefrontal. Sometimes (eg. *Atheris*, *Bitis*, *Cerastes*) there is a single ligament arising from the postorbital, that bifurcates anteriorly.

In *Causus*, there is no ligament running between the postorbital and the maxilla; only a single ligament remains, attaching to a prominent posteriorly-directed spine at the ventro-lateral extremity of the prefrontal. The lateral maxillo-prefrontal ligament is unusually lateral in position, and is exposed laterally due to the absence of the typical maxillo-postorbital ligament, that when present is the most superficial ligament. I interpret this pattern as a synapormorphy of the *Causus* species (this particular instance of loss may result from an apparent overall simplification of the fang apparatus in this genus).

The maxillo-postorbital ligament is thin in many specimens of the *Echis carinatus* complex, and is absent in some specimens; similarly it is thin in most *Atheris*, (s.s., not *superciliaris* or *hindii*), and absent in *A.hispida*. I regard these as independent losses. It is possible to speculate that prevention of maxilla hyperextension is performed by the maxillary portion of the *M.retractor pterygoidei* (character 29) in the *Echis carinatus* lacking the maxillo-postorbital ligament, but this muscle branch is not present in *Causus* or *Atheris hispida.*

The maxillo-postorbital ligament is modified or lost in a few crotalines (Kochva, 1962), but not *Agkistrodon piscivorus* (Kardong, 1973) or various Asian crotalines (pers. obs.).

A - primitive

B - 'maxillo'-postorbital ligament runs only to spine on prefrontal *Causus*

C - ligament absent in some individuals, *Echis carinatus*

D - ligament absent, *Atheris hispidus* (parallelism)

$$\begin{tikzcd}
B & A \arrow[l] \arrow[r] \arrow[d] & C \\
 & D &
\end{tikzcd}$$

24,25,26.

Venom gland and associated muscles (with particular reference to Causus) (Figs 84-87)

Typically the viperid venom gland, located in the temporal region is a rather pear-shaped structure, tapering anteriorly into the venom duct, and surrounded posteriorly by a loop of muscle fibres, the M.compressor glandulae (Kochva, 1958, 1962, 1979). The compressor arises dorsolaterally from the capsule of the venom gland, encloses the posterior end of the venom gland in a loop, and inserts on the compound bone of the mandible. Kochva (1962,1963) has shown, on the evidence of development and adult anatomy (eg. innervation, that the compressor is derived phyletically from the immediately posterior add.ext.profundus (illustrating a fundamental difference from elapid snakes, in which the 'compressor' is the add.ext.superficialis). The profundus typically runs from the anterior edge of the quadrate to the postero-lateral portion of the mandible. A quadrato-glandular ligament runs between the dorsal head of the quadrate and the dorso-medial extremity of the venom gland; in many viperids this ligament is incorporated into a connective tissue sheath covering the junction of the compressor and profundus and adjacent areas of the gland.

The venom gland and associated musculature are modified in Causus. In 4 species (C.resimus, rhombeatus, and 2 forms until recently regarded as conspecific with the latter, C.maculatus and C.bilineatus), the venom gland is greatly elongated, extending posterior to the head well into the neck region (Haas, 1952, 1973; Kochva, 1962). Elongate venom glands are also found in the 2 species included in Maticora (Elapidae), and in certain species of Atractaspis (of possible aparallactine affinities). It is of interest that in Causus and Atractaspis the elongate venom glands are situated superficial to the ribs and are overlain by the skin and dermal musculature, but in Maticora the gland penetrates into the body cavity deep to the ribs. It has been suggested that elongation of the venom gland may be a means of increasing venom secretion and storage capacity; elongation has certainly occurred separately in each of the 3 groups noted above.

In the *Causus* species with long venom glands, the *compressor* is superficially highly dissimilar to that of other vipers; it forms a ribbon of muscle fibres extending posteriorly along the dorsal edge of the elongated gland, and back anteriorly along the ventral edge, to the temporal region. Kochva (1967) has shown that in its early development this muscle is identical to the *compressor* of other vipers. Anteriorly the ventral strip of *compressor* joins the ventral portion of the divided *profundus* (see below), fibres of the dorsal strip tend to fade out anteriorly (especially in *resimus*) and are connected via a thin aponeurosis of the dorsal portion of the *profundus* (and frequently with some association with the *superficialis*).

This configuration of the extended venom glands and modified *compressor* is not seen in other snakes (only certain *Atractaspis* are somewhat similar, see Kochva, 1979:111, and Kochva *et al*, 1967, for differences), and is here regarded as a synapomorphy of *Causus resimus*, *C.rhombeatus*, *C.maculatus*, and *C.bilineatus*.

In the remaining *Causus* species, (*C.défilippii*, *C.lichtensteini*), the venom gland is of an almost standard viperid form, but is slightly modified in that it has a small bulbous postero-ventral extension (Fig.85). The *compressor* is likewise quite similar to that of other viperids (except for its position in relation to the posterior extremity of the gland), but it is accompanied by a well-defined band of muscle fibres arising from the head of the quadrate and inserting on the bulbous posterior extension of the venom gland. I am uncertain whether this muscle (muscle 'X') is to be regarded as a portion of the *profundus* that has shifted its ventral attachment from the mandible to the venom gland, or as a portion of the *compressor* that has shifted its anterior attachment from the venom gland to the quadrate. The former appears most probable (and is favoured by Haas, 1952, 1973), but is difficult to decide on one view or the other because of the intimate association of the two muscles in phylogeny and ontogeny. This muscle is absent from all other viperids, and is here regarded as a synapomorphy of Causus defilippii and C.lichtensteini.

In all Causus the profundus is nearly completely divided into dorsal and ventral portions; the former, with its near vertical fibres passing between the anterior edge of the quadrate and the mandible, is very similar to the profundus of other snakes, the latter is a compact almond-shaped mass with diagonal fibres inserting on the lateral face of the posterior portion of the mandible. This condition is not seen in other viperids (or other snakes) and is here regarded as a synapomorphy of all 6 Causus species.

It would seem possible to interpret the slightly extended venom gland of Causus defilippii and C.lichtensteini as an intermediate stage toward the evolution of fully extended glands in other Causus species, but I do not follow this interpretation since the structure is associated with 'muscle 'X', unique to the 2 noted Causus, and may likewise be a derived feature unique to these species. This matter is complicated by the fact that Azemiops also seems to have a slight postero-ventral extension of the venom gland (Haas, 1973:Fig.167; Kochva et al, 1967:Fig. 7a, Liem et al, 1972: Fig. 8; pers.obs. on FMNH 152987). Because Azemiops and Causus retain primitive states of many characters, it may be that this configuration is also primitive for viperids; in all viperids other than these genera, fibres of the compressor encircle the gland posteriorly without passing slightly medial to it posteriorly and thus producing the appearance of a postero-lateral extension of the gland.

In Azemiops and the Causus without extended venom glands, compressor muscle fibres that insert on the venom gland are not restricted to the dorsal and dorso-lateral portions of the gland as their area of origin, but arises also from the quadrato-glandular ligament. There is a degree of continuity between the main *profundus*, the fibres arising fromthe quadrato-glandular ligament, and the typical *compressor*. The actual course of the intermediate fibres is different in *Azemiops* and the 2 noted *Causus*. In *Azemiops* the fibres are continuous dorsally with the *compressor* (anteriorly), but become separate at the rear of the venom gland, where a few fibres attach to the gland, and antero-ventrally become confluent again with the *compressor* at its insertion. In *Causus*, the fibres arising from the quadrato-glandular ligament mostly overlie the main *compressor*, and insert almost entirely on the bulbous posterior portion of the gland.

The various subdivisions of the *profundus-compressor* system in the generally primitive *Azemiops* and *Causus* may be primitive to the condition in other viperids in which there is typically a clear separation dorsally between the *profundus* and the *compressor* (in none of 6 specimens of *Bitis gabonica* was found the condition reported by Haas, 1952, in which many fibres of the *compressor* pass posteriorly from their origin to mingle with *profundus* fibres on the quadrate; the condition in my single specimen of *B.nasicornis* was also typical, unlike the specimen examined by Kochva, 1963:247).

This complex may be treated as three separate characters, as overleaf.

24. Venom gland

A - primitive

B - considerably elongated

<u>Causus bilineatus</u>, <u>maculatus</u>, <u>resimus</u>, <u>rhombeatus</u>

A → B

25. Muscle 'X'

A - primitive

B - present

<u>Causus defilippii</u>, <u>lichtensteini</u>

A → B

26. <u>M.add.ext.profundus</u>

A - primitive

B - divided

<u>Causus</u>

A → B

27.
M.hyotrachealis (Figs 88-89)

The M.hyotrachealis is a muscle of the throat region that is unique to snakes and present in all forms so far investigated (Langebartel, 1968:79-81). Typically it arises on the hyoid cornua and passes anteriorly along the buccal floor to insert on the anterior portion of the trachea immediately posterior to the larynx. The action of the muscle is to retract the larynx and associated elements, particularly following protraction of the larynx by the M.geniotrachealis (the latter action in order to facilitate breathing during deglutition).

The major variation in the hyotrachealis among snakes is in its site of origin. Langebartel, in his valuable survey of the hyoid and its musculature in snakes, states (1968:79) that "in most snakes the site of attachment is upon the respective cornu, but there are exceptions" (Langebartel believed that the hyoid cornua are derived from different visceral arches in different groups of snakes, hence the word 'respective' but this seems implausible, see McDowell, 1972). He then notes some such exceptions in Scolecophidia; in leptotyphlopids the origin is on the buccal floor, in typholopids it is on the rib musculature (the statement that in anomalepidids the origin is on the buccal floor is erroneous, the origin is on the hyoid as in the great majority of snakes, Groombridge 1979c.Langebartel then states (1968:80), "nearly all of the remainder of snakes have the origin upon the cornu", and also "in the colubrids (s.l.) and the poisonous snakes, there are a few exceptions to the otherwise straightforward situation". Thus in what is probably the least highly modified group of Scolecophidia (the anomalepidids), in almost all Henophidia (except Tropidophis, origin on deep face of the M.neurocostomandibularis, Langebartel, 1968:80, and in the majority of Caenophidia (exceptions noted by Langebartel: Heterodon, Pseudaspis, origin on rib musculature; Thamnophis elegans, split origin, on hyoid and to neurocostomandibularis; and three viperid species), the origin of the hyotrachealis is from the hyoid cornua. I suggest that this form of origin is the primitive state, and that other conditions are derived.

The primitive hyoid origin of the hyotrachealis is retained among viperids only in Azemiops and Causus, two genera that also retain primitive states of several other characters. All crotalines examined and all viperines except Causus show a derived state in which the hyotrachealis has shifted its origin off the hyoid; it arises instead from the deep face of the neurocostomandibularis near the region of the anterior tendinous inscription. This situation has been found universally in viperines other than Causus (from 1-4 specimens of all species included in this study). It has also been reported by Kardong for the crotalines Crotalus viridis (1972) and Agkistrodon piscivorus (1973), and has been found in all crotalines dissected in the present study; Agkistrodon blomhoffi, A.intermedius, A.piscivorus, A.rhodostoma, Bothrops alternatus, B.jararaca, B.nigoviridis, B.nummifer (4 specimens, including B.n. mexicana), and Lachesis mutus. Langebartel (1968:142, Fig. 18A) indicated that the origin is on the hyoid in Bothrops mexicana (=B.nummifer mexicana), but I cannot confirm this. He also noted (1968:80) a variable origin in Agkistrodon (A.piscivorus leucostomus according to his species list, 1968:   ), on the rib cage or also on the hyoid, I cannot confirm this and agree with Kardong (1973:331). Edgeworth (1935:202) reported a similar split origin in Vipera, I have not found this in any specimen of Vipera. Although coverage of the crotalines is less complete than of viperines, it is reasonable to conclude that a derived form of hyotrachealis origin (from the deep face of the neurocostomandibularis, not from the hyoid) is characteristic of both crotalines and viperines other than Causus.

At first sight the derived hyotrachealis origin shared by crotalines and viperines other than Causus would appear to be a probable synapomorphy indicating that these two groups are jointly monophyletic. While other evidence is congruent with this arrangement, it is perhaps contradicted by features of retinal anatomy (see discussion, p.200). The problem is whether the derived state was uniquely derived (among viperids) in the common ancestry of crotalines and viperines except *Causus*, or was derived in parallel in each of the two groups. As noted by Langebartel (1968), a few other snake taxa have also departed from the primitive state in which the *hyotrachealis* arises from the hyoid.

A - primitive

B - *M.hyotrachealis* shifts attachment off hyoid, to *M.neurocostomandibulari* complex,

Viperinae except *Causus*, also Crotalinae - homologous ?

A→B

28.

Occipital head of the M.depressor mandibulae (Figs 90-92)

The depressor mandibulae (= occipito-quadrato-mandibularis) in snakes arises from the cartilaginous cap over the head of the quadrate at the quadrate-squamosal articulation, and the postero-lateral surfaces of much of the length of the quadrate (frequently with anterior fibres associated with the M.adductor externus profundus). The muscle runs more or less parallel to the quadrate, and inserts on the dorsal surfaces of the retroarticular process of the mandible. Dorsally, there is frequently one (or more) partly separate occipital heads of the depressor mandibulae, arising from the occipital region of the skull and the parieto-squamosal ligament, in addition to the main quadrate head.

The function of the main quadrate portion of the depressor is to depress the mandible (by rotation at the quadrate-mandible articulation) during opening of the mouth; contraction of the occipital portion would add a degree of dorso-medial rotation of the quadrate and the posterior tip of the squamosal (to which the quadrate head articulates) and possibly slight protraction of the palato-maxillary arch (Dullemeijer, 1956:65). The cross-sectional area of the occipital head, when present, is typically somewhat or considerably less than that of the quadrate head.

An occipital head of the depressor mandibulae is present in most Henophidia and many Caenophidia (Cundall, 1974: Frazetta, 1966:248, Haas, 1955, 1973; Varkey, 1973; Weaver, 1965). Among the Caenophidia, it is present in a majority of viperids, including Azemiops (Liem, Marx & Rabb, 1972:93), most crotalines (Kardong, 1973:328; Kochva, 1962:269; pers. obs.), and many viperines. Given the wide distribution of this muscle within snakes, and within viperids in particular, it would seem probable that the occipital head is primitively present in the family, and its absence (loss) is a derived state.

There is considerable variation within the Viperinae; an occipital head is very prominent in some species, moderately-developed in others, and absent in some; there is also occasional intraspecific variation.

In the apparently most conservative of the smaller Eurasian *Vipera* (*V.ursinii*, *kaznakovi*, *berus*) the occipital head is typically very prominent, with a broad transverse origin on the parietal-supraoccipital ridge, and approaching contact with the occipital head of the other side in the midline. This pattern is also found in *Echis*, most *Atheris*, *hindii*, and *Adenorhinos* (very well-developed in the latter 2). A quite similar pattern, but with the occipital head relatively narrower and/or shorter (reaching around the head of the quadrate only to the parieto-squamosal ligament, not to the cranium) is typically found in the remaining smaller European *Vipera* (*seoanei*, *latastei*, *aspis*, *ammodytes*), in *Cerastes* and the remaining 'true' *Atheris*, (*desaixi*, *hispidus* - much reduced on one side in the single specimen examined). A further degree of reduction is seen in two of the smaller *Vipera* of the '*xanthina*-complex' (*bornmuelleri*, *latifii*), and in most *V.russelli*, and in *superciliaris*.

A quadrate head alone is found in *Bitis*, *Causus*, (very slight development of an occipital head in some specimens), most of the *xanthina*-complex *Vipera* (*xanthina*, *raddei*, *palaestinae*), *V.lebetina*, some *V.russelli*, and the probable close relatives of these large *Vipera*, *Pseudocerastes* and *Eristicophis*.

Significant intraspecific variation was found in some *Vipera*. Of 5 *V.berus* examined, the occipital head was wide and long in 3, but narrower in 2; of 5 *V.ammodytes*, it was long and narrow in 4, but absent in 1; of 5 *V.russelli* it was very short and very narrow in 3 (highly asymmetrical in one of these, being indistinct on one side), but absent entirely in 2; of 2 *V.x.xanthina* it was represented by only a very few muscle fibres on one side in 1, but absent in the second.

The gradual modifications in degree of development of the occipital head of the depressor mandibulae, and the intraspecific variation, make interpretation of this feature rather difficult. There would seem to be a persistent tendency to reduction and loss of the occipital head; this is particularly clear in the Eurasian group of species, where the apparent polarity is concordant with that in several other characters, with the most derived state (complete loss of the occipital head) being shared by most larger Vipera, Pseudocerastes and Eristicophis. Loss of the occipital head has also occurred in Bitis and again in Causus. It is possible that occipital head fibres are secondarily present in some V.russelli. The apparent trend toward reduction and loss of the occipital head of the depressor raises some doubts about the functional significance of the possession of a separate occipital origin.

Although, the derived state being a loss condition, this character cannot be given primary importance in a cladistic analysis, it is significant in illustrating concordance with other trends in the Eurasian group of species, and also in showing the probability that if Echis and Cerastes (and their possible relatives in Africa) share a common ancestor with some segment of the Eurasian radiation, that ancestor would have to be a form in which the occipital head was not yet lost (ie. similar to the small European Vipera, not the larger Mid-East forms in which the occipital head is typically absent).

29.
Lateral branch of the M.retractor pterygoidei (Figs 93-94)

The retractor pterygoidei is a muscle of the deep CId complex (Haas, 1973), running from the ventrolateral or ventral surface of the braincase (from a depression in the parietal immediately dorsal to the sphenoid in most viperids), to the anterior extremity of the pterygoid and/or the posterior portion of the palatine. The function of the retractor pterygoidei (with other muscles) is to retract the palato-maxillary arch, primarily during deglutition.

In certain viperids, a variably-distinct lateral bundle of muscle fibres diverges from the main portion of the retractor pterygoidei to insert on the antero-medial extremity of the ectopterygoid and/or the ventro-medial surface of the maxilla. It may be that the precision presumably afforded by a retractor muscle inserting directly on the ectopterygoid/maxilla is of adaptive significance in the viperid fang protraction-retraction system (another muscle, the pterygoideus, inserts directly on the ectopterygoid/maxilla, but it does not arise from the braincase and influences other cranial elements in addition. To the best of my knowledge such a lateral branch of the retractor pterygoidei has not been reported for any snakes other than vipers.

In the generally primitive viperid Azemiops, some lateral fibres of the retractor insert on the dorsal surface of the ectopterygoid (Liem, Marx & Rabb, 1972:94); in the crotaline Agkistrodon piscivorus similar fibres insert on the antero-medial articular knob of the ectopterygoid (Kardong, 1973:327; the same occurs in the two Asiatic Agkistrodon, A.halys and A.intermedius, and in Crotalus viridis, pers.obs.).

In several viperines lateral fibres of the retractor insert either directly, or by a distinct tendon, or by relatively diffuse fibrous connective tissue, onto the ventro-medial surface of the maxilla, occasionally extending across the ectopterygoid-maxilla articulation. There is typically also a small insertion on the skin lining the mouth. The lateral branch in viperines differs from that in *Azemiops* and examined crotalines in that it inserts entirely or nearly entirely on the maxilla, not on the ectopterygoid alone.

Despite differences in the precise area of insertion, the presence of a lateral branch of the *retractor pterygoidei* in *Azemiops*, crotalines, and many viperines, suggests that such a branch may be primitively present in most or all groups of vipers. Within viperines, the further enlargement of the lateral branch, or its loss, would be derived conditions.

In most *Vipera* (some *ursinii*, *berus*, *aspis*, *ammodytes*, *latastei*, the *xanthina* group, *lebetina*, *russelli*) and in *Pseudocerastes*, the lateral branch of the *retractor* is moderately well-developed and typically inserts by a thin tendon (and with many fibres attaching directly to the maxilla in *x.palaestinae*, *lebetina*, and some *russelli*). The lateral branch is less well-defined in *V.kaznakovi*, *seoanei*, and some *ursinii*, and inserts via relatively diffuse fibrous connective tissue; a similar condition is found in *Eristicophis*. The lateral branch appears to be best developed in *V.x.palaestinae*, *lebetina*, and *russelli* (contrary to Kochva, 1963:235, in my 3 specimens of *palaestinae* the insertion was primarily on the maxilla, not the ectopterygoid); because *Pseudocerastes* and *Eristicophis*, on other evidence very probably share a common ancestor with some member of this group, the lateral branch of the *retractor* would seem to have been somewhat reduced in *Pseudocerastes* and further reduced in *Eristicophis*.

In *Bitis*, *Echis*, and *Cerastes*, the lateral branch is large, more prominent than in any *Vipera* (especially so in *Bitis* and *Echis*), and has a quite extensive direct fibrous insertion on the ventro-medial face of the maxilla (noted for *Bitis arietans* by Boltt & Ewer, 1964:90). This would seem to be a derived condition, but it is possibly not to be regarded as a synapomorphy of these 3 genera; it is a small difference from the typical *Vipera* condition, and no other evidence suggests that *Bitis*, *Echis*, and *Cerastes* form a monophyletic group.

In *Atheris*, *hindii*, *superciliaris*, and *Adenorhinos*, no distinct lateral branch of the *retractor* is present; this would seem to be a derived loss, and a probable synapomorphy of these forms, since it is congruent with other evidence.

No lateral branch is present in *Causus*; I am uncertain if this is a primitive absence or a secondary loss.

A - primitive (small medial head)

B - medial head of *M.retractor pterygoideus* large
    Bitis, *Echis*, *Cerastes* less so (parallelism ?)

C - medial head absent
    hindii, *superciliaris*, *Adenorhinos*, *Atheris*

$$B \leftleftarrows A \rightarrow C$$

30.

Origin of M.retractor pterygoideus (Figs 95-98)

In most viperids the origin of the M.retractor pterygoideus is confined to the posterior part of the descending walls of the parietal, which is usually hollowed out somewhat in this region, with the posterior extremities sometimes developed into a low flange marking the limit of muscle fibre attachments (a few fibres may extend onto the prootic, eg. in Atheris). Two different derived trends are apparent in viperines.

In Bitis nasicornis the posterior portion of the retractor transgresses onto the prootic, there is no flange at the posterior edge of the parietal; this tendency is further developed in B.gabonica, where the retractor extends well across the prootic, which itself, instead of the parietal, becomes hollowed out to form a distinct posterior flange.

In Cerastes, instead of muscle fibres extending onto the prootic, the parietal itself is much extended postero-laterally. The prootic is considerably deformed, and the foramen for exit of the maxillary branch (V_2) of the trigeminal comes to lie dorsal to the parietal instead of posterior to it.

These would seem to represent two different ways of increasing the length of M.retractor pterygoideus fibres, or of providing an increased attachment area for a more bulky muscle.

A - primitive
B - prootic modified
    Bitis nasicornis, gabonica
C - parietal modified
    Cerastes

$$B \leftarrow A \rightarrow C$$

31.

Origin of the M.add.ext. superficialis (Figs 99-100)

Typically in viperids the origin of the superficialis (of the adductor mandibulae externus muscle group) is thin and wide, extending anteriorly along the parietal to the postorbital, and thus covering the origins of the deeper levator pterygoidei (of the CId complex) and pseudotemporalis (of the adductor mandibulae internus group). In all 5 specimens of Vipera russelli dissected (from Sri Lanka, India, Pakistan and Thailand), the origin of the superficialis is situated more posteriorly, thus exposing the origins of the levator pterygoidei and the pseudotemporalis. The origins of the two deep muscles appear to be slightly more dorsal in position, as if taking the place of the superficialis.

This unique condition in Vipera russelli was noted by Kochva (1962:238-240). Contrary to Kochva (1962:240), all specimens of V.russelli examined in the present study possessed an add.ext.medialis.

The exposure of the deep muscles noted above is here interpreted as an autapomorphy of Vipera russelli (it is a derived feature and unique to this taxon); this condition thus provides no information on the cladistic affinities of russelli, but adds to the considerable morphological gap between russelli and the other species of Vipera.

32.
Posterior attachment of the M.pterygoideus (Figs 101-102)

The form of the M.pterygoideus in viperids has been summarised by Kochva (1962:265-266; see also Kardong, 1973, and Kochva, 1958). Typically 2 or 3 bundles of muscle fibres and associated ligaments arise anteriorly from the antero-lateral edge of the ectopterygoid (immediately posterior to its articulation with the maxilla), and from the connective tissue surrounding the developing fangs and the base of the maxilla. These bundles coalesce into a prominent bulky muscle, the major portion of the pterygoideus, passing posteriorly medial to the mandible. At its posterior attachment the muscle wraps ventrally around the posterior end of the mandible and inserts onto the ventral surface of the retroarticular process (which may be more or less hollowed out to receive muscle fibres), and with some fibres inserting on the medial face of the mandible close to the quadrate-mandible articulation. A further distinct portion, the M.pterygoideus accessorius, also attaches here, and passes to the posterior lamina of the pterygoid. Another branch, the M.pt.glandulae, present in most crotalines (Kochva, 1962:266; Liem, Marx & Rabb, 1972:104-105), passes from the main body of the pterygoideus to the venom gland capsule.

The above general description applies to all viperines (s.l.) examined in the present study, except Causus. In all species of Causus the posterior attachment of the main portion of the pterygoideus is not restricted to the retroarticular process and adjacent portions of the mandible, but passes also well anteriorly along the medial face of the mandible.

Because of the wide distribution of the typical condition in Azemiops, crotalines, and viperines (and similar, although less complex, in other snakes), I interpret this condition as primitive for viperids, and the Causus condition as derived, constituting a synapomorphy of the 6 species assigned to the genus.

A - primitive

B - M.pterygoideus with attachment extending anteriorly along compound bone, Causus

A→B

33.
Compound bone: posterior laminae (Figs 103-104)

In snakes the posterior bones of the mandible (articular, prearticular and surangular) are fused in the adult, forming the compound bone. A more or less extensive aperture is present in the compound bone, opening dorsally, bordered laterally by the surangular component of the compound bone, and medially by the prearticular component. Usually one or both of these elements form an elevated lamina adjacent to the aperture. The mandibular branch of the trigeminal nerve (V_3) and mandibular blood vessels enter the mandible through this aperture, and posterior elements of the adductor muscle group insert in and around it. The aperture is variously termed, Meckelian vacuity (Liem, Marx & Rabb, 1971;81), adductor fossa (Romer, 1956:199), primordial canal, or mandibular fossa.

In lizards and most lower snakes (Henophidia) the lateral (surangular) lamina is typically well-developed and larger than the medial (prearticular) lamina, and usually contributes, with the coronoid itself, to the coronoid process. In all higher snakes (Caenophidia) the coronoid is absent and a typical coronoid process is likewise absent, perhaps correlated with this the lamina bordering the mandibular fossa are frequently somewhat reduced, but in contrast to most Henophidia the medial lamina is usually larger than the lateral lamina, if the latter is present at all.

Two different patterns are present in viperids. In species of Causus both lateral and medial laminae are present and moderately well-developed, the medial is frequently slightly larger in most species, the lateral slightly larger in C.defilippii. Because of the fairly continuous variation between species and the significant variation within species, I would not agree with the clear distinction implied by Marx & Rabb (1972), who assigned lichtensteini and "lieneatus"(= bilineatus)to their state VI (2 laminae, medial largest) and other Causus to a different state (IV, 2 laminae, equal development). In all viperids (including Azemiops)other than Causus only the medial lamina is present.

Because the presence of a large medial lamina alone is the condition most widespread both in viperids and in other Caenophidia (75% of those examined by Marx & Rabb, 1972), it would seem likely that this state is primitive for viperids and the Causus state is derived, and a probable synapomorphy of the Causus species.

A - primitive

B - moderate or low lateral and medial laminae present

Causus

A→ B

34.

Angular and splenial (Figs 105-111)

The angular and splenial are two mandibular dermal bones lying ventral and posterior to the dentary (Romer, 1956). In snakes they form part of the medial face of the mandible and are only slightly exposed in lateral view (the angular more so than the splenial). The splenial is the anterior bone of the pair and has a long anteriorly-tapering contact with the dentary, primarily ventromedial to Meckel's cartilage in snakes; posteriorly it has a short contact with the angular that itself has a long posteriorly-tapering contact with the compound bone (=fused articular, prearticular, and surangular).

In the great majority of snakes (and almost all lizards) the angular and splenial are both present, in a few snakes only one bone is present within the area usually occupied by the two. There can be little doubt that presence of both bones is primitive for viperids, and that presence of a single bone is derived. This is in agreement with Marx & Rabb (1972:248).

Both the angular and splenial are present in Azemiops and in most crotalines (including certain Asiatic species of Agkistrodon, such as halys and intermedius, that are among the least derived crotalines). Among viperines, the angular and splenial are both present in Vipera, Pseudocerastes, Eristicophis and Causus (except C.maculatus, until recently regarded as a subspecies of rhombeatus, the 'rhombeatus' of Marx & Rabb, 1972:248, may be maculatus); but only a single bone is present in Atheris, Adenorhinos, hindii, superciliaris, and Bitis. Marx & Rabb (1965:165) stated that Echis and Cerastes "are conveniently distinguished from the other Palaearctic genera by their lack of a splenial bone". However they later (1972:248) noted that both angular and splenial are present in some specimens of Echis carinatus. In the present study I have found both bones present in Echis coloratus (3 specimens) but a single bone present in

This is on the basis of this character, and the postorbital-parietal relationship. These must be serious reservations about giving such high weight to a character with clear evidence for parallel evolution of the derived state.

However, Echis and Cerastes do differ consistently from other Palaearctic forms (Vipera, Pseudocerastes, Eristicophis) in another feature of the angular-splenial complex, resembling the advanced African forms (Adenorhinos, Atheris s.l., and Bitis) in the overall reduction in size of these bones.

The primitive condition would seem to be that found in Causus and the Eurasian viperines (including forms that are primitive in other respects), in which the angular is separate (except Causus maculatus) and rather prominent, extending in height (dorsal process) from the ventral edge of the mandible to near its dorsal edge where it approaches or contacts the dentary. In the most widespread derived state the angular-splenial complex, whether separate, partially fused, or fused (ie. accepting parallel fusions), is much reduced in height to a sliver-like form lacking close approach to the dentary or lacking a dorsal process altogether. The primitive state is shown by Causus, Vipera (except russelli), Pseudocerastes and Eristicophis; the derived state is shown by Adenorhinos, Atheris, hindii, superciliaris, Bitis (except the three big Bitis), Echis and Cerastes.

Two further derived states have a very restricted distribution. In Vipera russelli the separate angular has a long dorsal process forming an extensive overlapping articulation with the dentary (slight overlap or mere contact in other Eurasian species). In the big Bitis (arietans, nasicornis, gabonica) there is just a slight contact between a dorsal process of the fused angular-splenial and the dentary (dorsal process absent or very short in other Bitis, Adenorhinos, Atheris sl., Echis and Cerastes). Although this latter state superficially resembles the condition in most Vipera, the angular and splenial are fused not separate in

E.carinatus (5). Similarly, both bones are present in Cerastes cerastes (3), but a single bone in C.vipera (3). In one of the C.vipera there is a partially open line of fusion across the posterior part of the bone (in both left and right mandibles), precisely in the position of the line of contact between the separate angular and splenial in C.cerastes; this indicates that in some cases at least, and probably in all the viperine examples, the presence of a single bone is due to fusion of the centres of ossification of angular and splenial. This is in agreement with Marx & Rabb's modification (1972:245) of their earlier suggestion (1965; that presence of a single bone is due to loss of the splenial) to include the possibility of angular-splenial fusion.

I am also in agreement with Marx & Rabb (1972) that the derived state in which only a single bone is present has evolved in parallel in more than one lineage. For example, it is rather certain that the three species in Echis and the two in Cerastes are each more closely related to their congeners than to other forms, yet the derived state is found in species of each genus, indicating two separate transformations. Similar variation was reported within genera of crotalines by Marx & Rabb (1972), and a single bone is also present in Causus. This definite evidence for parallel evolution means that this character cannot be used as primary cladistic evidence in distinguishing lineages of viperines; without significant other evidence there is no more reason to associate the advanced African forms Atheris (s.l.), Adenorhinos, and Bitis, on this character (e.g. Marx & Rabb, 1965:181, 192) than there is to associate them with species of Echis and Cerastes also.

Marx & Rabb (1965:164) divide the "advanced viperines" (ie., not including Causus) into two lineages (1965:Fig.46), the Palearctic Vipera, Eristicophis, Echis and Cerastes, on one hand, and the Ethiopian Adenorhinos, Atheris, and Bitis on the other.

Bitis, and because the big *Bitis* are derived on other evidence, and other *Bitis* (including *worthingtoni*, the most primitive *Bitis*) lack 'angular' (-splenial) contact with the dentary, I have accepted that the big *Bitis* state is derived ('pseudoprimitive', perhaps reinforcing the mandible against increased forces acting on it following size increase in these species).

A - primitive
B - angular/splenial much reduced
  hindii, *superciliaris*, *Adenorhinos*, *Atheris*, *Bitis* (except big *Bitis*), *Echis*, *Cerastes*
C - angular/splenial contacts dentary (secondary ?)
  Bitis arietans, *nasicornis*, *gabonica*
D - angular extensively overlaps dentary
  Vipera russelli

$$D \leftarrow A \rightarrow B \rightarrow C$$

35.

Premaxilla: vomerine process (Figs 112-120)

The premaxilla is a dermal bone composed of left and right portions that, in Squamata, fuse along the sagittal plane during early ontogeny. Typically the snake premaxilla has a median ascending process, a ventral posterior (vomerine or palatal) process, that is frequently bifurcate posteriorly (presumably indicating incomplete fusion of left and right rudiments), and a pair of antero-ventral lateral processes. This basic pattern is seen in viperids, but there is much variation in detail, particularly in the vomerine process.

In *Azemiops*, most crotalines, *Causus*, and the Eurasian group of viperines (*Vipera*, *Pseudocerastes*, *Eristicophis*), the vomerine process is well - or moderately developed, and frequently bifurcate posteriorly (this is subject to significant intraspecific variation). This would seem to represent the primitive state in viperids. *Echis* and *'Atheris' superciliaris* are quite similar, and may also be primitive in this respect.

In *'Atheris' hindii* (one of two skulls examined was more similar to true *Atheris*), and especially in *Adenorhinos* and *Atheris* (*s.s.*), the vomerine process is very much reduced or virtually absent in some *Atheris*; this probably represents a single derived sequence.

Cerastes typically retains a vomerine process intermediate in size between those of *Echis* and *hindii*; if *Echis* and *Cerastes* are sister groups, this must be a parallel reduction (in *Cerastes* and *Atheris*). *Cerastes* is not cladistically intermediate between *Echis* and *hindii*-*Atheris* in any other characters.

Conditions vary within *Bitis*. In most species there is a vomerine process that is rather broad anteriorly, with two postero-lateral lobes each perforated by a blood vessel foramen (such foramina may also be present in other viperines, e.g. *hindii*, *Cerastes*), and with a median posterior process. This pattern is present in *Bitis arietans*, nasicornis and gabonica (posterior process turned ventrally in these two), caudalis, cornuta (posterior process reduced), and xeropaga. Bitis atropos is quite similar but with a broad vomerine process, lacking a separate posterior median spine. In B.peringueyi and schneideri the premaxilla as a whole is much reduced, especially the ascending process, and the vomerine process; this is a probable synapomorphy. The premaxilla was damaged in the single B.heraldica skull available. Bitis worthingtoni differs conspicuously from its congeners in that only the two postero-lateral lobes of the vomerine process are present, with no median spine; this appears to be a derived state.

A - primitive

B - vomerine process much reduced or virtually absent

hindii, Adenorhinos, Atheris

homologies in other taxa unclear

A → B

36.
Divided premaxilla (Figs 121-123)

In Adenorhinos ( ) and in Atheris hispidus ( ) the anterior portion of the premaxilla, composed of the two ventro-lateral arms, is separate from the rest of the maxilla, composed of the ascending process. The two parts are in contact, but considerable motion between them is possible.

This two-part premaxilla is not a single result of failure of the two rudiments of the premaxilla to fuse during ontogeny, because the division is into anterior and posterior portions, not into left and right portions. In Atheris (s.s.) the premaxilla is reduced to a very narrow 'waist' in the region of the divisions present in Adenorhinos and A.hispidus. It appears that loss of the vomerine process in this group (character 35) has enabled formation of the articulation in this region in these two taxa.

At first sight such an unusual feature (apparently unique among snakes) would seem to be a definite synapomorphy, however, no other features link Adenorhinos with A.hispidus in particular (beyond those linking Adenorhinos with all Atheris), and within this group these species are at opposite extremes in overall morphology. Adenorhinos is a relatively short and stout little snake, with highly modified head scalation and proportions, possibly semi-burrowing, whereas A.hispidus is extremely elongate, highly arboreal, with trunk scale keels highly developed into 'leafy' processes. It seems most probable that the two-part premaxilla has evolved in parallel in Adenorhinos and Atheris hispidus from the nearly two-part condition seen in other Atheris.

A - primitive
B - two-part premaxilla, Adenorhinos
C - two-part premaxilla, Atheris hispidus (parallelism)

B← A →C

37.

Horizontal anterior lamina of septomaxilla (Figs 112-120)

Anterior to the main portion of the septomaxilla that forms a domed laterally-directed wing situated ventral to the nasal capsule but dorsal to the vomeronasal organ (completing the bony enclosure of that organ formed mainly by the vomer), the septomaxilla may bear a horizontal lamina extending between the nasal capsule dorsally and the superficial palate ventrally.

This horizontal lamina is weakly-developed or absent in *Bitis*, *Causus*, and *Vipera*, but moderately - or strongly-developed in other viperine taxa. When present it may take one of two forms; either a wide sheet that may extend anteriorly to approach or contact the lateral arms of the premaxilla, or a narrow shelf not broadly underlying the nasal capsule but continuing anteriorly for the entire length of the palatine process of the premaxilla and extending a short distance lateral to it. The former condition is present to varying degrees in *Cerastes*, *Echis*, *hindii*, *superciliaris*, *Adenorhinos* and *Atheris*. The latter condition is present in *Pseudocerastes* and *Eristicophis*, and foreshadowed to some extent in the mid-East *Vipera* such as *V.x.palaestinae* and *V.russelli*.

The definition of formal states for this character, and their evolutionary polarity, has been subject to some difficulty. Because an anterior horizontal lamina of the septomaxilla is absent in the diverse forms in the taxa *Bitis*, *Causus*, and *Vipera*, I originally considered that this is likely to be the primitive state within viperines. This proposal is reinforced by the observations that *Vipera* and particularly *Causus* retain primitive states of more characters than other viperines, that these three genera themselves do not form a monophyletic group (ie. it is not simply that a lamina has been lost in one lineage of viperines), and also that there is other evidence suggesting that those forms in which the wide form of lamina (not the Pseudocerastes-Eristicophis type) is present may be very closely related and possibly form a monophyletic group. However, it later became evident that a similar lamina is present to a varying extent in Azemiops, several crotalines, and many other Caenophidia examined. Although this makes it probable that at least a moderately-developed lamina is the primitive state for the viperids as a whole, the distribution of character states within the Viperinae alone still leads to the original proposal that the absence of such a lamina is the primitive state for viperines. This interpretation implies that the lamina was reduced in the immediate ancestry of viperines (and separately in Causus if it is not monophyletic with other viperines) and subsequently redeveloped in certain viperine taxa, where it is to be regarded as derived. As noted above there are suggestions (eg. characters 35, 38) that these latter taxa (Echis, Cerastes, hindii, superciliaris, Adenorhinos, Atheris) may form a monophyletic group. An alternative hypothesis, not so consistent with other evidence, is that the lamina was primitively present in viperines but was lost three times in Bitis, Causus, and Vipera.

In Echis and Cerastes the lamina is not so well-developed as in superciliaris and Atheris. The lamina is somewhat less well-developed in hindii than in the latter taxa. In Adenorhinos the lamina is only weakly developed, but in view of the good evidence (pp.215) that this form is monophyletic with Atheris and probably hindii, and the several other peculiarities of Adenorhinos, including features of the snout, I have concluded that this is a secondary reduction.

The second type of lamina, in which a narrow shelf of the septomaxilla is visible in ventral view bordering the vomerine process of the premaxilla, would perhaps not deserve recognition in a higher-level analysis, but is recognised here because it is relevant to relations within the Eurasian group of viperines. This form of lamina is very weakly-developed in the larger *Vipera* (*V.x.palaestinae*, some *V.lebetina*, *V.russelli*) but distinctly more prominent in *Pseudocerastes* and *Eristicophis* (especially the latter). This state is here regarded as an independent derivation from the primitive state.

The suggestion that *hindii*, *superciliaris* and *Atheris* share an apparently derived state of the anterior lamina of the septomaxilla tends to confirm the proposal of Marx & Rabb (1965), made on the basis of other evidence, that these taxa are closely related (see discussion, pp.213-217). It is of interest that *Echis* and *Cerastes* share an intermediate state.

A - primitive

B - wide lamina moderately developed
    Echis, *Cerastes*

C - wide lamina strongly developed
    hindii, *superciliaris*, *Atheris*

D - wide lamina weakly developed (reduced ?)
    Adenorhinos

E - narrow lamina present
    Pseudocerastes, *Eristicophis*

E ← A → B → C → D

38.

Latero-dorsal process of septomaxilla (Figs 124-129)

The laterally-directed wing of the septomaxilla that extends ventral to the nasal capsule and dorsal to the vomeronasal organ (forming part of the bony enclosure of the latter) bears a thin process in the form of a spike or elongate plate of bone extending dorsally from its lateral extremity. This process curves up laterally around the nasal capsule, forming a strong indentation in the lateral wall of the primary nasal cavity (cavum nasi proprium) and is partially embedded therein. This process forms a bony support for the concha, (that extends posteriorly from it), and anteriorly is bound locally by fibrous connective tissue to the nasal capsule. This local attachment of connective tissue may be associated with a distinct concavity in the septomaxillary process.

In what I suggest is the primitive state, due to its presence in *Azemiops*, *Causus*, *Vipera*, *Pseudocerastes*, and *Eristicophis* (the former three taxa showing primitive states of other characters, variously including ingroup and outgroup polarity criteria), the process is relatively simple and spatulate, wider from anterior to posterior in *Causus* and the smaller (apparently more primitive) *Vipera* than in the other taxa, and there is a moderately-developed horizontally-oriented concavity (weak or absent in *Causus*) formed partly in the lateral wing of the septomaxilla and partly in the extreme proximal region of the process. A wide variety of conditions occur in crotalines and other Caenophidia.

In one derivation from the primitive condition, present in species of *Bitis*, the process is spike-like, the variably-developed concavity is in a similar proximal position, but immediately anterior to it is a second short peg-like process (this second anterior process is much reduced in *B.atropos*, but because it is present in

B.worthingtoni, the most primitive *Bitis* on other evidence, see pp. 209-210, and all other *Bitis*, I conclude that it is secondarily reduced in *atropos*).

In the remaining viperines (*Echis*, *Cerastes*, *hindii*, *superciliaris*, *Atheris*, *Adenorhinos*) the form of the lateral process is modified, partly due to the fact that the concavity is located entirely within it, typically at its distal extremity. In *superciliaris*, *Atheris*, and *Adenorhinos*, the concavity is near vertical instead of horizontal in the orientation of its long axis. In *hindii* the lateral process is somewhat reduced, while retaining the noted features in common with *Atheris*. In *Adenorhinos* the process is very much reduced, but on the evidence of other characters, very probably reduced from an *Atheris*-like condition. I have recognised one derived state for *Echis*, *Cerastes*, *hindii*, *superciliaris*, and *Atheris*, and another state, derived from it for *Adenorhinos*.

The suggestion that *hindii* and *superciliaris* share a derived state of the latero-dorsal process of the septomaxilla with *Atheris* is additional evidence, not noted by Marx & Rabb (1965), for the close relationship proposed by Marx & Rabb for these taxa. An apparently homologous state is also shared by *Echis* and *Cerastes*, and is one reason to suspect that this entire group may be monophyletic.

A - primitive

B - spike-like process with small anterior process
Bitis

C - concavity at tip of process
Echis, *Cerastes*, *hindii*, *superciliaris*, *Atheris*

D - as 'C' but smaller (reduced ?)
Adenorhinos

B ← A → C → D

39.

Inclination of latero-dorsal process of septomaxilla (Figs 130-132

This character applies only among the Eurasian group of viperines. In all Vipera species (and in Causus, Azemiops and the examined crotalines) the process is more or less vertical in orientation when seen in lateral view, this condition appears to be primitive within the group. In Pseudocerastes the process is attenuated distally and prominently curved toward the anterior, this condition is further developed in Eristicophis.

A - primitive

B - process prominently curved

Pseudocerastes, Eristicophis

homologies unclear in other taxa

A → B

40.
Foramen in septomaxilla (Figs 133-134)

In snakes the vomeronasal organ (Jacobson's organ) is enclosed by the septomaxilla and vomer. In Caenophidia the vomeronasal nerve emerges from the bony enclosure by way of very many small foramina in the globular portion of the vomer (by one or a very few foramina in Henophidia; Groombridge (1979d).

In *Causus*, *Echis*, *superciliaris*, and most *Vipera* there is a relatively large separate foramen in the septomaxilla, in addition to those in the vomer. In a specimen of *Causus rhombeatus* examined a branch of the vomeronasal nerve was traced through this foramen. I take this to be the case in the other taxa in which a septomaxillary foramen is present. In *Azemiops*, *Vipera lebetina* and *V.russelli*, *Eristicophis*, and *Pseudocerastes*, this foramen is open ventrally, ie., the septomaxilla is sharply emarginated (on one side of one of the two *superciliaris* skulls examined there is an emargination instead of a foramen). In *Adenorhinos*, *Atheris*, *hindii*, *Cerastes*, there is neither a foramen nor a strong emargination. All crotalines examined had either a moderate emargination or no emargination nor foramen.

Among a wide variety of non-viperids only *Anilius* and *Cylindrophis* had a separate foramen in the septomaxilla, about half the Caenophidia examined had a moderate or strong emargination while the other half had no trace of emargination or foramen. It is thus very probable that the presence of a foramen in the septomaxilla for a branch of the vomeronasal nerve is a derived state for viperids.

A simple hypothesis would be that the presence of a separate foramen is a synapomorphy of *Causus* and the other viperine taxa noted above, but this grouping runs contrary to all other characters (notably the *M.hyotrachealis*, Char. 27)and overall it seems out of the question that the group *Causus*, *Echis*, *superciliaris*, and *Vipera* (except lebetina and russelli) is monophyletic. It does seem probable that loss of a separate foramen has occurred within the Eurasian group of viperines;it is present in the small mainly European Vipera that are primitive on other evidence, but only an emargination is present in related forms (V.lebetina, V.russelli, Eristicophis, Pseudocerastes) that on other evidence are derived. An alternative hypothesis would be that the presence of a foramen is a synapomorphy of Causus and all the other viperines, with Azemiops and crotalines retaining more primitive states in which only an emargination is present or absent, but this would require that reversal (loss of a complete foramen) has occurred not only in some of the advanced Eurasian viperines but also in Cerastes and the strictly African viperines other than Causus. If loss is so 'easy' there would be little reason to reject a third possible hypothesis, that a full foramen is a synapomorphy of all viperids, but reversal has occurred in Azemiops and crotalines as well as in several viperines.

Because an intermediate state 'emargination present' is found in Azemiops some crotalines, and intermittently among other Caenophidia, it may well be possible that a separate foramen has evolved from the intermediate state in parallel in Causus and in other viperines.

The distribution of the state 'foramen present' among viperids, which suggests the probability of reversal and perhaps of parallel evolution, has made it impossible to construct a rigorous hypothesis for the evolution of this character. Other characters must be considered. In purely phenetic terms the difference between Echis (foramen) and Cerastes (no foramen), superciliaris (foramen or emargination), and hindii (no foramen), and primitive Eurasian viperines (foramen) and advanced Eurasian viperines (emargination), are of interest since the taxa in each pair appear closely related on certain other evidence.

41.

Septomaxilla: anterior ridge (Figs 135-136)

This character applies only within Bitis. In B.atropos there is a distinct ridge of bone running transversely from the base of the laterodorsal process of the septomaxilla toward the midline. Posteriorly this ridge demarcates a concavity in the lateral wing of the septomaxilla, and anteriorly produces a forward-directed facet. B.heraldica is similar, and these features are present although somewhat less prominent in caudalis, cornuta, peringueyi, schneideri and xeropaga. This form of septomaxilla is considered to be a derived feature. The ridge and concavity are extremely prominent in B.arietans, nasicornis and gabonica.

These features are not developed in B.worthingtoni, a probably primitive resemblance to other viperines, in which they are not present.

A - primitive
B - anterior ridge present
Bitis, except worthingtoni

A→B

42.

Prefrontal-frontal articulation (Figs 137-140)

The prefrontal is a dermal bone that forms the anterior wall of the orbit in snakes. It typically articulates dorso-medially with the frontal, ventro-medially with the palatine, and ventro-laterally with the maxilla. In a majority of snakes the syndesmotic joint with the frontal allows only slight relative movement between the two bones, however, in pythons (Frazzetta, 1966; and presumably in some related boids) and especially in advanced vipers, there is considerable mobility at this articulation, and the prefrontal is a key element in jaw kinesis during striking and swallowing. Kardong (1973:352) has noted that in pythons the articulation of the prefrontal with the palatine is of greatest functional importance (second to the articulation with the frontal), whereas in vipers its articulation with the maxilla is of greatest importance (apart from the frontal). Typically in vipers there is no actual contact between prefrontal and palatine.

Within vipers, a highly kinetic frontal-prefrontal joint will both increase the extent to which the fang-bearing maxilla is rotated during protraction, thus directing the fang more anteriorly during the strike, and also produce a dorsal component to the motion of the maxilla during protraction, thus minimising interference with the passage of prey items during deglutition (Kardong, 1977:343).

In most non-viperid caenophidians, the prefrontal articulate with the frontal along a relatively firm syndesmosis. The suture line visible dorsally is typically almost straight, and at an oblique angle to the long axis of the skull. A mid-lateral process of the frontal also restricts prefrontal movement.

In *Azemiops* and *Causus* the prefrontal is little, if any, more mobile on the frontal than is the case in non-viperid caenophidians. An anterior mid-lateral frontal process is present. This would appear to be primitive in relation to the high mobility seen in other viperids. A difference from most Caenophidia in Azemiops and Causus is that (in dorsal view) the frontal appears to extend antero-laterally into the prefrontal, the latter thus bears lateral and anterior dorsal processes. This would also seem to be primitive to conditions in other vipers, because of correlation with lack of extensive mobility, and with primitive states of other characters.

In all viperines except Causus, the prefrontal lacks a lateral dorsal process, but the anterior dorsal process is extended toward the midline of the skull. The midlateral frontal process is somewhat reduced (very much so in 'true' Atheris and Bitis), and is grooved dorsally to receive the anterior dorsal process of the prefrontal. This forms a hinge joint, oriented nearly horizontally in the transverse plane, that allows quite extensive rotation of the main body of the prefrontal (carrying the maxilla) in a para-sagittal plane.

In crotalines the lateral dorsal process is absent, as in viperines (s.s.). or is present as a small knob. However, unlike viperines, there is no development of the anterior dorsal process. Instead, the antero-lateral extremity of the frontal, and the reduced processes of the dorsal part of the prefrontal form a complex double-saddle articulation. This allows considerable mobility of the prefrontal, but it is not restricted by the bony articulation to a near para-sagittal plane, as in viperines.

Marx & Rabb (1972:181) considered the crotaline state to have been derived from the Azemiops-Causus state, with the latter, and the viperine s.s. state, forming two independent derivations from a primitive state in which dorsal prefrontal process are absent. This interpretation differs from Liem et al (1971:110), who suggested that both the crotaline and viperine statescould be independent derivations from the Azemiops-Causus state. The latter view seems reasonable, but it would be more parsimonious, considering this character alone, to suggest that crotalines and viperines may have shared a common ancestor (above the Azemiops-Causus level) with reduced or absent lateral dorsal process of the prefrontal, and subsequently diverged along two different pathways.

A - primitive

B - latero-dorsal process reduced or absent

Viperinae except Causus, also Crotalinae (homologous ?)

A → B

43.

Prefrontal form (Figs 141-143)

The prefrontal varies appreciably in detailed form throughout the viperines, and homologies are difficult to define. However, within the Eurasian group there is a general trend to increasing robustness of the prefrontal from the slim form seen in *Vipera ursinii*. There is a distinct gap between the majority of *Vipera* and *lebetina*, *palaestinae* and *russelli*, where the bone is robust, the exit of the lachrymal duct is concealed (in anterior view), and with rounded extensions of the anterior and posterior surfaces the body of the prefrontal encloses a deep concavity. The *aspis* and *xanthina* groups (not *palaestinae*) are intermediate, with the former closer to *berus*-*ursinii*.

In *Pseudocerastes* and *Eristicophis* the posterior face of the prefrontal is reduced, and there is a prominent ventro-medial process (especially in the latter).

A - primitive (généralised)
B - prefrontal robust, deeply concave
    Vipera lebetina, *palaestinae*, *russelli*
C - prefrontal robust, ventro-medial process
    Pseudocerastes, *Eristicophis*

A → B → C

Maxilla-ectopterygoid articulation (Figs 144-153)

As noted in section A3b, the maxilla in vipers is highly modified in comparison with other snakes, and is a key element in the venom injection system.

The anterior end of the ectopterygoid articulates with a portion of the posterior face of the maxilla. Protraction of the pterygoid and ectopterygoid (by muscles of the CId group) rotates the distal fang-bearing portion of the maxilla anteriorly into a striking position, as the proximal portion pivots at its articulation with the pre-frontal (which itself pivots extensively around the frontal in advanced vipers). The force generated by the protracting components of the CId group is transmitted to the maxilla entirely through the ectopterygoid-maxilla articulation. The articular surfaces here are covered with cartilage, and the joint is bound by fibrous connective tissue (that may be concentrated into distinct ligaments). The orientation of the articular surfaces and associated connective tissue results in a near-perfect hinge-joint, restricting the line of action of the maxilla to a near parasagittal plane.

In Azemiops (Liem, Marx & Rabb, 1971:108-9) and viperines (s.l.), the anterior head of the ectopterygoid articulates with a fossa in the maxilla, the dorsal edge of which is typically developed into a transverse ridge. In crotalines this relationship is largely reversed; ridges and condyles on the posterior face of the maxilla articulate partly with a shallow fossa in the head of the ectopterygoid. This appears to be correlated with the presence of a deep excavation in the maxilla, housing the crotaline sensory facial pit-organ. It is suggested that the crotaline maxilla would be excessively weakened if it retained a viperine-like articulatory fossa also, hence the maxilla is strengthened by the articular condyles and the ectopterygoid bears the articular fossa (Dullemeijer, 1959:949). Kardong (1974:339) has described the ectopterygoid-maxilla articulation in the crotaline Agkistrodon piscivorus.

The functional importance of the hinge-like design of the ectopterygoid-maxilla articulation has been stressed (Dullemeijer, 1956:80, 1959; Kardong, 1974, 1977). In the interests of precision and economy of effort, any lateral motion during fang protraction, striking, and retraction, should be minimised; the gross morphology of the articulation is thus of great functional importance, and the smaller scale variation, noted below, may well be of some significance. Presumably the design of the articulation will reflect a balance between the opposing requirements of eliminating wastage of energy (of ectopterygoid protraction) that would occur with too 'sloppy' an articulation, and still retaining sufficient rotatory motion of the maxilla.

In Azemiops (Liem et al, 1971:25) and viperines there are two ligaments, associated with the maxillo-prefrontal articulation, that attach on or near the dorsal ridge of the articulatory fossa in the maxilla. The lateral maxillo-prefrontal ligament runs from the lateral portion of the maxilla at the level of the ridge to the ventrolateral corner of the prefrontal, the medial maxilloprefrontal ligament runs from the medial portion of the ridge to the antero-ventral part of the prefrontal. These ligaments assist in maintaining the relative positions of the maxilla and prefrontal, and in resisting hyperextension of the maxilla. In some forms the ligaments fuse into one before attaching to the maxilla. These ligaments are noted here because they appear to be a major factor contributing to the form of the posterior face of the maxilla, in particular the ridges and protrusions dorsal to the articulatory fossa.

All crotalines possess a facial sensory pit and the correlated crotaline pattern ectopterygoid-maxilla articulation, these are both clearly synapomorphies of crotalines and are not discussed further.

In Azemiops, Causus, and the smaller Vipera (all being forms that appear to retain primitive states of other characters), the maxilla has a rather simple overall form, and bears a shallow rectangular, or somewhat triangular, fossa for articulation with the ectopterygoid. This would seem to be a primitive condition, but the possibility of secondary simplification should be considered.

In the Eurasian group of species (see section A4c), there is an apparent trend towards elaboration of the rather simple morphology seen in *Vipera ursinii*, *kaznakovi*, and *berus*. The lateral portion of the maxilla is modified to form a distinct 'shoulder', above the fang-bearing section. The anterior end of the ectopterygoid, instead of forming a nearly straight horizontally elongate surface, bears a small anteriorly-directed lateral projection that fits over the shoulder on the maxilla. The antero-lateral edge of the ectopterygoid has a curled-over margin, fitting ventro-lateral to the shoulder. The transverse dorsal ridge of the articulatory fossa is relatively large. These features are most prominent in the larger *Vipera* (eg. *xanthina palaestinae* and *lebetina*), and this development may involve a simple allometric relationship. Because of the fairly continuous spectrum of variation throughout the Eurasian group, it would be a matter of some difficulty to define the limits of discrete character states, although a clear primitive to derived sequence is apparent, from the '*berus* group', through the '*aspis* group', to the *xanthina* and *lebetina* complexes.

A pattern rather similar to that of the larger *Vipera* is also seen in *Cerastes*. There is a prominent dorsal ridge to the articulatory fossa, but this differs significantly from *Vipera* in being very short and perhaps more like a single knob, particularly in *C.vipera*. The lateral shoulder of the maxilla is developed into a distinctive projecting knob, not found in the Eurasian group. The head of the ectopterygoid is correspondingly hyperdeveloped. There is a very deep excavation in the medial aspect of the dorsal portion of the maxilla (for passage of blood vessels). This pattern would seem to be derived in relation to the suggested primitive form, however it is morphologically a small step to make, and I am doubtful if it indicates a close cladistic affinity with the large *Vipera*, to which there is most resemblance. For example, the prominence of the dorsal ridge seen in both groups could well be an allometric consequence of a shared increase in size, and/or a consequence of an increase in the functional importance of the maxillo-prefrontal ligaments attaching to the dorsal ridge, or of an increase in importance of the dorsal ridge as a 'stop' acting against the dorsal surface of the head of the ectopterygoid to assist in preventing hyper-extension of the maxilla and fang. These factors are all linked with the magnitude of forces acting on the maxilla and fang, which would increase as the relative size of the prey increases. It seems quite possible that another resemblance between *Cerastes* and large *Vipera*, in the form of the postorbital process of the parietal (Character 49), is also a parallelism linked with the same functional system.

A somewhat different pattern is found in *Echis*, *'Atheris' superciliaris*, and further modified in true *Atheris* (also *hindii* and *Adenorhinos*). Here the articulatory fossa is distinctly more triangular in shape than rectangular (with the partial exception of *E.coloratus*), and the maxillo-prefrontal ligaments attach to a medial knob developed on the diagonal dorsal ridge of the fossa. In *Echis* (especially the *carinatus*-complex), there is a single knob, partly extended dorsally into the diagonal ridge, in *superciliaris* this dorsal extension bears a distinct second knob. There is no distinct lateral shoulder. The head of the ectopterygoid is simple, a probably primitive resemblance to the smaller Vipera. A similar pattern to *superciliaris* is found in *Atheris nitschei* (that also appears among the most conservative true *Atheris* in certain other characters, p.213), but the triangular articular area is extended dorsally, and the overall degree of relief of the posterior face of the maxilla is less than in *superciliaris.* The remaining true *Atheris* continue these two trends further, accompanied by the appearance of a dorso-ventral 'stretching' of the maxilla.

The articulatory surface in *hindii* is rather weakly defined, but otherwise most resembles that of true *Atheris*. Considering the other evidence linking *hindii* to *superciliaris*, *Atheris* and *Adenorhinos*, this would appear to be a secondary reduction (presumably correlated with the small body size of *hindii*). The same is true of *Adenorhinos*, where the maxilla has a very small contact with short lateral prong of the head of the ectopterygoid. There is a quite extensive gap between these two bones, filled with a diffuse connective tissue. The maxilla has a simple peg-like form, with the barest trace of a fossa for articulation with the ectopterygoid. The ectopterygoid is weakly forked anteriorly with a unique antero-medial prong (see Character 45). This is rather certainly a secondary reduction in the feeding apparatus, and is indeed suggestive of "radically different feeding habits..." (Marx & Rabb, 1965:184).

Because of other evidence linking *Echis* with *superciliaris*, *hindii*, *Adenorhinos*, and *Atheris*, it is possible that the derived form of ectopterygoid-maxilla articulation (secondarily reduced in *Adenorhinos*, and probably so in *hindii*) is a synapomorphy of the group. It is also possible that *Echis* and *Cerastes* form a monophyletic group (this suggestion is based almost entirely on the shared presence of serrated keels on the flank scales and the shared pattern of orientation of these scales, Character 13). If this is the case it would appear that *Cerastes* has diverged considerably from the *Echis*-*Atheris* trend suggested above, and has independently come to resemble the large *Vipera* in some features. The *Echis* condition is the most conservative among this group.

In all *Bitis*, except *B.worthingtoni*, there is a very deep fossa in the maxilla, the very prominent dorsal ridge is developed laterally into a strong process (note that this is lateral rather than the more medial location of the process in *Cerastes*-*Echis*-*Atheris*). There is a distinct lateral shoulder. In *B. worthingtoni* the articulatory fossa is rather more triangular in form, the dorsal ridge is much more weakly developed, similarly the lateral shoulder is weaker. Overall the maxilla of this species is rather similar to that of *Echis* (perhaps these forms retain a morphology close to that possessed by the basal stock of advanced African viperines). As in other features (Characters on p.209) *worthingtoni* appears primitive to the remaining *Bitis*. In these latter species the dorsal ridge and its lateral extremity may be very prominent indeed. The attachment of the maxillo-prefrontal ligaments to the tip of the process is mechanically advantageous for their role in resisting fang hyperextension, and the process itself may act as a 'stop' against the ectopterygoid (Dullemeijer, 1959:946). Correlated with this, the floor of the canal for the lachrymal duct in the prefrontal is emarginated from behind to a greater or lesser extent in order to accommodate the maxillary process when the maxilla is fully retracted. This emargination is not found in *B.worthingtoni*.

In *Causus* there is an appearance of secondary reduction, possibly connected with the dietary specialisation on anurans. The overall relief of the posterior face of the maxilla is low. There is no prominent lateral shoulder. It is unclear if the resemblance to small *Vipera* and *Azemiops* is a shared primitive resemblance or a result of parallel simplification.

Overall, because of the strong possibility of parallel development of certain features (eg. increasing depth of the articular fossa, increasing development of the dorsal ridge in association with the maxillo-prefrontal ligaments), and for parallel simplification of the articulatory surface, this character complex is of clear cladistic significance mainly at lower taxonomic levels. Of greatest interest are the suggestions that *B.worthingtoni* is the sister group of the other *Bitis*, and that *Echis* (and possibly *Cerastes*) is closely related to the *superciliaris*-*Atheris* group. Also significant is the trend to increasing complexity through the Eurasian group, concordant with trends in several other characters.

A - primitive

B - articular fossa rather triangular, ligaments attach to knob on diagonal ridge
    Echis, *superciliaris*, *hindii*, *Atheris*

C - articular fossa weakly developed (reduced ?)
    Adenorhinos

D - very prominent dorsal transverse ridge
    Bitis, except *worthingtoni*

$$D \leftarrow A \rightarrow B \rightarrow C$$

45.

Ectopterygoid (Figs 154-159)

The ectopterygoid is a dermal bone connedting the pterygoid and the maxilla. Its role in the viperid fang protraction-retraction system has been noted (p.24). Dullemeijer (1956, 1959) gives discussions of the form-function relationship in this bone.

In vipers the ectopterygoid is an elongate bone, oriented parallel with the long axis of the skull. Posteriorly there is a near vertically oriented syndesmosis with the pterygoid, allowing motion primarily in the parasagittal plane, anteriorly there is a horizontally oriented articulation with the maxilla (character 44). This basis pattern is seen in _Azemiops_ (rather slender), crotalines, and most viperines, and is thus probably primitive for viperids. Three derived variations are seen within viperines.

In _Bitis_ species, as noted by Marx & Rabb (1965:182), the head of the ectopterygoid is broadened, robust, decurved somewhat laterally, and with a pointed projection at the postero-lateral extremity. Fibres of the _M.pterygoideus_ attach to this projection. This pattern is regarded as a synapomorphy of the species currently assigned to _Bitis_.

A postero-lateral projection is also present in _Causus_, but the ectopterygoid as a whole is very much more slender, and the projection is smaller, usually more rounded, and not turned ventrally. Although phenetically similar in this one respect to _Bitis_, the cladistic evidence (pp.198-205) indicates that these genera are not very closely related, and I regard the _Causus_ condition as a separate derived state.

Unique to _Adenorhinos_, the head of the ectopterygoid is slightly forked, with a small lateral process forming a very small articulation with the maxilla, and a long medial process extending anteriorly medial to the maxilla. Most of the head of the maxilla, including the long medial spine, is separated from the maxilla by a gap filled with diffuse connective tissue. The specimen examined by Marx & Rabb (1965:186) apparently lacked any forking of the ectopterygoid head, and they make no mention of its relation to the maxilla.

Some small-scale variation is present within the generally primitive ectopterygoid morphotype present in other viperines, but it has not been possible to partition this into separate states. In general there is a trend toward increasing specialisation of the ectopterygoid head through the Eurasian group (from *Vipera ursinii*, to *V.lebetina*, *Pseudocerastes*, *Eristicophis*).

A - primitive

B - ectopterygoid with broad head and pointed postero-lateral projection
Bitis

C - ectopterygoid slender, rounded postero-lateral projection
Causus

D - ectopterygoid slender, head forked, long antero-medial spine
Adenorhinos

$$\begin{tikzcd}
D & A \arrow[l] \arrow[r] \arrow[d] & B \\
& C &
\end{tikzcd}$$

46.

Pterygoid-palatine articulation: type of joint (Figs 160-161)

As noted by Liem, Marx & Rabb (1971:111) and Marx & Rabb (1972:163), in all viperines (including Causus) except *'Atheris' superciliaris* the pterygoid and palatine articulate at a relatively simple syndesmosis. The lateral surface of the posterior extremity of the palatine overlaps the medial surface of the anterior extremity of the pterygoid. This joint allows appreciable dorso-ventral rotation of the anterior portion of the palatine, and contrary to Liem *et al* (1971:111) significant lateral motion is typically also possible owing to the looseness of the fibrous connective tissue at the joint surface.

Liem *et al* note that in most crotalines a more complex interlocking articulation formed of opposing saddle-shaped surfaces is present, apparently allowing relatively extensive mobility of the palatine relative to the pterygoid. A similar pattern is found in *Azemiops*.

This situation is complicated by the fact that the viperine *'Atheris' superciliaris* has a complex crotaline-like articulation, and a simple viperine-like articulation is present in the crotalines *Agkistrodon strauchi*, *A.*(or *Calloselasma*) *rhodostoma*, and *Hypnale hypnale* and *H. nepa* (formerly *Agkistrodon*, Gloyd, 1977). Therefore, whichever is the derived condition, it must have been evolved separately in at least 2 lineages.

Excellent studies of the jaw apparatus have been performed on the crotaline *Agkistrodon* (Kardong, 1973, 1974, 1977), but in the absence of parallel work of similar depth on viperines it is difficult to assess the functional significance (if any) of the different forms of palatine-pterygoid articulation. It seems probable that in all viperids the degree of mobility of the palatine is limited more by connective tissue links to adjacent elements of the snout than by the form of the palatine-pterygoid articulation itself.

I agree with Marx & Rabb (1972:165) that a simple overlap articulation is probably primitive for Caenophidia in general, because it is found in the vast majority of caenophidian species examined; because it is likewise present in *Causus*, in viperines *s.s.* (except *superciliaris*), and a few crotalines, it is probably also primitive for viperids in particular. An alternative hypothesis, that the interlocking articulation is primitive for viperids because it is found in the generally-primitive *Azemiops* and most crotalines is rejected because those crotalines with a simple overlap articulation are among the most primitive crotalines, and also because of the significant variation in the detailed construction of the articulation among crotalines and viperines. For example in several viperines (eg. *Vipera ursinii renardi*, *Causus lichtensteini*) the articulation is not a simple overlap but moderately-developed grooves and processes are also present, thus approaching the *Azemiops*-crotaline pattern. Similar intermediate conditions are found in some crotalines (eg. *Agkistrodon* (*halys*) *intermedius*).

If the crotaline pattern is primitive for viperids, then reversal has occurred in viperines (except *superciliaris*, unless reversed again to the crotaline pattern) and in certain lower crotalines. If the viperine pattern is primitive for viperids (and if the viperine pattern shown by certain crotalines is not a reversal from a crotaline pattern), then the crotaline pattern has evolved in parallel in *Azemiops*, most crotalines, and *superciliaris*. Thus whichever permutation is adopted, there is clear evidence for parallel evolution (and/or reversal) in this feature, and because of this ambiguity the character of the palatine-pterygoid articulation cannot be used as primary evidence in a cladistic analysis.

Although the palatine-pterygoid joint in *Azemiops* contributes in purely phenetic terms to its appearance as a "pitless pit-viper" (Liem, Marx & Rabb, 1971:113), it seems more probable that <u>Azemiops</u> and most crotalines (and <u>superciliaris</u>) merely share a derived state evolved in parallel rather than a true synapomorphy. The <u>superciliaris</u> condition is regarded as an autapomorphy. Within viperines it is possible to recognise 2 states.

A - primitive
B - interlock joint
<u>superciliaris</u>

A→B

47.

Pterygoid-palatine articulation: extent of overlap (Figs 162-164

In most viperines (s.l.) there is only a short extent of pterygoid-palatine overlap at their articulation. Two different autapomorphous conditions are shown by *Vipera russelli* and *Adenorhinos barbouri*, in both species there is a relatively extensive palatine-pterygoid overlap. In *V.russelli* the posterior extremity of the palatine extends ventrally along the medial side of the pterygoid, and the anterior extremity of the pterygoid extends dorsally along the lateral side of the palatine. In *A.barbouri* the extent of overlap is similar, but here the palatine extends dorso-medially over the pterygoid (as opposed to ventro-medially in *V.russelli*).

48. Anterior process of palatine (Fig 164)

Unique among viperines, the palatine of Vipera russelli bears a toothless anterior blade-like extension, directed slightly dorsally, especially at its anterior tip. This process appears to form a sliding contact with the medial face of the prefrontal more extensive than that found in other viperines, the functional significance of this is not clear. This condition is regarded as an autapomorphy of V.russelli.

49.
Postorbital region (Figs 165-173)

The postorbital is a dermal bone forming the postero-lateral margin of the orbit in snakes. It is mounted dorso-medially on the postorbital process of the parietal, and may or may not also contact the frontal; distally it typically contacts the maxilla, to which it is connected by a tough ligament, but in vipers, with their highly modified maxilla, the postorbital is remote from the maxilla. The postorbital is reduced in size in several groups, and is occasionally absent, especially in burrowing forms. In vipers the postorbital is typically rather slender, laterally compressed, and tapering distally, but has a relatively wide blade-like form in most Bitis. It is much reduced in crotalines, and in Echis coloratus among viperines.

There is some variation within viperines in the form of the postorbital process of the parietal, Marx & Rabb (1965) give the greatest possible weight to this character, and divide "advanced viperines" (ie. not Causus) into two geographical groups, considered as two monophyletic groups (1965:198, Fig.46), on the basis of this character and the presence or absence of a separate splenial bone. They state (1965:163-4) "the four genera that we recognise (Vipera, Eristocophis (sic), Echis, and Cerastes) are set off from the Ethiopian advanced vipers by the nature of the postorbital area of the skull. In all of them, the postorbital bone is a moderate-sized element that is firmly sutured posteriorly and medially to a lateral process of the parietal... In the three Ethiopian genera" (ie. Adenorhinos, Atheris s.l., Bitis) "the postorbital abuts on the parietal, but does not form a common unit with it".

In view of its supposed primary cladistic significance, it has been necessary to examine this character in some detail; it appears that the morphological situation is not so clearly-defined as Marx & Rabb suggest, and the cladistic interpretation is somewhat ambiguous due to non-concordance with other characters.

Where a relatively narrow postorbital is present, apparently the primitive condition in vipers, the posterior part of the origin of the *M.levator pterygoidei* (of the CId group) extends slightly dorsally at the posterior extremity of the head of the postorbital, into a variably-developed fossa immediately ventral to the ridge marking the origin of the *M.adductor externus superficialis*. In viperines with a relatively broad postorbital head (*Atheris*, *hindii*, *superciliaris*, *Bitis*) the *levator* origin is largely or entirely deep to the postorbital head (entirely so in most *Bitis*, where the postorbital head has a posterior extension contacting the proctic). In all viperines the *levator* origin extends deep to the postorbital, where there is a ridge on the lateral descending wall of the parietal, and on the postorbital process of the parietal, marking its anterior limit (see below). The *levator* is noted here because the nature of its area of origin appears to be a significant factor determining the form of postorbital-parietal relationship.

In *Azemiops* (Liem *et al*, 1971:75, these workers call the postorbital the postfrontal), the postorbital has a weak articulation with the parietal, there is a rather shallow fossa in the parietal accommodating the rather well-developed head of the postorbital. There is no distinct postorbital process of the parietal. This would appear to be a derived condition (the postorbital is frequently lost or reduced or its articulation with the parietal weakened in the 'streamlined' skull of burrowing or secretive snakes, which *Azemiops* may be, judging by its rarity in collections). Contrary to Liem *et al* (1971:75) the postorbital does contact the frontal (in FMNH 152987, and in USNM 84363, in the latter the postorbital has been separated from the skull, but if replaced in articulation in the parietal fossa, it contacts the frontal).

In Causus, conservative crotalines such as Agkistrodon halys, and the smaller Vipera (ursinii, berus, seoanei, kaznakovi), the parietal has a short and simple tapering lateral process upon which the postorbital lies. Because of its taxonomically widespread occurrence in vipers, that also appear to retain primitive states of certain other characters , this would seem to be a primitive condition. It is necessary to disagree with the statement of Marx & Rabb (1965:192) that the postorbital process of the parietal serves as a "substantial bolster" for the postorbital in all Vipera, this is simply not true in the Vipera species noted above (especially V.ursinii). Their figure (1965: Fig.32) illustrating the supposed "Palaearctic condition" is of V.russelli, a species that is highly divergent from its congeners in many characters, and certainly has a parietal process that is about twice as large as the largest found in other Vipera.

In Vipera other than the four species cited above, the parietal process becomes progressively enlarged (least so in the European forms aspis, ammodytes,and latastei, and greatly so in russelli), and no longer forms a simple tapering process but has a distinct "shoulder" posteriorly. In the smaller Vipera (also Causus; smaller Asiatic Agkistrodon) the antero-ventral limit of the origin of the levator is barely indicated by a slightly rounded ridge running up the descending wall of the parietal and extending centrally along the ventral surface of the parietal process, in the larger Vipera this ridge remains central along the process but is accentuated, leaving a postero-ventrally facing surface to which the levator attaches. The parietal process is similar in Pseudocerastes and Eristicophis, but the posterior shoulder is notably more prominent. In Vipera russelli the parietal process is greatly enlarged, but without a distinct posterior shoulder, and extends ventro-laterally nearly to the tip of the postorbital. Although these latter two variations are clearly derived in relation to other members of this Eurasian group, it is rather difficult to assign the remaining species to discrete character states due to the regularity of the trend from *V.ursinii* to *lebetina*, for example. As with the form of maxilla (Character 44), in general terms there is a progressive development of the postorbital and its parietal process from the '*berus* group', through the 'aspis group', to the *xanthina* and *lebetina* complexes.

The parietal process in *Cerastes* and *Echis* is very prominent, and in this respect resembles that in certain Eurasian group species (large *Vipera*, *Pseudocerastes*, and *Eristicophis*), as noted by Marx & Rabb (1965:163 & 192). While not true of all *Vipera* it is certainly so in *Cerastes* and *Echis* that the parietal process "serves as a substantial bolster for the postorbital" (Marx & Rabb, p.192). However I am uncertain whether the condition in *Cerastes* and *Echis* is strictly homologous to that in large *Vipera* (etc.), or is a parallelism; the grouping of *Cerastes* and *Echis* with large *Vipera* is incongruent with certain other characters (p.227-230), also, differences between *Cerastes* and *Echis* are problematic.

It is *Cerastes* in particular that most closely resembles certain Eurasian species; there is a distinct posterior shoulder to the parietal process which is quite long, but it is formed distally by the exceptionally well-developed central ventral ridge, giving a blade-like appearance to the process, and defining a distinct posterior concavity for the *levator* origin. Distally, the postorbital and the process are directed anteriorly. Although the *Cerastes* condition in detail differs from all other species, it is possible to visualise it as arising from a *Vipera*-like, or especially a *Pseudocerastes*-like, state.

In *Echis* the parietal process is larger than that of *Cerastes*, and is of similar length to *Vipera russelli* in *E.carinatus*, but of even greater length in *E.coloratus*.

In the latter species the postorbital is reduced to a tiny sliver of bone, so that the tip of the parietal process is exposed distally (I am unable to understand the statement of El-Toubi & Abdel Magid, 1961:312, that the postorbital is "extremely small" in E.carinatus and "completely absent" in E.coloratus). While in Cerastes the central ventral ridge forming the anterior limit of the levator origin is very prominent and blade-like, in Echis the parietal process is broadened and laterally compressed, or even somewhat concave ventrally, and the ridge marking the anterior limit of the levator origin has shifted to a position entirely anterior to the parietal process. The levator, instead of arising from the parietal posterior and ventral to the postorbital and from the postero-ventral aspect of the parietal process (as in large Vipera, Pseudocerastes, Eristicophis, and Cerastes) now arises from the flattened ventral surface of the parietal process and even extends anterior to it. This is a special derived resemblance to Atheris (s.l.) and Bitis in which the levator also extends anteriorly beneath the postorbital, although there is never a very large process in the latter two genera.

It is necessary to disagree with the statement of Marx & Rabb (1965:192) that the east African form Adenorhinos "lacks the anterolateral process of the parietal, but has a somewhat complex articulation of the two bones". Adenorhinos does not lack the parietal process (at least not in the single skull I have been able to examine, this feature is not intraspecifically variable to any significant extent in other species), and the two bones do not have a somewhat complex articulation, in fact the condition in Adenorhinos is superficially very similar to that of the small Vipera and Causus (ie. the possible primitive viperid condition). There is a short simple tapering lateral parietal process, and the levator origin does not extend anterior to the weak ventral ridge of the process. The postorbital itself is rather slender, and not at all widened dorsally as in other African forms (other than *Causus*). The evidence of other characters (p.215) makes it possible that this is a secondary reduction from a more complex condition. Regardless of this point, the example of *Adenorhinos* obscures Marx & Rabbs' supposed clear-cut difference between "Palaearctic" and "Ethiopian" groups (besides raising the possibility of secondary reduction in other species).

'*Atheris*' *hindii* is very similar to *Adenorhinos* but the head of the postorbital is slightly expanded (although little more developed than in *Azemiops*), and is supported by a very slight supplementary process of the parietal, posterior to the small main process. As in *Echis*, *Atheris*, and *Bitis* the *levator* origin extends beneath the parietal process and reaches well beyond it, as in *Echis* in particular, to a definite anterior ridge on the parietal.

Conditions are fundamentally similar to *hindii* in *superciliaris*, *Atheris*, and *Bitis*, although the postorbital itself is much broadened in *superciliaris* and *Bitis* other than *B.worthingtoni*, and less so in *Atheris*. In *superciliaris* this broadening is mainly anterior to the major parietal process (and there is a distinct postorbital-frontal contact, present or absent in *hindii* and absent in *Atheris*), whereas in *Bitis* (except *worthingtoni*) the head of the postorbital has a very prominent posterior lobe reaching back to contact the prootic; these two features would seem to be derived. The parietal process is somewhat larger in most *Atheris* *s.s*. than in *hindii*, *superciliaris* or *Bitis*. In *A.chloroechis* the process extends laterally at its posterior shoulder and is less flattened ventrally than most other *Atheris*, it resembles some *Vipera* (eg. *V.aspis*) quite closely. There is no significant postero-dorsal extension of the postorbital in some *Atheris* (eg. *chloroechis*), this is a resemblance to *Adenorhinos*, *Vipera*, *Cerastes* & *Echis*.

The cladistic interpretation of these states is subject to some difficulty. As a first step it is possible to suggest, as above, that the morphologically quite simple state shown by some Asiatic Agkistrodon, Causus, and small Vipera, a taxonomically diverse group that appear to show primitive states of several other characters, is the primitive extreme. If primitive, this state has persisted in both African viperines (Causus) and Eurasian viperines (small Vipera). The apparent progressive enlargement of a shouldered parietal process supporting the postorbital in the Eurasian group is perfectly congruent with other characters (p.218), as is the occurrence of derived extremes in Vipera russelli, and linking Pseudocerastes with Eristicophis, suggesting that these three forms are the morphologically most modified of the Eurasian radiation.

The major problem arises over the relationship of Cerastes and Echis to each other and to other advanced African and Eurasian groups. The differences, noted above, between the two genera are consistent with independent evolution from a more primitive condition; the two genera are very dissimilar and this character affords no support for the suggestion (characters 12,13) that they may form a monophyletic group. Certain characters (p.228) suggest that Echis (and Cerastes less clearly so) may be closely related to Atheris (s.l.) and Adenorhinos, but the postorbital region suggests that Cerastes (and Echis less clearly so) may be closely related to advanced Eurasian vipers such as Pseudocerastes.

An apparently primitive morphology is shown by Adenorhinos and partly by hindii, among the advanced African viperines; a similarly small parietal process is present in Atheris, superciliaris, and Bitis, but in these forms is accompanied by a distinct widening of the dorsal portion of the postorbital, notably in the latter two taxa, (but probably independently evolved). The general phenetic resemblance between Atheris and Bitis is this character may be partly due to retention of a primitive feature (small parietal process), and partly due to a derived similarity (postorbital widened dorsally). There is quite close similarity in trunk patterning between certain Bitis, hindii, and superciliaris; like the postorbital region this suggests the possibility of a close relationship between Bitis and Atheris sensu lato. However, if the primitive-like condition in hindii and Adenorhinos is truly primitive, not secondary reduction, this would mean that these two taxa are less closely related to Atheris (s.s.) than is Bitis; this is certainly not suggested by any other characters.

The differences between Echis and Cerastes, and between hindii, Adenorhinos, and their undoubtedly close relatives superciliaris and Atheris, also the resemblance of Atheris chloroechis to some Vipera, indicate a rather high lability in the postorbital region. As with the ectopterygoid-maxilla articulation (character 44), I suggest that functional demands linked with the fang protraction-retraction system should be considered as a possible source of selective forces promoting parallel evolution of phenetically similar features in different groups.

It may be noted that, in contrast to the appearance of dried anatomical specimens, bone in the living organism is a dynamic not a static entity, and its outward form is frequently able to change within individuals in response to functional demands. It is also apparent that in cranial anatomy, 'soft' structures such as sense organs, nerves, blood vessels, and muscles, frequently appear to dictate some parameters of the form of adjacent 'hard' bones, rather than vice versa (Dullemeijer, 1974:125,145).

Although direct electromyographic evidence is currently lacking for vipers, it is apparent that two muscles of the CId group, the M.protractor pterygoidei and the M.levator pterygoidei, are responsible for fang erection during the strike and ingestion of prey; the former arises from the sphenoid complex and inserts on the posterior third of the pterygoid, the latter arises from the parietal and its postorbital process and inserts on the middle third of the pterygoid (Kardong, 1973, 1974; Liem, Marx & Rabb, 1971; Boltt & Ewer, 1964). The area of attachment of the levator to the parietal would be expected to increase (relatively faster than the volume of the muscle) as a consequence of allometric growth as the adult size of the animal increases, or as the fang protraction-retraction system is presented with the task of transmitting increased forces (if there is specialisation toward taking larger prey or an increase in safety margins with existing prey items). Dullemeijer (1959: 939) has suggested that the extremely wide cerebral skull of large Bitis species is due to the larger postorbital process of the parietal forming an increased surface area for attachment of the levator, enlarged in response to an increased prey size. The anterior limit of the levator origin is set by the posterior margin of the eye and adjacent structures, the eye is of fixed volume in relation to the size of the animal, hence expansion must be lateral rather than anterior. This lateral expansion is simply provided by enlargement of the postorbital process.

Another relevant factor is that the more lateral is the levator origin (from the long postorbital process as in Echis and large Vipera such as russelli), the more the resultant vector of forces generated by the protractor and levator pterygoidei is channelled directly anteriorly; under the principle of optimum design any deviation from an anterior resultant would presumably represent wasted energy and a more lateral origin would thus be subject to positive selection pressure. The formation of a wide transverse lamina by the postorbital process, as in Cerastes, is another means of increasing the levator origin.

Given these considerations it seems unwise to place too great a weight on the form of the postorbital-parietal relationship, not only would it appear to be relatively labile in response to functional demands of the fang erection system, but it is totally erroneous to suggest (as do Marx & Rabb, 1965) that an absolute distinction exists between advanced "Palaearctic" and "Ethiopian" taxa.

It would seem prudent to consider the possibility of parallel evolution in cases of non-concordance with other characters. I have in mind particularly the evidence indicating that Cerastes may be monophyletic with Echis (p.226), and that Echis (and presumably Cerastes) is monophyletic with Atheris (s.l.) and Adenorhinos (p.228). If this relationship is accepted, it is necessary to assume that the resemblance in the postorbital process of the parietal between Cerastes and Pseudocerastes in particular among the Eurasian species (and the lesser resemblance of Echis is a parallelism. In Cerastes, the hyperdeveloped parietal process is accompanied by hyperdevelopment of the postero-lateral portions of the parietal, forming the origin of the retractor pterygoidei, such as to deform the prootic and the trigeminal foramina (char. 30). This peculiarity is also functionally linked with the fang apparatus, as it appears the parietal process may be.

The formation of a robust postorbital-parietal articulation may also be functionally linked with the "quadrato-mandibular" ligament. As noted in Character 23 in the larger and/or generally more advanced viperines the anterior section of this ligament (maxillo-postorbital ligament) arises entirely from the distal tip of the postorbital, rather than being diffusely connected with it and arising mostly from the connective tissue of the venom gland capsule. Kardong (1974) has suggested that this ligament functions to resist hyperextension of the maxilla and fang during the strike. It would thus seem possible that a relatively firm postorbital-parietal articulation would be selected for, since the ligament arises from the distal tip of the postorbital (or indeed from the tip of the parietal process in Echis coloratus). The development of an expanded postorbital head (especially Bitis, also superciliaris, and to a lesser extent hindii and Atheris s.s.), or a laterally extended postorbital process of the parietal (in large Vipera, Pseudocerastes, Eristicophis, and especially Echis and Cerastes), would appear to be alternative pathways to attain postorbital stability. However, if the ligament is functionally of such significance, it is difficult to conceive of the factors allowing loss of the ligament in some Echis carinatus, Atheris hispidus, and a few crotalines.

Enlargement of the postorbital process of the parietal has also occurred in crotalines; the process is small in most of the more conservative Agkistrodon, but is massive, with reduced postorbital, in several advanced lineages.

50.

Postorbital: dorsal portion

This character applies only within Bitis. In all Bitis, except B. worthingtoni, the head of the postorbital has a prominent posterior lobe, extending back to contact, or almost contact, the prootic. This is clearly a derived condition. Bitis worthingtoni lacks this process, a primitive resemblance to other viperines.

A - primitive

B - postorbital contacts prootic

Bitis, except worthingtoni

A → B

51.

Postorbital: distal tip (Figs 174-176)

This character applies only among the Eurasian group of viperines. In nearly all Vipera species (and in Causus, Azemiops, most crotalines) the postorbital is a gently curved bone, its distal tip directed anteriorly, and tapering somewhat.

In Vipera russelli the distal tip of the postorbital is turned posteriorly. In Pseudocerastes the postorbital has a weakly developed twist distally, this is further developed in Eristicophis.

This character provides another autapomorphy of Vipera russelli (see also pp. 221-222), and another synapomorphy of the advanced Eurasian viperines, Pseudocerastes and Eristicophis.

A - primitive

B - tip of postorbital turned posteriorly
 Vipera russelli

C - postorbital 'twisted' distally
 Pseudocerastes, Eristicophis

$$C \leftarrow A \rightarrow B$$

52.

Separation of posterior Vidian foramen and cerebral foramen

Underwood (1967:18) has reported that in the viperids he examined the cerebral foramen (for entry into the braincase of the cerebral branch of the internal carotid artery) is separate from the posterior foramen of the Vidian canal (for passage of the palatine branch of the facial nerve). In most snakes only a single foramen is visible externally; both the cerebral artery and the palatine nerve enter the posterior foramen of the Vidian canal, but since the cerebral foramen lies just within the Vidian canal the cerebral artery passes through only the posterior-most portion of the canal, the palatine nerve continues anteriorly to emerge from the anterior Vidian foramen.

Because a single foramen is typically present in lizards and the great majority of snakes, this appears to be the primitive state, and the typical viperid state in which there is a separate external cerebral foramen appears to be derived.

There is some variation within viperids. In Azemiops, which on other evidence is the most primitive viperid, there is only a single external foramen (Liem, Marx & Rabb, 1970: 76, 107), the Vidian canal and the cerebral foramen are visible just within. A similar pattern persists in a few other viperids, but in these cases the two foramina are typically more readily visible externally, or are closely visible within a shared excavation in the sphenoid. There may also be individual asymmetry, with the cerebral and posterior Vidian foramina separate on one side, but with a single external aperture on the other.

Causus is quite variable. Of the three C.lichtensteini examined there are separate foramina in one but single foramina in the other two. Of six defilippii the two foramina are separate in two specimens, separate on one side but not on the other in three specimens, and there is only a single foramen on each side in the sixth. In two resimus the foramina are separate in one specimen but single in the second.

In all specimens of the remaining Causus species, bilineatus (1 specimen), maculatus (2), and rhombeatus (4), the cerebral and posterior Vidian foramina are clearly separate.

The two foramina are separate in all other viperines examined except some Echis carinatus. In two Echis c. ocellatus from Nigeria there is only a single external foramen, but in 5 other specimens (3 from India, 1 from Aden, 1 without locality) the two foramina are separate. This variation may reflect on the biological status of populations usually referred to the single species E.carinatus; Hughes (1976) prefers to treat ocellatus as a full species pending a full revision of all the relevant populations. The foramina are separate in the closely related species Echis coloratus.

Liem, Marx & Rabb (1970:107) note that among crotalines in some Crotalus the two foramina are not closely separate; this has also been found on one side of 2 specimens of Trimeresurus gramineus and one side of 1 Agkistrodon halys but the remaining crotalines examined (species of Agkistrodon, Bothrops, Crotalus, Hypnale, Trimeresurus) have the two foramina clearly separate, as in almost all viperines.

While there can be little doubt that, as suggested above, the typical viperid condition with separate cerebral and posterior Vidian foramina is a derived state in relation to other Caenophidia, the variation encountered in Causus, Echis carinatus, and some crotalines, is problematic. The question is whether character state reversals have occurred, and those taxa with only a single external foramen are secondarily 'primitive' (pseudoprimitive) in this respect. Considering the evidence of other characters it seems probable that Azemiops retains a genuinely primitive state and equally probable that the West African Echis carinatus with a single foramen are secondarily 'primitive'. The situation in Causus and a few crotalines where there is intrageneric and interspecific variation (some specimens with separate foramina, with the foramina barely separable, or with a single foramen) and occasional individual asymmetry, is difficult to interpret. After consideration of the other cladistic evidence, it seems quite possible that the shift to fully separate foramina has occurred in parallel in three lineages; within Causus, within crotalines, and in viperines other than Causus (with reversal in at least some populations of Echis carinatus).

53.

Emargination of Vidian canal (Figs 177-178)

The standard condition of the Vidian canal in viperids has already been described. In Vipera (xanthina) raddei and a currently undescribed form from northwest Iran, very closely allied to raddei, the floor of the Vidian canal is perforated by a window through which the palatine nerve is visible, and/or is emarginated from the posterior (Fig. 178).

A - primitive

B - floor of Vidian canal reduced
Vipera raddei (and raddei-like form)

A→B

54.

Prootic foramina

The maxillary and mandibular branches of the trigeminal, and the facial nerve, emerge from the braincase via foramina in the prootic bone. There is considerable detailed variation among viperines in the arrangement of these foramina, and frequent individual asymmetry. However, two apparently derived conditions can be distinguished.

Among *Bitis* species, *caudalis*, *schneideri* and *peringueyi* differ from their congeners in having an isolated foramen in the mid-portion of the prootic, for exit of a twig of V_4.

In *Echis carinatus* (*coloratus* less so), *hindii*, *superciliaris*, and *Atheris* (and one side of the *Adenorhinos* skull examined), there is a relatively large excavation in the prootic (frequently extending into the parietal or sphenoid) widely exposing the course of a V_4 twig passing anteriorly into the Vidian canal (to CId muscles).

Because of difficulties in defining homologies across all taxa, and frequent individual asymmetry, these features are not of the highest significance.

A - primitive (or generalised)

B - separate V_4 foramen

Bitis caudalis, *schneideri*, *peringueyi*

C - anterior twig of V_4 widely exposed

Echis carinatus, *Atheris*, *hindii*, *superciliaris*, *Adenorhinos* (partial) some *Echis coloratus*.

$$B \leftarrow A \rightarrow C$$

55.

Colour pattern

There is a rather wide range of head and trunk colour patterns among viperines, and because of the apparent lability of this feature, it is difficult to define homologous states. However, certain apparently derived conditions can be noted.

In the trunk pattern of *Bitis caudalis* each of the median line of dark patches (usually two separate offset patches in other *Bitis*) is accompanied by a lateral dark patch, typically each with a light central spot. These occeli are accentuated in *B.schneideri*, although most pattern elements are reduced. In *B.peringueyi* they are still visible, although other elements are diffuse and fragmented.

Within the Eurasian group, *Eristicophis* is unique, and somewhat resembles *Bitis peringueyi*, in that lateral occeli are present, and the typical Eurasian zigzag or chequered pattern is visible on the tail.

Unlike other *Vipera*, in *palaestinae* and *russelli* dark colouration extends over much of the dorsal head surface, but leaving two light stripes laterally, converging toward the snout. These stripes are frequently more precisely defined in the latter than the former. This is interpreted as a synapomorphy of these two taxa.

C. DISCUSSION

1. The higher taxa of Viperidae: are the viperines monophyletic?

As noted above (section A3c), in the currently most widely-used taxonomic arrangement of the Viperidae (Liem, Marx & Rabb, 1971), three subfamilies are recognised; Azemiopinae, containing only Azemiops; Crotalinae, containing all the vipers with sensory facial pits; and Viperinae, containing all the pit-less vipers except Azemiops.

The Azemiopinae, containing a single species, cannot be other than monophyletic. The Crotalinae is certainly a monophyletic group, the facial pit-organ (and correlated ectopterygoid-maxilla articulation pattern) constituting an undoubted synapomorphy. Within the crotalines, the smaller Central and East Asian species of Agkistrodon (sensu stricto, Gloyd, 1979) appear to be generally the most primitive crotalines, lacking a specialised ectopterygoid-pterygoid joint, and a connection between the M.pterygoideus and the venom gland (developed in two different forms in different crotaline lineages; work in progress). A form such as A.halys or intermedius would also provide a suitable candidate for a primitive crotaline in its small size, slender habitus, colour pattern, head scalation, etc., and of course the geographic position is consistent with such a status.

No synapomorphy of 'Viperinae', comparable to the crotaline facial pit, has become apparent in the present study; however, a probable synapomorphy of viperines other than Causus has emerged. In Acrochordidae and Caenophidia generally, the facial carotid artery passes forward dorsal to the mandibular branch of the trigeminal nerve, as the latter emerges from the prootic. This is the case also in Azemiops, crotalines, and Causus, whereas in viperines other than Causus the facial carotid passes ventral to the mandibular nerve. The distribution of the states of this character throughout snakes strongly suggests that the viperine (*s.s.*) state is derived within Caenophidia, and constitutes a good synapomorphy. Hereafter in this report the term 'viperine' or Viperinae should be understood to refer to the Viperinae *sensu* Liem *et al* (1971) after the removal of *Causus*.

The occurrence of derived states shared between viperines and crotalines tends to further dissociate *Causus* and true viperines, and suggests that crotalines and viperines may form a monophyletic group (with *Causus* as their sister group). These states are noted here, but discussed more fully above as Characters:-

(1) Character 27 *M.hyotrachealis*
(2) Character 17 superficial palate
(3) Character 42 prefrontal

Primitively in snakes the *M.hyotrachealis* attaches posteriorly to the hyoid cornua, this is also the case in *Azemiops* and *Causus* among the vipers, but examined crotalines and viperines (*s.s.*) share a derived state in which the posterior attachment has shifted off the hyoid; instead the muscle fibres merge with the deep face of the adjacent *M.neurocostomandibularis*. A very few other snakes show a similar condition, but the most parsimonious interpretation is that the derived state shared by crotalines and viperines is a synapomorphy.

Primitively in caenophidian snakes there is no elaboration of the posterior margin of the superficial palate (the choanal arc), this is also the case in *Azemiops* and *Causus*, but all crotalines and nearly all viperines share a derived state in which the choanal arc bears a median choanal papilla, usually bifurcate in viperines. I interpret this as a probable synapomorphy of crotalines and viperines; there is some complication in that the papilla is very small and intraspecifically variable (occasionally absent) in two viperine species (that appear primitive on certain external characters) it is suggested above that these are probably examples of secondary reduction.

In Azemiops and Causus, and thus probably primitively in vipers, the prefrontal has both lateral and anterior dorsal processes, at its articulation with the frontal. In viperines the lateral process is absent, but the anterior process is hyperdeveloped; in crotalines both processes are very much reduced or absent. On the grounds of parsimony alone it may be suggested that viperines and crotalines share a common ancestor in which the lateral dorsal process was much reduced, and that the two groups subsequently developed their own differing patterns of articulation. This is admittedly rather slender evidence, but it is fully congruent with the evidence of the M.hyotrachealis and the superficial palate.

A fourth feature, not discussed above, is congruent with crotaline-viperine monophyly, but like the prefrontal, affords only rather weak evidence. In Azemiops and Causus the dorsal trunk scales are smooth (or the dorsal-most rows are weakly keeled in some Causus); this condition is widespread in snakes and may be primitive for vipers. In viperines and crotalines (except Calloselasma rhodostoma where absence of keeling is almost certainly secondary), the dorsal trunk scales are moderately to very strongly keeled. This may be the derived state within vipers.

The proposal that Crotalines and Viperinae (s.s.) form a monophyletic group is possibly incongruent with the retinal anatomy of viperids, so far as this is known (Underwood, 1967,1970,1979), although a cladistic interpretation of this evidence is somewhat uncertain.

Underwood (1979:19-20) distinguishes three grades of retinal organisation in Caenophidia. In the first, probably primitive grade, the retina resembles that of the majority of henophidian snakes in having many close-packed rods, few cones (simple cones only), and outer (visual) cell nuclei outnumbering inner (bipolar, horizontal, amacrine) cell nuclei by about 2:1, the pupil usually closes to a vertical ellipse. In the second, intermediate, grade there are still densely-packed rods, but there may be up to three types of cone, including double cones, often in a second tier extending scleral to the rods; the outer nuclei usually still outnumber the inner, but may be fewer, the pupil usually closes to a vertical slit. In the third, most advanced, grade, there are few rods or none at all, accompanying up to three cone types, there is never a 2-tier arrangement, the inner nuclei now well outnumber the outer nuclei, the pupil is usually circular.

As noted by Underwood (1979:20), the Crotalinae retain densely-packed rods, and the outer nuclei somewhat outnumber the inner nuclei, whereas the Viperinae (here including Causus) are generally more advanced with "a reduced proportion of rods... a gradation from two tiers to a single tier - with the inner nuclei outnumbering the outer". Underwood suggests that the retention of an apparently more primitive retina by crotalines may be related to the development of the infrared-sensitive facial pit-organ in the group. The significant point is that Causus has a retina similar to that of Viperinae (s.s.); if Causus is primitive to the combined group Crotalinae-Viperinae, the implication is that a more advanced retina has evolved in parallel in Causus and true viperines. Thus the hypothesis of crotaline-viperine monophyly is unparsimonious with respect to retinal anatomy.

However, I would not be inclined to give great weight to this character. Firstly, the crotaline retina may in fact be derived rather than primitive, in particular the lack of 'type C' (small) cones would appear to be a derived loss. Secondly, the obvious difficulties in the preparation of specimens means that taxonomic coverage for this character is very sparse (for this level of analysis), and the full extent of interspecific variation within Viperinae is unknown. Thirdly, in any event Underwood suggests (1979:20) that "it is probable that the transition from second grade to third grade has taken place more than once". If Causus has in fact independently transformed to a 'third grade' retina, it may be that the presence of a round pupil in the genus is a derived state, not primitive, all other vipers retaining a vertical pupil, including the generally most primitive form *Azemiops*.

The conclusions to be drawn from the above considerations are that not only is the Viperinae (of Liem, Marx & Rabb, 1971) not demonstrably monophyletic, but that one 'viperine' genus, *Causus*, is probably primitive to a monophyletic group formed of crotalines and viperines other than *Causus*, the two latter groups being distinguished by two unique derived states, the facial pit-organ and the ventral course of the facial carotid, respectively.

It remains to discuss the phyletic position of Azemiops. While undoubtedly a member of the monophyletic group Viperidae (section A3b), the work of Liem *et al* (1971), and my own examinations, reveal no uniquely derived state shared between *Azemiops* and any other viperid lineages. For all characters susceptible to cladistic interpretation *Azemiops* has either the primitive state, or a unique derived state, or the cladistic interpretation is ambiguous.

However, two characters seem unequivocally to place *Azemiops* primitive to *Causus*, crotalines and viperines. In the great majority of snakes (Underwood, 1967:23; Liem *et al*, 1971:111), and thus probably primitively in viperids, the palatine bone bears a dorso-medial process, the choanal process, arching dorsally over the internal choanae (deep to the buccal mucosa) toward the midline. The process may be broad or narrow-based as it arises from the main shaft of the palatine. A long narrow choanal process is present in *Azemiops* but in no other viperids, this absence is regarded as a derived condition. In a very few viperines (eg. *Atheris*) and (more prominent) in many crotalines, the palatine has a low vertical dorsal extension. This extension may be inclined slightly medially, and is particularly prominent in

Calloselasma rhodostoma and Deinagkistrodon acutus, but is absent in the primitive Asiatic Agkistrodon, and is of fundamentally different form in Azemiops.

In the vast majority of caenophidian snakes (Liem et al, 1971:112), and thus probably primitive in vipers, the prefrontal bears a near vertical wing or spine arising immediately dorsal to the anterior opening of the lachrymal canal. This spine is retained in Azemiops but is absent or vestigial in other vipers.

Although the above two derived states shared by Causus, crotalines and viperines, are 'loss' states, and so perhaps questionable as synapomorphies, there is no good evidence that is incongruent with the hypothesis of the monophyly of these three groups.

I would reject the suggestion of Liem et al (1971:118), that Azemiops "arose as an early offshoot of the main line of vipers near the evolutionary paths of the crotalines and viperines", and (p.113) represents a "pitless pit-viper". It is uncertain if any significance should be attached to the fact that in the phyletic diagram illustrating their hypothesis (p.118), the lettering of the 'Azemiopinae' stem starts off nearest the Viperinae but ends up nearest the Crotalinae. It is certainly true that "Azemiops can be seen to combine elements of crotaline and viperine morphology", but these resemblances cannot simply be taken as evidence for the "intermediate" position of Azemiops, since they include both primitive and derived features, and phyletic relationship is revealed only at the level of shared derived features.

As noted above, of the characters shown by Azemiops that appear amenable to a cladistic interpretation, there is no derived state shared by Azemiops and Causus alone, or by the former and Viperinae alone; similarities such as the lack of a M.pterygoideus glandulae, lack of the sensory pit-organ (and correlated lack of excavation in the maxilla), the form of the ectopterygoid-maxilla articulation, are all primitive for vipers, Likewise, there is no clearly derived state shared by <u>Azemiops</u> and crotalines alone; a major similarity, the dorsal course of the facial carotid artery, is primitive for vipers. Similarities in the palatine-pterygoid articulation (character 46) and in the venom duct shape are cladistically ambiguous. In <u>Azemiops</u> and most crotalines the palatine-pterygoid articulation is a double-saddle joint; at first sight this seems a possible synapomorphy of <u>Azemiops</u> and crotalines, however, several crotalines lack a double-saddle joint and thus resemble viperines. These crotalines, comprising species of <u>Agkistrodon</u>, <u>Hypnale</u> and <u>Calloselasma</u>, include what are probably the least derived crotaline snakes, thus the 'viperine' articulation may well be primitive for crotalines, and thus no synapomorphy of crotalines and <u>Azemiops</u>. Furthermore, one viperine, '<u>Atheris' superciliaris</u>, resembles the crotaline pattern, indicating significant lability in the precise form of joint. Overall, it seems likely that the <u>Azemiops</u>-advanced crotaline resemblance is a parallelism. The 'kinked' form of the venom duct is shared by adult <u>Azemiops</u> (not young, Liem <u>et al</u>, 1971:105) and most crotalines (reported by Kochva, 1962:256), but again certain probably primitive crotalines (<u>Agkistrodon halys</u>, <u>Hypnale hypnale</u>) retain a straight venom duct, as in viperines, young <u>Azemiops</u>, and <u>Causus</u>. Again, this feature is ambiguous, and in any event there is not a clear distinction between 'kinked' and 'non-kinked', since several viperines dissected show a near-crotaline pattern.

The suggestion of Liem <u>et al</u> (1971:109) that the motion at the ectopterygoid-maxilla articulation in <u>Azemiops</u> "foreshadows the condition in Crotalinae" appears to be without foundation, no significant evidence is provided for this statement. At one point (p.99) it is said that the maxilla moves "not in a pure hinge fashion", while elsewhere (p.109) it is said to "move like a hinge". Kardong (1974) should be consulted for a clear and concise account of jaw kinesis during the strike in <u>Agkistrodon piscivorus</u>.

It is not possible to arrive at an acceptable hypothesis regarding the absence of a typical viperid M.levator anguli oris in Azemiops; this muscle is present in all vipers but absent or weakly-developed in Azemiops (Haas, 1973:462; Liem et al 1971:105). Haas suggests that this is a secondary (derived) loss, but the point made by Liem et al (p.106), that the 'levator' is quite possibly not homologous in all taxa possessing a muscle of that name, is well-taken.

Overall, the hypothesis most consistent with available evidence is that, firstly, Azemiops is a generally primitive viper, possessing a forward pocket of the right lung, a vestigial left lung and lacking a tracheal lung (character 22), also showing an unmodified anterior azygos vein (character 21), the primitive cranial features noted above and by Liem, Marx & Rabb (1971), and a preponderance of primitive external features (Liem et al, 1971:114; Marx & Rabb, 1972); and secondly that Azemiops is the sister group of the remaining viperids (comprising Causus, crotalines and viperines). Evidence suggesting the monophyly of the inclusive group Viperidae has been noted above (section A3b).

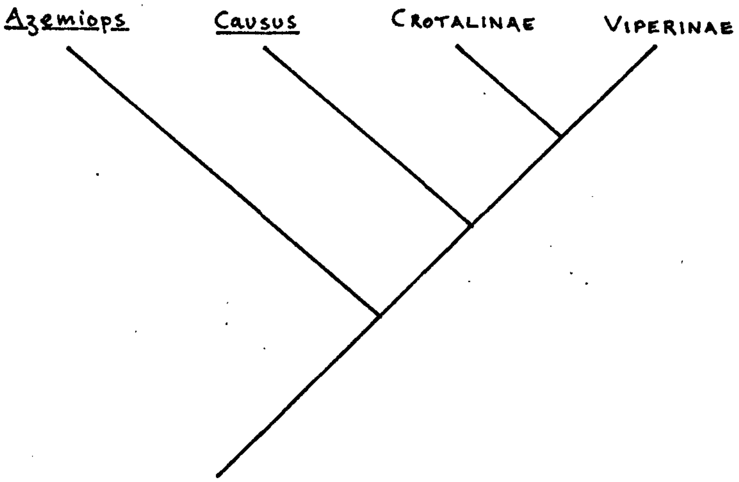


Fig. 7, Hypothesis of cladistic relationships among the major viperid lineages.

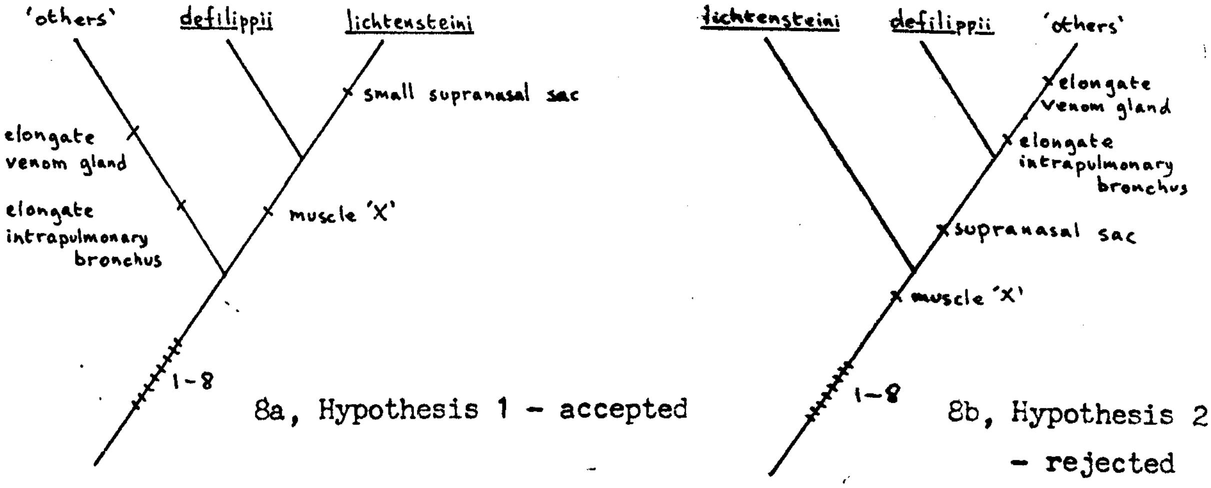
2.Cladistic relationships within *Causus*

The six species of *Causus* share several probable synapomorphies, and there can be little doubt that they form a monophyletic group, phenetically highly aberrant relative to other vipers. Proposed synapomorphies are: -

1. Form of supranasal sac (character 3, probably reduced in *C.lichtensteini*)
2. Scale surface microornament (character 12)
3. Hemipenial morphology (19)
4. Pulmonary arterial pattern (22)
5. Loss of maxillo-postorbital ligament (23)
6. Area of *M.pterygoideus* origin (32)
7. Form of compound bone (33)
8. Form of ectopterygoid (45)

It is possible to distinguish two monophyletic lineages within *Causus*. *Causus defilippii* and *C.lichtensteini* share a probable synapomorphy, the presence of 'muscle X' (character 25) running from the quadrate head to the short posterior extension of the venom gland present in these two species. The remaining *Causus* (*bilineatus*, *maculatus*, *resimus*, *rhombeatus*) share two synapomorphies; elongation of the venom gland (character 24), and elongation of the intrapulmonary bronchus (22, p.122).

The weak development of the *Causus*-type supranasal sac in *C.lichtensteini* is here interpreted as a secondary reduction, because of the incongruence of this feature with the apparently higher-weight character involving the venom gland musculature. If the weighting is reversed, and 'muscle X' interpreted as primitive for *Causus*, or a parallelism, then *lichtensteini* would be regarded as the sister group of the remaining species (sharing full development of the supranasal sac). The presence of two autapomorphies in *lichtensteini*, single subcaudals (paired in other *Causus*), and a very high pterygoid tooth count (42-44 teeth per pterygoid, between ¼ and ½ this number in other vipers, but generally highest in *Causus*), could be consistent with either arrangement.



8a, Hypothesis 1 - accepted

8b, Hypothesis 2 - rejected

Fig. 8, Cladistic relationships within *Causus*

Three features unique to *Causus* among viperids are of uncertain polarity; incomplete fusion of the fang venom canal suture (thus forming a much-extended distal orifice of the venom canal), presence of paired transverse ridges on the sphenoid (providing attachment for muscles of the CId group), and a high dentary, pterygoid and palatine tooth count (e.g., 8-9 teeth per palatine, compared with 4 or less in other vipers, including *Azemiops*). The incomplete development of the fang venom canal has been interpreted as primitive, but it seems perhaps more likely to be a secondary reduction, the relatively simple nature of the ectopterygoid-maxilla articulation and the general lightness of construction of the skull, may similarly be simplifications, but this is uncertain. Transverse sphenoid ridges are of widespread but scattered occurrence in Caenophidia; if primitive for *Causus* and vipers, such ridges must have been lost in *Azemiops* and other vipers, perhaps more likely they may have been developed independently in *Causus*. Superficially, the high palatine tooth count would seem to be primitive (since Caenophidia usually have a higher count than most vipers), but rather more likely, with the high dentary and pterygoid counts, be adaptively associated with dietary specialisation on anurans (perhaps affording a better grip on anuran skin).

The retention of 'colubroid' dorsal head scalation is one of the undoubted primitive features of Causus, others include the presence of an anterior azygos vein, relatively immobile prefrontal-frontal articulation, lack of carination on trunk scales (or weakly present dorsally), unspecialised superficial palate, origin of M.hyotrachealis on hyoid; presence of round pupil (instead of vertical pupil as in other vipers) is possibly derived in the genus rather than primitive.

3. Cladistic relationships within the Viperinae

The taxon Viperines as used here does not include the genus Causus (see above) and is distinguished as a monophyletic group by the shared derived ventral course of the facial carotid artery (character 20).

It has not been possible to produce a completely resolved hypothesis of the cladistic interrelations of all the viperine species. I propose to delimit first the groups whose monophyletic status appears clearly established, and then to discuss how these may relate to one another.

a. The genus Bitis

Species currently assigned to the genus Bitis are united by four apparent synapomorphies:-

1. Supranasal sac morphology (character 3)
2. Form of ectopterygoid (45)
3. Scale surface microornament (12)
4. Form of laterodorsal process of septomaxilla (38)

Within Bitis, B.worthingtoni would seem to be the sister taxon of the remaining species combined, the latter group distinguished by four synapomorphies: -

1. Postorbital-prootic contact (50)
2. Scalation of snout region (2)
3. Anterior ridge of septomaxilla (37)
4. Form of maxilla (and correlated modifications of prefrontal - 44)

In terms of the characters discussed here, B.worthingtoni is generally the most primitive of the species Bitis. By this interpretation, tracheal lungs have been 'invented' twice within Bitis, once in worthingtoni, and again in the 'big Bitis' group (arietans, nasicornis, gabonica; condition in parviocula unknown). The difference in pulmonary arterial pattern between these lineages is consistent with parallel evolution of tracheal lungs; as noted above (character 22), I have given low weight to the degree of tracheal lung development because of the strong evidence for multiple parallel evolution within many groups of snakes. The presence of single subcaudals in worthingtoni (paired in other Bitis) may equally be primitive or derived for the genus.

Bitis worthingtoni is in a rather isolated geographic position, being restricted to relatively high altitudes in the Rift Valley, centred around the Gilgil and Naivasha regions of Kenya. In common with certain other plant and animal taxa occurring in highlands of East Africa, this has the appearance of a relict distribution, an impression that is fully congruent with the primitive status of worthingtoni within Bitis suggested on anatomical grounds.

The big Bitis (arietans, nasicornis, gabonica) appear to form a monophyletic group, sharing the derived features noted below. B.parviocula, known only from the recently described type specimen, has not been examined, but from Böhme (1977), and colour slides kindly provided) it appears to be generally intermediate between arietans and nasicornis in external morphology.

1. Tracheal lung and pulmonary artery pattern (character 22, p.121)
2. Large body size (16)
3. Angular/splenial contacts dentary (34)

Within the big Bitis group, nasicornis and gabonica share many synapomorphies:-

1. Snout horns (6)
2. Superficial palate (17)
3. Transverse scale rows frequently duplicated (15)
4. Prootic modified in relation to M.retractor pterygoideus (30)
5. Tracheal cartilages end near anterior level of heart (22 p.114)
6. Hemipenis ornament (19)
7. Extent of nasal-rostral separation (2)

While B.arietans is the most widely-ranging of all Bitis species, occurring in savanna and semi-desert throughout Africa (to S.W. Morocco and S.W. Arabia), the morphologically closely-related pair *nasicornis* and *gabonica* share a further similarity in geography, being largely restricted to forested regions of west and central Africa.

The remaining *Bitis* are all small species restricted to southern Africa. It has not been possible to find morphological characters suggesting either that these southern African 'small *Bitis*' form a monophyletic group, or that one or other subgroup is more closely related to the big *Bitis* than are other subgroups. On zoogeographic grounds it seems most probable that the small south African *Bitis* are in fact monophyletic, but this cannot be substantiated by any intrinsic morphological features; it is thus necessary to accept a trichotomy at this point, uniting the big *Bitis* and two apparently monophyletic lineages within the small *Bitis*. Of the latter, one group comprises *caudalis*, *schneideri* and *peringueyi*, while the second comprises *atropos*, *cornuta*, *xeropaga* and *heraldica*.

The '*caudalis* group' share a probably derived similarity in colour pattern (55), and in the arrangement of trigeminal foramina in the prootic (54). Within the group, *caudalis* and *schneideri* resemble each other in the sharply acuminate apex of the trunk scales (modified to a rounded apex in *peringueyi*), and presence of supraocular horns; *schneideri* and *peringueyi* resemble each other in premaxilla and nasal form (most modified in *peringueyi*), in progressive modification of colour pattern, and in absence of a median sphenoid keel and basioccipital tubercles. I was unable to trace the *M.add.ext.superficialis* in the two specimens of *peringueyi* examined, however it was present in the *peringueyi* dissected by Kochva (1962:248); perhaps there is between-population variation in the degree of development of the *superficialis* (it is often very thin in other dwarf *Bitis*). *B.schneideri* is distinguished by fusion of transverse scale rows outnumbering occasional duplications, and the very low ventral count and correlated small body size. *B.peringueyi* is unique among Bitis in its dorsal eye position, as in Cerastes vipera, associated with a sand-sinking 'sit and wait' feeding strategy (Robinson & Hughes, 1978:192). The caudalis group also share a broadly similar hemipenial form, with terminal awns present (only in arietans among other Bitis); this similarity is suggestive of a close relationship, but it is not possible to determine if this hemipenial form is derived or primitive for the genus.

The second apparent lineage of small south African Bitis, the 'atropos group', is distinguished by more certainly derived hemipenial similarities (character 19). B.heraldica is included in this group because its unique hemipenial form (p.102) is most easily derived from an atropos-like state. Several features of the trunk colour pattern are shared between the atropos group and B.worthingtoni, the sister taxon of all other Bitis, suggesting that these similarities are primitive for the genus (similarities between these taxa and 'Atheris' hindii and superciliaris may be homologous, eg. Kramer 1961a, or a parallelism, see below).

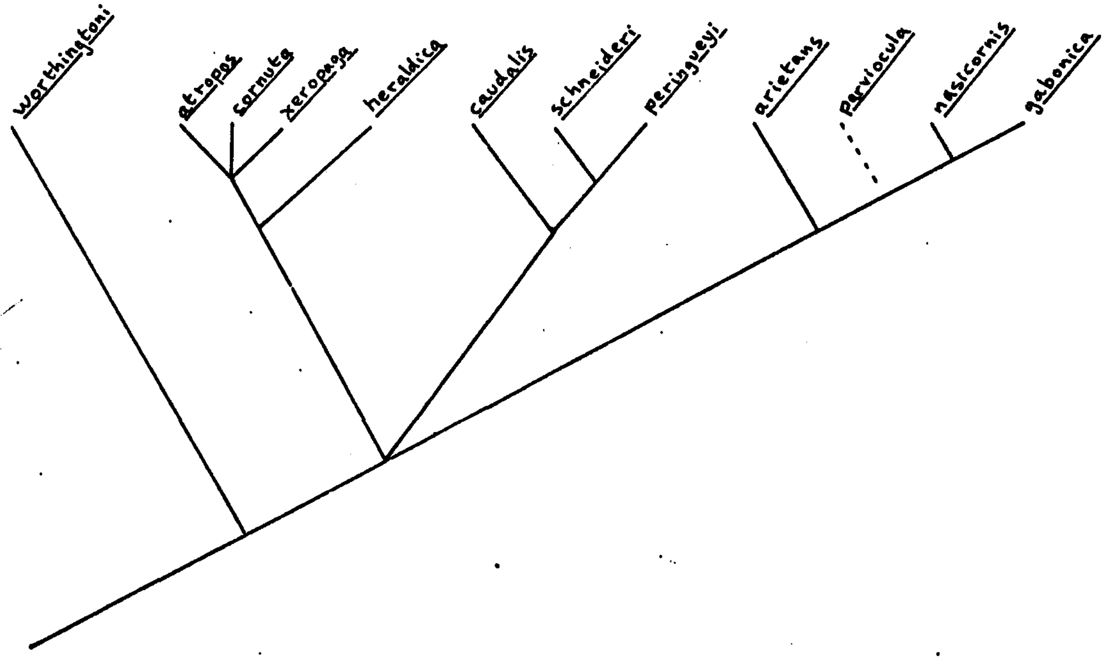


Fig. 9, Hypothesis of cladistic relationships within Bitis

b. The Atheris group

The 'true' arboreal Atheris species are distinguished as monophyletic by shared possession of a derived, highly attenuated body form (character 16), with high ventral and subcaudal counts, single subcaudals, short and wide head plan, and also typically have squarish gular scales. Atheris nitschei appears to be the sister taxon of the other arboreal Atheris species which, unlike nitschei, possess strongly keeled gular scales (char. 11); the colour pattern, head and trunk proportions of nitschei are also less modified. The division of the 'upper rostral' (1) is a derived state shared by A.ceratophorus, chloroechis and desaixi. A.hispidus is the most aberrant species, with a divided premaxilla (36), frequent transverse scale row fusions (15), highly accentuated scale keels and apices (p.36), and absence of the maxillo-postorbital ligament (23). A.ceratophorus is unique in the genus possessing supraocular horns (8).

Certain of the Atheris species (nitschei, desaixi, ceratophorus, weak in chloroechis) show a feature nearly unique in snakes, in that the lower flank scales are inclined (apex ventrally) and their keels are serrated. The only other snakes to possess a similar feature are the viperines Echis and Cerastes (with a more distinct array of modified flank scales, see character 13), where the serrated keels are rubbed against each other as the trunk is coiled upon itself, to produce a warning display, and in the possible Echis-Cerastes mimic, the egg-eater Dasypeltis (and much less developed in the South American Tropidodryas serra). Two species of Atheris (nitschei and desaixi have also been recorded to perform the same warning behaviour.

Such an unusual combination of morphology and behaviour would seem to deserve the highest weight in a cladistic analysis, and to strongly suggest that Echis-Cerastes-Atheris s.s. is a monophyletic group. This is indeed indicated by other characters(37,38,12, with the inclusion of *hindii*, *superciliaris* and *Adenorhinos*). However, a very close resemblance has evolved in *Dasypeltis*, certainly in parallel; the problem is whether this makes parallelism more likely in *Echis-Cerastes* and *Atheris*. A further problem is that certain *Atheris* species and also species undoubtedly closely related to *Atheris* (*superciliaris*, *hindii*, *Adenorhinos*) lack keel serration (and *hindii* alone has inclined flank scales); thus in any event it is necessary to postulate either parallel development of scale modifications or parallel losses.

I feel unable to resolve this question conclusively, but suspect that the presence of inclined flank scales with serrated keels in *Echis*, *Cerastes* and some *Atheris* does indicate a relatively close cladistic relationship; possibly these taxa share a derived similarity in structural gene sequences, but the appropriate regulatory gene sequences, resulting in phenotopic expression of the character complex, have evolved in parallel in *Echis*-*Cerastes* and *Atheris* (see Davidson & Britten, 1973, on gene regulation).

Three individually distinctive species '*Atheris*' *superciliaris*, '*A*'.*hindii*, and *Adenorhinos barbouri*, appear to be related to *Atheris* (*sensu stricto*). All four taxa are here hypothesised to form a monophyletic group, on the basis of:-

1. Scale surface morphology (character 12) further modified in *hindii*)
2. Loss of lateral branch of *M.retractor pterygoidei* (29)

The group is further divisible into two lineages, *superciliaris* being the sister taxa of *hindii*, *Adenorhinos* and *Atheris*. The species *superciliaris* is distinguished by two autapomorphies; form of palatine-pterygoid articulation (character 46), long intra-pulmonary bronchus (p.122), and also has a high pterygoid tooth count (23 per pterygoid usually 12-18 in other viperines, occasionally to 20; 25-26 in *Adenorhinos*; 21-42 in the non-viperine *Causus*)

A large supraocular scale is present in superciliaris, apparently a primitive retention, consistent with the suggested phyletic position of the species; the supraocular is fragmented in hindii, Adenorhinos, Atheris, Bitis, also Cerastes, Echis (except some E.carinatus), and advanced Eurasian group species.

Adenorhinos, hindii, and Atheris, together forming the sister group of superciliaris, share four synapomorphies:-

1. Hemipenial form (character 19)
2. Divisions of rostral (1)
3. Presence of naso-rostral (2)
4. Reduction of vomerine process of premaxilla (35)

Adenorhinos is ecologically (section A4c) and morphologically highly distinct; it has unique nasal scalation (character 4) and other features of head scalation and proportion, see Marx & Rabb, 1965: Fig.41,C-D), unique palatine-pterygoid articulation (47), unique ectopterygoid (45) and ectopterygoid-maxilla articulation (p.169), septomaxilla modifications (characters 37, 38), divided premaxilla (also seen in Atheris hispidus, but almost certainly in parallel, see p. 151), and other unique cranial features. Although both specimens I have been able to examine have been melanistic, Loveridge (1933:278) records a colour pattern that reads as if similar to that found in certain Atheris (eg. nitschei).

'Atheris' hindii is distinguished by a unique scale surface microornament (12), and also by ecology, inhabiting montane grassland in Kenya.

Despite the individual peculiarities of Adenorhinos and hindii, the features noted above lead unambiguously to the hypothesis that these two taxa, with Atheris ss., form a strictly monophyletic group. What is a little less certain is how the three lineages relate to one another; hindii and Atheris share the derived feature of regular transverse scale row duplications (15), whereas Adenorhinos and Atheris share the derived features of extreme reduction of the premaxilla vomerine process (35), and hemipenial morphology (19). It thus seems most probable that *hindii* is the sister taxon of the group *Adenorhinos* plus *Atheris* *ss*. (and that scale row duplication has either been lost in *Adenorhinos*, or evolved in parallel in *hindii* and *Atheris*, as again in big *Bitis* and *Eristicophis*).

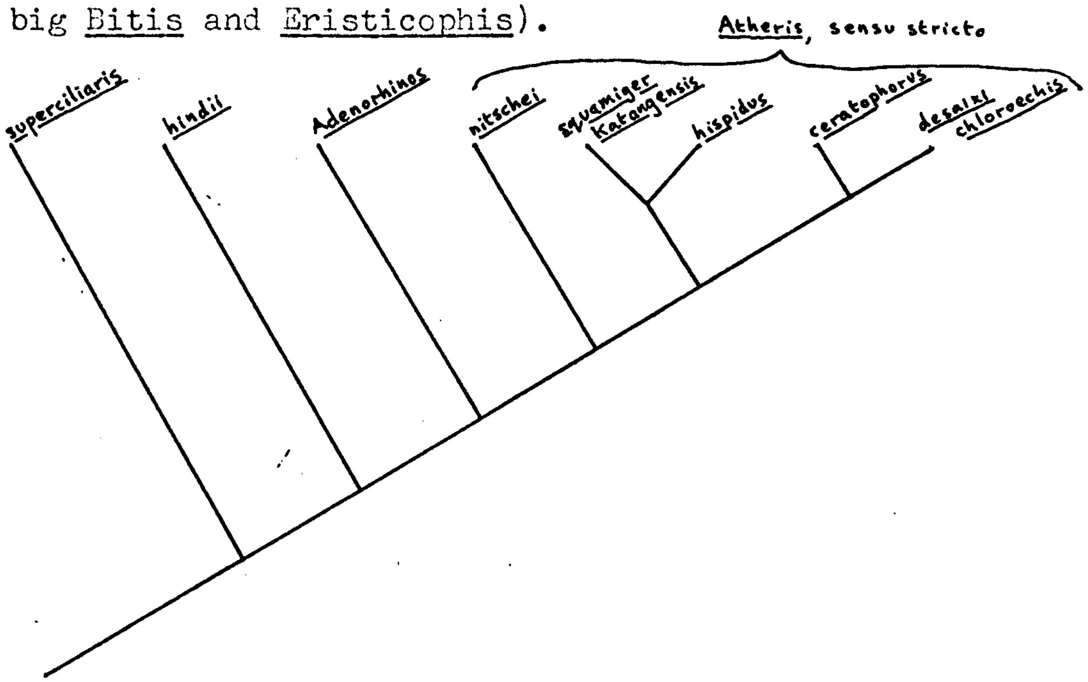


Fig. 10, Hypothesis of cladistic relationships within the '*Atheris* group'.

Regarding the formal nomenclature of the species in this group, it seems inappropriate to recognise one taxon (*barbouri*) as a monotypic genus (*Adenorhinos*, Marx & Rabb, 1965:184) on the grounds of distinct morphology and ecology, when two other taxa, the terrestrial *superciliaris* and *hindii*, are lumped with the arboreal *Atheris* (Marx & Rabb, 1965:182), all groups being morphologically and ecologically highly distinct (see section A4c).

Although Marx & Rabb grouped *superciliaris* and *hindii* with *Atheris* on the basis of three strong similarities (ectopterygoid form, lack of supranasal sac, narrow postorbital), these all transpire to be primitive for vipers, and thus no indication of phyletic affinity. However, the characters noted above do in fact suggest agreement with the broad conclusions of Marx & Rabb (that *superciliaris*, *hindii*, and *Atheris* are closely related, although certainly not with the actual argument on which the conclusion was based. The major disagreement with Marx & Rabb is to their proposal that *Adenorhinos* is not closely related to *Atheris* (as illustrated in their Fig40, p.183). On the contrary, the evidence presented here suggests that *Adenorhinos* and *Atheris* *ss*. form a strictly monophyletic group, ie. the former is closer to the latter than *superciliaris* and *hindii* are. Taxonomically, one solution would be to recognise two additional monotypic genera, for *superciliaris* and *hindii*; an alternative would be to lump all these taxa, including *Adenorhinos*, in an enlarged genus *Atheris*. The first solution is most complicated in terms of nomenclature, but seems perhaps of most practical use.

c. The Eurasian group

The only synapomorphy proposed for *Vipera* species, *Pseudocerastes* and *Eristicophis*, is the presence of a naso-rostral scale (character 2). The scalation of the snout region is further modified in the larger, more eastern, *Vipera* ('*xanthina* group', *lebetina*, *russelli*) by proportional changes and partial re-fusion of the nasal and naso-rostral, and is most modified in *Pseudocerastes* and especially *Eristicophis*. I have concluded that the 'naso-rostral' present in *hindii*, *Adenorhinos* and *Atheris* is most probably non-homologous to that in the Eurasian group; conditions are most similar in *hindii* and the small *Vipera*, but the several derived states linking *hindii* to the '*Atheris* group' are numerous (pp.214-215), and there is no evidence whatsoever suggesting that *hindii* and *Vipera* are monophyletic.

Although reinforced by only one clear synapomorphy, the general phenetic similarity across all members of the Eurasian group is striking, and especially noteworthy are the congruent trends apparent in many characters, where the primitive condition is present in the smaller European *Vipera* of the '*berus* group' (*ursinii*, *berus*, *seoanei*, and *kaznakovi* somewhat divergent), intermediate in the '*aspis* group' (*aspis*, *latastei*, *ammodytes*), while the mid-East '*xanthina* group' species are more derived, with *lebetina*, *palaestinae*, *russelli*, *Pseudocerastes* and *Eristicophis* being at the derived extreme. Saint Girons (1978) discusses this phenomenon with reference to the European *Vipera*. Features involved include:-

1. Head scales (increasing numbers, typically increasingly keeled; 10)
2. Scale surface microornament (12)
3. Body size (increasing, involving transverse scale rows, ventral count, and correlated cranial features, eg. size of basioccipital spine)
4. Maxillo-postorbital ligament (stronger attachments, 23)
5. Occipital branch of *M.depressor mandibulae* (reduction and loss, 28)
6. Lateral branch of *M.retractor pterygoidei* (increasing development, reversed in *Pseudocerastes* and *Eristicophis*, 29)
7. Septomaxilla (37,38,39)
8. Maxilla-ectopterygoid articulation (44)
9. Postorbital and postorbital process of parietal (49)
10. Prefrontal form (43)
11. Attachment of *M.retractor quadrati* (shifts from head of quadrate to midway down quadrate, character not noted above)
12. Superficial palate (17)

Within the Eurasian radiation, the '*xanthina*' group', *Vipera lebetina*, *russelli*, *Pseudocerastes* and *Eristicophis*, form a monophyletic group, united on the basis of four synapomorphies:-

1. Nasal scalation (2)
2. Dorsal head scalation (10)
3. Anterior azygos vein present (21)
4. Occipital branch of *M.depressor mandibulae* (reduction/loss, 28)

The presence of an anterior azygos in this group is superficially a primitive feature, however, because these larger Eurasian forms are strictly monophyletic on three other characters, and are at the derived extreme in all the other characters listed above (1 - 12), and the small European *Vipera* do not appear to form a monophyletic group (which would allow the hypothesis of a two-lineage Eurasian group, with a derived loss of the azygos in one line and a primitive retention in the other), the most parsimonious hypothesis is that a derived character state reversal has occurred in the larger *Vipera*, *Pseudocerastes* and *Eristicophis*.

Five taxa, *V.lebetina*, *'x'.palaestinae*, *russelli*, *Pseudocerastes* and *Eristicophis* (for convenience, termed the '*lebetina* group' below) are distinguished as monophyletic by:-

1. Prefrontal form (further modified in *Pseudocerastes* and *Eristicophis*, 43)
2. Size increase (16)

These species, with the '*xanthina* group', are also distinct in geographical distribution, being mainly mid-Eastern, Central Asian and Oriental (*russelli*) in occurrence, in contrast to the mainly European distribution of the smaller *Vipera*. The two groups overlap chiefly in Turkey, and *lebetina* has an isolated population in northwest Africa, where *V.latastei* also occurs.

The *xanthina* group of species, other than *'x'palaestinae*, is morphologically intermediate between the most advanced of the smaller European species of *Vipera* (the *aspis* group) and the large *lebetina* group. They are also intermediate in geography, not extending so far east as *lebetina* and *russelli*, for example. *Vipera 'xanthina' raddei*, the Iran form close to *raddei*, and *V.latifii*, appear to form a monophyletic group on the basis of:-

1. Supraocular form (8)
2. Complete circumocular ring (7)

They also share a similar form of maxilla, with a narrow shaft above the main tooth-bearing portion, with a distinct medially-directed dorsal tip.

Within this group of three taxa, *Vipera latifii* is suggested as the sister group of *raddei* and the *raddei*-like form; *latifii* is the most easterly of the '*xanthina* group' (except *palaestinae*), being restricted to the Lar valley in the Elburz Mtns. of Iran (Mertens *et al*, 1967; Andren & Nilson, 1979), and is unique in its trunk pattern polymorphism. The *raddei* complex is centred on the Armenian region, and is distinguished by a generally high ventral count, 'reversed' trunk colour pattern, and emargination of the Vidian canal (53).

It is difficult to precisely place *V.x.xanthina* and *V.bornmuelleri* in relation to *raddei-latifii* on one hand, and the *lebetina* group on the other; there is no synapomorphy shared by *x.xanthina* and *bornmuelleri* and either of the latter groups, thus available evidence enables no greater degree of precision than a trichotomy at this point.

It is proposed elsewhere (in preparation) that it is most consistent to treat *bornmuelleri* as a subspecies of *xanthina*, with *raddei* and *palaestinae* as full species. The trichotomy thus involves the *raddei*-*latifii* group, *xanthina* (*x.xanthina* and *x.bornmuelleri*), and the *lebetina* group.

The *lebetina* group is divisible into two branches, one lineage comprising *Vipera palaestinae* and *V.russelli*, united by:-

1. Head colour pattern (55)
2. Nasal scalation and snout shape (5)
3. A strong phenetic resemblance, probably a derived state, is reduction (*palaestinae*) or absence (*russelli*) of peritoneal pigment (darkly pigmented in most vipers and in the other Eurasian species).

The second lineage comprises *V.lebetina*, *Pseudocerastes* and *Eristicophis*, united by several derived resemblances, although no complex synapomorphy; these features include:-

1. Increasing fragmentation of head scales, involving increased subocular count and break-up of the supraocular (still distinct only in some *lebetina*).
2. Snout shape (relatively broad and rounded, less so in some *lebetina*).
3. Scale surface microornament (tendency to reticulate microsculpture and squarish cell outlines: 12)
4. Reduced keeling on head scales (secondarily prominent in *Eristicophis*)
5. Similar trunk colour pattern (except *lebetina mauritanica*, more similar to *palaestinae*; *Eristicophis* most modified).

Within the *palaestinae-russelli* branch, *V.russelli* is phenetically extremely divergent, although most contributing features are internal and so *russelli* is not superficially as distinct as *Eristicophis*, for example. Although *palaestinae* has usually been treated as a subspecies of *V.xanthina*, after Mertens (1951, 1952), a cladistically much more acceptable arrangement was that of Tristram (1888) and Gray (1842,1849), who included *palaestinae* and *russelli* in the genus *Daboia* (also including Turkish *xanthina*, with less justification). Autapomorphies of *russelli* comprise:-

1. Anterior process of palatine (48)
2. Palatine-pterygoid overlap (47)
3. Dorsal exposure of CId muscle group origins (31)
4. Splenial-dentary relation (34)

5. Postorbital process of parietal (49)
6. Superficial palate (choanal papillae reduction)(17)
7. Postorbital (distal tip, 51)
8. Trunk colour pattern
9. Hemipenis (19)
10. Scale surface microornament (12)
11. Increased transverse scale rows (27-33, max. in other Eurasian group 25-27)
12. Lack of peritoneal pigment (p221)

In the *lebetina*-*Pseudocerastes*-*Eristicophis* group, the latter two species are distinguished by many features:-

1. Supranasal sac morphology (3)
2. Superficial palate (17)
3. Scale surface microornament (12)
4. Prefrontal form (43)
5. Shortened keels on trunk scales
6. Snout form (broad, depressed rostrally in dorsal view)
7. Septomaxilla, laterodorsal process (38)
8. Septomaxilla, anterior shelf (37)
9. Sidewinding locomotion
10. Tendency to fewer ventrals (compared with other *lebetina* group)
11. Head shape (very distinct from neck)
12. Terminal awn (reduction-loss, 19)
13. Nasal scale (nearly or completely separated from supralabials)

Marx & Rabb (1965:169) synonymised *Pseudocerastes* with *Vipera* (correctly noting the resemblance of the former to *V.lebetina*) on the grounds of "the marked differences between *Eristocophis* (sic) on the one hand and *Pseudocerastes* and *Vipera* on the other...and the negligible differences between *Pseudocerastes* and some species of *Vipera*". I feel unable to accept this argument. On the basis of one complex cladistically unambiguous character (supranasal sac, see character 3 ; note that a "proto-sac" is not present in any

Vipera), among many other shared derived resemblances, it is evident that *Pseudocerastes* and *Eristicophis* are sister species. It seems unacceptable to sink one of these species in another taxon in the face of such strong evidence, although the actual preferred classification may be subject to some dispute. In phenetic terms both *Pseudocerastes* and *Eristicophis* are jointly very distinct from *Vipera* (eg. *lebetina*), and *Eristicophis* is further modified to a comparable degree from its sister species, *Pseudocerastes*. Table 7 of Marx & Rabb (1965:178), comparing certain characters of *Eristicophis*, *Pseudocerastes* and *Vipera*, simply indicates that in the balance of the few effective characters examined *Pseudocerastes* is more similar to *Vipera* than is *Eristicophis*; when a larger set of characters is examined the phenetic distance between *Pseudocerastes* and *Vipera* increases very considerably, and is accentuated by clear cladistic evidence linking *Pseudocerastes* with *Eristicophis*. It is certainly erroneous that the differences between *Vipera* and *Pseudocerastes* are "negligible".

Autapomorphies of *Eristicophis* include:-

1. Lateral branch of *M. retractor pterygoideus* much reduced (29)
2. Hyoid lingual process much reduced (18)
3. Snout scalation (p.58)
4. Postorbital form (51)
5. Dorsal trunk scales rounded
6. Duplication of transverse scale rows (15)
7. Orientation of transverse scale rows (14)
8. Keeling of ventrals and gulars (11)

9. Premaxilla form (Marx & Rabb, 1965, Fig.39A)
10. Superficial palate (17)
11. Trunk colour pattern (55)
12. Loss of postorbital-frontal contact (present in other Eurasian taxa)

Eristicophis is also distinct geographically, being restricted to sandy deserts in the Baluchistan region, enclosed within the range of its sister species, *Pseudocerastes persicus*, but ecologically separate (section A4c).

It remains to discuss the smaller European *Vipera*, whose cladistic relations with the rest of the Eurasian radiation, and amongst each other, have proved difficult to resolve. A neat solution, and one very convenient for nomenclature, would be to propose that the Eurasian species fall into two lineages, One branch, marked by the derived loss of the anterior azygos vein (21), would include the European forms; the second branch, marked by fusion of the naso-rostral with the nasal (2) and primitive retention of the azygos, would contain all other Eurasian forms (ie. from the *xanthina* group onwards). But, recalling the very many congruent trends evident through the Eurasian group as a whole (p.218), the above arrangement would require extensive parallelism in derived features shared by the more advanced European forms (*aspis* group) and the larger mainly mid-East forms (*xanthina*, etc.). Such features include, maxilla-ectopterygoid articulation, ectopterygoid head form, increase in dorsal and lateral head scales, increase in development of postorbital and postorbital process of parietal, reduction of occipital head of *M.depressor mandibulae*, and others (see above).

It would thus seem likely that the small European species show more of a 'pectinate' phylogeny, with the main stem leading toward the *xanthina* group and its more derived relatives. In general, the *aspis* group is more derived than the *berus* group in respect of the characters noted above; while there is moderate evidence that the *aspis* group is monophyletic (snout form, 6), the *berus* group may well be paraphyletic, but at the level of resolution possible here, *ursinii*, *berus*, *seoanei* and *kaznakovi*, have all been lumped together. Rejection of the 'diphyletic' hypothesis for the

Eurasian group requires either that the anterior azygos vein has been lost in parallel in however many lineages are present in the European species or that it was primitively absent in the stem of the Eurasian group and is secondarily present, as a result of a developmental shift (failure to regress in early ontogeny), in the mid-East forms from *xanthina* onward. I have adopted the latter hypothesis on the grounds of parsimony.

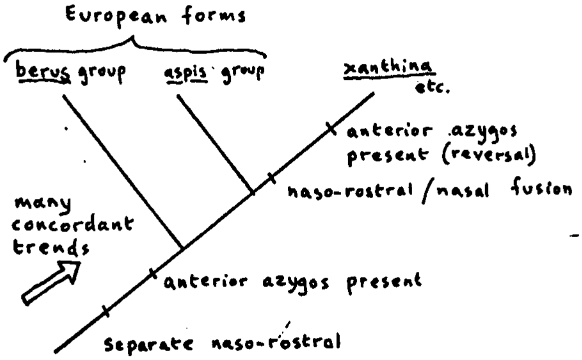


Fig. 11a

Hypothesis 1 - accepted

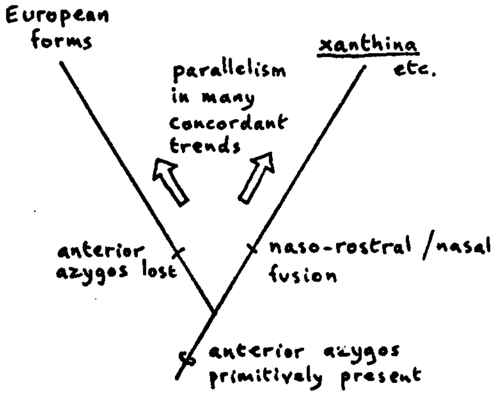


Fig. 11b

Hypothesis 2 - rejected

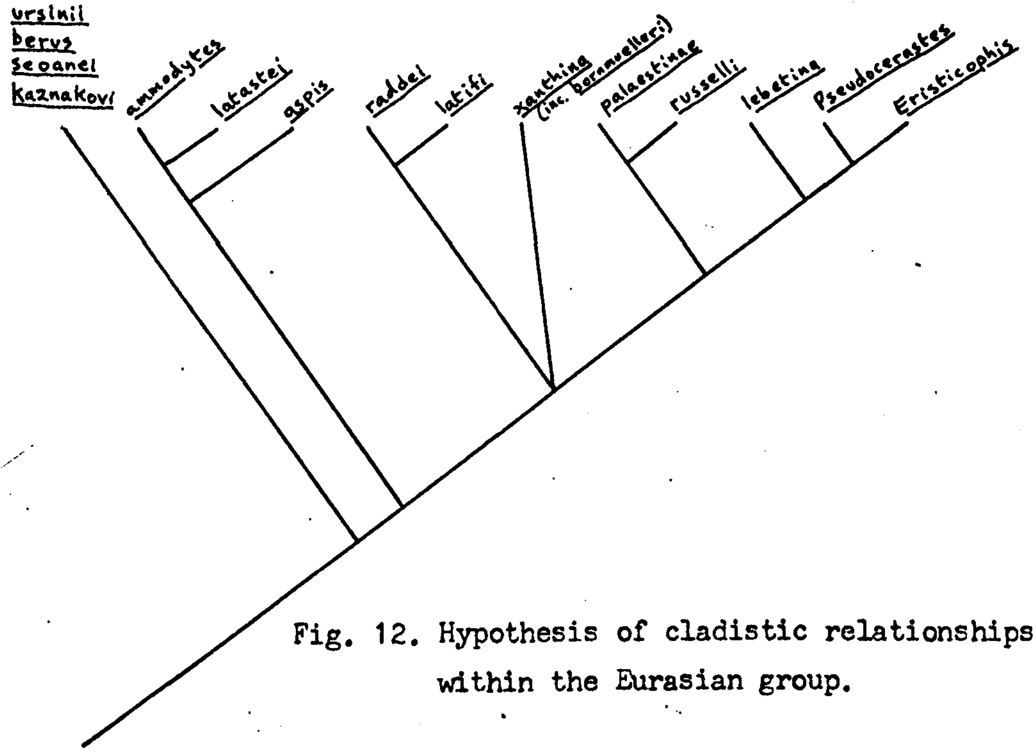


Fig. 12. Hypothesis of cladistic relationships within the Eurasian group.

d. *Echis* and *Cerastes*

It remains to discuss the major persistent problem of this study, namely, how do *Echis* and *Cerastes* relate to each other and to the three main monophyletic viperine groups outlined above? (*Bitis* species, '*Atheris* group' the Eurasian group).

Marx & Rabb (1965:165) state, "*Cerastes* and *Echis* are apparently closely related. They are conveniently distinguished from the other Palaearctic genera by their lack of a splenial bone. In addition to common general internal anatomy, a striking external feature that they share is the oblique lateral rows of scales with serrated keels".

These similarities require some comment, Firstly, they do not both lack the splenial (Marx & Rabb, 1972, have subsequently proposed that in viperines with only a single bone in the place of the separate angular and splenial of other taxa, this is a result of angular-splenial fusion, not loss of the splenial). In the *Echis* and *Cerastes* specimens examined here , one species of each genus was found to have separate bones, in the other the bones were fused; ie. only one species of each genus is "distinguished from the other Palaearctic genera" on this basis. As for "common general internal anatomy", as much could be said for any viperine species, and in fact *Echis* and *Cerastes* are perhaps more different than any other pair of taxa, for example, *Cerastes* lacks a tracheal lung (22) whereas the tracheal lung and anterior pulmonary arteries are well-developed in *Echis*, there are also numerous cranial differences, eg. in the postorbital region (49), and in the hemipenes (19). Thirdly, it has already been noted (13) that certain *Atheris* possess oblique lateral scales with serrated keels, although not so prominently modified.

One striking and detailed resemblance is in scale surface microornament (12). *Echis* and *Cerastes* share a pattern in which there is a dense reticulate microsculpture and distinctly raised polygonal cell margins superimposed on an underlying relief of rounded elevations, of the same order of size as the Oberhautchen cells, but not coincident with them. At first sight this morphology would seem to constitute a good synapomorphy of *Echis* and *Cerastes*. However, a somewhat similar pattern can be seen at the proximal (overlapped) ends of the trunk scales in *Bitis* (before the characteristic laminae are developed on the exposed scale surface); also the scales of *B.peringueyi* resemble a flattened version of the *Echis*-*Cerastes* pattern. Some similarity with *Pseudocerastes* is also evident. Because *Cerastes* and *B.peringueyi* are hot sand desert species, and *Echis* and *Pseudocerastes* are also arid zone forms, it seems possible that the scale surface similarities are parallel adaptive responses to a particular demanding environment; and if the moderate *Cerastes*-*B.peringueyi* resemblance is a parallelism the same may conceivably be true for *Cerastes* and *Echis*.

However, in the absence of persuasive evidence to the contrary, the very close derived resemblances in orientation and serration of flank scales, and in scale surface morphology are here accepted as sufficient indication that *Echis* and *Cerastes* do form a monophyletic group (although phenetically divergent in many other characters). It is also significant that *Echis* antivenin will neutralise *Cerastes* venom, indicating high antigenic similarity (Christensen,1968:45).

e. Interrelations of the four major viperine lineages.

There are now four major monophyletic groups to assemble:-

1. *Bitis* species
2. '*Atheris*' group
3. *Cerastes-Echis*
4. Eurasian group

It is at this point that considerable difficulties arise, for there are no entirely unambiguous synapomorphies uniting any of these four groups (beyond the fact that all are recognisable as viperines *ss*. by virtue of the ventral course of the facial carotid artery).

There are three apparently derived features that link *Cerastes* and *Echis* (especially) with the '*Atheris* group';

1. Laterodorsal process of septomaxilla (38)
2. Anterior shelf of septomaxilla (37)
3. Reduction of vomerine process of premaxilla (35)

Three more features suggest the same grouping (although they are subject to some variation within the group);

4. Presence of a distinct extension of the parietal separating the frontal and the head of the postorbital (most frequently in contact in other viperines)
5. Presence of a very wide occipital head of the *M.depressor mandibulae* (28)
6. Tendency toward greater exposure of the V_4 nerve to the *M.retractor pterygoideus* and *r.vomeris* (running in a bony canal from the anterior trigeminal foramen in the prootic to join the Vidian canal) (54)
7. A seventh feature, orientation and serration of flank scales, is proposed as a synapomorphy of *Echis* and *Cerastes*, and thus cannot strictly be interpreted at the same time as linking *Echis*-*Cerastes* and *Atheris*; but as suggested above (p.82) presence of a similar condition in some *Atheris* *ss*. does tend to suggest a close phyletic relationship, and would be congruent with the features just noted above.

Furthermore, Christensen (1968:453) notes that *Atheris squamiger* venom is strongly neutralised by *Echis* antivenin indicating a high antigenic similarity between the two venoms.

The postulated *Cerastes*-*Echis*-'*Atheris* group' lineage shares one derived state with the Eurasian group, namely, loss of the anterior azygos vein (retained in most *Bitis* species). The above features suggest:-

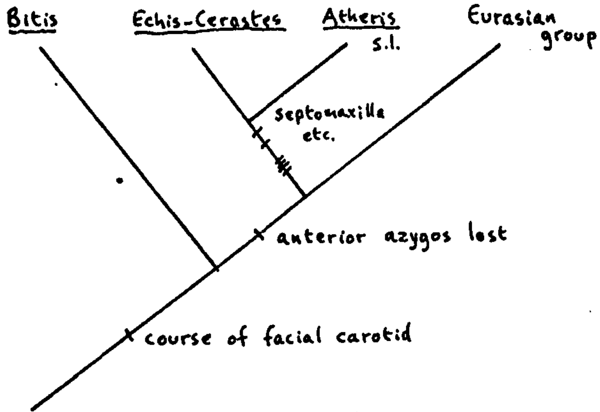


Fig. 13

A problem with this arrangement is that Bitis and most of the 'Atheris group' share a rather similar postorbital region, perhaps derived, whereas Echis and Cerastes (especially the latter) more closely resemble the condition seen in advanced Eurasian species (especially Pseudocerastes). Another similarity shared by most Bitis (including the most primitive, worthingtoni) and two of the Atheris group (again, the most primitive taxa, superciliaris and hindii), is in trunk colour pattern, whereas Echis and Cerastes (especially the latter) more closely resemble advanced Eurasian species (eg. lebetina, Pseudocerastes). These features suggest:-

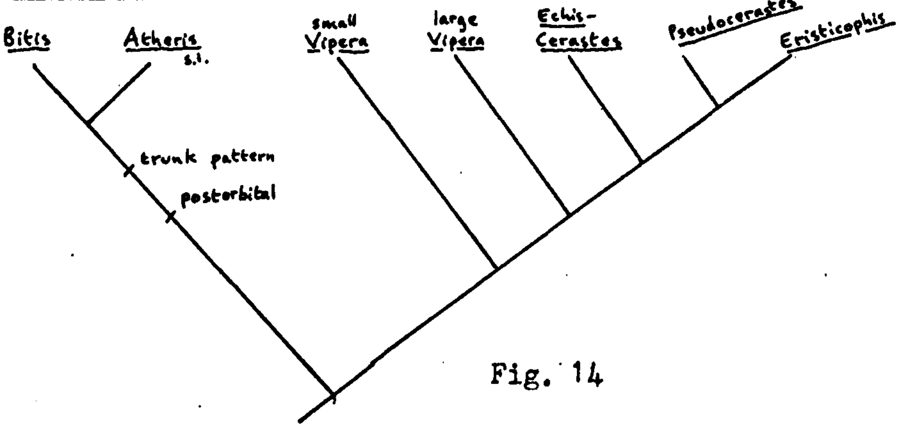


Fig. 14

Although a particularly close Atheris-Bitis relationship remains a possibility, I am inclined to reject a Cerastes-Echis / advanced Eurasian relationship because Cerastes-Echis are not like Pseudocerastes, for example, in the balance of other features (the former pair lack the anterior azygos, have a differently modified nasal region, etc.).

I would also tend to give a low weight to colour pattern similarity, no matter how striking superficially; very considerable intraspecific variation is known in viperines, indicating a high lability (eg. Bruno, 1976, on *Vipera aspis*), and there are additional complications raised by the phenomenon of mimicry, in which connection both *Bitis* and *superciliaris* have been cited (Gans, 1974; Stevens, 1973). It is also suggested above that only low weight can be given to characters of the postorbital region (49).

Two probably derived states shared by *Echis*-*Cerastes*, *Atheris* and *Bitis*, are the presence of a dense reticulate scale microsculpture (12) and much reduced angular-splenial (34). A further common factor linking these three groups, although purely extrinsic and thus of low significance, is their distribution centred on the Afro-Arabian continental plate (the phenetically intermediate *Cerastes*-*Echis* group being geographically intermediate with the Eurasian group also in extending into southwest Eurasia).

The above considerations do not permit any robust cladistic hypotheses, but on balance it seems most probable that *Echis*-*Cerastes* are monophyletic with the *Atheris* group (*Echis* in particular being phenetically rather similar to *superciliaris*, the most primitive *Atheris* group taxon), and that *Bitis* is more closely related to this combined group than to the Eurasian group, and may be the sister group of *Cerastes*-*Echis*-'*Atheris* group'.

Although the present study has fallen well short of the ideal goal of full resolution of the cladistic interrelations of all viperine species, a possible virtue is that problem areas have been clearly identified, and may yield to future investigation by different methods (eg. chromosomes, venom, or blood protein analysis).

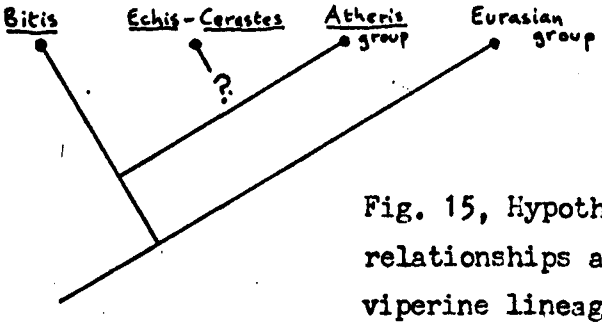


Fig. 15, Hypothesis of cladistic relationships among the major viperine lineages.

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E. FIGURES

16. Rostral region, *Vipera kaznakovi*
17. " " *'Atheris' hindii*
18. " " *Atheris desaixi*
19. Nasal region, *Causus lichtensteini*
20. " " *Vipera kaznakovi*
21. " " *V.lebetina*
22. " " *Pseudocerastes persicus*
23. " " *Bitis worthingtoni*
24. " " *B.atropos*
25. Nasal region of *Causus defilippii*, showing extent of supranasal sac (dashed) beneath supranasal scale
26. As '25', for *Bitis caudalis*
27. *B.caudalis*, supranasal lifted to show branch of ophthalmic nerve in floor of sac
28. As '25', for *Pseudocerastes persicus*
29. *P.persicus*, supranasal lifted to show branch of ophthalmic nerve in roof of sac
30. Snout region, *Adenorhinos*
31. Nasal scale, *Adenorhinos*
32. Snout region, *Vipera lebetina*
33. " " *V.palaestinae*
34. " " *V.russelli*
35. " " *V.ursinii*
36. " " *V.aspis*
37. " " *V.ammodytes*
38. " " (dorsal), *Bitis arietans*
39. " " " *B.gabonica*
40. " " " *B.nasicornis*
41. Circumocular scales, *Vipera bornmuelleri*
42. " " *V.raddei*
43. Supraocular scale, *V.xanthina*
44. " " *V.raddei*
45. Gular scales, *Atheris nitschei*
46. " " *A.desaixi*
47. Flank scales, *Cerastes cerastes*
48. " " *Echis coloratus*
49. " " *Adenorhinos*
50. " " *Atheris ceratophorus*

51. Superficial palate, *Causus maculatus*
52. " " *Vipera ursinii*
53. " " *V.berus*
54. " " *V.aspis*
55. " " *Pseudocerastes persicus*
56. " " *Eristicophis macmahonii*
57. " " (variations), *V.russelli*
58. " " *V.kaznakovi*
59 " " (a crotaline), *Trimeresurus jerdoni*
60. Hyoid, *V.aspis*
61. Anterior portion of hyoid, *V.aspis*
62. " " " " *Causus maculatus*
63. " " " " (variations), *'Atheris' superciliaris*
64. " " " " " *Bitis worthingtoni*
65. Hemipenis (sulcate and asulcate faces). *Causus maculatus*
66. " *Vipera berus*
67. " *Atheris squamiger*
68. " *Bitis arietans*
69. " *B.gabonica*
70. " *B.atropos*
71. Facial carotid artery, dorsal course, *Causus defilippii*
72. " " " , ventral course, *Vipera russelli*
73. Anterior azygos vein, *Causus maculatus*
74. " " " *Bitis atropos*
75. " " " *Atheris squamiger*
76. Heart and pulmonary elements, *Azemiops*
77. " " " " *Bitis cornuta*
78. " " " " *B.arietans*
79. " " " " *B.worthingtoni*
80. " " " " *Causus maculatus*
81. Maxillo-postorbital ligament, *Vipera ursinii*
82. " " " *Eristicophis*
83. " " " *Echis carinatus*
84. Venom gland and muscles, *Vipera palaestinae*
85. " " " " *Causus defilippii*
86. Divided *M.add.ext.profundus*, *C.defilippii*
87. Venom gland(extended), *C.rhombeatus*
88. *M.hyotrachealis*, *Causus maculatus*
89. " *Vipera berus*
90. *M.depressor mandibulae*, occipital head, *Vipera xanthina*
91. " " " " *V.berus*
92. " " " " *'Atheris' hindii*

93. *M.retractor pterygoideus*, *Bitis schneideri*
94. " " *Causus lichtensteini*
95. Origin of *M.retr.pterygoideus*, *Bitis arietans*
96. " " " *B.gabonica*
97. Parietal, *Echis carinatus*
98. " *Cerastes cerastes*
99. *M.add.ext.superficialis* origin, *Vipera ursinii*
100. " " *V.russelli*
101. *M.pterygoideus*, posterior attachment, *Vipera ursinii*
102. " " " *Causus rhombeatus*
103. Compound bone, posterior laminae, *Vipera ammodytes*
104. " " " " *Causus maculatus*
105. Angular and splenial, *Echis coloratus*
106. " " " *Vipera ammodytes*
107. " " " *Echis carinatus*
108. " " " *Cerastes vipera*
109. " " " *Causus maculatus*
110. " " " *V.russelli*
111. " " " *Atheris chloroechis*
112. Snout bones (ventral), *Vipera berus*
113. " " *Echis carinatus*
114. " " *'Atheris' superciliaris*
115. " " *'Atheris' hindii*
116. " " *Cerastes vipera*
117. " " *Adenorhinos*
118. " " *Atheris ceratophorus*
119. " " *Bitis caudalis*
120. " " *B.worthingtoni*
121 " " (lateral), *Adenorhinos*
122. " " *Atheris hispidus*
123. " " *Atheris squamiger*
124. Septomaxilla (top - lateral, below - oblique), *Causus maculatus*
125. " *Vipera seoanei*
126. " *Bitis caudalis*
127. " *Echis coloratus*
128. " *Cerastes vipera*
129. " *Atheris squamiger*
130. Latero-dorsal process of septomaxilla, *Vipera xanthina*
131. " " " *Pseudocerastes*
132. " " " *Eristicophis*

133. Septomaxilla, Vipera kaznakovi
134. " Bitis xeropaga
135. " B.caudalis
136. " B.worthingtoni
137. Prefrontal - frontal articulation, Azemiops
138. " " " Causus rhombeatus
139. " " " Agkistrodon halys
140. " " " Vipera seoanei
141. Prefrontal (top - anterior, below - posterior), Vipera ursinii
142. " Vipera palaestinae
143. " Eristicophis
144. Maxilla (posterior), Causus defilippii
145. " Vipera ursinii
146. " V.latastei
147. " Cerastes vipera
148. " Bitis cornuta
149. " 'Atheris' superciliaris
150. " Echis carinatus
151. " Atheris nitschei
152. " A.squamiger
153. " Bitis worthingtoni
154. Ectopterygoid (anterior portion), Vipera ursinii
155. " V.latastei
156. " Atheris desaixi
157. " Echis carinatus
158. " Bitis cornuta
159. " Adenorhinos
160. Palatine (right) - pterygoid (left) articulation, Vipera ursinii
161. " " " 'Atheris' supercili
162. Palatine - pterygoid articulation (bones in situ), Vipera xanthina
163. " " " Adenorhinos
164. " " " Vipera russelli
165. Postorbital region (top - lateral, bottom - ventral)
Causus lichtensteini
166. " " Vipera ursinii
167. " " V.ammodytes
168. " " V.russelli
169. " " Echis carinatus
170. " " Cerastes vipera
171. " " Bitis worthingtoni
172. " " Atheris chloroechis

173. " " *Bitis atropos*

174. Postorbital, *Vipera palaestinae*

175. " *Pseudocerastes*

176. " *Eristicophis*

177. Sphenoid, *Vipera berus*

178. " *V.raddei*

179. Scale surface microornament (x 2,000), *Azemiops*

180. " " " *Vipera kaznakovi*

181. " " " *V.lebetina*

182. " " " *Pseudocerastes*

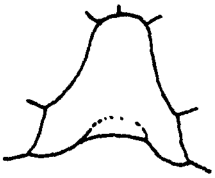
183. " " " *Echis carinatus*

184. " " " *Atheris squamiger*

185. " " " *'Atheris' hindii*

186. " " " *Bitis atropos*

187. " " " *Causus defilippii*



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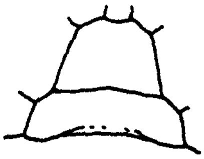

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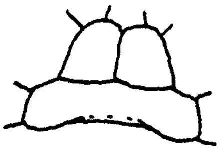

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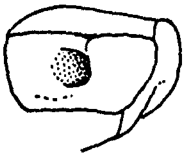

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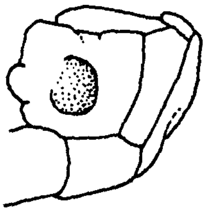

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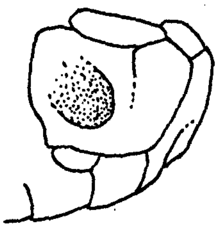

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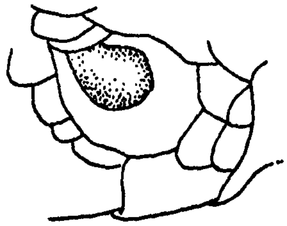

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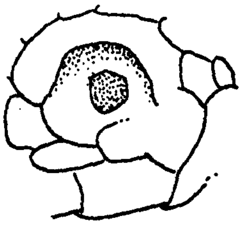

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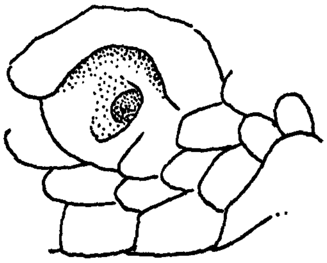

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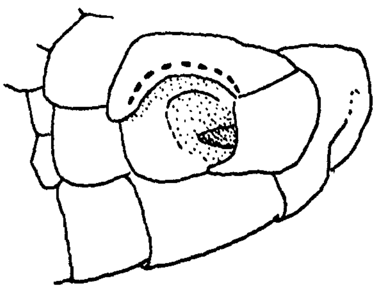

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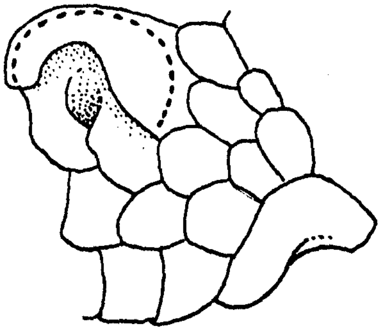

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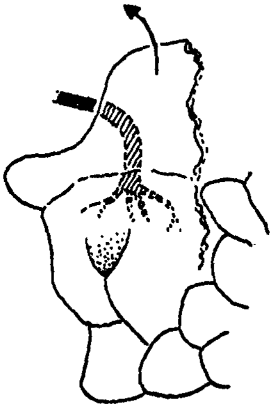

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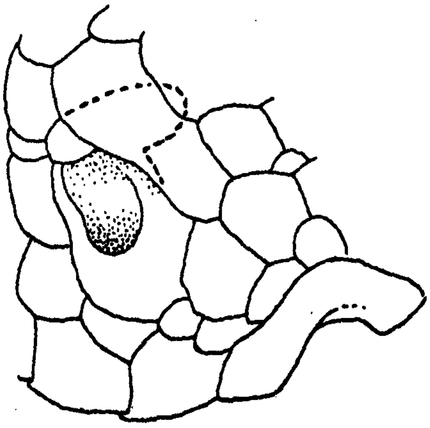

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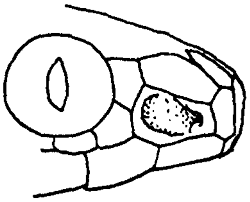

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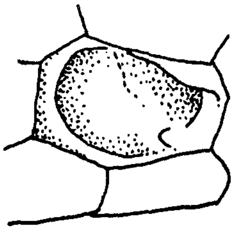

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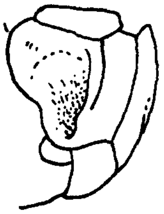

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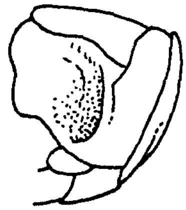

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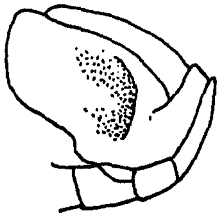

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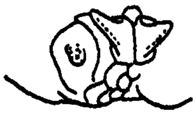

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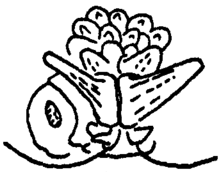

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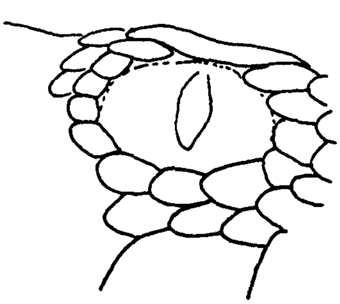

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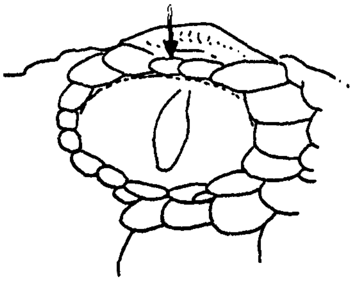

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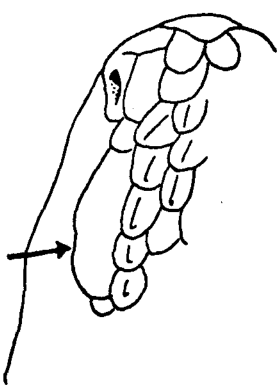

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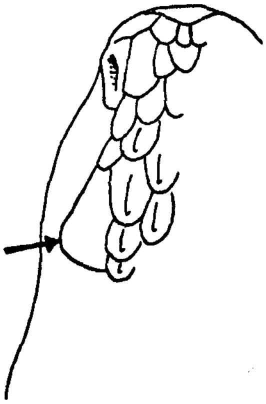

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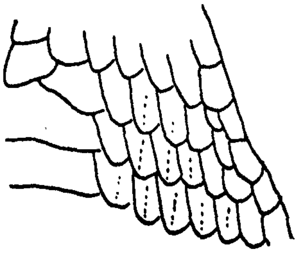

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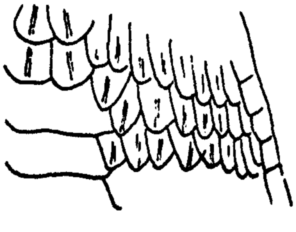

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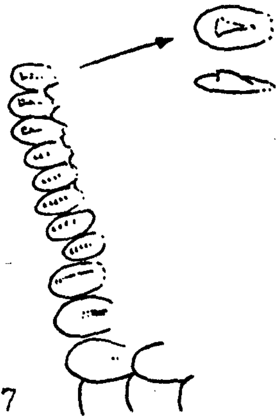

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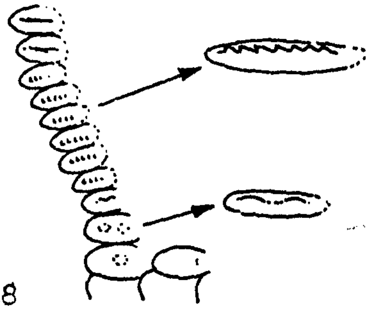

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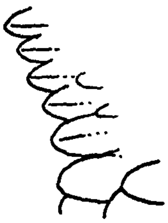

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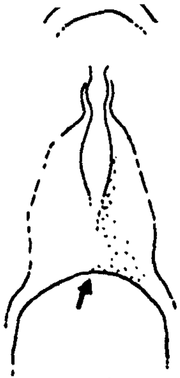

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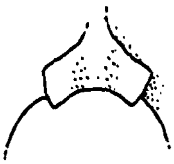

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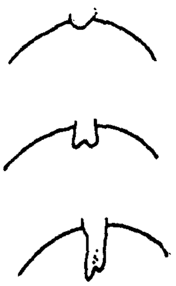

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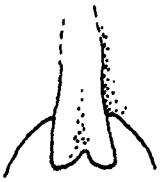

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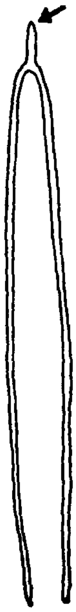

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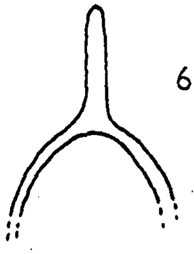

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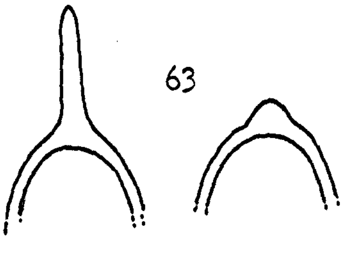

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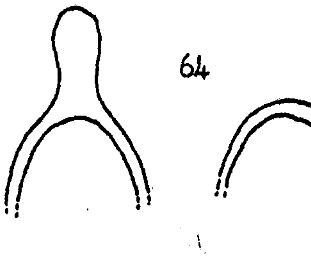

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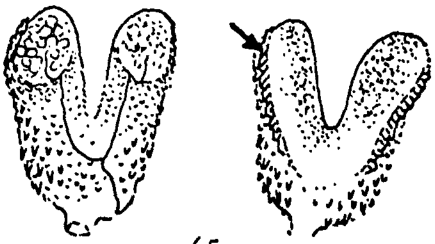

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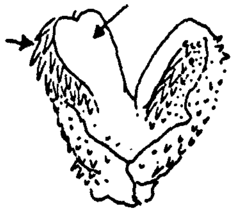

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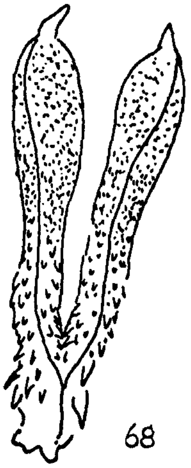

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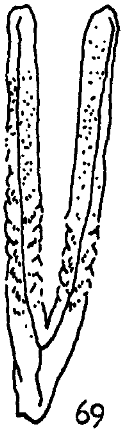
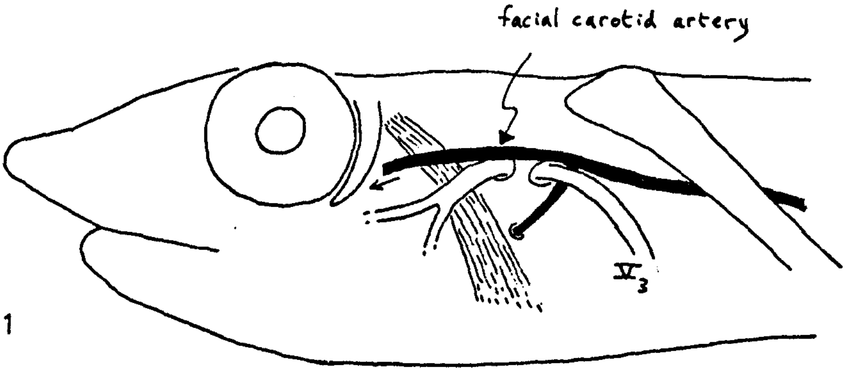
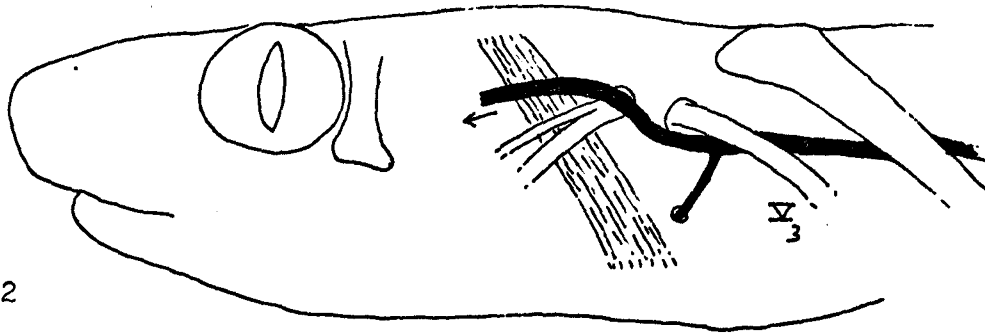


69

70

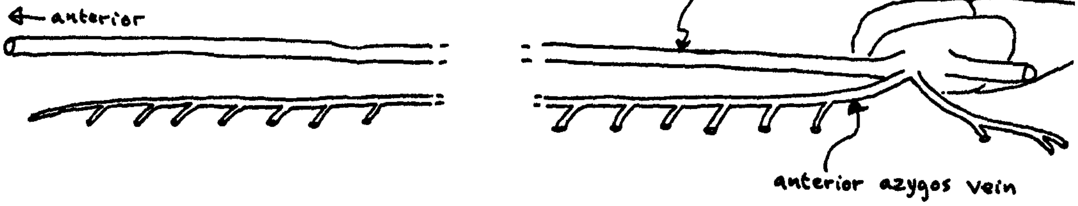

facial carotid artery
V3

71

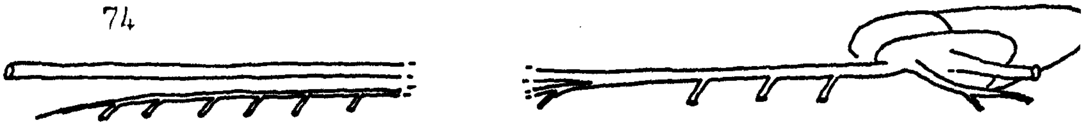

V3

72

73


← anterior
jugular vein
anterior azygos vein

74



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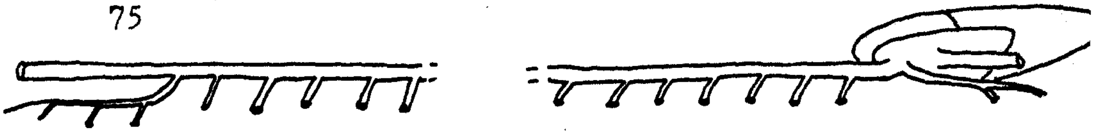
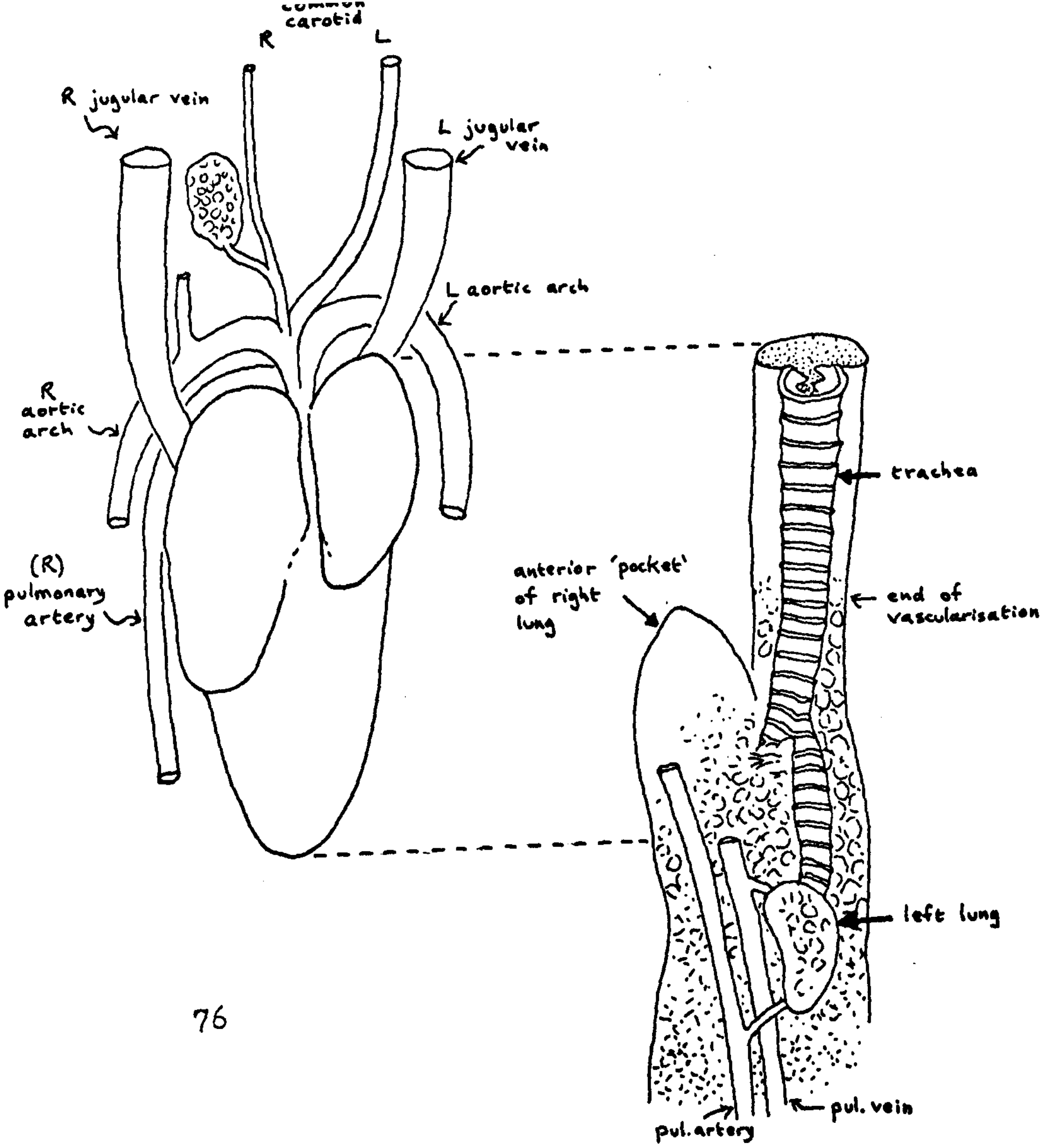
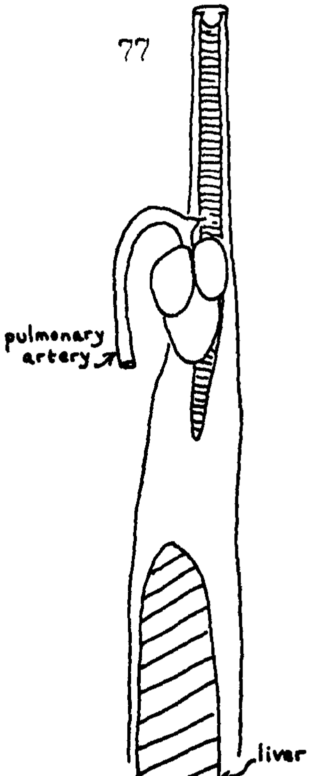
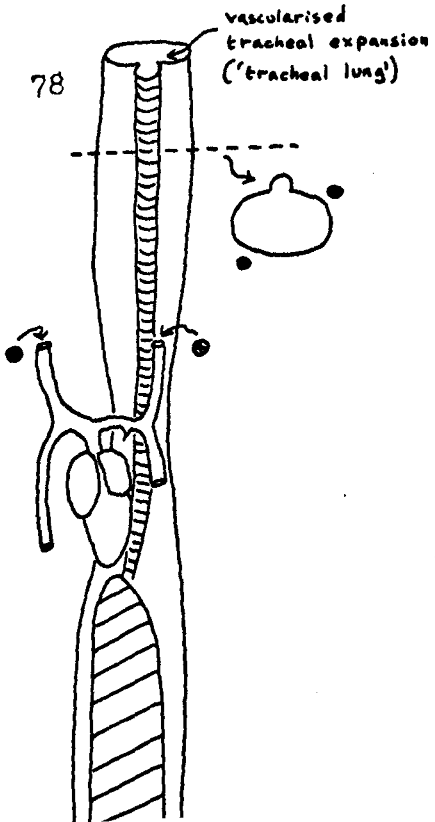



carotid
R
L
R jugular vein
L jugular vein
L aortic arch
R aortic arch
(R) pulmonary artery
anterior 'pocket' of right lung
trachea
end of vascularisation
left lung
pul. vein
pul. artery

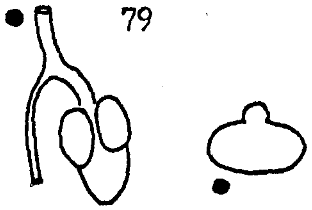
76


pulmonary artery
liver

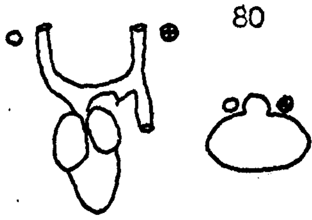
77


vascularised tracheal expansion ('tracheal lung')

78



79



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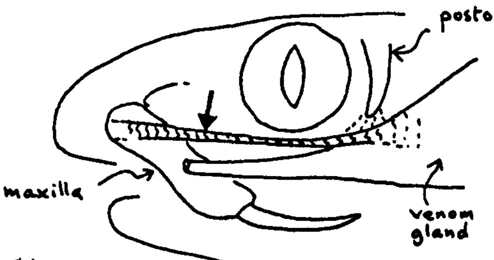

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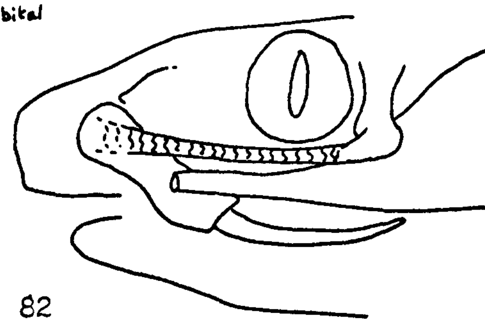

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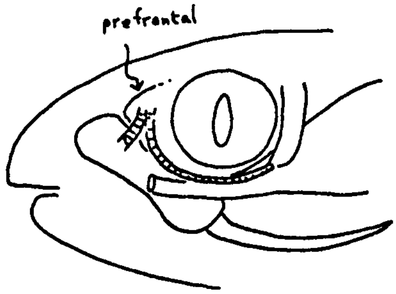

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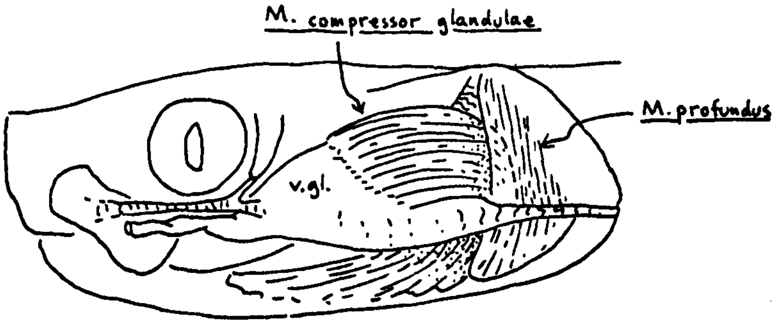

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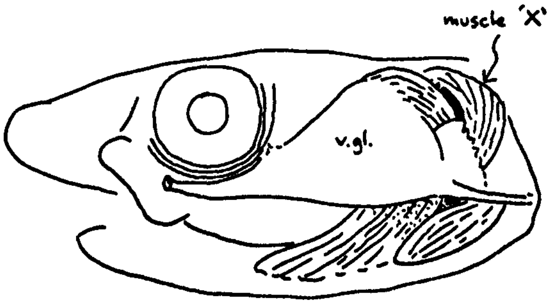

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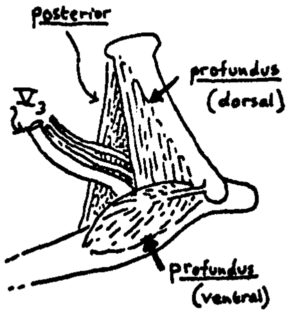

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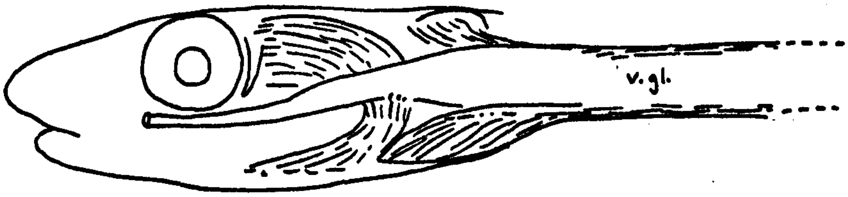

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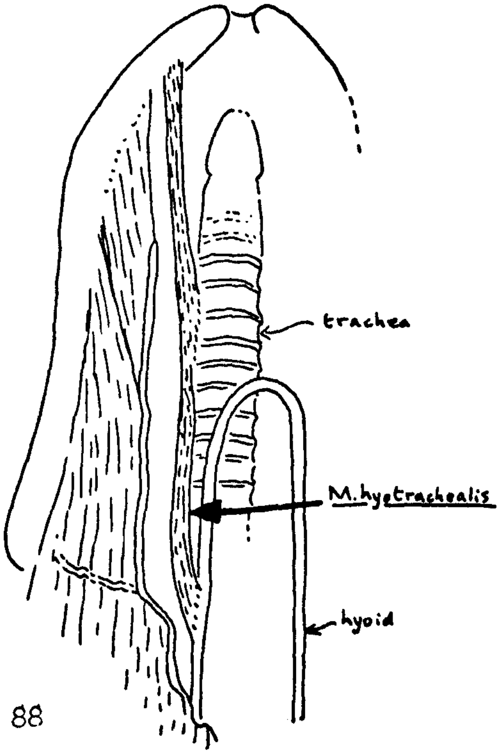
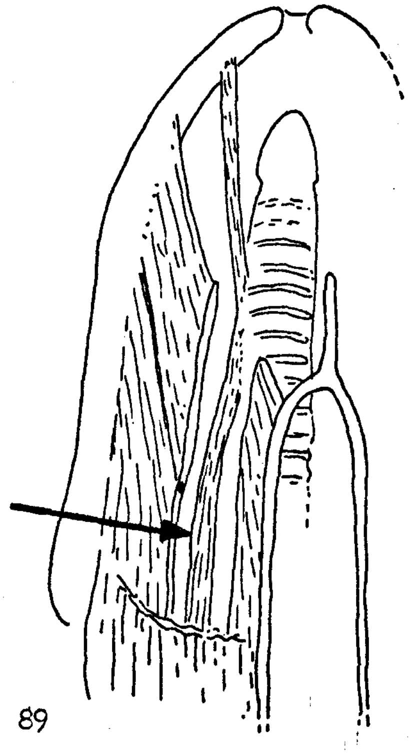

trachea
M.hyotrachealis
hyoid

88

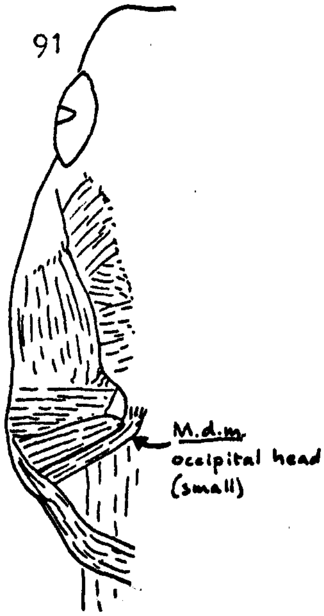


89

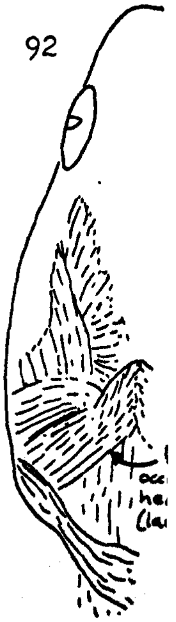
90

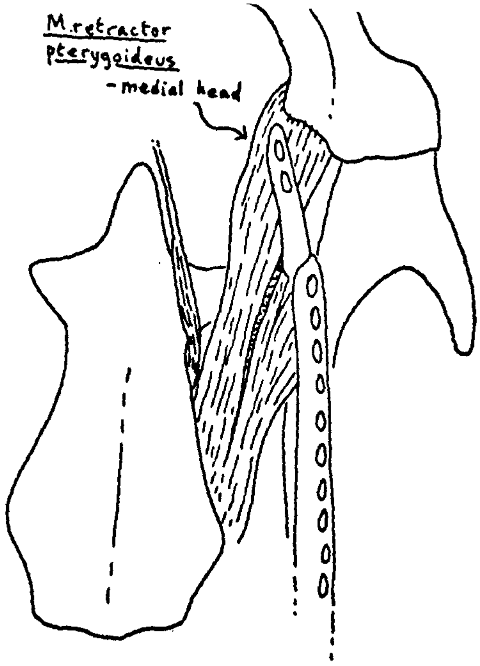

M.depressor
mandibulae

91

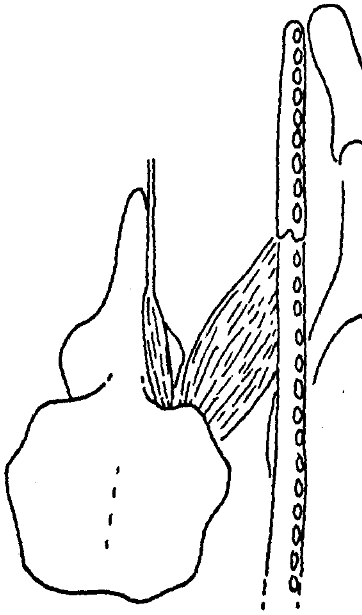

M.d.m.
occipital head
(small)

92


occ
he
(la



93



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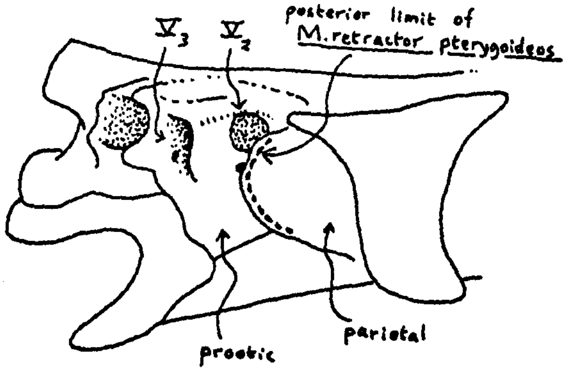

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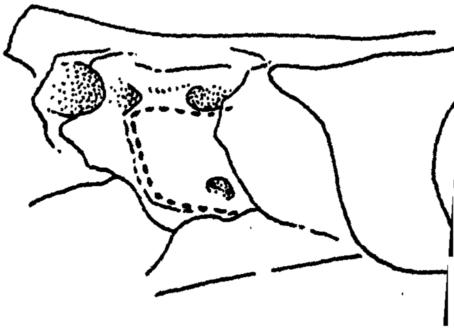

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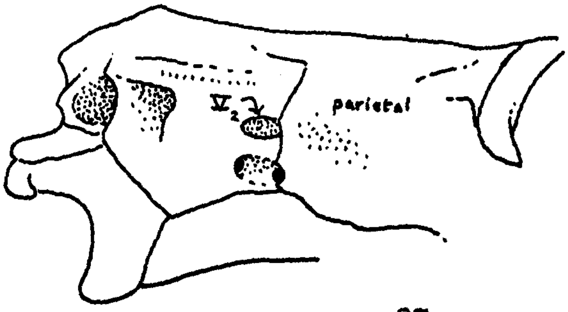

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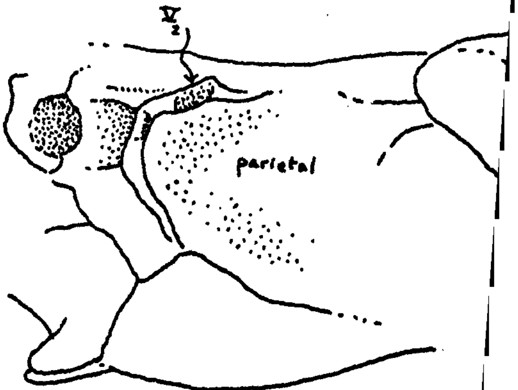

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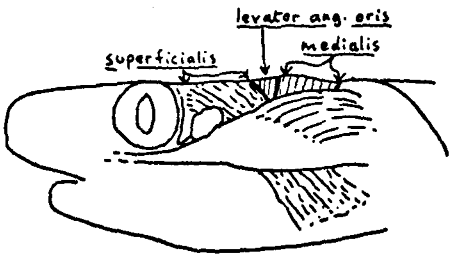

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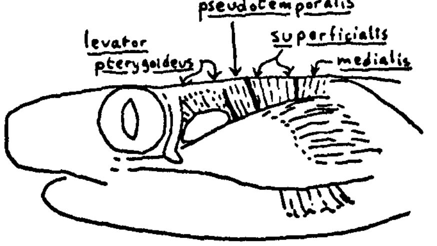

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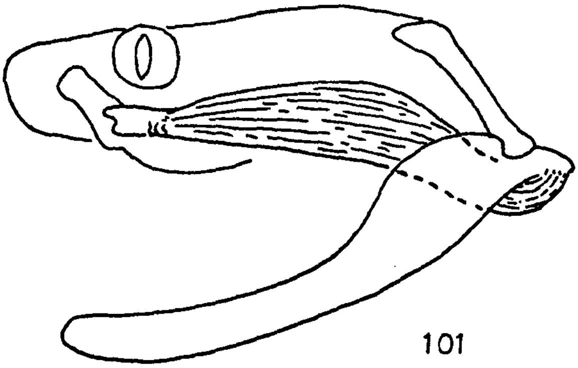

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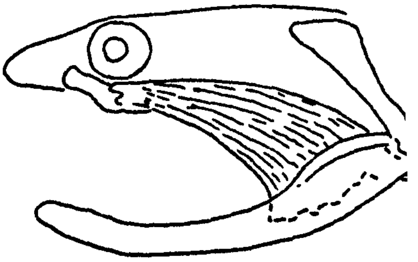

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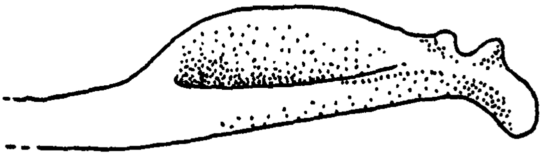

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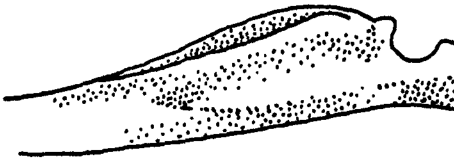
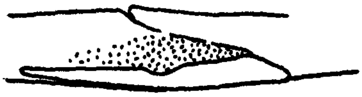


104

105

106

107



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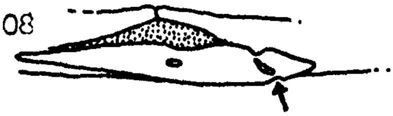

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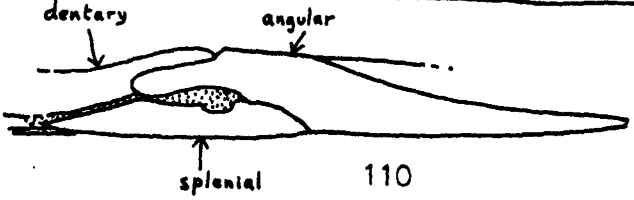

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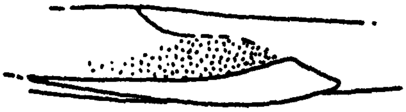

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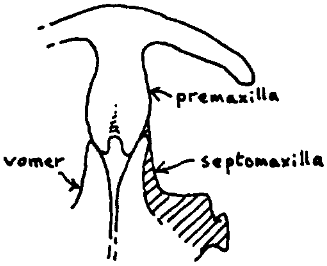

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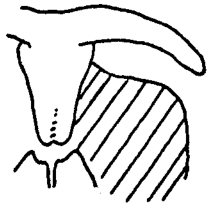

114

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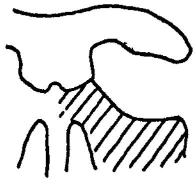

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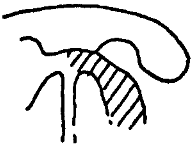

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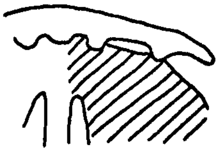

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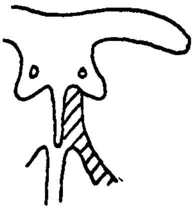

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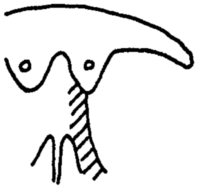

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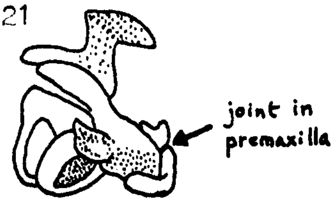

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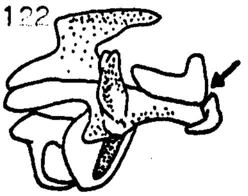

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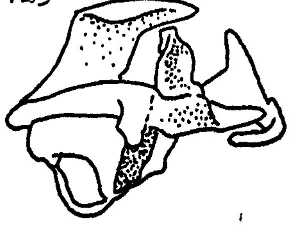

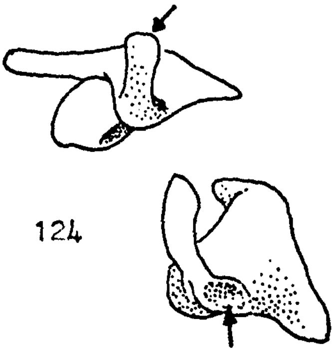

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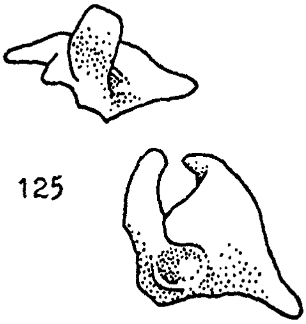

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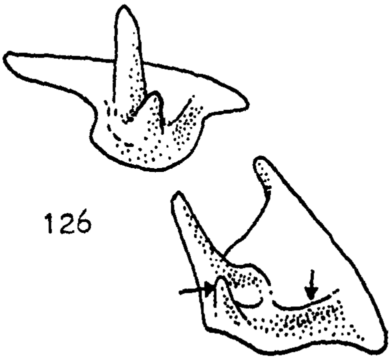

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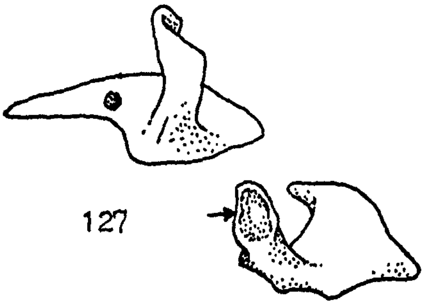

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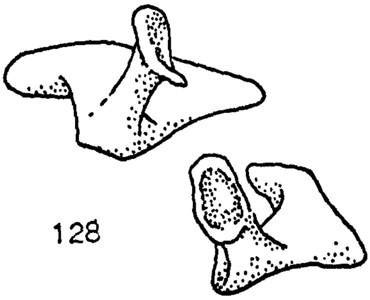

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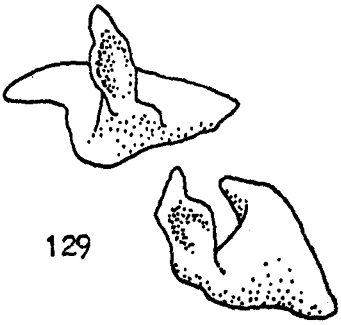

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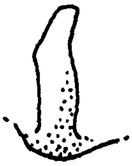

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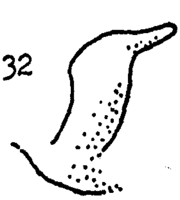

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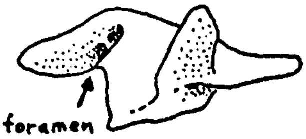

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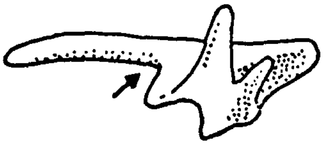

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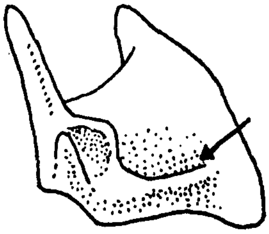

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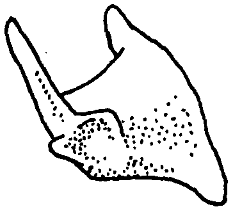

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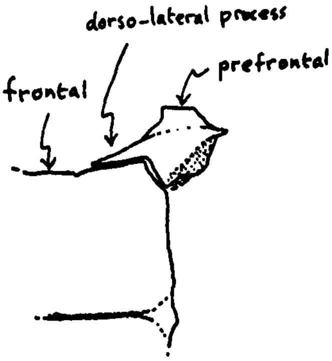

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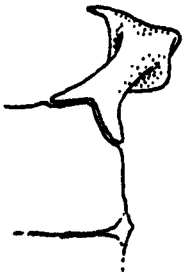

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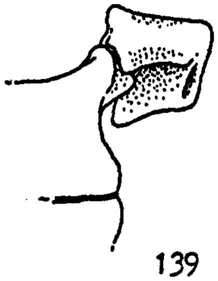

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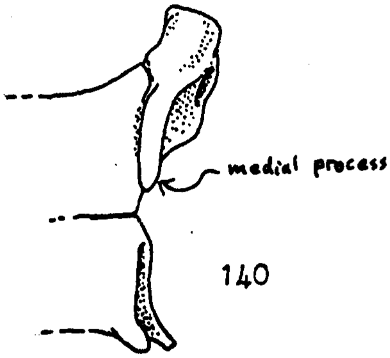

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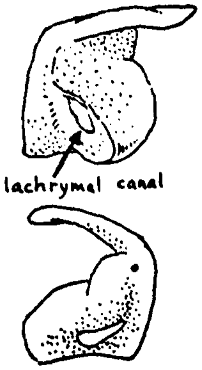

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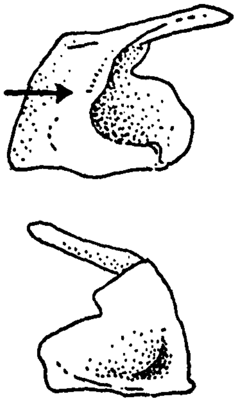

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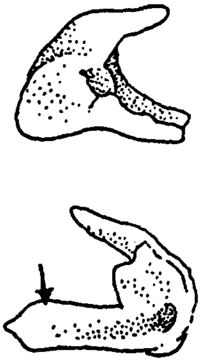

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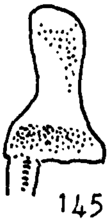
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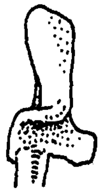
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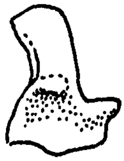
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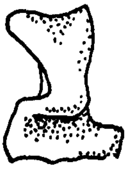
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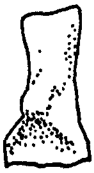
149


150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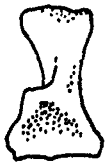
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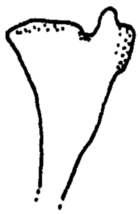
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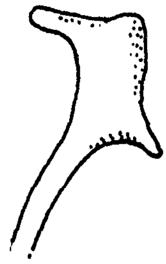
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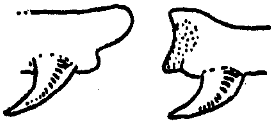
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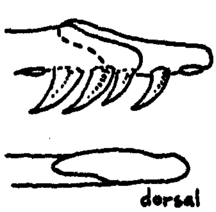

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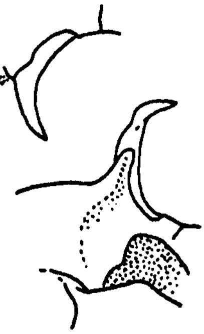
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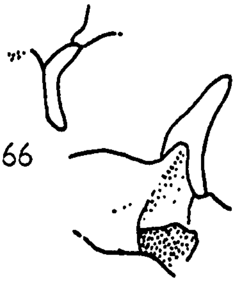
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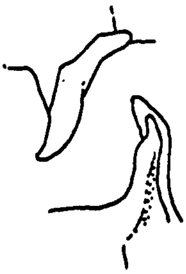
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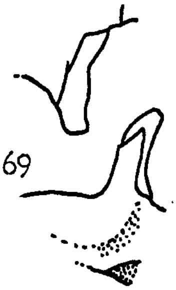
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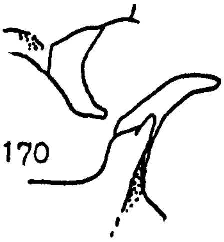
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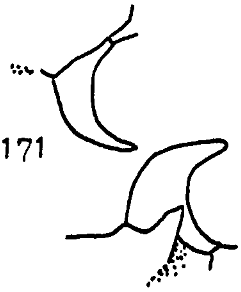
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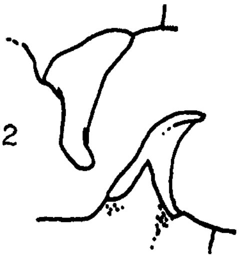
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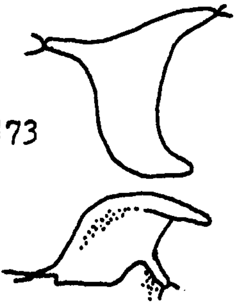
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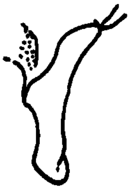
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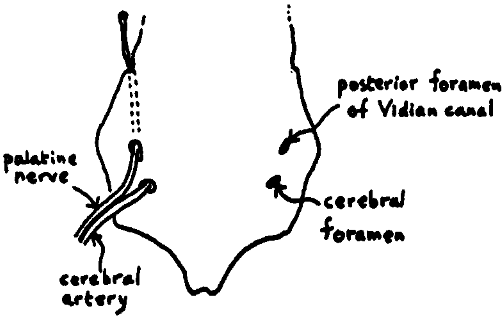

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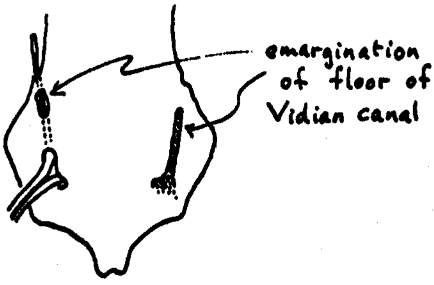

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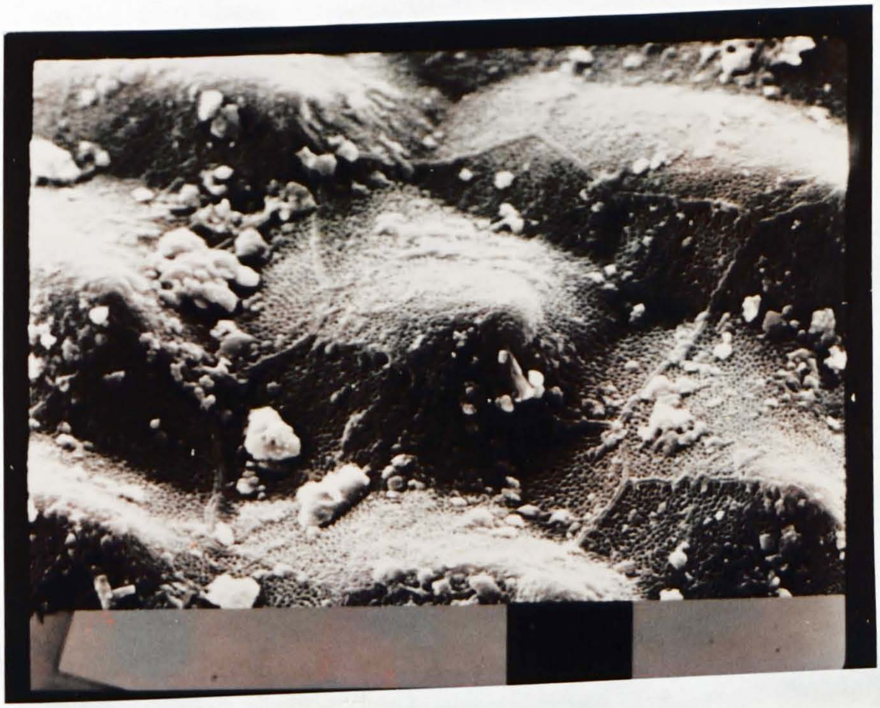

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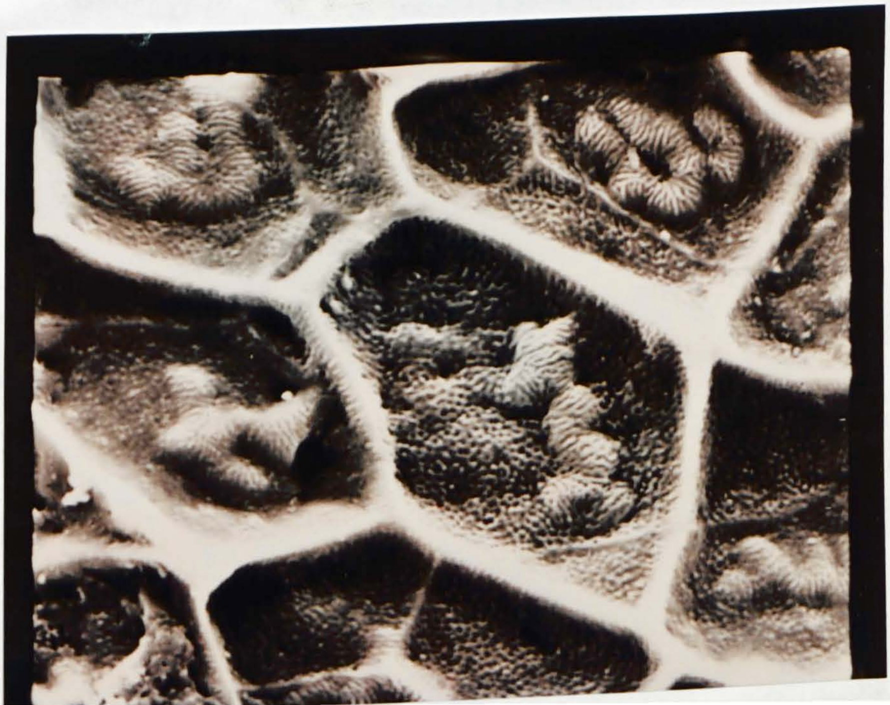

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F. ACKNOWLEDGEMENTS

I owe an enormous debt to Dr Garth Underwood with whom I worked as Research Assistant during a major portion of this study, and whose good humour and breadth of knowledge of snake morphology and systematics have been an inspiration during his supervision of this work.

I am also indebted to Miss A.C.G. Grandison, Curator of the Amphibia and Reptilia section at the British Museum (Natural History), and other staff of the section, notably Dr E.N. Arnold, for their continual assistance and encouragement.

APPENDIX

Copies of published papers arising from this study.

Reprinted from *J. Zool., Lond.* (1979) **189**, 559–567

On the vomer in Acrochordidae (Reptilia: Serpentes), and its cladistic significance

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c/o Reptile Section, British Museum (Nat. Hist.), Cromwell Road, London

(*Accepted 25 June 1979*)

(With 3 figures in the text)

It is reported that in certain features the form of the vomer is significantly different in Caenophidia than in Henophidia (except acrochordids). In Henophidia the vomer typically has one or a few apertures for the exit of the vomeronasal nerve from the bony surround of the vomeronasal organ, well- or moderately-developed vertical and horizontal (palatal) posterior laminae, and only a partially-developed cup-like enclosure for the vomeronasal organ. In Caenophidia the vomer typically has very many tiny foramina for the passage of the vomeronasal nerve, the horizontal posterior lamina in particular is much reduced or absent, and the vomer forms a globular enclosure for the vomeronasal organ. A comparison with the vomer in lizards suggests that the henophidian type of vomer is primitive within snakes and the caenophidian type is derived. Scolecophidia are not discussed. The vomer in acrochordids closely resembles that of Caenophidia, and this form of vomerine morphology is proposed as a synapomorphy indicating the strict monophyly of the group acrochordids-Caenophidia. The acrochordids have been treated very differently by various snake taxonomists and their phyletic position has always been highly problematical. The synapomorphy proposed herein contributes to a solution of this problem.

Contents

Introduction

The purpose of this paper is to report an observation of systematic interest arising from a recent survey of the form of the septomaxillae and vomers in snakes.

Prepared skulls of most henophidian genera, a representative selection of Caenophidia, and the acrochordids *Acrochordus* and *Chersydrus* (Wart snakes), have been examined (see Appendix for list of taxa). In several cases the bones of the snout, including the septomaxillae and vomers, have been disarticulated. In a few species, microscopic transverse sections have been examined to confirm results obtained by gross dissection.

The taxa Henophidia and Caenophidia used herein are defined by Underwood (1967). In very general terms, the Henophidia are "lower snakes", and include species retaining primitive (lizard-like) features such as the presence of premaxillary teeth, pelvic elements, a coronoid bone, a large left lung with two pulmonary arteries, and two carotid arteries (not

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all these features are present in all Henophidia). The Caenophidia are "higher snakes", distinguished by the presence of derived states of the above and other characters, involving the costal cartilages (Hardaway & Williams, 1976; Persky, Smith & Williams, 1976), jaw and throat musculature (Groombridge, in press *a*), and other features (Underwood, 1967).

The Caenophidia is very probably a strictly monophyletic group (*sensu* Hennig, 1966). The Henophidia equally probably is not, since the included forms are grouped largely by presence of primitive snake features, not by synapomorphies, such as distinguish the Caenophidia. In Hennig's approach to phyletic analysis, a synapomorphy is a feature shared exclusively by a particular group of taxa, that is hypothesised to have arisen in the most recent common ancestor of the group, and to be derived (advanced or apomorphous) in relation to the ancestral condition. Such a group, comprising all lines of descent from a common ancestor, distinguished by an apomorphous feature (or further modifications thereof), is strictly monophyletic. Hennig's approach is frequently termed "cladistic", because primary attention is given to the cladistic parameter of phylogeny, pertaining to the branching sequence of lineages.

The phyletic position of the Acrochordidae has been a persistent problem for snake systematists; in two recent accounts they have been treated either as a tribe within the natricine group of higher snakes (Dowling, 1975), or as isolated derivatives of a very primitive snake stock, at superfamily level (McDowell, 1975). Underwood (1967), although assigning the Acrochordidae to the Henophidia, noted the possibility that the group may be cladistically intermediate between the Henophidia and Caenophidia.

FIG. 1. The vomer in certain Henophidia and a lizard. Anterior is to the right in all figures, scale-lines represent 1 mm.

A, right lateral view of skull of *Cylindrophis rufus*. B, area enclosed within rectangle in A, slightly enlarged, after removal of prefrontal (p) and maxilla (m) to expose elements of the snout complex; the vomeronasal organ (Jacobson's organ) is enclosed between the septomaxilla (smx) and vomer (vom), the bony enclosure has openings ventrally (fv) for passage of the duct of Jacobson's organ to the superficial palate, and posteriorly for exit of the vomeronasal nerve bundles (vn); in *C. rufus* there is one foramen in the septomaxilla and one in the vomer, for the vomeronasal nerve. C, right septomaxilla of *C. rufus*, removed from articulation with the vomer (Fig. 1D, E) and turned to expose ventral surface, showing excavation (j) for the dorsal portion of the vomeronasal organ, and internal opening of aperture (fn) for a vomeronasal nerve bundle. D, E, right vomer of *C. rufus* in lateral (D) and dorsal (E) views; showing excavation (j) for the vomeronasal organ with weakly-developed cup-like enclosure (x) formed by the vomer, and short canal (in dashed lines) with its external foramen (fn) for passage of a vomeronasal nerve bundle. F, G, right vomer of *Python recticulatus* in lateral (F) and dorsal (G) views, showing well-developed vertical (v) and horizontal (h) posterior laminae. H, I, similar views of *Tropidophis haetianus*. J, K, *Xenopeltis unicolor*. L. M, *Boa constrictor*, note that in this specimen the vomeronasal nerve is not completely enclosed by the vomer; the approximate planes of section in Fig. 3A, B are shown. N, O, *Iguana iguana*, to show a typical lizard vomer; note that the vomer does not enclose the vomeronasal nerve, there is a fairly weak excavation for the vomeronasal organ—and thus no cup-like enclosure, and the vomer forms a relatively simple elongate horizontal plate.

Overall, the henophidian vomer is characterised by presence of: one or two apertures for exit of the vomeronasal nerve, weak or moderately-developed cup-like enclosure of the vomeronasal organ, moderately or well-developed posterior laminae. *Key to abbreviations:*—f, frontal; fn, foramen (or foramina) for vomeronasal nerve; fp, foramen for branch of palatine ramus of facial nerve; fv, opening for duct of Jacobson's organ (fenestra vomeronasalis externa), complete fenestra shown in Fig. 1B only, the fenestra is completed laterally by the septomaxilla in snakes but by the maxilla in lizards; h, horizontal (palatal) posterior lamina; j, excavation for Jacobson's organ; m, maxilla; n, nasal; p, prefrontal; pm, premaxilla; pr, parasphenoid rostrum; smx, septomaxilla; v, vertical posterior lamina; vn, vomeronasal nerve bundles; vom, vomer; x, cup-like enclosure of Jacobson's organ.

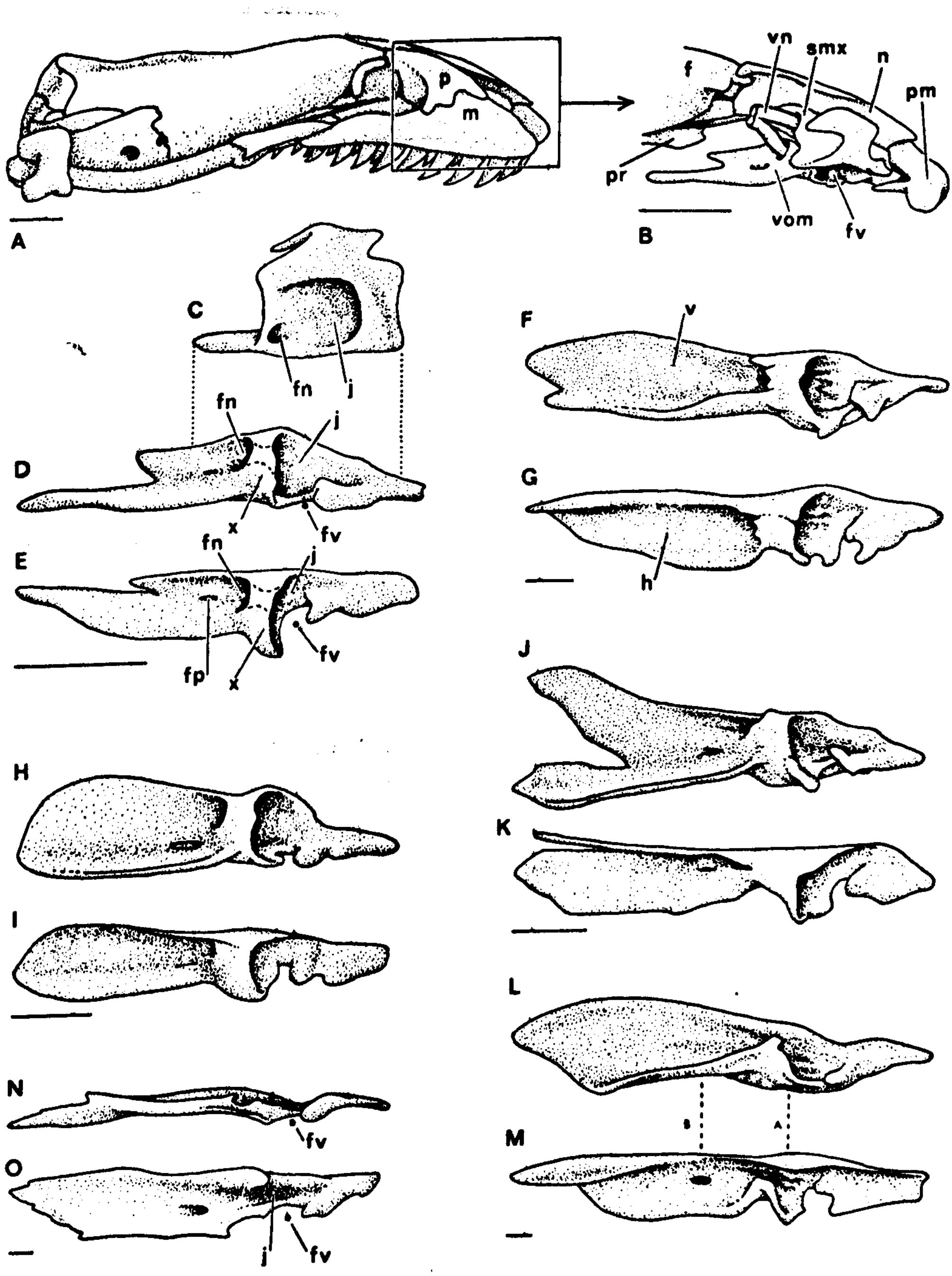
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FIG. 1.

During the present study it has emerged that the vomer has a significantly different form in Caenophidia as compared with Henophidia (except acrochordids), it is remarkably constant in form within each of these groups with respect to the features noted below, and the vomer in acrochordids closely resembles that of Caenophidia. Attention is given herein to the latter observation, which is relevant to a hypothesis of the cladistic position of the Acrochordidae.

The present paper is concerned only with a restricted aspect of snout morphology. Further information on the relations of the vomer to other elements of the snout may be found in such works as, Albright & Nelson (1959), Bellairs (1949, 1969), Frazzetta (1959), and Rieppel (1977, 1978). Quite possibly some of the differences in the form of the vomer are correlated with differing modes of snout kinesis and patterns of articulation between the bones of the snout and the frontals (Frazzetta, 1959, 1966, 1970; Rieppel, 1978; Underwood, 1967); these aspects are beyond the scope of this report.

The vomer in Henophidia and Caenophidia

As in Squamata generally, the highly-developed vomeronasal organ (Jacobson's organ) is enclosed to a greater or lesser extent by two dermal bones, the septomaxilla antero-dorsally, and the vomer postero-ventrally. There are openings in this bony enclosure, ventrally for passage of the duct of Jacobson's organ (opening onto the palate), and posteriorly for the passage of the vomeronasal nerve bundles (to the accessory olfactory bulb of the forebrain).

The intention in this section is to establish the essential features of the vomer in Henophidia (except acrochordids), Caenophidia, and the Acrochordidae.

The following features are characteristic of Henophidia (Figs 1, 3A, 3B):

(1) The exit of the vomeronasal nerve from the bony capsule of the vomeronasal organ is visible externally as one, two or rarely three, apertures. Frequently, a major aperture is found in the posterior line of contact of the septomaxilla and vomer; a distinct notch is then present in the septomaxilla or vomer, or in both bones. Alternatively, there may be separate foramina in each bone (e.g. *Anilius*, *Loxocemus*, *Cylindrophis*, one aperture in the septomaxilla and one in the vomer), or foramina are restricted to the vomer (e.g. *Python*, *Trachyboa*, one aperture in the vomer). Occasionally (e.g. *Eryx*) the one or two apertures visible externally are partially subdivided internally into a few separate channels or foramina by thin struts of bone. Postero-ventral to the vomeronasal nerve foramen the vomer frequently bears another small foramen, presumably for passage of a branch of the palatine ramus of the facial nerve.

(2) The vertical and usually also the horizontal (palatal) laminae of the posterior portion of the vomer are well-developed (although reduced in the short-snouted burrowing forms, *Calabaria* and the erycines).

(3) The vomer forms only a partially-developed globular enclosure for the vomeronasal organ.

The following features are characteristic of Caenophidia (Figs 2, 3C):

(1) The exit of the vomeronasal nerve is visible externally as a cluster of many or very many small foramina (resembling the lid of a pepper-pot), almost always within the vomer alone.

(2) The horizontal posterior lamina of the vomer is typically absent, but occasionally present although much reduced. The vertical lamina is frequently perforated by a foramen

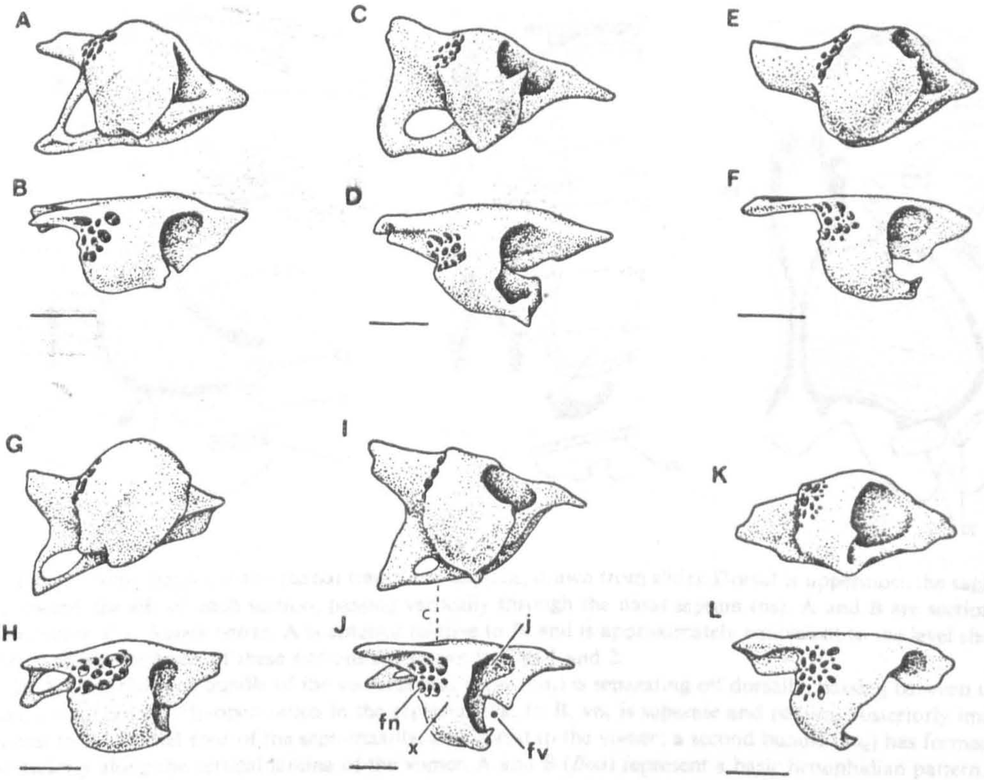

FIG. 2. The vomer in representative Caenophidia and Acrophordidae. Anterior is to the right in all figures scale-lines indicate 1 mm. Relevant features are labelled in I and J, and approximate plane of section illustrated in Fig. 3C is shown by the dashed line (nb. different species are figured, the line is indicated here for orientation only). Abbreviations as in Fig. 1.

A, B, right vomer of *Pseudoboa neuwiedii* in lateral (A) and dorsal (B) views. C, D, similar views of *Macropisthodon plumbicolor*. E, F, *Causus rhombeatus*. G, H, *Oligodon cyclurus*. I, J, *Coluber viridiflavus*. K, L, an acrochordid, *Chersydrus granulatus*.

Features characteristic of Caenophidia and Acrochordidae are presence of: multiple small foramina for exit of the vomeronasal nerve, moderate (acrochordids) or well-developed globular enclosure for the vomeronasal organ, reduced posterior laminae.

or is emarginated posteriorly (in the latter case the posterior portion of the vomer is reduced to two processes of bone arising from the globular main body of the vomer). (3) The vomer forms a well-developed globular capsule, completed by the septomaxilla antero-dorsally, around the vomeronasal organ.

Although occasionally one or another of these features may not be found in a given species of either group, each category remains distinctive overall, and it was found possible to identify any isolated vomer as either henophidian or caenophidian in origin. There is some variation within each category in features of the vomer not considered here, more so in Henophidia than in Caenophidia.

The observation prompting this report is that the vomer in Acrochordidae differs significantly from that of all other henophidians examined, but closely resembles that of Caenophidia in respect of the features noted above. The vomer in acrochordids (Fig.

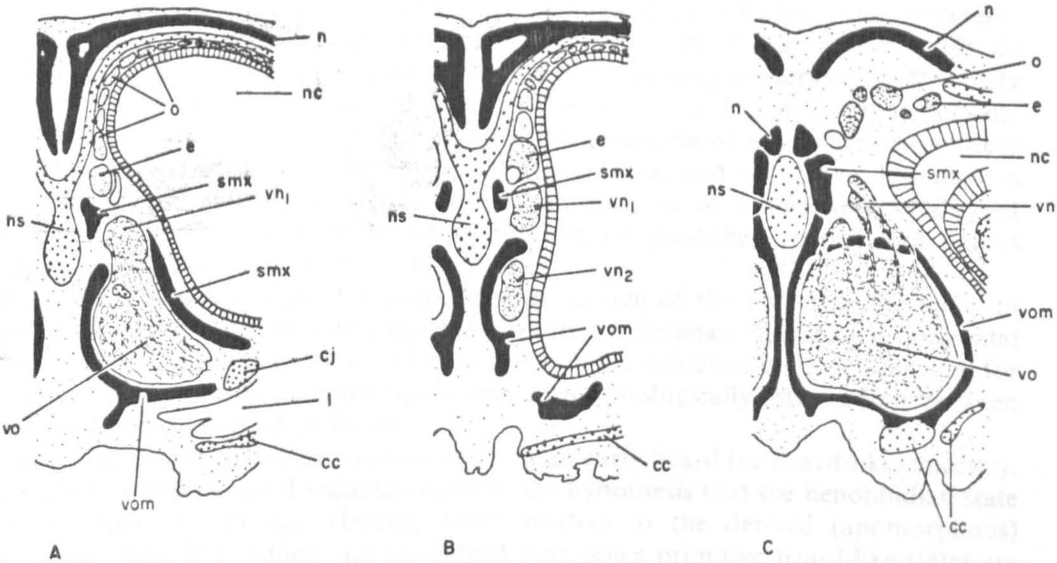

FIG. 3. Semi-diagrammatic partial transverse sections, drawn from slides. Dorsal is uppermost, the sagittal plane is toward the left of each section, passing vertically through the nasal septum (ns). A and B are sections of *Boa constrictor*, C is *Natrix natrix*. A is anterior relative to B, and is approximately equivalent to the level shown in C; the approximate levels of these sections are shown in Figs 1 and 2.

In A, note that one bundle of the vomeronasal nerve (vn_1) is separating off dorsally, passing between the vomer and a wide posteriorly-open notch in the septomaxilla. In B, vn_1 is separate and passing posteriorly immediately lateral to the medial spur of the septomaxilla, and dorsal to the vomer; a second bundle (vn_2) has formed, passing posteriorly along the vertical lamina of the vomer. A and B (*Boa*) represent a basic henophidian pattern.

In C (*Natrix*), note that several bundles of the vomeronasal nerve (vn) are passing postero-dorsally through multiple perforations in the extensive globular enclosure of the vomeronasal organ formed by the vomer (only a few of the perforations can show up in any one transverse section).

Abbreviations: cc, choanal cartilage (ecto- and hypochoanal components shown in C); cj, cartilage of Jacobson's organ; e, ethmoidal (nasal) branch of ophthalmic nerve; l, lachrymal duct; n, nasal bone; nc, nasal cavity; ns, nasal septum; o, olfactory nerve; smx, septomaxilla; vn (vn_1, vn_2), branches of vomeronasal nerve; vo, vomeronasal (Jacobson's) organ; vom, vomer.

2K, L) differs from that of Caenophidia chiefly in the somewhat lesser development of the globular enclosure of the vomeronasal organ, but a very striking resemblance to Caenophidia, found in no other henophidians, is in the emergence of the vomeronasal nerve from the vomerine cup via a cluster of very many tiny foramina. Hoffstetter & Gayrard (1965: 683) have already noted that the vomer in *Acrochordus* "evoquent surtout ceux des Colubroides (= Caenophidia) par leurs proportions", but they did not discuss the detailed similarity and supported the assignment of the Acrochordidae to the Henophidia.

A cladistic interpretation of the form of the vomer

A comparison of the two states of the form of the vomer defined above (henophidian type, caenophidian type) with the vomer in lizards makes it possible to suggest the primitive-to-derived polarity of these states.

In lizards (Fig. 1N, O) the vomeronasal nerve typically emerges from the bony surround of the vomeronasal organ by a wide opening bordered by both the septomaxilla and vomer. The vomer itself forms a relatively thin and elongate plate, horizontally orientated and very widely exposed in the palate, with a depression and a notch antero-laterally marking the position of the vomeronasal organ and its palatal duct. It may bear virtually no trace of the course of the vomeronasal nerve (the nerve passing posteriorly immediately dorsal to the vomer), it may bear a distinct groove, or (as in *Varanus*) it may partially enclose the nerve in a deep channel. The vomer forms much less of a cup-shaped enclosure for the vomeronasal organ than is the case in Henophidia, and very much less than in Caenophidia. These statements are based on examination of a relatively small, but taxonomically diverse, sample of lizard skulls, and on published reports and figures (notably Bellairs, 1949, 1950; Oelrich, 1956).

In having only one or a few foramina for the passage of the vomeronasal nerve, in typically having well- or moderately-developed posterior laminae (including a horizontal portion well-exposed in the palate), and in forming only a moderate cup-like surround for the vomeronasal organ, the henophidian vomer is morphologically intermediate between the lizard and the caenophidian forms.

If it is accepted that snakes are descended from an early lizard (or lizard-like) ancestry, then the above morphological sequence leads to the hypothesis that the henophidian state is primitive (plesiomorphous; Hennig, 1966) relative to the derived (apomorphous) caenophidian state. It is widely acknowledged that other primitive lizard-like states are retained by various henophidian taxa (noted in Introduction), whereas all Caenophidia show derived states of these and other characters.

The only major group of snakes not examined in this study is the Scolecophidia. These snakes appear aberrant in many respects, and the bones of the snout are highly modified (presumably associated with subterranean habits and diet of small invertebrates). Scolecophidia appear primitive to all other extant snakes in several characters (lack of mediun processes of the frontals partly or entirely separating the olfactory tracts; undivided trigeminal foramen; lack of toothed anterior ramus of the palatine; possession of a throat muscle probably homologous to a lateral portion of the *M. genioglossus* inserting on the buccal floor, as is found in diverse lizards, Groombridge, in press *b*). The combination of aberrant and primitive states in Scolecophidia suggests that they form an isolated line of descent from an archaic snake stock. The view is taken here that conditions within Scolecophidia do not affect the hypothesis that the caenophidian vomer is derived relative to that of Henophidia. Haas (1964: 20; 1968: 79) has reported that in anomalepidid Scolecophidia the vomeronasal nerve passes through the septomaxilla. The relevant portions of the skull of the Late Cretaceous fossil snake *Dinilysia* (Estes, Frazzetta & Williams, 1970) are too poorly-preserved to allow comparison.

Conclusions

The essential point of this report is that the Acrochordidae and Caenophidia are seen to uniquely share a derived state, the caenophidian-type vomer. An initial hypothesis is that this state constitutes a synapomorphy (see Introduction) indicating the strict monophyly of the group Acrochordidae plus Caenophidia.

As discussed more fully elsewhere (Groombridge, in prep.), the hypothesis of acrochordid-Caenophidia monophyly is supported by other evidence (insertion of the *M. intermandibularis anterior, pars anterior*, Groombridge, in press *a*; vertebral morphology, Rage, 1978; also shared derived states of the hyoid, hemipenis, and septomaxilla-frontal relationship), but is not contradicted by any other significant evidence susceptible to cladistic interpretation.

The optimum taxonomic assignment of the acrochordids may remain for future discussion; however, it should be noted that if the hypothesis of acrochordid-Caenophidia monophyly is adopted it would be clearly inappropriate on cladistic grounds to retain the acrochordids within the Henophidia (assuming the latter taxon is to be recognised at all). The fact that acrochordids possess several primitive states characteristic of Henophidia (Underwood, 1967: 63, 66–67; Hardaway & Williams, 1976: 385) is irrelevant to the problem of finding the nearest relatives of the Acrochordidae, since such states only indicate that acrochordids retain a predominantly henophidian grade of organisation, they do not indicate which particular group acrochordids are monophyletic with.

My thanks are due to Miss A. G. C. Grandison, Dr E. N. Arnold, and Dr G. Underwood, for critically reading a first version of this report. I am grateful to Miss Grandison (Curator of Amphibians and Reptiles at the British Museum, Nat. Hist.) also for allowing access to specimens in her care. I am indebted to Dr A. d'A. Bellairs for giving me advice and access to his slide collection.

Appendix

List of species examined

Achalinus braconnieri, Acranthophis dumerili, Acrochordus javanicus, Aipysurus duboisii, Alsophis sp., *Anilius scytale, Azemiops feae, Boa constrictor, Boiga ocellata, Bolyeria multocarinata, Bothrochilus boa, Bungarus fasciatus, Calabaria reinhardtii, Candoia carinata, Casarea dussumieri, Cerberus rhynchops, Charina bottae, Chersydrus granulatus, Chondropython viridis, Coluber viridiflavus, Corallus enydris, Demansia* sp., *Dispholidus typus, Dryocalamus davisonii, Elaphe flavolineata, Elaphe taeniurus, Eryx jayakari, Eryx johnii, Eunectes murinus, Lapemis hardwickii, Laticauda colubrina, Leimadophis poecilogyrus, Leptodeira annulata, Liasis amethistinus, Lichanura roseofusca, Loxocemus bicolor, Macrophistodon plumbicolor, Morelia argus, Naja naja, Natrix natrix, Natrix tessellata, Oligodon cyclurus, Pareas monticola, Psammodynastes pulverulentus, Pseudoboa neuweidii, Python regius, Sanzinia madagascariensis, Sibon nebulatus, Stoliczkaia borneensis, Telescopus dhara, Trachyboa boulengeri, Trimorphodon biscutatus, Tropidophis haetianus, Tropidophis taczanowskii, Uropeltis brevis, Vipera berus, Xenelaphis hexagonatus, Xenopeltis unicolor.*

Although most of these species were presented by a single specimen, three specimens of each of the two acrochordid species were examined.

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Note added in press:

McDowell (1979) has recently described a new acrochordid species and no longer recognizes the genus *Chersydrus* (thus the group now contains three species, all assigned to the genus *Acrochordus*). McDowell also reiterates (1979: 71) his earlier (1975) proposals concerning the phyletic position of acrochordids, however, I see no evidence requiring modification of the conclusion of the present paper, that acrochordids and Caenophidia form a monophyletic group. Rieppel (in press) has already countered a major component of McDowell's argument. It is intended to discuss the problem at greater length elsewhere (in preparation).

McDowell, S. B. (1979). A catalogue of the snakes of New Guinea and the Solomons, with special reference to those in the Bernice P. Bishop Museum. Part 3, Boinae and Acrochordoidea (Reptilia, Serpentes). *J. Herpet.* **13**: 1–92.

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Variations in morphology of the superficial palate of henophidian snakes and some possible systematic implications

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Introduction

During a present study of relationships among viperine snakes, some variation was noted in the gross morphology of the superficial palate. Originally in an attempt to distinguish primitive and derived character states within viperines, a survey was made of some aspects of the superficial palate of many species from several snake families. Part of this survey is reported here, with the purpose of establishing the potential value of palatal characters in the discovery of supra-specific groupings.

Attention is here primarily confined to henophidian snakes (Underwood 1967), where the palate of nearly all genera and many species has been examined, and where the systematics of the group has been previously well-studied (McDowell 1975, Underwood 1967, 1976). A basis is thus available on which to evaluate the significance of palatal characters. Scolecophidia have not been examined in this survey. Only a small, but taxonomically diverse, sample of caenophidian snakes has been examined to date. Some brief comments on this group are given.

Recent studies on the morphology of the snout of snakes (and other reptiles) have been made by Bellairs (1949), and Bellairs and Boyd (1950, 1957). A review is provided by Parsons (1970). A useful work that includes figures and reference to the palate (including Scolecophidia) is that of McDowell (1972). Other works that incidentally give some information on the palate of various snakes include; Frazzetta (1966), Gans (1952), and Haas (1959, 1968).

Materials and methods

All specimens examined are in the collection of the British Museum (Natural History), they are listed in the appendix. Most specimens are unsuitable for direct examination of the palate since the mouth is typically firmly shut and the jaw adductors fixed in this position. Many specimens have been utilized in which a previous worker has forced the jaws fully open, presumably in order to examine the teeth. In several other cases the palate has been exposed to ventral view by spreading the mandibles laterally after reflecting the skin of the lower jaw, and making a dissection of the lower jaw muscles. Some points of interest emerged from these dissections and are reported elsewhere (Groombridge 1979). In other specimens the jaws have simply been opened as far as possible without causing damage to the specimen.

When interest is concentrated on only a few millimetres of soft tissue, it is clearly necessary to be aware of the possible effects of differential preservation and of intra-specific variation. An attempt was made, within the limits of time and material available, to counter these problems by the examination of several specimens of one species whenever possible. Apart from a few exceptions, noted below, the amount of intra-specific variation encountered was small.

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Basic morphology of the superficial palate

The superficial palate comprises the expanse of soft tissue lying between the bony palate and the oral cavity (Bellairs 1949, p. 117).

The *vomerine cushion*, a median pad of soft tissue lying superficial to the vomers, forms much of the superficial palate of snakes (fig. 1). Anteriorly is a median ridge termed the *vomerine raphe* in snakes by McDowell (1972) after Oelrich (1956). The weaker posterior section of this ridge separates the two palatal openings of the paired ducts of Jacobson's organ. There is typically a distinct constriction between this part of the ridge and the more anterior section mostly lying superficial to the premaxilla. The vomerine cushion and the vomers themselves are derived during ontogeny from the vomerine process, a postero-median extension of the frontonasal process of the embryonic face. In early ontogeny the frontonasal process and its vomerine extension is separated by a cleft on each side from the encroaching palatine extension of each maxillary process (Bellairs and Boyd 1957, fig. 7 B). In most lizards extensive fusion between these processes occurs on each side anteriorly and continues posteriorly to just behind the ducts of Jacobson's organ. More posteriorly, fusion occurs dorsally only, leaving much of the primitive choana intact to form the choanal groove of adult anatomy. By contrast, in snakes this extensive fusion is continued posteriorly much further, thus extending the surface of the superficial palate. No well-developed choanal grooves remain. Insofar as the precise margins of the vomerine cushion of snakes are obscured in adult anatomy, due to the absence posteriorly of choanal grooves, it is sometimes convenient to refer broadly to the general surface of the superficial palate between the palatine bones as the *palatal surface*.

In most snakes the palatal surface is continued posteriorly as a horizontal lamina for a variable distance beyond the median nasal septum, thus forming the floor of a common nasopharyngeal duct. This posterior portion is termed the *palatal velum* by McDowell (1972, p. 249), and would constitute a type of soft secondary palate to the extent that the definitive choana is posterior to the posterior end of the primitive choana, and thus encompasses a portion of the original oral cavity. This cannot be established by examination of adult anatomy, and interpretation of embryonic material has been debated in the literature; Parsons (1959, 1970) follows Fuchs (1908, 1911) in suggesting that the palate in snakes is an extended primary palate.

It will be necessary to refer below to the posterior-most margin of the palatal surface (irrespective of whether a palatal velum is formed) and its postero-lateral confluence with the side walls of the orbitonasal trough; this is here termed the *choanal arc*.

It seems unlikely that the grooves immediately flanking the anterior part of the vomerine raphe in snakes are homologues of the choanal grooves of lizards, contrary to the suggestion of McDowell (1972, p. 246 and fig. 20), since in the cleft palate specimens figured by Bellairs and Boyd (1957, plate 1) these grooves are still present medial to the cleft entirely within the area of frontonasal derivatives. By the same argument it seems unlikely that the fleshy ridges enclosing these grooves laterally are homologues of the choanal folds of lizards, although their weaker posterior extensions may be. These ridges largely conceal the openings of the ducts of Jacobson's organ in ventral view. They then diverge, diminishing posteriorly where variably developed longitudinal folds and creases may be present lateral to the vomerine cushion, and continue, joining with the lateral extremities of the choanal arc, onto the side walls of the orbitonasal trough.

Much of the postero-lateral portions of the palatal surface, including the choanal arc and the lateral ridges in this region, are supported internally by the ectochoanal cartilages (see McDowell 1972, pp. 248–249, for discussion of the ecto- and hypochoanal cartilages in snakes), and are thus probably homologous to the choanal folds of lizards.

Henophidia: Observations

It has been found that the variation in superficial palate morphology among the sample of Henophidia examined can be partitioned quite clearly into eight categories or character states. Descriptions and figures are given in terms of these character states, lettered A to H, rather than within a particular classification. It is intended to relate these states below to other taxonomic characters and to previous systematic proposals. Reference to the figure of a representative species, and the names of the genera included, precede the description of each character state. Reference to the genus of the selected representative species, for comparative purposes, should be understood to include all associated genera unless stated otherwise.

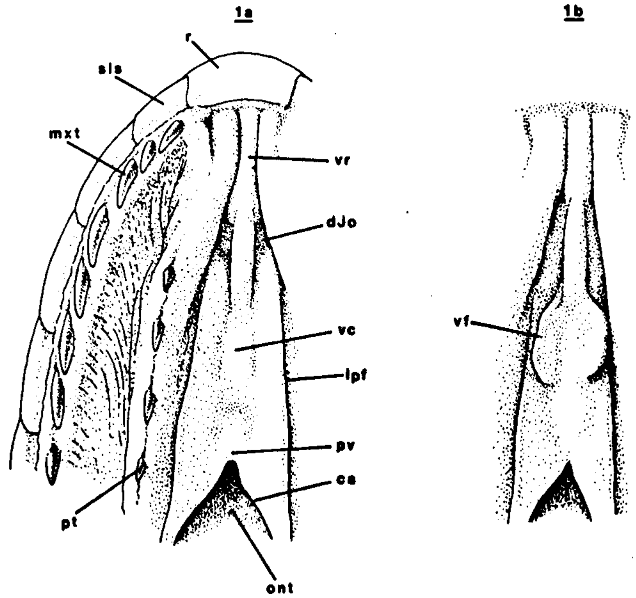

FIG. 1. *Cylindrophis maculatus*. In this and subsequent figures, the area illustrated is the anterior part of the roof of the mouth, showing the region of the superficial palate discussed in the text. Only the median, or median and righthand, portions are shown. In (*a*), some basic features of the snake palate are indicated. The internal choanae open dorsal to the palatal velum (*pv*), into the deep orbitonasal trough (*ont*). The maximum extent of the vomerine flaps (*vf*) found in group A is shown in (*b*). In most individuals of this group, the vomerine flaps are absent, as in (*a*), or weakly indicated.

Abbreviations (for all figures): *ca*, choanal arc; *cc*, choanal cleft; *cn*, posterior part of concha; *cp*, choanal papilla; *ct*, choanal tongue; *dJo*, duct of Jacobson's organ; *ec*, ectochoanal cartilage; *fJo*, fenestra for passage of duct of Jacobson's organ; *gl*, glottis; *lpf*, lateral palatal fold; *mxt*, maxillary tooth; *ont*, orbitonasal trough; *ots*, opening of tongue sheath; *pl*, lobe of palatal surface; *pmx*, premaxilla; *pmt*, premaxillary tooth; *pt*, palatine tooth; *pv*, palatal velum; *r*, rostral scale; *sls*, supralabial scale; *smx*, septomaxilla; *tt*, tongue tip; *vc*, vomerine cusion; *vf*, vomerine flaps; *vom*, vomer; *vr*, vomerine raphe.

STATE A: *Cylindrophis maculatus*, fig. 1

(*Anomochilus*, *Cylindrophis*, *Xenopeltis*, uropeltids:- *Melanophidium*, *Platyplectrurus*, *Plectrurus*, *Pseudotyphlops*, *Rhinophis*.)

Certain additional features can be distinguished besides those common to most snakes, as discussed above. In *Cylindrophis* and *Xenopeltis* a pair of folds arise a short distance postero-lateral to the proximal end of the vomerine raphe. These folds continue posteriorly, where they are most clearly defined, before fading out on the side walls of the orbitonasal trough. The free edges of these folds, where clearly defined, are directed laterally and thereby enclose dorsally a pair of medially directed grooves. These folds may be termed *lateral palatal folds*, and appear to lie superficial to, rather than themselves constituting, the region corresponding to the choanal folds of lizards. They are weakly developed or absent in uropeltids and *Anomochilus*.

In many individuals of the *Cylindrophis* species examined and in many uropeltids, a more medial and much shorter pair of folds are also present, superficial to the vomers. These vary in degree of development from virtual absence, to a simple longitudinal crease, to a more well-defined flap with a rounded free lateral margin. The latter extreme, seen in a minority of *Cylindrophis* specimens only, and intraspecifically variable, is shown in fig. 1 (*b*). Similar structures in *Loxocemus* were called *vomerine flaps* by McDowell (1972, p. 246). This term is retained here to avoid additional names, but with the reservation that the structures in this group form a series from 'creases' to 'flaps'. One specimen of *Xenopeltis* examined had an irregular fold on one side only.

The fact that the taxa grouped here are quite diverse in respect of certain other characters, but share a basically similar, relatively simple, type of superficial palate, suggests that this palatal morphology may be primitive among Henophidia. This is supported by the presence of probable primitive states of some characters in these taxa and in *Anilius*, and of derived states of these and other characters in other Henophidia. This matter is pursued further in the discussion section below. Among the probable primitive states (not known for *Anomochilus*), are presence of a distinct *levator anguli oris; adductor externus medialis* and *profundus* partly bipinnate and (except *Xenopeltis*) divided by tendinous aponeuroses (Haas 1955, 1973); squamosal immobile and incorporated in braincase (except uropeltids, squamosal absent or fused; and *Xenopeltis*, squamosal partly free of braincase posteriorly but still immobile); quadrate short and concave posteriorly; ascending process of maxilla present, firmly contacting prefrontal (except *Xenopeltis*).

STATE B: *Anilius scytale* only, fig. 2

A pair of lateral folds are found in about the same position as the lateral palatal folds of *Cylindrophis*. However, these are typically better developed and, presumably depending on circumstances of preservation, the free margin may be variously directed medially or ventro-laterally.

The posterior part of the palatal surface is extended and turned dorsally into the orbitonasal trough, and is deeply bilobed. The lateral margins of these lobes, which are extensively free posteriorly, are variably continuous with weak folds that appear to arise anteriorly in about the same position as the vomerine flaps of *Cylindrophis* (the resemblance is increased in some specimens by a distinct expansion of the folds at this point). In all specimens, the posterior lobes approach the transverse plane and appear to entirely block the internal choanae unless pulled aside manually, or,

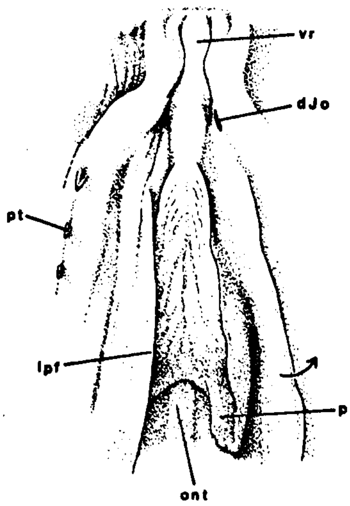

FIG. 2. *Anilius scytale*. The lateral palatal fold (*lpf*) of the animal's left has been pulled aside to show the palatal surface turned dorsally into the orbitonasal trough (*ont*). Also revealed is one of the two lobes (*p.l.*) closing off the internal choanae. Complete list of abbreviations under fig. 1.

presumably, by the inspiration of air. It is difficult to suggest the functional significance of these 'valves'. Possibly they prevent debris being pushed into the nasal passages from the mouth during the taking of prey within the confines of a burrow. This does not seem too convincing bearing in mind the absence of such structures from other burrowers (*Cylindrophis*, uropeltids, *Calabaria*, *Atractaspis*). Perhaps there is a connection with the partially aquatic habits of *Anilius* (Gans 1975, p. 96, McDowell 1972, p. 263). Despite the unusual structure of parts of the superficial palate of *Anilius*, it is otherwise similar to that of *Cylindrophis*, and is most reasonably derived from that kind of morphology.

STATE C: *Python sebae*, fig. 3

(*Loxocemus*, *Aspidites*, *Chondropython*, *Liasis*, *Morelia*, *Python*)

Characteristic of the group is the consistent presence of well developed vomerine flaps. Anteriorly they are variably confluent with the proximal end of the vomerine raphe. Well-developed lateral palatal folds are present and enclose a distinct medially-directed groove or pocket postero-lateral to the vomerine flaps. Medially and posterior to the vomerine flaps the palatal surface frequently (e.g. *Python*, *Chondropython*) bears several irregular ridges, converging from the posterior ends of the vomerine flaps, toward the mid-point of the choanal arc. In most Asiatic and Australasian pythons examined, this point, or the posterior edge of the nasal septum dorsal to the palatal surface, bears a small more or less bifurcate papilla (fig. 3 (*c*), (*d*)). The precise form of this structure is quite variable intra-specifically, and its apparent absence from African *Python* may well be an artefact of small sample size. This structure may be termed the *choanal papilla*.

As in other snakes much of the palatal surface is supported internally by the ectochoanal cartilages, which are here closely adjacent in the mid-line nearly up to the posterior tip of the vomers, (fig. 3 (*b*)) before diverging postero-laterally and

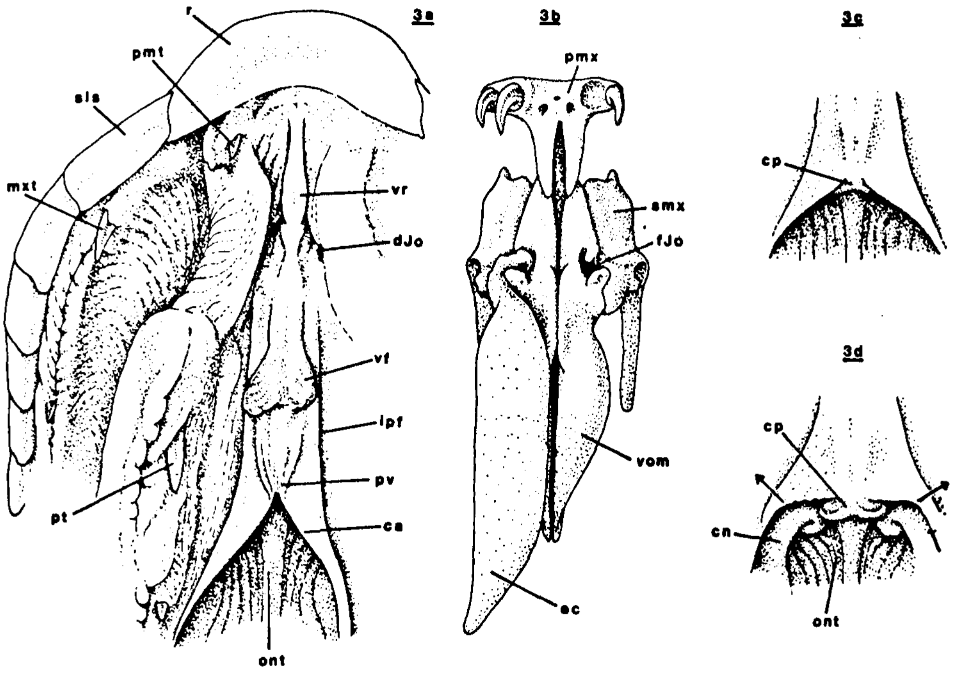

FIG. 3 (*a*, *b*). *Python sebae*; (*c*, *d*). *Aspidites melanocephalus*. In (*a*), note the well-developed vomerine flaps (*vf*), also the irregularities of the palatal surface running posteriorly from the flaps toward the midpoint of the choanal arc (*ca*). In (*b*) the bones of the snout complex (in ventral view) and the ectochoanal cartilage (*ec*) of the animals' right are shown, the medial margin of the latter is near the midline until the posterior tip of the vomers (*vom*). The choanal papilla (*cp*) is shown in (*c*) and (*d*), in (*d*) the choanal arc is pulled aside to fully reveal the papilla, note also the conchae (*cn*). Complete list of abbreviations under fig. 1.

forming the sides of the choanal arc. This feature is relevant to the following account of the different superficial palate of boas (*sensu lato*).

It is suggested that this state is derived relative to state A (*Cylindrophis*, etc.) by virtue of the constant presence of well-developed vomerine flaps, and typically, of ridges in the posterior palatal surface, and choanal papillae. The latter two features appear to foreshadow the condition of the boa palate (states D to G).

STATE D: *Bolyeria multocarinata*, fig. 4 (*a*), (*Casarea dussumieri*, fig. 4 (*b*))
(*Bolyeria*, *Casarea*)

There is a pair of vomerine flaps which appear to be probable homologues of those of *Python*: they are in a similar position relative to the palatine bones and to the openings of the ducts of Jacobson's organ. However, they are confluent posteriorly with the narrower ventro-lateral margins of a fleshy wedge of soft tissues, here termed the *choanal tongue*, that projects in the sagittal plane into the front of the orbitonasal trough. The vomerine flaps of *Bolyeria* and most other boas are thus extended posteriorly. The side walls of the orbitonasal trough appear to continue anteriorly relatively further than in *Cylindrophis* or *Python*, and, separated on each side by a short *choanal cleft* from the choanal tongue, they do not meet medially to form a continuous choanal arc.

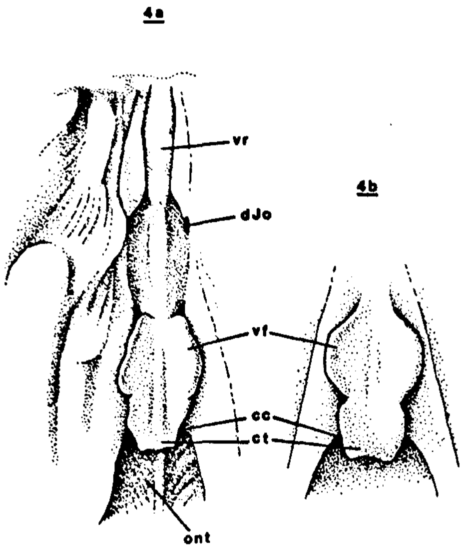

FIG. 4. (*a*). *Bolyeria multocarinata*; (*b*) *Casarea dussumieri*. Note the short choanal tongue (*ct*), short choanal cleft (*cc*) and absence of an entire choanal arc. Note also the anterior increase in width of the long vomerine flaps (*vf*). It is suggested that this wide anterior portion is homologous to the complete, but shorter, vomerine flaps of *Python*. Complete list of abbreviations under fig. 1.

In *Boa constrictor* (whose palate is basically similar to that of *Bolyeria*, except as noted below) the ectochoanal cartilages diverge from each other more anteriorly relative to the vomers and the palatines (and forming the lateral margins of the choanal cleft) than is the case in *Cylindrophis* and *Python*. It is suggested that much of the posterior palatal surface, as it exists in *Cylindrophis* and *Python*, has been disrupted in boas by the relative anterior migration of the point of divergence of the ectochoanal cartilages and thus of the palatal arc. The choanal tongue would correspond to the median irregular section of the posterior palatal surface of *Python*, that has become isolated at the front of the orbitonasal trough. The wider anterior part of the long vomerine flaps would correspond to the entire shorter vomerine flaps of *Python*. If this interpretation is correct, the anterior increase in width of the long vomerine flaps is a primitive state for boas (*s.l.*). In boas other than *Bolyeria* and *Casarea*, the flaps are equally developed or taper anteriorly; this would appear to be the more derived state. The choanal papillae of some pythons may represent a first stage in the formation of a choanal tongue, having been 'left behind' by a slightly more anterior divergence of the ectochoanal cartilages.

In *Bolyeria* the lateral palatal folds are not clearly defineable as a simple structure. *Casarea* somewhat more closely resembles *Python* in this respect.

The above considerations lead to the suggestion that *Bolyeria* and *Casarea* retain a palatal morphology structurally and cladistically intermediate between that of pythons and that of other boas. This is subject to the significant reservation that I have been able to examine the intact superficial palate of only one specimen each of *Bolyeria* and *Casarea*, both extremely rare in collections. A more general hypothesis is that the boa (*s.l.*) palate, including that of *Bolyeria* and *Casarea*, is derived relative to that of pythons. With the few exceptions (among erycine boas) noted below, all boas show an emarginated choanal arc, with the correlated presence of long vomerine flaps, and a distinct choanal tongue.

STATE E: *Boa constrictor*, fig. 5

(*Acrantophis*, *Boa*, *Candoia*, *Corallus*, *Epicrates*, *Eunectes*, *Lichanura*, *Sanzinia*.)

Much of the preceding discussion of *Bolyeria* is equally relevant to *Boa*. The major difference in this group is that the anterior parts of the long vomerine flaps are never wider than their posterior continuations, as in *Bolyeria*; in contrast, the flaps are either of approximately constant width (as in *Boa*) or more typically are tapered anteriorly. In some species the choanal tongue is bilobed posteriorly to a varying extent, particularly so, for example, in *Corallus enydris* and *Epicrates cenchria*. In some forms, e.g. *Corallus canina* and *Acrantophis*, the degree of anterior extension of the side walls of the orbitonasal trough appears to be somewhat greater than in others of this group, such that a more distinct choanal cleft is formed. The nasopharyngeal ducts are thus disrupted and the posterior sections of the nasal cavities and conchae are well-exposed when the sides of the choanal cleft are manually separated. The resemblance between this choanal cleft and the posterior section of a complete cleft palate (as described for *Eunectes* by Bellairs and Boyd 1957) is very striking. It may be suggested that since a fully cleft palate appears to result from the failure of the vomerine extension of the frontonasal process to fuse with the palatine extensions of the maxillary processes, the distinctive boa (*s.l.*)

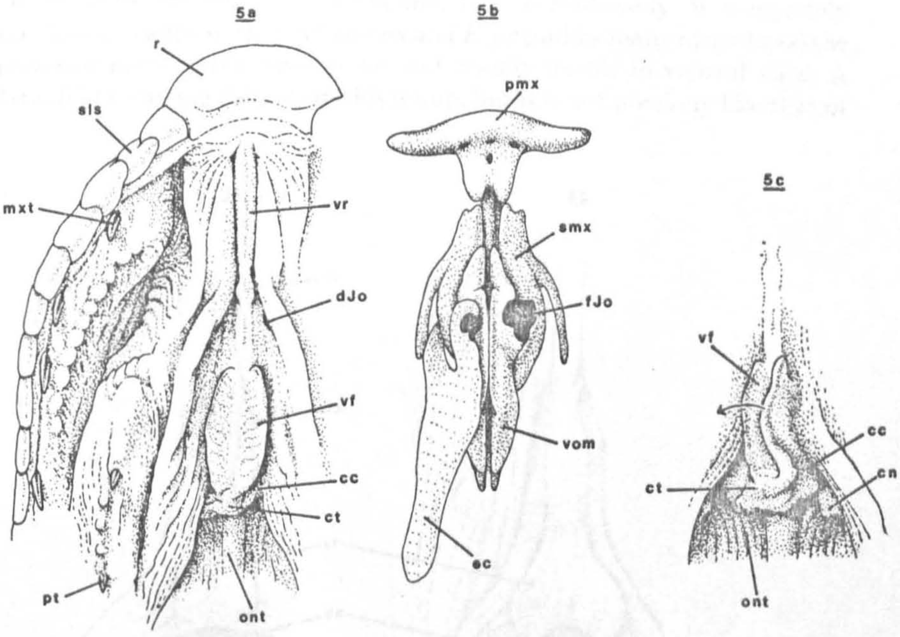

FIG. 5. *Boa constrictor*. In (*a*), note the long vomerine flaps (*vf*), that lack an anterior increase in width. In (*b*), note that the ectochoanal cartilages (*ec*), shown on the animals right, diverge from the midline considerably anterior to the tips of the vomers (*vom*); this is correlated with emargination of the choanal arc, and isolation of a distinct choanal tongue (*ct*). In (*c*), one of the vomerine flaps is pulled medially to show its full depth; the choanal clefts (*cc*) are somewhat opened to show their complete length, and the extent of the choanal tongue. Complete list of abbreviations under Fig. 1.

palatal morphology may result from the failure of fusion to occur posteriorly as compared with *Cylindrophis* and *Python*.

As in *Bolyeria*, but not *Casarea*, the lateral palatal fold is not clearly definable as a single simple structure.

As noted above, it is suggested that boas in general (including *Bolyeria*) have a palatal morphology that is derived relative to that of *Python* by virtue of the emargination of the choanal arc and the correlated presence of a choanal tongue. The *Boa* (and also the *Eryx* and *Tropidophis*) groups appear to be more derived than *Bolyeria* in respect of their palate due to the lack of an anterior increase in width of the vomerine flaps (which in *Bolyeria* is suggestive of the short vomerine flaps of *Python*).

STATE F: *Eryx jaculus*, fig. 6 (*a*), (*Calabaria reinhardti*, fig. 6 (*b*))
(*Calabaria*, *Charina*, *Eryx*.)

While *Lichanura* is quite *Boa*-like, and is here included in that group, the vomerine flaps are more distinctly tapered anteriorly than usual, and there is not such an extensive choanal tongue. These features are more conspicuously developed in the three genera included here. The anterior tapering of the vomerine flaps is accentuated and they appear relatively short (especially *Calabaria* and *Charina*). In most *Eryx* the depth of the flaps is also much reduced. The choanal tongue is shortened so that there is a tendency toward the formation of a complete choanal arc (complete in most *Eryx* and nearly so in *Calabaria*). This is accentuated by the apparent tendency for the lateral segments of the near complete choanal arc to converge more distinctly toward the midline, thus considerably or completely reducing the choanal clefts, so that in *Charina* and *Eryx* (unlike many other boas) the extreme posterior roots of the conchae are not readily visible in ventral view. A lateral palatal fold is distinguishable in this group, but it is not precisely like that of *Python*.

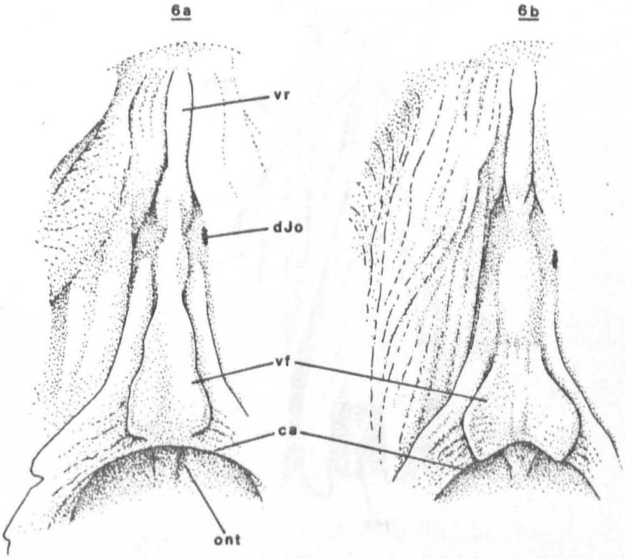

FIG 6. (*a*) *Eryx jaculus*; (*b*), *Calabaria reinhardti*. In (*a*), note the anteriorly-tapered vomerine flaps (*vf*) and the entire choanal arc (*ca*). In (*b*), note the relatively short vomerine flaps, and the almost complete choanal arc. Complete list of abbreviations under Fig. 1.

It may be significant that among those *Eryx* (*s.l.*) examined, it is *conicus* that retains the most developed vomerine flaps and choanal tongue. Rage (1972) suggests, in the course of revalidating the genus *Gongylophis* for this species, that it is primitive to other *Eryx* in respect of cranial osteology. However, this apparent palatal difference may well be obscured by the examination of more specimens.

Since the choanal arc in this group appears to be more anterior in position relative to that of *Python*, and since *Lichanura* and *Charina* form a structural series with respectively greater and lesser resemblance to *Boa*, the complete (most *Eryx*) or near-complete palatal arc found in this group is here interpreted as a secondary development from a *Boa*-like morphology by reduction of the choanal tongue. In the case of *Eryx* at least, this interpretation is supported if other characters are also considered (Underwood 1976). In the case of *Calabaria*, consideration of other characters reveals a distinct phenetic resemblance to erycines, but its cladistic position is not fully clarified and so the near complete palatal arc of *Calabaria* could conceivably have been independently derived from either a *Python*-like condition (by anterior retreat of the choanal arc, without formation of a choanal tongue) or from a *Boa*-like condition.

STATE G: *Tropidophis caymanensis*, fig. 7
(*Trachyboa*, *Tropidophis*.)

Like *Eryx*, *Trachyboa* and *Tropidophis* differ from most *Boa*-like forms and *Bolyeria* in the tapering anterior origin of the vomerine folds which are quite weakly developed. The major difference however, is that the choanal tongue is long and extensively bifurcate posteriorly. Although this condition is somewhat developed in some boas (as noted above), there is a distinct morphological gap between them and

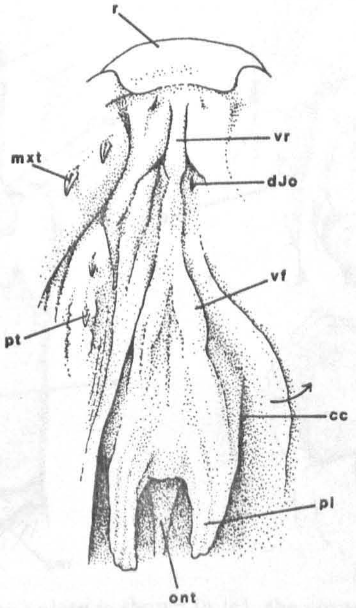

FIG. 7. *Tropidophis caymanensis*. The extent of the long choanal clefts (*cc*) is shown on the animals left, by lateral deflection of adjacent tissues. Note the long palatal surface, deeply bifurcate posteriorly, forming long lobes (*p.l.*). Complete list of abbreviations under Fig. 1.

Tropidophis. There is also some resemblance to *Anilius*, although details differ, and the forks (shorter in *Anilius*) are not turned up to cover the internal choanae.

In *Tropidophis caymanensis* (the only species dissected, but presumably so in others) the ectochoanal cartilages diverge abruptly and apparently more anteriorly than in *Boa*. Long choanal clefts are thus present as in some of the *Boa* group.

As in *Bolyeria* (not *Casarea*) and *Boa*, a lateral palatal fold is not clearly definable.

Since *Trachyboa* and *Tropidophis* differ from pythons and *Calabaria*, and resemble other boas (except *Charina* and *Eryx*) in possessing a well-developed choanal tongue projecting into the orbitonasal trough, and further resemble certain of the *Boa* group (e.g. *Corallus*) both in having a bifurcate choanal tongue and in having long choanal clefts, it is most parsimonious (considering palatal characters alone) to derive these two genera from an ancestor with a *Boa*-like palate. Possibly there is some significance in the geographical proximity of these genera and those boas they most resemble.

STATE H: *Acrochordus javanicus*, fig. 8
(*Acrochordus*, *Chersydrus*.)

The superficial palate of *Acrochordus* and *Chersydrus* is quite peculiar and apparently unique in several respects, as are so many other aspects of their anatomy, (Brongersma 1952, respiratory system, Hoffstetter and Gayrard 1965, osteology, Langebartel 1968, throat muscles, Miller 1968, cochlear duct, McDowell 1975 and Underwood 1967, general accounts).

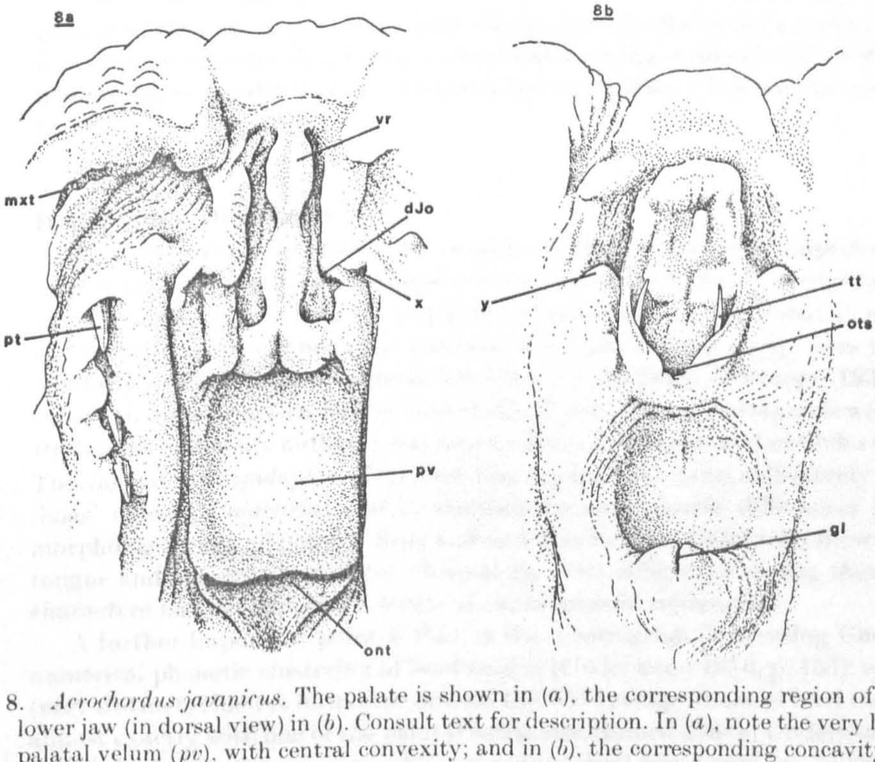

FIG. 8. *Acrochordus javanicus*. The palate is shown in (*a*), the corresponding region of the lower jaw (in dorsal view) in (*b*). Consult text for description. In (*a*), note the very long palatal velum (*pv*), with central convexity; and in (*b*), the corresponding concavity in the dorsal part of the tongue sheath, in the lower jaw. Note also the similarly corresponding pocket (*x*), and protruberance (*y*). Other abbreviations listed under fig. 1.

The grooves lateral to the vomerine raphe are typically terminated abruptly posterior to the ducts of Jacobson's organ by a pair of variably developed fleshy swellings which partly join with each other in the mid-line and with the proximal end of the vomerine raphe. Lateral to the ducts, and separated from them by a ridge of tissue, are another pair of grooves, each with a short anteriorly-directed pocket. There are a corresponding pair of prominences in the lower jaw, adjacent to the rim of the outer tongue sheath, which appear to fit into these grooves when the mouth is closed. In this position the tips of the retracted tongue are in very close proximity to the openings of the ducts of Jacobson's organ.

Posterior to the aforementioned fleshy swellings is a transverse groove from which arises the posterior part of the palatal surface. Much of this surface is posterior to the nasal septum and thus constitutes a palatal velum forming the floor of a long, dorso-ventrally compressed, common nasopharyngeal duct. This sheet of tissue bears a slightly toughened central convexity. There is a corresponding concavity in the lower jaw, in the dorsal surface of the outer tongue sheath, which separates (to an unusual extent) the glottis from the orifice of the tongue sheath. In view of the correspondence between these surfaces, it is tempting to suggest that some kind of functional link exists. Possibly, juxtaposition of the two surfaces facilitates the formation of a close fit between the glottis and the nasopharyngeal duct, a continuous airway would then exist from external naris to trachea, separate from the oral cavity; but the precise adaptive significance of this is uncertain. The same applies to the suggestion of Smith (1943, p. 19), that the long palatal velum serves to separate the nasal and oral cavities.

The *Acrochordus* type of palate does not closely resemble that of any other snake examined thus far, it is perhaps most easily derived either from a *Cylindrophis*-like morphology, or from that found in most Caenophidia (quite simple overall, with a moderately long palatal velum, and an entire choanal arc). It is not discussed further below.

Henophidia: Discussion

It is important to note that certain of the categories of superficial palate morphology defined above correspond very closely with widely recognized taxa of varying supra-generic rank ranging from subfamilial to superfamilial, depending on the taxonomist concerned. For instance, the *Cylindrophis* group, plus the fundamentally similar *Anilius*, corresponds with the Aniliidae of Romer (1956, p. 570), except that *Loxocemus* is here excluded. The *Python* group corresponds well with the Pythoninae (of many authors), but here includes *Loxocemus* and excludes *Calabaria*. The *Bolyeria*, *Tropidophis*, *Eryx* and *Boa* groups have been collectively known as 'boas' (except *Calabaria*) and in addition to recognisable differences in palatal morphology, they all (except *Eryx* and to a lesser extent *Calabaria*) show a choanal tongue and emargination of the choanal arc. The differences among them in other characters has led to various levels of supra-generic recognition.

A further important point is that in the dendrogram illustrating Underwood's numerical phenetic clustering of boid snakes (Underwood 1976, p. 165), each of the (very distinct) clusters formed at around the 400 average distance level corresponds almost exactly with one of the palatal categories defined above. Underwood's study (which included phenetic and phyletic approaches) was based on 28 species each scored for 76 characters, and did not include the palatal characters considered here.

While it is of interest that groups of taxa sharing a similar state of superficial palate morphology correspond closely both with higher taxa formed by traditional systematic procedures, and also with groups formed by a purely phenetic numerical approach, it may be further asked whether palatal characters can contribute to a cladistic analysis of Henophidia.

It is suggested that primitive and derived states of the superficial palate can be distinguished with a fair degree of confidence, most of the relevant lines of argument have been included above with each character state description. Whether any of the relatively derived states are uniquely so (and thus cladistically useful), and not derived in parallel, can be decided at present with a little less confidence. In other words, a plausible transformation series (Hennig 1966) or morphocline (Maslin 1952) can be constructed and a primitive to derived polarity suggested, as illustrated in fig. 9. However, if it is attempted to interweave this series with those for other characters, it is found that either some palatal states, or some non-palatal states, or both, cannot be uniquely derived and thus do not delimit monophyletic groups. Some of these areas of agreement and of conflict are outlined in the following discussion.

McDowell (1975) has recently included several henophidian taxa (*Anilius*, *Anomochilus*, *Cylindrophis*, *Loxocemus*, uropeltids, and *Xenopeltis*) in his superfamily Anilioidea. This was apparently not intended to be a monophyletic group (*sensu* Hennig, 1966). In this case the inclusion of *Loxocemus* would not contradict the present cladistic arrangement of palatal states, in which most of these taxa are interpreted as showing the primitive condition, but *Loxocemus* shares a derived state with pythons.

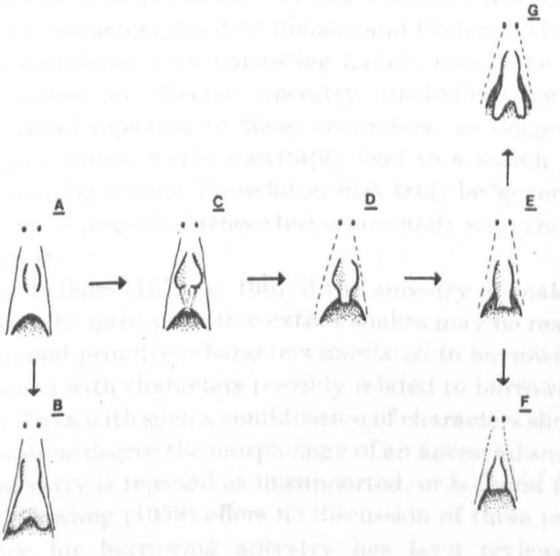

FIG. 9. Suggested transformation series, with polarity indicated, of palate character states (A to G only; State H, *Acrochordus* and *Chersydrus*, is not included). The two dots in each diagram represent the position of the paired ducts of Jacobson's organ. Presence of a distinct lateral palatal fold is indicated by a continuous lateral line, this line is broken in other taxa. State A is represented by an individual with weak vomerine flaps; as noted in the text, these are better developed in a few specimens, but absent in many.

It is here suggested that these 'anilioid' taxa are not united by any clear synapomorphy, and further that at least some of the major characters defining the superfamily or found in some or most of its members may be primitive for Henophidia. These include, large stapedial footplate; short stapedial shaft with contact high on quadrate; short quadrate, concave posteriorly due to longitudinal expansion of head of quadrate; ascending process of maxilla present and in firm articulation with prefrontal; lack of an *M. intermandibularis anterior, pars posterior* (Groombridge 1979); very long papilla basilaris (Miller 1968); presence of a distinct *levator anguli oris, adductor externus medialis* and *profundus* partly bipinnate and divided by tendinous aponeuroses (Haas 1955, 1973); squamosal immobile and incorporated in braincase.

There are various interpretations possible of character states such as these, some of which are likely to have functional significance for a burrowing snake. They may have been independently derived among these 'anilioid' genera in the separate adoption of burrowing habits from a non-burrowing ancestry; or represent true synapomorphies indicating the joint monophyly of the genera (thus requiring parallel evolution in those characters such as the palate in which *Loxocemus*, for example, resembles pythons); or represent a primitive inheritance from a burrowing or semi-burrowing ancestor. The latter hypothesis is most parsimonious, and there appears to be no convincing argument against it at present.

Dowling (1959) appears to reject the hypothesis that the ancestry of snakes passed through a burrowing phase, although he does not specifically say so. He states that of the characters proposed by Bellairs and Underwood (1951) as primitive, only four (coronoid present, teeth on premaxilla, pelvic rudiments present, left lung relatively large) are both typical of lizards and also found in snakes of various adaptive types. Dowling groups snakes showing these character states in his Boidae, which is seen as the 'most generalized' or as a 'primitive and generalized' family. The remainder of the characters listed by Bellairs and Underwood are correctly noted to be apparently correlated with burrowing habits, and to be approached in some respects by snakes of diverse ancestry (including both Henophidia and Caenophidia). Blind rejection of these characters, as suggested by Dowling, as possible primitive states, would inevitably lead to a search for primitive snakes among non-burrowing groups. These latter may truly be 'generalized' but are not as a consequence 'most primitive' (these terms are surely not synonymous, as Dowling appears to suggest).

As noted by Bellairs (1972, p. 166), if the ancestry of snakes passed through a burrowing phase, the most primitive extant snakes may be reasonably expected to combine undisputed primitive characters unrelated to burrowing (such as presence of a coronoid bone) with characters possibly related to burrowing (such as reduced cranial kinesis). Taxa with such a combination of characters should only be rejected as preserving to some degree the morphology of an ancestral snake if the hypothesis of burrowing ancestry is rejected as unsupported, or is found to be outweighed by other evidence. Dowling (1959) offers no discussion of these points.

The evidence for burrowing ancestry has been reviewed in Bellairs and Underwood (1951) and Bellairs (1972). Apart from cranial osteology, much of the evidence is derived from the peripheral visual system (Underwood 1957, 1970, Walls 1942), this is supported by details of the organisation of the central visual pathways (Senn and Northcutt, 1973, p. 150, Northcutt and Butler 1974, p. 134). This body of evidence is not here considered to be outweighed by alternative arguments (e.g.

McDowell 1972, pp. 262–265). The viewpoint of Dowling (1959) is thus not followed here and states possibly correlated with burrowing are not *a priori* excluded from consideration as primitive states.

By this interpretation the 'anilioid' taxa appear to include some of the most primitive Henophidia; a proposal that rests on two lines of argument. First, the co-existence in 'anilioids' of states possibly primitive but related to burrowing; and states not so related, but undoubtedly primitive. Secondly, by the presence of some 'anilioid' states in the late Cretaceous *Dinilysia* (Estes, Frazetta and Williams 1970), such as the form of the quadrate (except its articulation with the mandible, of unique structure in *Dinilysia*), intercalation of the squamosal in the braincase, large stapedial footplate. *Dinilysia* combines these states with others that are distinctly lizard-like (e.g., absence of an anterior tooth-bearing ramus of the palatine, absence of a crista circumfenestralis, presence of a bony element interpreted by Estes *et al.* as a jugal); this tends to support the proposal that these former states are likely to be primitive for snakes.

This is the main basis on which rests the suggestion that palatal State A shared by *Anomochilus*, *Cylindrophis*, uropeltids, and *Xenopeltis*, is the primitive extreme of the transformation series. State B (*Anilius*) is considered to be an isolated derivation from this kind of morphology. The somewhat aberrant condition of the superficial palate of *Anilius* is accompanied by the similarly aberrant lack of a separate angular and splenial, and is consistent with McDowell's (1975, p. 23) proposal that *Cylindrophis* and uropeltids are more closely related to each other than either is to *Anilius*. In addition to characters cited by McDowell, this is further supported by distinct points of resemblance (personal observation) between the skull of *Cylindrophis* (*rufus* and *maculatus*) and that of, for example, *Platyplectrurus madurensis* (probably among the most conservative of the uropeltids, by virtue of the retention of a supraocular scale, absence of extreme modifications of the rostrum and tail tip, optic foramen between frontal and parietal).

The existence of symplesiomorph links between the anilioids (*sensu* McDowell 1975), as suggested above, does not preclude the existence of synapomorph links between any of them and other Henophidia.

The posterior extension of the squamosal, so that it is no longer fully incorporated in the braincase, appears to be a possible synapomorphy of *Xenopeltis*, *Loxocemus*, and 'higher' Henophidia (and Caenophidia, where exceptions are more certainly secondary). In *Loxocemus* (82.8.17.17.) and higher Henophidia, the squamosal is typically more or less mobile on the braincase; this appears not to be the case in *Xenopeltis* (1925.5.25.6.) and is reasonably regarded as cladistically intermediate between the fully intercalated state of, for example, *Cylindrophis* and the non-intercalated state of *Loxocemus*.

A second possible synapomorphy of this same group is the formation of the complex composite throat muscle, the *M. neurocostomandibularis* (Langebartel 1968, p. 93). Langebartel reported that this muscle is not present in Scolecophidia, *Anilius*, *Cylindrophis*, or uropeltids. However, McDowell (1972) gives a different interpretation, and states that this muscle complex is present in all snakes except the scolecophidian Anomalepididae. Also, Lubosch (1933, fig. 1 d; repeated as fig. 141 in Haas 1973), appears to show a *neurocostomandibularis*-like muscle present in *Cylindrophis*, where Langebartel reports it to be absent.

I have re-examined the relevant taxa and would support Langebartels' original findings. The *M. neurocostomandibularis*, as characterised by Langebartel (1968), is found only in *Xenopeltis*, *Loxocemus*, pythons, *Calabaria*, boas, and Caenophidia. In other snakes, the various components of the *neurocostomandibularis*, where present, are more separate elements and do not come into the appropriate relationship with each other. In *Typhlops*, for example, where McDowell (1972, p. 239) states that the *neurocostomandibularis* is present, the *M. geniohyoideus* (='ceratomandibularis' of Langebartel), an anterior component of the *neurocostomandibularis*, is entirely separate from the other throat muscles: therefore the *neurocostomandibularis* is not present. Langebartels' suggestion that the presence of the *neurocostomandibularis* complex is a derived state in snakes appears to be well-founded; it is unique among Squamata, is correlated in most taxa with derived states of other characters, and what could be interpreted as preliminary stages in its formation occur in *Anilius* and *Cylindrophis*.

The throat muscles of *Acrochordus* show a pattern unique among snakes, according to Langebartel. He did not find the *neurocostomandibularis* in this form; however, it does not particularly resemble those lower Henophidia in which the muscle complex is also absent. Considering the numerous other unique features of acrochordids, the *neurocostomandibularis* may well be secondarily absent ('pseudo-primitive'): this interpretation is adopted in the cladistic arrangement of fig. 10 (see Groombridge 1979 for comments on the cladistic position of acrochordids).

Underwood (1976, p. 167) has recently argued that *Loxocemus* is cladistically close to pythons; this is independently supported by their joint possession of a similar superficial palate morphology (State C) which it is suggested above is derived relative to that of *Xenopeltis* and other lower Henophidia.

Underwood (1976) has recently placed both *Xenopeltis* and *Loxocemus* in his subfamily Xenopeltinae of the Boidae. Dowling and Gibson (1970) have made a similar proposal, but their Xenopeltinae also provisionally included *Calabaria* (see below for comments on this genus). These were apparently not intended to be monophyletic taxa (*sensu* Hennig 1966). If these taxa were actually monophyletic, the course of evolution of the superficial palate would have been more complex than is suggested here. Either *Xenopeltis* may have secondarily lost its vomerine flaps, or *Loxocemus* may have developed its vomerine flaps independently of true pythons. It is proposed here that *Xenopeltis* is primitive to *Loxocemus* and pythons; the superficial palate, the squamosal (noted above), the form of the quadrate, and the Vidian canals (Underwood 1976), are some characters of which *Xenopeltis* appears to show primitive states. This would imply that *Xenopeltis* and other 'anilioid' taxa lacking a separate postfrontal have attained this state separately from boas and Caenophidia. There do not appear to be any convincing apomorphic states shared between *Xenopeltis* and *Loxocemus* (or *Calabaria*) that require the association of these genera in a monophyletic group. The observation by Cole and Dowling (1970), utilized by Dowling and Gibson (1970) that *Xenopeltis* shares a similar karyotype with most (not all) boids, (and *Loxocemus*; Fischman, Mitra and Dowling 1972), is of restricted value cladistically until that of *Anilius*, *Anomochilus*, *Cylindrophis*, and uropeltids is reported. Although almost all snakes so far reported (Gorman 1973) have a diploid number of 36, with 16 macrochromosomes and 20 microchromosomes; *Xenopeltis*, *Loxocemus*, and most boids resemble each other (and differ from almost all Caenophidia) in having 8 metacentric (or near metacentric) and 8 acrocentric (or near acrocentric) macrochromosomes. It has just been suggested above that these taxa are derived relative to *Anilius*, *Cylindrophis*, and uropeltids in respect of the squamosal and the *M. neurocostomandibularis*; it would not be unexpected, by this argument, were the latter group of taxa shown to have a somewhat different karyotype. The hemipenes of *Xenopeltis* and *Loxocemus* as figured by Dowling and Gibson (1970) do appear quite similar, and together differ from those of other boids in possessing a disc-like structure without ornament terminating both lobes of the hemipenis. The cladistic interpretation of this similarity is also uncertain until a report on the everted hemipenis of *Anilius* (which alone among the remaining lower Henophidia has a forked hemipenis, typical of most Henophidia) is available. On present evidence, the hemipenial morphology noted above could as well be primitive for *Xenopeltis*, *Loxocemus*, and other boids, as a synapomorphy demonstrating the joint monophyly of these two genera. It is here suggested that the condition of the palate argues against the latter possibility, until stronger evidence is available.

That the palate of pythons is cladistically intermediate between that of *Cylindrophis* on one hand, and that of boas on the other (see below), is supported by the presence of an intermediate state of the *intermandibularis anterior* muscle in true pythons (Groombridge 1979). Lower Henophidia have a thin usually weakly defined muscle; this muscle is present in pythons, but is typically better developed. In *Calabaria* and boas (also acrochordids and Caenophidia) this muscle is divided into a *pars anterior* (in *Calabaria* and boas, retaining an insertion similar to that of the undivided muscle in pythons) and a *pars posterior*. The presence of a divided *intermandibularis anterior* is interpreted as a derived state.

The remaining henophidian snakes (possibly except *Calabaria*) share a probable synapomorphy, namely, the emargination of the choanal arc and presence of a median choanal tongue. This argues against the opinions expressed by certain workers (Hoffstetter 1968, p. 208, Smith 1943, p. 103) that the boas do not share an immediate common ancestor. *Calabaria* and *Eryx* are partial exceptions in that they possess a complete or near complete palatal arc, and thus no choanal tongue (some *Eryx*) or a very reduced one. It is conceivable that this condition has been reached from a *Python*-like state, simply by the anterior retreat of the palatal arc up to the rear of the vomerine flaps. In the case of *Eryx*, consideration of other characters strongly suggests origin from a *Boa*-like state. Underwood (1976) notes evidence (see also Bogert 1968; Hoffstetter and Rage 1972) that the erycines (*Lichanura*, *Charina*, *Eryx*) form a monophyletic group, with *Lichanura* the most primitive, *Charina* intermediate, and *Eryx* most derived. The palatal states run parallel to this sequence; *Lichanura* is most *Boa*-like, *Charina* is modified, *Eryx* is more modified (reduction of vomerine flaps, reduction of choanal tongue, near complete or complete choanal arc). It is suggested that the weight of other characters demonstrates that the relatively simple palatal morphology of *Eryx* is secondarily so. This is an important point because it sets a precedent that may have been followed by the ancestors of Caenophidia (which typically have a quite simple palate) if they stem from a *Boa*-like form.

Calabaria phenetically resembles *Eryx* and *Charina* in respect of its palate, and clusters with erycines in the phenetic part of Underwood's (1976) study. Cladistically its position is uncertain; other than the palate initially, no characters clearly link *Calabaria* with erycines when interpreted cladistically. The phenetic proximity of these taxa could well be due to parallel adaptions to a semiburrowing or burrowing niche, the palatal similarity between *Calabaria* and *Eryx*, in particular, could follow from a common remodelling of the proportions of the snout region in this connection.

Dowling (1975, p. 193) has figured the distinctive hemipenial morphology of erycines; interestingly, the unusual hemipenis of *Calabaria* (Dowling 1975, Dowling and Gibson 1970, photograph in Doucet 1963) would seem to be more similar to that of *Eryx* than to those of *Xenopeltis* and *Loxocemus*, with which latter taxa *Calabaria* is provisionally associated by Dowling and Gibson.

Arguing against a close cladistic proximity, among other characters, is the presence of a postfrontal in *Calabaria*; accepting a close relationship between *Calabaria* and *Eryx* would require postulating the multiple loss of this bone in other erycines and other boas (since *Eryx* seems to be the end of a side branch of boa evolution), assuming it to be primarily present in *Calabaria* and not secondarily so. It would also require postulating reversals (in *Calabaria*) in those derived states relating erycines to boines, and the erycines to each other (Underwood 1976). The weight of other characters thus appears to indicate that the shared derived state of the superficial palate in *Calabaria* and *Eryx* is not uniquely derived.

Although the palate alone does not appear to settle the cladistic position of *Calabaria*, certain other characters do suggest that its ancestry was more boa-like than python-like. The sole reason for the traditional inclusion of *Calabaria* with true pythons seems to be the possession of a post-frontal, but (if not a neomorph) this is surely a symplesiomorphy and no clue to cladistic affinity. Some states shared by *Calabaria* and boas include; single subcaudals, loss of pre-maxillary teeth, and presence of both anterior and posterior portions of the *M. intermandibularis anterior*. It is suggested elsewhere that this latter state is a probable synapomorphy in respect of which *Calabaria* and other boas (also acrochordids and Caenophidia) are more derived relative to pythons and other Henophidia. This would agree well with Underwood's (1976) phyletic arrangement of boids, in which *Calabaria* is intermediate between the pythons and the more derived boas.

Underwood (1976) has noted a degree of affinity, in both phenetic and cladistic senses, between his taxa Bolyeriinae and Tropidophinae: they are accordingly associated in the Tropidophidae. McDowell (1975) also notes some similarities between these two groups, but they are each ranked as super-families in his treatment. Beyond the fact that in palatal morphology these groups resemble boas in general, and not pythons, they are not particularly similar in this respect. It has been suggested above that *Bolyeria* and *Casarea* are the most primitive of boas in palatal morphology, while *Tropidophis* and *Trachyboa* are further derived from a Boa-like condition. The palate of two other probable tropidophiine genera, *Exiliboa* and *Ungaliophis*, has not yet been examined.

The combined evidence of several characters (see Underwood, 1976) indicates that bolyeriines and tropidophiines are primitive to the other boas; e.g. the latter group generally having the right Vidian canal larger than the left (except *Candoia*), an open palatine foramen, and the palatine process of the maxilla close to or contacting the pterygoid (all interpretated as derived states).

If it is accepted that bolyeriines are primitive to tropidophiines and other boas in respect of their superficial palate, and that bolyeriines and tropidophiines are primitive to boas in respect of these skull characters, it would then follow that the basic *Boa* palate had evolved in the common ancestry of tropidophiines and other boas, and the derived skull characters subsequently evolved in the other boas alone. It would also follow that tropidophiines are not the sister group of bolyeriines, as Underwood suggests, but are the sister group of other boas.

The actual physical feature forming the basis of the suggestion that the bolyeriine palate is primitive to that of other boas, i.e., the anterior increase in width of the vomerine flaps, is composed of about a square millimetre of soft tissue. This would seem to be an impossibly weak foundation on which to argue against the evidence proposed by Underwood for the joint monophyly of bolyeriines and tropidophiines. However, considering the palatal similarity of *Bolyeria* and *Casarea* (but only one specimen of each) despite several differences in other characters (indicating that the state is likely to be a real feature of the group, and not an artefact of a small sample), and the apparent conservatism of the superficial palate; it is suggested that the major evidence proposed for monophyly may bear further examination.

Pelvic spurs are absent from female bolyeriines (and from males), and from female *Trachyboa* and *Tropidophis* (and from male *Tropidophis semicinctus*, Stull 1928) among tropidophiines. Of the two genera only provisionally included in the Tropidophinae of Underwood (1976), vestigial pelvic spurs are present in female *Exiliboa* (Bogert 1968) and are variably present or absent in *Ungaliophis* (Corn 1974). Most other henophidian genera retain spurs: except uropeltids, *Xenopeltis*, and acrochordids. Since this is a 'loss' state, and has occurred in at least three other lineages, and is intra-specifically variable in *Ungaliophis panamensis*, it cannot be given great significance in a cladistic analysis.

The hyoid cornua of Caenophidia, acrochordids, tropidophiines (Dowling 1975, p. 196, McDowell 1975, p. 13), and *Casarea*, are parallel†; those of other Henophidia, including *Bolyeria* (Underwood 1967, p. 72), are divergent posteriorly. The latter state is very probably primitive (Langebartel 1968). *Bolyeria* and *Casarea* are linked by a very probable synapomorphy, the division (unique among vertebrates) of the maxilla into anterior and posterior portions. The parallel condition of the hyoid in *Casarea* must therefore have been arrived at independently from that of tropidophiines: unless *Bolyeria* is secondarily 'primitive' in its resemblance to other Henophidia, having returned to a divergent condition from a parallel condition shared by the ancestry of bolyeriines, and possibly of tropidophiines. The evidence of the hyoid is thus not conclusive of cladistic proximity.

Underwood has noted shared derived features of the respiratory system that appear to associate bolyeriines and tropidophiines. Among boids, only tropidophiines possess a well-developed tracheal lung. *Casarea* has a very slightly developed tracheal lung. Most tropidophiines are unique, among boids, in lacking a left lung (a vestige remains in *Ungaliophis panamensis*, Butner 1963), it is extremely reduced in bolyeriines. The weight to be assigned to these features is perhaps diminished by the observation that, among other Henophidia, *Anilius* and *Cylindrophis* also show extreme reduction of the left lung (Underwood 1967), *Anomochilus* lacks a left lung (Brongersma and Helle 1951), acrochordids lack a left lung and possess a tracheal lung, although the latter is of unique form (Brongersma 1952). Also, many separate stocks of Caenophidia have lost or reduced the left lung, and acquired a tracheal lung (Underwood 1967). The terminal entry of the trachea into the lung is a further derived state shared by bolyeriines and tropidophiines (Underwood 1976, p. 155).

Although, taken separately, these character states cannot be regarded as convincing synapomorphies, when considered together they do suggest the possibility of a close cladistic relationship between bolyeriines and tropidophiines.

At least four alternatives can be considered, in order to account for the states of the superficial palate, as noted above. Firstly, that the bolyeriine palate is actually *not* primitive to that of other boas; bolyeriines and tropidophiines are monophyletic

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† See addendum.

(as suggested by Underwood 1976), and cladistically the palate can only separate boas from pythons without indicating a primitive boa condition. Secondly, that the palate of bolyeriines *is* primitive; bolyeriines and tropidophiines are monophyletic, and tropidophiines have evolved a palate more similar to that of most other boas in parallel. Thirdly, the palate of bolyeriines *is* primitive; the bolyeriinae and the tropidophiinae do *not* form a monophyletic group, and tropidophiines and other boas share a common ancestry with a *Boa*-like palate subsequent to that shared with bolyeriines. Fourthly, it is more remotely possible that tropidophiines share an ancestry specifically with the large South American boas (*Corallus*, *Epicrates*) that they most closely resemble in palatal morphology; this would require reversals in those characters in respect of which tropidophines appear to be primitive to other boas.

It is here suggested that the third of these possibilities deserves serious consideration. At least, the evidence of the palate would indicate that the cladistic position of the Bolyeriinae and Tropidophiinae should be a matter for continued investigation.

The salient points of the above discussion are summarised in the cladogram of fig. 10. It must be stressed that this is in no way intended to approach a complete phylogeny of the Henophidia, but is simply an explicit visual statement of the suggested cladistic implications of the few characters considered herein (and in Groombridge 1979). Hopefully, areas of concordance, or otherwise, with interpretations of other characters can thus be more readily located and subjected to useful examination. An extensive analysis of the Boidae is to be found in Underwood (1976). A somewhat different scheme (but with full documentation delayed), is to be found in Frazzetta (1975).

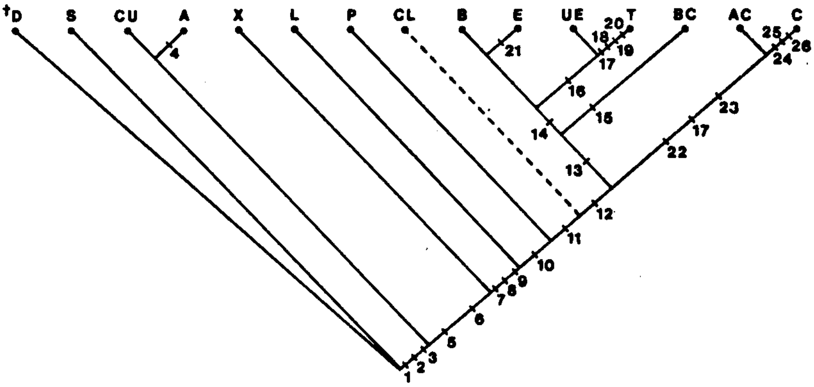

FIG. 10. Diagram to illustrate suggested cladistic implications of characters considered herein, and in Groombridge (1979). Numbered bars indicate transformation to derived character state (mostly proposed as synapomorphies) present in hypothetical ancestor at following node, or in terminal group. Key to group abbreviations (left to right):—D, *Dinilysia* (Upper Cretaceous); S, Scolecophidia; CU, *Cylindrophis*, *Anomochilus*, uropeltids; A, *Anilius*; X, *Xenopeltis*; L, *Loxocemus*; P, pythons; CL, *Calabaria*; B, boine boas and *Lichanura*; E, erycine boas except *Lichanura*; UE, *Ungaliophis*, *Exiliboa*; T, *Trachyboa*, *Tropidophis*; BC, *Bolyeria*, *Casarea*; AC, acrochordids; C, Caenophidia. Key to proposed derived character states: 1, presence of toothed anterior ramus of palatine; 2, presence of antero-median pillars of frontals, between olfactory tracts; 3, separate prootic foramina for both maxillary and mandibular branches of trigeminal nerve (occasional exceptions certainly secondary, at least in Caenophidia); 4, palatal 'valves' of *Anilius*; 5, formation of the composite

Since the above material was written, an interesting work by Rieppel (1977), a comparative study of the skulls of several Henophidia, has appeared. His basic division of the Henophidia (except acrochordids) into the two superfamilies Anilioidae (group CU + A in fig. 10 of this paper), and Booidea (groups X to BC inclusive), appears to be a useful concept, and is broadly compatible with the cladistic arrangement suggested here. While the Anilioidae (of Rieppel, not of McDowell 1975) may well be a monophyletic group (*sensu* Henning 1966), the Booidea would be paraphyletic on the interpretation given here. Whether a purely cladistic classification is to be considered theoretically desirable or not, it will surely

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M. neurocostomandibularis; 6. squamosal somewhat elongate and free of braincase posteriorly; 7. quadrate without distinct posterior concavity; 8. squamosal mobile on braincase; 9. presence of fully-developed vomerine flaps; 10. *M. intermandibularis anterior* (= *ima*) well-developed, exposed medial to *M. genioglossus*; 11. *ima* divided into *pars anterior* and *pars posterior*; 12. loss of postfrontal (but also in groups S, CU + A, and X); 13. emargination of choanal arc and presence of a choanal tongue, correlated with relatively more anterior divergence of ectochoanal cartilages; 14. vomerine flaps lose anterior increase in width; 15. maxilla divided into anterior and posterior portions; 16. presence of tracheal lung; 17. caenophidian-type hyoid, with closely parallel cornua and adpressed *M. hyoglossi* (see addendum); 18. posterior palatal surface extended and deeply bifurcate; 19. long intra-pulmonary bronchus; 20. non-lobed kidneys; 21. reduced choanal tongue; 22. shift in insertion of *ima*, *pars anterior* onto postero-median portion of intermandibular 'ligament' (secondarily paired posteriorly in acrochordids); 23. spines on hemipenis (exceptions in some Caenophidia probably secondary); 24. specialised costal cartilages (Hardaway and Williams, 1976; Persky *et al.* 1976); 25. presence of *M. protractor quadrati*; 26. presence of *M. protractor laryngeus*. *Notes*: (*a*) the basal trichotomy between the Upper Cretaceous fossil *Dinilysia*, Scolecophidia, and other snakes is not resolvable on evidence considered herein; (*b*) in most cases autapomorphies of individual lineages are not shown, among the exceptions are character states distinguishing group T from other 'tropidophiines', and three states(in addition to those in Underwood 1967) that rather clearly indicate the monophyly (*sensu* Hennig) of the Caenophidia (Colubroidea of McDowell 1975). (*c*) most groups can be further divided on evidence not considered here. (*d*) the two groups CU plus A lack any clear synapomorphy, but share primitive states, and lack derived states of their sister group (remaining Henophidia and Caenophidia); other evidence is thus required to decisively demonstrate their joint monophyly or otherwise. (*e*) the position of *Calabaria* (CL) indicated here rests on weak evidence, the presence of a postfrontal appears to place *Calabaria* primitive to the boas (groups B to BC inclusive) and the group formed of acrochordids and Caenophidia (AC + C), in which the postfrontal is absent, but this bone has also been lost in groups S, CU + A, and X. In terms of parsimony there seems little to choose between postulating four rather than five losses of the postfrontal. However, Underwood (1976), also considering other characters, similarly places *Calabaria* cladistically between pythons and boas. The resemblance of the superficial palate of *Calabaria* to that of *Charina* and *Eryx* (group E), by this interpretation, must have been derived in parallel. (*f*) if other characters emerge to indicate that the superficial palate of bolyeriines (group BC) is actually not primitive to that of other boas, I suggest that the derived state of the superficial palate of boas (State 13 in Fig. 10) would still support the more general hypothesis that the boas collectively form a monophyletic group. (*g*) see Underwood (1976) for derived states of the group B + E. (*h*) the 'semi-parallel' hyoid (see addendum) must have arisen (from the typical henophidian divergent 'V' type) at least twice, in *Casarea* (of group BC, but not in *Bolyeria* of this group), and in *Ungaliophis*, *Exiliboa* (or probably in the common ancestry of the group UE + T). The observation that the intermediate state has arisen in parallel in two lineages has led me to postulate that the caenophidian 'parallel-type' hyoid (State 17 in fig. 10) has also arisen twice, in the group T, and in the ancestry of the group AC + C. (i) this scheme implies that loss of vomerine flaps occurred in the ancestry of group AC + C.

remain necessary and useful to recognise paraphyletic 'grade' taxa, such as the Booidea or the Henophidia, while so many ambiguous or controversial aspects of the branching sequence of snake phylogeny persist.

The above account of morphological variation in the superficial palate could be extended to consider possible functional aspects. Two areas for investigation may be suggested. Firstly, could the vomerine flaps be involved in some way in the transfer of particles from the tongue tips to the ducts of Jacobson's organ for sensing? Secondly, could the appearance of choanal clefts (i.e. emargination of the palatal arc) be correlated with increased independence of mobility of the lateral palato-maxillary arches relative to the median snout complex? These areas were beyond the scope of the present study.

Comments on Caenophidia

As stated in the Introduction, attention was first drawn to the possible taxonomic value of the superficial palate by the observation of variation within viperines, during a study of relations within the subfamily. This study is still in progress, but it may be noted here that *Causus* has a simple palatal structure with a non-emarginate choanal arc, similar to that of most other Caenophidia examined, and thus probably primitive. *Causus* also appears at present on other evidence to be primitive to other viperines. The latter typically (there are a couple of exceptions) show some elaboration rather similar either to the choanal papillae of pythons, or to the short vomerine flaps of *Calabaria*. Crotalines also show some elaboration of the palate (that is not identical to that of viperines); this is contributing to the investigation of relationships between the sub-groups of Viperidae. There is good concordance here, as in Henophidia, between palatal characters and other characters.

Although a taxonomically diverse sample of other Caenophidia has been examined, no variation of a similar magnitude or of such evident systematic relevance has emerged. The sample is still numerically extremely restricted however. Three of the major variations encountered to date may be noted here without attempting comprehensive description.

Achalinus braconnieri and *A. spinalis* (but not *A. rufescens* or *A. werneri*) have a median cleft in the rear of the palatal surface, the nasopharyngeal ducts thus each form a separate lateral tube opening into the orbitonasal trough. A rather similar condition was also found in *Xenodermus javanicus*, it was not found in another xenodermatine, *Fimbrios klossi*.

The dipsadines and pareines examined all have a relatively long palatal velum. In *Sibon nebulata*, *Dipsas albifrons*, and *Sibynomorphus turgida*, this has a medium stiffened portion. In the latter species (two specimens) this is turned dorsally into the orbitonasal trough and forms a median 'valve' over the internal choanae. The palatal velum appears longest in *Aplopeltura boa*. All these forms apparently specialize in molluscs as a food source, possibly the long palatal velum becomes pushed up into the orbitonasal trough during prey intake, thus closing off the internal choanae and preventing mucus from occluding the nasal passages. The palatal similarity between the two groups may well be a parallelism, it would be a very small step from the more typical caenophidian condition.

In several Old World colubrids (*sensu* Underwood 1967) the posterior palatal surface bears on each side, a short longitudinal fold (in addition to the usual, more lateral, folds). The posterior end of this fold intersects the choanal arc. These forms include. *Coluber rhodorhachis*, *Elaphe longissima*, *Spalerosophis arenarius*, and *Ptyas mucosus* (for palate of the latter, see Fig. 9(*c*) in Parker and Grandison 1977).

The superficial palate is relatively simple in most Caenophidia examined. Typically there is a short palatal velum, the posterior margin of which forms a simple approximately semi-circular choanal arc. Some variation was noted in the depth and degree of pleating of the lateral folds flanking the vomerine cushion region.

Conclusions

I would suggest that the morphology of the superficial palate in Henophidia is sufficiently stable within groups, and shows states that can be hypothesised as either primitive or derived with sufficient confidence, such as to contribute usefully to the clarification of the broad outlines of cladistic relations among henophidian snakes.

Anilius (with a unique palatal morphology), *Cylindrophis*, uropeltids, and *Xenopeltis*, appear primitive to other Henophidia in respect of their superficial palate. *Loxocemus* and pythons, with consistent full development of vomerine flaps, and typically with choanal papillae present, appear derived relative to the above group. Boas (*sensu lato*; the Boinae, Erycinae, Tropidophiinae, and Bolyeriinae of Underwood 1976) share a probable synapomorphy, namely, emargination of the choanal arc with correlated presence of choanal clefts and a choanal tongue. It is suggested that, within boas, *Bolyeria* and *Casarea* may retain the most primitive palatal morphology. *Eryx*, *Charina*, and *Tropidophis*, *Trachyboa*, form two distinct derived sub-groups. The palate of *Calabaria* resembles that of *Eryx* and *Charina*, other characters suggest that this resemblance was derived in parallel. Acrochordids have a unique palatal morphology, of uncertain derivation.

Among boids, with the exception in particular of *Xenopeltis* and the Tropidophiinae, there is quite good agreement here with the recent arrangement of Underwood (1976, p. 168) made on the basis of many more characters.

A diagram of the suggested cladistic implications of the characters considered herein is provided (fig. 10).

The situation in Henophidia and in viperids suggests that workers in snake systematics should be alert to the possibility of useful variation in the superficial palate(and should take care not to destroy the palatal region, before examination, in the preparation of skulls or removal of the palato-maxillary arch).

Acknowledgments

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Addendum

Since the above was written, the British Museum (Natural History) has acquired a specimen of *Exiliboa placata* (BMNH 209.1977), through the kind cooperation of Dr. C. M. Bogert and Dr. W. G. Degenhardt (of the University of New Mexico). Although there are points of difference, the palate of *Exiliboa* (a possible tropidophiine) most closely resembles that of the *Boa* group. The palate of *Exiliboa* could be interpreted as showing some divergence toward the *Tropidophis* condition; the choanal tongue forms two distinct, but short, lobes posteriorly, it then tapers postero-dorsally into the roof of the orbito-nasal trough. The long vomerine flaps are of approximately equal depth throughout (there is a superficial appearance of a *Bolyeria*-like anterior increase in width of these vomerine flaps, but this is due to the fact that their middle portions are somewhat adpressed in this specimen). Unlike *Trachyboa* and *Tropidophis*, the choanal tongue is not considerably extended and deeply bifurcate.

I have also subsequently been able, through the courtesy of Dr. R. G. Zweifel of the American Museum of Natural History, to examine a specimen of *Ungaliophis continentalis* (representing a fourth possible tropidophiine). The soft oral tissues of this specimen (AMNH 70205) are not well-preserved (the specimen is severely decalcified), however, it is clear that like *Exiliboa* but unlike *Trachyboa* and *Tropidophis*, the choanal tongue is not greatly extended and deeply bifurcate. The resemblance is chiefly to *Exiliboa* and members of the *Boa* group.

Thus of the four 'tropidophiine' genera, two (*Exiliboa* and *Ungaliophis*) retain a rather *Boa*-like palatal morphology, while the other two (*Trachyboa* and *Tropidophis*) share what I interpret as a more derived condition. It will be noted below that certain other characters indicate the same distinction.

The above observations are at least not inconsistent with the suggestion that 'tropidophiines' and other boas (except bolyeriines) share a common ancestor, with a *Boa*-type palate, and form the sister-group of bolyeriines.

I have also examined the hyoid apparatus of *Exiliboa*, *Ungaliophis*, *Trachyboa*, *Tropidophis*, *Bolyeria*, and *Casarea*. The following comments expand and modify those given in the discussion section above (p. 465).

Of these six genera, only *Bolyeria* has a hyoid similar to those of the majority of Henophidia, i.e. the 'V' type of Langebartel (1968, p. 12), with the cornua broadly divergent posteriorly. In *Bolyeria*, the posterior tips of the cornua lie superficial to the ventral portions of the ribs and their musculature. A small muscle ('omohyoideus' of Langebartel 1968, p. 70, not present in all Henophidia) arises from the posterior tip of the cornua and inserts over the rib musculature. The cornua are close together anteriorly, but do not meet. These observations were made on the same specimen (BMNH 96.3.25.2) reported by Underwood (1967, p. 72), and confirm his account. If the contrary report of Anthony and Guibé (1952, p. 196), that *Bolyeria* has parallel cornua and a lingual process, is correct for their specimen, then unprecedented intraspecific variation occurs in *B. multocarinata*.

The specimen of *Casarea* examined does agree with the report of Anthony and Guibé (1952): the cornua are near parallel and joined anteriorly, with a lingual process. However, there is a very significant difference from the caenophidian condition ('parallel type' of Langebartel 1968, p. 13), which *Casarea* otherwise resembles; the cornua are not *closely* parallel. Correlated with this, their posterior tips still lie in the usual henophidian position, superficial to the ribs, and the *M. hyoglossi* (arising from the cornua, and entering the main body of the tongue) are *not* in close contact with each other along the whole length of the cornua. The same is true of *Exiliboa*, except that the lingual process is virtually absent. The cornua of *Ungaliophis* are similar, with their posterior tips superficial to the ribs, and the *hyoglossi* not adpressed.

It thus emerges that, among Henophidia, it is only *Trachyboa*, *Tropidophis*, and acrochordids, that resemble Caenophidia in respect of the hyoid apparatus. In all these forms the hyoid cornua are closely parallel, and the *M. hyoglossi* are typically closely adpressed. The cornua and *hyoglossi* are bound together in a thin fascia, and lie, not superficial to the ribs, but in the ventral mid-line, entirely medial to the rib tips. In this position they are able, posteriorly, to lie deep to the *M. transversus abdominis* and *M. obliquus abdominis internus*, running from the medial surface of the ribs of the ventral mid-line (Langebartel 1968, pp.5–6, 82–83).

Perhaps the most significant morphological distinction can be made, not (as previously) between divergent, as opposed to parallel, cornua; but between divergent or parallel, but widely separated, cornua and *hyoglossi*, on the one hand; and closely parallel cornua, medial to the rib tips, with adpressed *hyoglossi*, on the other (see fig. 11). The assumption is made here, in the absence of good evidence to the contrary, that the hyoid cornua in all these snakes are derived from the same visceral arch elements.

The above reinterpretation reduces the similarity between the four tropidophiine genera, and between *Casarea* and tropidophiines; they do not all possess the same form of hyoid apparatus.

Bogert (1968, p. 33), after noting several differences between the four 'tropidophiine' genera, suggested that the presence of a tracheal lung is "perhaps the most nearly conclusive evidence of their relationship". Underwood (1976, p. 153), only provisionally included *Exiliboa* and *Ungaliophis*, with *Trachyboa* and *Tropidophis*, in his subfamily Tropidophinae. Dowling (1975, p. 196) and McDowell (1975, p. 13),

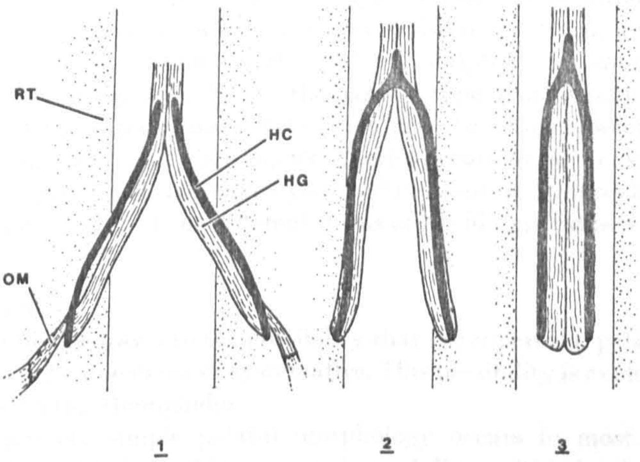

FIG. 11. Diagram of the hyoid and *M. hyoglossi* of certain snakes. Shown in ventral view, anterior is toward the top of the page. Muscles attaching to the hyoid, other than the *hyoglossus* (and *omohyoideus*), are not included. The *hyoglossi* continue anteriorly into the main body of the tongue. The Scolecophidia are not considered.

(1) Divergent type or 'V' type (Langebartel 1968); cornua and *hyoglossi* divergent posteriorly, terminating posteriorly superficial to the ribs and their intrinsic musculature; cornua joined or separate anteriorly; 'omohyoideus' present or absent. Characteristic of the majority of Henophidia, including *Bolyeria*.

(2) Semi-parallel type; cornua approximately parallel, but widely separate, *hyoglossi* not adpressed in midline; cornua and *hyoglossi* somewhat divergent posteriorly, still terminating superficial to ribs. Found in *Casarea*, *Ungaliophis*, *Exiliboa*.

(3) Parallel type; cornua parallel and close together, *hyoglossi* adpressed in midline; cornua and *hyoglossi* entirely medial to the tips of the ribs. Found in *Trachyboa*, *Tropidophis*, Acrochordidae, and Caenophidia.

Key: RT, rib tips and costal musculature; OM, *M. omohyoideus* (of Langebartel); HC, hyoid cornua; HG, *M. hyoglossus.*

both group the four genera together, at family and superfamily level, respectively; but a major part of their evidence for this association was what now appears to have been a misleading interpretation of the hyoid apparatus. While there remains perhaps just enough evidence, mainly from the respiratory system(Bogert 1968, Underwood 1976). to suggest the monophyly of the 'tropidophiines', more investigation is desirable. However, it is more certain that, within the group, *Trachyboa* and *Tropidophis* are distinguished as a distinct sub-group by several probably derived states. These include, the condition of the superficial palate and of the hyoid apparatus (both described above), the presence of a long intrapulmonary bronchus (Underwood 1976, p. 155; not long in *Exiliboa* and *Ungaliophis*, personal observation), presence of non-lobed kidneys (Brongersma 1951, not *Exiliboa* or *Ungaliophis*, Bogert 1968).

Although there are several points of resemblance between 'tropidophiines' and Caenophidia, neither McDowell (1975, p. 15) nor Underwood (1976, p. 172) suggest that the two groups share an immediate common ancestor. This view is concordant with the fact that only two 'tropidophiine' genera, and furthermore the most derived two (*Trachyboa*, *Tropidophis*), share the caenophidian parallel-type hyoid. It would thus appear that the parallel-type hyoid has arisen at least twice during snake phylogeny (assuming it to be derived relative to the henophidian 'V' type), and perhaps three times if acrochordids and Caenophidia are not jointly monophyletic (*sensu* Hennig 1966). It is however suggested elsewhere (Groombridge 1979) that they *are* monophyletic, with acrochordids forming a basal, and highly divergent, lineage. A double origin (in the group *Trachyboa–Tropidophis*, and the group Acrochordidae–Caenophidia), of the parallel-type hyoid is perhaps not too unlikely in view of the intermediate state (that may be termed 'semi-parallel') found in *Casarea*, *Exiliboa*, and *Ungaliophis*. There appears to be no experimental work on functional aspects of the snake hyoid and its associated musculature. The adaptive significance, if any, of the different forms of hyoid apparatus is a subject for future study.

Summary

Attention is drawn to the possibility that the superficial palate may afford some characters of value in snake systematics. This possibility is explored with particular reference to the Henophidia.

A relatively simple palatal morphology occurs in most lower Henophidia (*Anomochilus*, *Cylindrophis*, uropeltids, and *Xenopeltis*). In *Anilius*, the posterior palatal surface is turned dorsally and divided into two lobes that cover the internal choanae. *Loxocemus* and pythons are characterized by full development of vomerine flaps, weakly developed or absent in lower Henophidia. In boas (*s.l.*), the vomerine flaps are extended and contribute to a median choanal tongue, accompanied by emargination of the choanal arc. Further variation, of systematic interest, occurs within boas. Some cladistic implications of palatal and non-palatal characters are proposed, and compared with previous systematic arrangements.

Appendix: specimens examined

Acrantophis dumerilii, IV.12.1.9, 92.2.29.9, 1925.4.1.13.
Acrantophis madagascariensis, IV.12.1.a.
Acrochordus javanicus, 60.3.19.1321, 1966.12, 1974.3865, 1974.3866.
Anilius scytale, 95.3.29.4, 1904.10.29.35, 1920.1.20.1338.
Anomochilus leonardi, 1946.1.17.4.

Aspidites melanocephalus, 1931.12.2.2.
Boa constrictor, 1904.10.29.31, 1908.5.22.1, 1926.4.30.10, 1958.1.2.21.
Bolyeria multocarinata, 70.11.30.4B.
Bothrochilus boa, (McDowell 1975: 31, places this species in *Liasis*), 77.2.24.11.
Calabaria reinhardti, 63.12.1.1, 1962.257, 1962.258, 1967.116, 1969.515.
Candoia asper, 1904.3.17.9.
Candoia bibronii, 1962.524.
Candoia carinatus, 1967.778.
Casarea dussumieri, 70.11.30.4B.
Charina bottae, IV.24.1.a, 77.3.6.16, 94.3.4.5.
Chersydrus granulatus, 1905.11.29.17, 1969.1762, 1974.3863, 1974.3864.
Chondropython viridis, 87.3.2.1, 1922.11.24.32.
Corallus caninus, 49.11.8.100.
Corallus enydris, 87.6.29.24.
Cylindrophis aruensis, 1946.1.16.72.
Cylindrophis lineatus, 1901.5.17.1.
Cylindrophis maculatus, 1905.3.25.76, 1931.5.13.1–5.
Cylindrophis opisthorhodos, 1946.1.16.48.
Cylindrophis rufus, IV.23.2.a, 71.7.20.207, 71.7.20.213, 1938.9.8.1, unregistered spec.
Epicrates cenchria, 74.8.4.9, 89.8.23.1.
Epicrates striatus, 55.10.16.314.
Eryx colubrinus, 1963.863, 1973.3346.
Eryx conicus, (Rage 1972, places this species in *Gongylophis*), 46.11.22.9, 1955.1.2.67.
Eryx jaculus, 97.10.28.539.
Eryx jayakari, 1971.1655.
Eryx johnii, 1921.6.15.10.
Eunectes murinus, IV. 13.1.c, 1924.2.28.14.
Liasis amethistinus, (McDowell 1975:31, places this species in *Python*), 70.8.31.148, 95.10.17.36, 1913.11.1.94, 1969.2630.
Liasis childreni, 51.2.12.10, 90.12.2.22.
Liasis fuscus, 79.11.7.1, 1922.11.24.30.
Liasis olivaceus, 58.10.25.18.
Loxocemus bicolor, 1914.1.28.124.
Melanophidium punctatum, 97.7.19.9.
Melanophidium wynaudense, 1914.1.26.6.
Morelia argus, 63.7.29.24, 97.12.10.109. 1970.2387.
Platyplectrurus madurensis, 1923.10.13.29–31.
Plectrurus aureus, 89.7.6.7–8.
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Tropidophis melanurus, 58.4.20.65.
Uropeltis arcticeps, 93.4.18.4, 97.7.19.1.
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Comments on the intermandibular muscles of snakes

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Introduction

During a recent investigation into the morphology of the superficial palate of henophidian snakes (Groombridge 1979), dissections of the lower jaw muscles of several species were performed in the course of fully exposing the palate to ventral view. Some discrepancies became apparent between my findings regarding some of these muscles and those of certain previous workers. Although a degree of variation is to be expected in biological specimens, it appears that some misinterpretations may have been made on previous occasions. It is the purpose of this paper to make appropriate corrections, and to report some new variations of possible systematic significance.

In particular, this report is concerned with the *M. intermandibularis anterior* and the *M. transversus branchialis*, both terms in the usage of Cowan and Hick (1951). Their terminology for the intermandibular muscles of snakes has been used by several recent workers, e.g. Frazzetta (1966), Kardong (1973), and partly by Albright and Nelson (1959 a). Some comments are also made on the *M. protractor laryngeus* (Karlstrom 1952), and the *M. geniomyoideus*, a muscle described by Camp (1923) in anguimorph lizards, and subsequently described by McDowell (1972) in snakes. Attention is not given here to other small muscles (the 'constrictors' of Langebartel 1968, p. 82), attaching to the lateral sublingual glands, which are sometimes closely associated with the *intermandibularis anterior*.

All specimens used in this study are in the collection of the British Museum (Natural History). The muscles were exposed ventrally by reflecting the skin of the lower jaw posteriorly, after making an incision adjacent to the dorsal margin of the sublabial scales around the perimeter of the lower jaw. Although this method conserves the appearance and usefulness of the specimen for general taxonomic work, it means that only the anterior parts of the throat muscles can be adequately investigated. Dissections were carried out under a binocular microscope.

General morphology of the intermandibular muscles

The *intermandibularis* muscle of jawed vertebrates typically arises from the ventral or medial surface of the mandible, and inserts, with that of the opposite side, on a mid-ventral raphe in the throat region (Edgeworth 1935). In amphibians, reptiles other than Squamata, and birds, the *intermandibularis* ('mylohyoideus' of several authors) tends to form a simple, thin, superficial sheet of transverse muscle fibres. The muscle is derived during ontogeny from the ventral part of the mandibular muscle plate (Edgeworth 1935), and is innervated largely or entirely by the trigeminal nerve. The Squamata differ from other tetrapods in that the continuity of the *intermandibularis* sheet is interrupted by the interdigitation of one or more slips of the usually deeper hypoglossal-innervated *M. geniohyoideus*

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('mandibulohyoideus' of Oelrich 1956; 'ceratomandibularis' of Langebartel 1968. See Camp 1923, McDowell 1972). These slips pass postero-dorsally from an origin on the mandible superficial to the *intermandibularis*, penetrate the *intermandibularis* sheet, and insert more deeply on the hyoid apparatus. Typically in snakes (fig. 5, p. 486), there remains only one weakly-developed slip of the *intermandibularis* superficial to the *geniohyoideus* (the latter usually now forming an anterior portion of a complex muscle, the *neurocostomandibularis*; Langebartel 1968), even this slip is absent in many taxa. The rest of the *intermandibularis* is either deep to the *geniohyoideus*, or anterior to it; thus the relationship of these two muscles, with respect to depth, is largely reversed in snakes, and partially so in lizards, as compared with other tetrapods. Cowan and Hick (1951) divide the *intermandibularis* (of *Thamnophis*, a genus of natricine snakes) into three groups (see fig. 5). The first of these, the *M. intermandibularis posterior*, comprises two slips originating on the posterior part of the mandible and running antero-medially; the *pars posterior* superficial to the *geniohyoideus*, and the *pars anterior* deep to it. The second group, the *M. intermandibularis anterior*, comprises two slips originating at the anterior tip of the mandible, and running postero-medially, anterior to the *geniohyoideus*; the *pars anterior* and the *pars posterio.* Their third group is represented by the *M. transversus branchialis* (see below). This paper is primarily concerned with the *M. intermandibularis anterior*, hereafter abbreviated to *ima*, and the *M. transversus branchialis*.

Most Henophidia and Caenophidia are unusual among tetrapods in showing pronounced inter- and intra-mandibular kinesis. In these snakes the *intermandibularis*, in particular the *ima*, probably acts mainly to adduct the tips of the mandibles and raise the floor of the mouth, thus generally helping to maintain an effective grip during prey ingestion (Albright and Nelson 1959 b). The precise actions and adaptive significance of the various *intermandibularis* slips requires considerable further study. It will be shown in the following section of this paper than an *ima*, *pars posterior* is absent in several Henophidia. It is here suggested that the addition of a *pars posterior*, and the insertion of an enlarged *ima*, *pars anterior* onto an intermandibular ligament (in acrochordids, where the ligament is largely paired, probably secondarily, and in Caenophidia) may constitute progressive sophistications of the feeding apparatus of snakes. These two modifications, along with liberation of the tips of the mandibles and the ability to spread laterally the quadrate-mandibular articulation, are probably key factors in the mechanism of unilateral feeding (Gans 1961). In other tetrapods the *intermandibularis* acts mainly to raise the floor of the mouth; this motion may be variously involved in olfaction, respiration, or prey manipulation (in mammals, the anterior belly of the *digastricus*, a jaw-opening muscle, appears to be derived from the *intermandibularis*).

The *M. transversus branchialis* of snakes appears to be innervated by the trigeminal, and is likely to have been derived during phylogeny from the *intermandibularis* (Cowan and Hick 1951, p. 47). This muscle has an anterior attachment to the posterior end of the lateral sublingual gland and partly to the adjacent oral mucosa. It then passes posteriorly, looping laterally around the hypoglossal-innervated *geniotrachealis* and *genioglossus*, and turns medially to a ventral mid-line attachment in association with the *intermandibularis* and the skin of the throat (see *tb* in fig. 5). The *transversus branchialis* is present in all snakes adequately reported in the literature, and in all snakes I have examined (including Scolecophidia, where the posterior attachment is somewhat modified; work in progress). It has been termed 'portion f' of the symphyseal part of the *intermandibularis* by Lubosch (1933); the 'mentalis' by Sondhi (1958, p. 184); the 'dilator' of the lateral sublingual gland by Langebartel (1968, p. 82) and the 'intermandibularis posterior dorsalis' by Gibson (1966, p. 36).

This muscle attaches only to soft tissue, and not directly to any bony element. It may function to stretch, and thus assist to empty, the lateral sublingual gland (perhaps antagonistically to the 'constrictor' muscle fibres attaching to the anterior of the gland), and also to resist excessive dilation of the soft tissues of the throat during prey ingestion.

Camp (1923) figures a muscle that I would identify as a *transversus branchialis*, in the scolecophidian *Typhlops congestus* (=*T. punctatus congestus*), as the 'mylohyoideus anterior superficialis'. He also figures a muscle of the same name in lizards of several families (Anguidae, Cordylidae, Helodermatidae, Iguanidae, Lacertidae, Scincidae, Xenosauridae). He only illustrates the superficial aspect of the throat muscles, and nowhere describes or figures the entire course of the muscle, so it is not clear if he was aware of the detailed similarity between the muscle in *Typhlops* and in lizards. In at least one anguid, *Gerrhonotus caerulus* (personal observation), the origin anteriorly is actually from the posterior end of the lateral sublingual gland and the adjacent oral mucosa. The muscle in this lizard is thus identical in its course to the *transversus branchialis* of snakes. Oelrich (1956, p. 49) describes somewhat similar fibres in the iguanid *Ctenosaura pectinata*. The possibility should be considered that the similar muscle found in diverse lizards and all snakes is in fact homologous in each case, and that the presence of this muscle is a primitive state, not only for lizards (as suggested by McDowell 1972, p. 200), but for Squamata as a whole.

The M. intermandibularis anterior and the M. transversus branchalis in Henophidia and Caenophidia

Langebartel (1968, p. 76) reported that the *ima* is present in most snakes, "but is distinctly missing in *Anilius* and *Xenopeltis*, and is represented only by a tendon in the uropeltid *Rhinophis*". His illustrations of *Cylindrophis rufus* and *C. maculatus* (his figs. 12B and C) show a muscle labelled '*ima*' (*intermandibularis anterior*) apparently arising from the dentary and passing posteromedially to insert in the ventral mid-line in association with the *intermandibularis posterior*. In my examples of these species (*C. rufus*, fig. 1) a muscle is present with the same posteromedial insertion, however it does not attach anteriorly to the dentary, but passes close to it before looping dorso-medially around the *genio-trachealis* and *genioglossus* to attach to the posterior end of the lateral sublingual gland (and some fibres to the oral mucosa, particularly *C. maculatus*). This muscle is thus correctly identified as the *transversus branchialis*, and does not represent the *ima*.

McDowell (1972) has given an important account of the tongue and associated structures in lizards and snakes, and his ideas on their evolution. However, it appears that there has again been a similar misinterpretation. In McDowell's fig. 21, of *Loxocemus bicolor*, there is shown a muscle labelled 'IMA 2'. It is apparent from his text that this is intended to refer to a muscle generally termed the *ima, pars posterior*, although called the 'intermandibularis anterior, pars medialis' by McDowell. He states (p. 254), "in *Loxocemus*, it arises from the region of the splenial and dentary just anterior to the intramandibular hinge and runs backwardly and medially to insert on a pad of connective tissue just beneath the orifice of the outer sheathing fold of the tongue". In my specimens (*L. bicolor*, fig. 2) there is a muscle with the same postero-medial attachment as his 'IMA 2' but which anteriorly passes close to the dentary, and then (apart from a few fibres to the oral mucosa) loops dorso-medially around the *geniotrachealis* and *genioglossus* to attach to the posterior end of the lateral sublingual gland. This muscle is thus likewise correctly identified as the *transversus branchialis*, and does not represent the *ima*.

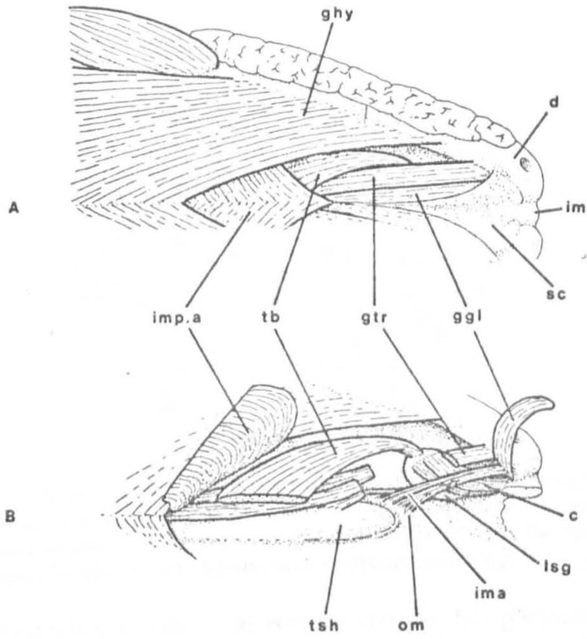

Fig. 1. *Cylindrophis rufus*. In this and other figures, certain muscles associated with the throat and mandibles are shown in ventral view. The animals' right side is toward the top of the page, the left side is not completed. Anterior is to the right. The uppermost view (A) is the most superficial, after removal of the skin and some connective tissue. The superficial connective tissue in the symphyseal region (*sc*) is left in place in A of fig. 1. Deeper dissections are shown in the lower views (B; and C in fig. 5) where the separation of the various components is exaggerated. In figs. 1 and 2, the muscle here identified as the *transversus branchialis* (*tb*) is shown with adjacent muscles in place in A; in B, the *imp.a* has been cut along the mid-line, the right-hand section is shown reflected. A segment has been removed from both the *gtr* and *ggl* (the latter reflected at its origin). The attachment of the *tb* to the lateral sublingual gland (*lsg*) is thus exposed. The *iml* is bisected in B of fig. 1. Note the thin undivided *intermandibularis anterior* (*ima*). Abbreviations for all figures: *c*, 'constrictor' muscle attaching to lateral sublingual gland; *d*, dentary; *ggl*, M. genioglossus; *ggl.l*, lateral head of genioglossus; *ggl.m*, medial head of genioglossus; *ghy*, M. geniohyoideus (in most forms figured here this muscle participates in the M. neurocostomandibularis complex, for uniformity it is here labelled *ghy* throughout); *gtr*, M. geniotrachealis; *ima*, undivided M. intermandibularis anterior; *ima.a*, M. intermandibularis anterior, pars anterior; *ima.p*, M. intermandibularis anterior, pars posterior; *iml*, intermandibular 'ligament'; *imp.a*, M. intermandibularis posterior, pars anterior; *imp.p*, M. intermandibularis posterior, pars posterior; *lsg*, lateral sublingual gland; *mc*, Meckels cartilage; *om*, oral mucosa; *pl*, M. protractor laryngeus; *sc*, superficial symphyseal connective tissues; *tb*, M. transversus branchialis; *tr*, trachea; *tsh*, tongue sheath.

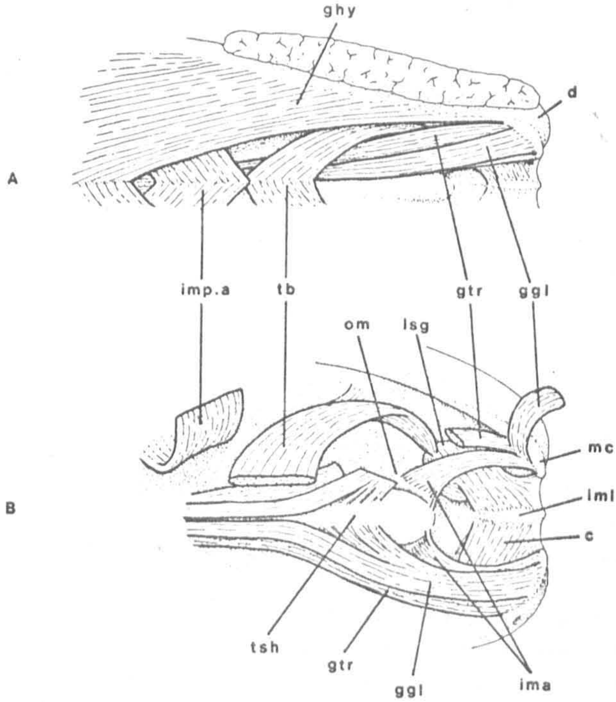

FIG. 2. *Loxocemus bicolor*. Note that the muscle here identified as the *transversus branchialis* (*tb*) shows the course typical for this muscle, and has no attachment to the dentary. Note also the *ima*, slightly exposed medial to the *ggl*, and compare with the much greater exposure in pythons (*Liasis*, fig. 3). Abbreviations listed under fig. 1.

Lubosch (1933) illustrates a muscle in several snakes, his portion 'f' of the *intermandibularis* group, that appears to be the same muscle as that subsequently termed the *transversus branchialis*. The course of this muscle is described specifically only for *Naja 'tripudians'* (*N. naja*). Lubosch notes (p. 618), "Der ursprung der transversalen Portion (f) liegt nicht mehr am Unterkiefer, sondern an der Kapsel der Glandula labii inf. (=lateral sublingual gland)". This would imply that the origin of the *transversus branchialis* in the other species in which Lubosch found the muscle is not from the lateral sublingual gland but from the lower jaw. This condition is clearly shown in his fig. 22 of '*Dryophis*' (*Ahaetulla*) and fig. 27 (a natricine) and also seems to be shown in his fig. 26 of *Cylindrophis maculatus*. I have examined an *Ahaetulla nasuta* (his was not identified to species); two Ceylon natricines, *Amphiesma stolata* and *Xenochrophis piscator* (his '*Tropidonotus*' was from Colombo); *Cylindrophis maculatus* (4 specimens) and *C. rufus* (3 specimens). In all cases the *transversus branchialis* has the typical course, noted above, and described correctly by Lubosch for *Naja naja*.

Lubosch (1933) also illustrates, but does not describe, some muscle fibres in *Cylindrophis maculatus* (his fig. 26) labelled 'b' and 'c' of his 'symphyseal portion' of the *intermandibularis*. As shown by Lubosch, these fibres closely resemble the typical *ima* of Caenophidia (e.g. *Xenochrophis*, fig. 5). These fibres were definitely not present in the *Cylindrophis* specimens (fig. 1) examined here (although it is suggested below that the *ima* is probably represented in this genus by some deep fibres, not shown by Lubosch). I am unable to account for the apparent presence of caenophidian-type *ima* fibres in *Cylindrophis*, as figured by Lubosch. It is perhaps not unreasonable to suggest, in view of the probably errors in observation made by Lubosch concerning the origin of the *transversus branchialis* (as noted above), that he may have mistaken some of the connective tissue extending from the symphyseal region for muscle fibres. An alternative explanation is that his specimen was misidentified, but *Cylindrophis maculatus* is a rather distinctive animal. Lubosch's figure of *C. maculatus* was reproduced with new labelling in the recent major review by Haas (1973).

The above observations appear to establish that *Cylindrophis maculatus* and *C. rufus* lack a typical *ima*. It was initially supposed that this is a resemblance to *Anilius*, uropeltids and *Xenopeltis*, in that they apparently lack an *ima*, as reported by Langebartel (1968). However, further investigation revealed that *Cylindrophis*, and also *Anilius*, *Xenopeltis*, and at least *Melanophidium* and *Platyplectrurus* among uropeltids, do in fact possess a thin variably-distinct band of muscle fibres with the same course as the more definite *ima* of *Loxocemus* and pythons, and the anterior portion (*pars anterior*) of the *ima* of *Calabaria*, most boas (*s.l.*), acrochordids and Caenophidia (insertion modified in the latter two taxa, see below). At present, there seems to be no compelling reason not to accept the homology of the muscle fibres found in these groups; accordingly, they are here provisionally assigned to the *ima*.

In *Cylindrophis rufus* (fig. 1) the muscle arises from the tip of the dentary just dorsal to the *genioglossus* and passes posteriorly to insert on the oral mucosa just lateral to the anterior tip of the tongue sheath (adjacent to its opening into the oral cavity). A few fibres appeared to join the *geniotrachealis* and the *genioglossus*. *C. maculatus* is very similar, but in one specimen the muscle was represented by only a very few diffuse fibres. *Melanophidium punctatum* and *Platyplectrurus madurensis* are also similar, but as with the *genioglossus*, the origin of the suggested *ima* is mostly from the connective tissue between the tips of the mandibles. In the probably more derived uropeltids, *Pseudotyphlops philippinus* and *Uropeltis arcticepts*, this muscle was not definitely seen; this group may thus be the only one in which the *ima* is entirely lacking, but this requires confirmation in further specimens. *Anilius* resembles the less derived uropeltids in that the origin of the *genioglossus* and of the *ima* (dorso-laterally) is from the connective tissue between the tips of the mandibles. In the *Anilius* figured by Langebartel (1968, fig. 12 A) the origin of the lateral head of the *genioglossus* is from the dentary. As in the other forms a very few fibres appeared to continue past the insertion on the oral mucosa to join the *geniotrachealis*. In *Xenopeltis* the muscle has an origin partly exposed dorso-medial to that of the *genioglossus*, on the tip of the dentary. The insertion is quite similar to that in the other forms, but near this point the muscle is only poorly separable from fibres of the medial head of the *geniotrachealis* (in the specimens of *Xenopeltis* examined the latter was divided into two parallel heads at its origin), and some fibres appeared to continue posteriorly with the *geniotrachealis*.

As noted above, *Loxocemus* has a very similar muscle (fig. 2), but it differs in being somewhat better developed and more clearly defined. The origin is similar to that of *Xenopeltis* in its partial exposure dorso-medial to the origin of the *genioglossus*, but in *Loxocemus* both muscles arise largely from the exposed tip of Meckel's cartilage. The insertion is as described for the other taxa above, with the exception that a very few fibres insert on the tongue sheath itself, and no fibres were definitely seen to join the *geniotrachealis*. It appears from McDowell's text (1972, pp. 252, 253) that this muscle may possibly correspond to at least some of the fibres labelled 'IMA 1' ('intermandibularis anterior, pars anterior' *sensu* McDowell) in his fig. 21.

In the true pythons (i.e. not *Calabaria*) examined the *ima* arises from the tip of Meckel's cartilage, mostly or entirely anterior to the origin of the *genioglossus*, and passes posteriorly closely parallel with the *genioglossus* to an insertion on the oral mucosa, just lateral to the anterior part of the tongue sheath adjacent to the position of its oral aperture (*Liasis amethistinus*, fig. 3). In *Aspidites melanocephalus* much of the origin of the muscle was more clearly dorsal to that of the *genioglossus*, and the muscle was thus more closely adjacent to the *geniotrachealis*. In *Aspidites*, *Liasis* and *Python sebae* a very few fibres appeared to continue posteriorly past the major insertion to join the *geniotrachealis*. In *Liasis amethistinus* a very few of these fibres turned antero-medially again from a point postero-lateral to the larynx, to fan out over the posterior extremity of the *M. dilator laryngis*, (thus somewhat resembling the insertion of the *M. protractor laryngeus* of Caenophidia, see below). In contrast to the report of Frazzetta (1966, p. 246), with reference to *Python molurus* and *P. sebae*, in none of my three specimens of *P. sebae* (from separate localities) did the *ima* join the *transversus branchialis* posteriorly.

The *ima* of pythons differs from the muscle found in the 'lower' Henophidia noted above in its greater development and typically in its greater exposure ventrally (i.e. its course is mostly medial to, rather than deep to, the *genioglossus*).

In *Calabaria* and most boas examined (*Epicrates cenchria*, fig. 4) a small muscle similar in its course to the *ima* of pythons is found, with a major insertion on the oral mucosa lateral to the anterior end of the tongue sheath (and occasionally associated with the lateral sublingual gland). Gibson (1966), describing the head muscles of *Boa constrictor*, does not appear to recognise this particular muscle, but I am uncertain of this in the absence of illustration; the muscle in my specimen of this species was rather poorly defined. In *Bolyeria* the origin is mostly dorsal to that of the *genioglossus*. In *Candoia asper*, *Tropidophis caymanensis* and *T. haetianus*, the origin is entirely dorsal to the *genioglossus* (and to the *geniotrachealis* in *Tropidophis*). In *Tropidophis* the muscle is relatively thin and weakly developed, it was not found at all in *Trachyboa boulengeri*. In *Calabaria* and the remaining boas the origin is ventral or ventro-medial to that of the *genioglossus*. In *Boa constrictor* and *Eunectes murinus*, a few of the anterior-most fibres have a median insertion on the posterior portion of a moderately developed connective tissue ridge present on the ventral surface of the oral mucosa between the widely separable tips of the mandibles. In *Epicrates cenchria* some slightly deeper fibres, posteriorly associated with the lateral sublingual gland, divert onto the ridge. This structure, termed the 'intermandibular ligament' by Cowan and Hick (1951) or the 'inter-ramal pad' by Langebartel (1968)†, is weakly developed in pythons and most boas but typically well developed in Caenophidia. In several species (e.g. *Epicrates cenchria*, *Sanzinia madagascariensis*) a very few *ima* fibres continued posteriorly to join the *geniotrachealis*. In most species, some fibres, not clearly separable at the origin, diverged posteriorly to join the *genioglossus*, resembling the medial head of the *genioglossus* frequent in Caenophidia. In *Calabaria* and *Charina*, these fibres were more closely associated at their origin with the larger lateral head of the *genioglossus*.

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† The former term is used here, but in a very general manner; perhaps a distinction should be made between the tough connective tissue directly joining the tips of the mandibles in some lower Henophidia (e.g. *Cylindrophis*), and the more elongate structure (not strictly a ligament) lying mainly in the soft tissues of the floor of the mouth in most forms with pronounced intermandibular kinesis (e.g. Caenophidia).

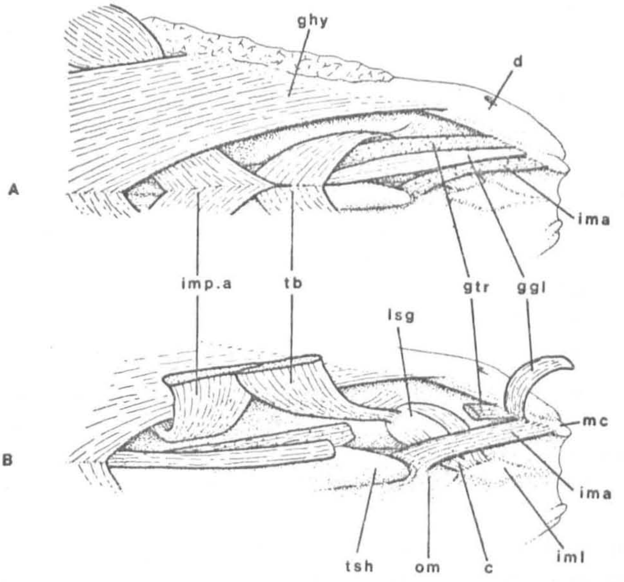

FIG. 3. *Liasis amethistinus*. In B of this and the remaining figures, the *imp.a* and *tb* are reflected together laterally from their mid-line attachment. Note the course of the relatively broad undivided *ima*, largely exposed medial to the *ggl* (shown in A), and compare with the divided *ima* of subsequent forms. As in figs. 1 and 2, a segment is removed from both the *gtr* and *ggl* (the latter reflected at its origin). Abbreviations listed under fig. 1.

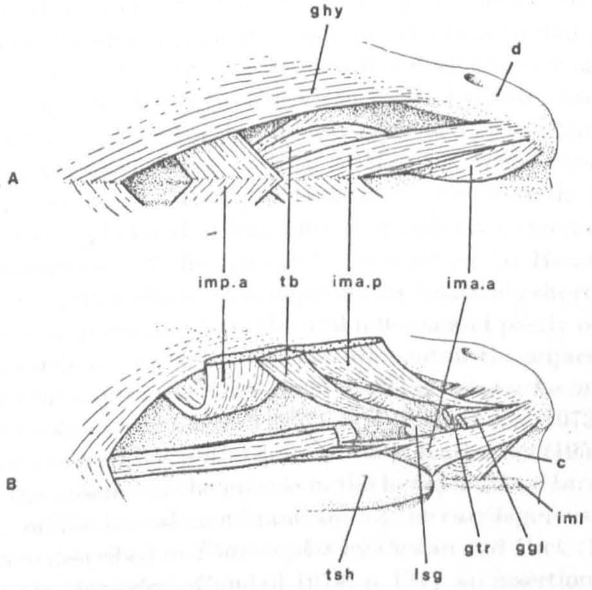

FIG. 4. *Epicrates cenchria*. Compare with fig. 3, and note here the presence of a divided *ima*, with a *pars posterior* (*ima.p*), whose posterior mid-line attachment is shared with the *imp.a* and *tb*, and a *pars anterior* (*ima.a*). The latter is similar in its course to the undivided *ima* of pythons, but typically has the origin (on the dentary) superficial to that of the *ggl*. As in figs. 1–3, a segment is removed from both the *gtr* and *ggl*. Abbreviations listed under fig. 1.

In *Acrochordus javanicus* and *Chersydrus granulatus* a rather more bulky muscle arises from the tip of the dentary. Like Caenophidia, but unlike other Henophidia (with the partial exception of some large boas, noted above), the fibres of this muscle have a more antero-medial insertion onto a well-developed intermandibular ligament. In contrast to all examined Caenophidia, and apparently unique to *Acrochordus* and *Chersydrus*, this ligament is not a single median structure, but is deeply bifurcate posteriorly, where it forms two parasagittal portions. This may be correlated with the specialized mental and rostral regions (see Smith, 1943, p. 132, for figure of head). Arising from the posterior end of each arm of the intermandibular ligament are two thin bands of muscle fibres that run posteriorly to join the *genioglossus* (as a medial head) and the *geniotrachealis* (with some fibres to the oral mucosa). Also arising from this position are a few fibres having an insertion similar to that of the *ima* of pythons and lower Henophidia, and to that of the more anterior of the two portions of the *ima* (see below) of *Calabaria* and boas. Thus although their various attachments are similar to those of other Henophidia, the *ima* (anterior portion) fibres in acrochordids radiate from the prominent, but largely paired, intermandibular ligament.

In Caenophidia (e.g. *Xenochrophis piscator*, fig. 5), the anterior-most muscle fibres arising from the tip of each dentary insert entirely on a single median intermandibular ligament. This ligament would seem to be a further development of the structure (frequently serving as an origin for the lateral sublingual gland 'constrictors'), found in, e.g., pythons and boas. Since some large boas show an incipient caenophidian state, and since the largely paired ligament in acrochordids appears to be associated with the specialized mental region, it is perhaps more likely that the acrochordid state is a derivative of the caenophidian state rather than a precursor of it. Also, in a single *Acrochordus* (from Thailand, BMNH 1966.12), there was found a single median ligament, appearing identical to that of Caenophidia. A third alternative is that they may be independent derivations from a boid condition.

Since in Caenophidia there is typically a single median intermandibular ligament, the origin of each medial head of the *genioglossus* (when present) are close together in the mid-line, at the posterior extremity of that ligament. Fibres similar to the posterior fibres that in many Henophidia are associated with the *geniotrachealis* are present in the Caenophidia that have been adequately examined, and also arise from the posterior end of the ligament. In contrast to Henophidia, including *Acrochordus*, these latter fibres in Caenophidia are relatively shorter, do not join the *geniotrachealis*, and insert partly on the oral mucosa and partly over the ***M. dilator laryngis*** of the intrinsic laryngeal musculature, and/or the adjacent portion of the trachea. These fibres appear to correspond to the *M. protractor laryngeus* described by Kardong in *Crotalus* and *Elaphe* (1972), and *Agkistrodon* (1973). The name used by Kardong derived from the initial description of Karlstrom (1952, not seen). Both authors noted the absence of the muscle in the henophidian *Charina*. Similar fibres that insert "... on the buccal membrane and/or the cartilaginous ring surrounding the glottis", were described in *Thamnophis* by Cowan and Hick (1951, p. 30). Such fibres also occur in *Opheodrys* (Cundall 1974, p. 131), an insertion on the laryngeal region was not reported, but is present in a specimen of *O. vernalis* examined (personal observation). A *protractor laryngeus* is consistently present, although frequently quite thin and obscured by connective tissue, in all other Caenophidia examined in the present study. This muscle may function, with the *geniotrachealis*, to protract the larynx and anterior part of the trachea clear of the prey during deglutition.

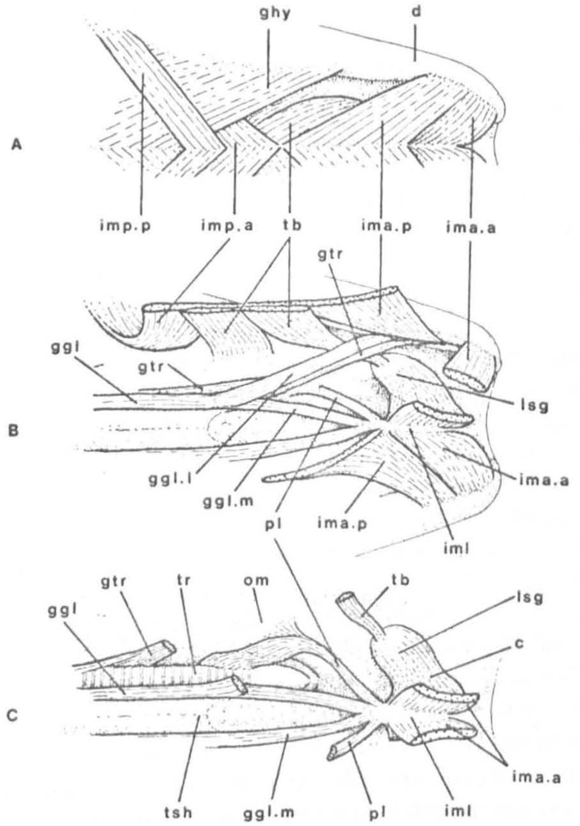

FIG. 5. *Xenochrophis piscator*. Note the presence of a divided *ima*, with the insertion of the *ima.a* onto the single postero-median extension of the intermandibular ligament (*iml*). In B, a segment of the *ima.a* is removed on the animals' right. In C the trachea is exposed dorso-lateral to the tongue, note the presence of a *protractor laryngeus* (*pl*); most other muscles, including the lateral head of the *ggl* (*ggl.l*) and *gtr*, are removed. Abbreviations listed under fig. 1.

In *Calabaria*, all boas, acrochordids (not pythons or remaining Henophidia), and Caenophidia, the *ima* is divided into two portions; the *pars anterior* and *pars posterior* (of Cowan and Hick 1951). The single *ima* of *Anilius*, *Cylindrophis*, uropeltids, *Xenopeltis*, *Loxocemus*, and pythons, has a course corresponding to that of the *ima*, *pars anterior* of those forms with a divided *ima* (except that the insertion is modified in acrochordids and Caenophidia). The *pars posterior* arises from the dentary superficial to the *genioglossus* and/or *geniotrachealis*, and passes postero-medially to a ventral mid-line insertion in association with that of the *transversus branchialis* and the *intermandibularis posterior*, and to a variable extent on the skin of the lower jaw. In some Caenophidia, the anterior-most fibres may insert on the posterior extremity of the intermandibular ligament. The major insertion of the *pars posterior* is always at a more superficial level, and largely or entirely posterior, to that of the *pars anterior* (the latter inserting more deeply, on the oral mucosa, in *Calabaria* and boas; or on the intermandibular ligament in Caenophidia). In most cases the two *ima* portions are more or less confluent at their origin on the dentary. In some Caenophidia the *pars anterior* and *pars posterior* are not clearly separate, e.g., Albright and Nelson (1959a) regard these fibres as a single muscle ('pars cutaneomandibularis') in *Elaphe obsoleta*, but the two portions are clearly separable in the related *Coluber viridiflavus* (personal observation). When there is a superficial appearance of a single muscle, a clear division is frequently found upon deeper dissection. Even if a clear division is not found the two different regions of insertion, appropriate for each portion, are still maintained. The single muscle of some Caenophidia is morphologically unlike the single muscle of pythons and lower Henophidia. I believe that where it does occur in Caenophidia, it is due to a secondary fusion of the two portions.

The only notable departure from the typical caenophidian condition encountered in the present study occurs in *Dasypeltis*. Here the *ima* is single, and the insertion resembles that of the *ima, pars posterior* of other Caenophidia (and with some fibres onto the hyoid lingual process in one specimen). There is no anterior portion inserting on the intermandibular ligament. This muscle was described by Gans (1952, p. 223) thus, "a pair of muscles runs from the lower surface of the dentaries' tips and attaches to the skin folds between the first pair of chin shields at their posteriormost point of junction". The intermandibular ligament and associated sublingual gland 'constrictors' are very prominent, and, unlike the situation in other Caenophidia, are exposed (in ventral view) in the mid-line between the right and left *ima*. The *ima* fibres are relatively long, and lie nearly in a longitudinal plane.

Very probably the *Dasypeltis* condition is related to the egg-eating habits of these snakes. The lack of the typically short and nearly transverse *ima, pars anterior* fibres (that in other Caenophidia appear to form one restraint on the extent to which the mandibles can separate from each other), would perhaps allow the longer fibres of the remaining *ima* portion to swing open into a mechanically advantageous transverse plane as the tips of the mandibles are spread widely apart during egg ingestion.

The *Dasypeltis* condition is almost certainly derived in relation to other Caenophidia. The condition to be found in *Elachistodon*, a possible relative of *Dasypeltis* (Rosenberg and Gans 1976), but very scarce in collections, is thus of some interest.

The variations in the condition of the *ima* and *protractor laryngeus* recorded above can be expressed as three separate characters, as follows:

Character A: divisions of the *ima*

State 1, undivided *ima* present; typically weakly developed, mostly deep to the *genioglossus* (except, e.g., *Loxocemus*, where the *ima* is partly exposed medial to the *genioglossus*); *Anilius*, *Cylindrophis*, *Loxocemus*, *Melanophidium*, *Platyplectrurus*, *Xenopeltis*.

State 2, undivided *ima* present; better developed, mostly exposed medial to the *genioglossus*: *Aspidites*, *Liasis*, *Python*.

State 3, *ima* divided into *pars anterior*, with a deep insertion corresponding to that of the undivided *ima* of other forms (modified in acrochordids and Caenophidia, see *Character B*), and *pars posterior*, with a more superficial insertion: *Calabaria*, boas, acrochordids, Caenophidia (except *Dasypeltis*, see above).

Character B: insertion of *ima*, *pars anterior*

State 1, *ima, pars anterior* inserts entirely, or almost entirely, onto the oral mucosa, between the lateral sublingual gland and the anterior portion of the tongue sheath: *Calabaria*, boas.

State 2. *ima*, *pars anterior* inserts into the postero-medial portion of the intermandibular ligament (paired in acrochordids); acrochordids, Caenophidia (except *Dasypeltis*, see p. 487).

Character C: M. protractor laryngeus

State 1. *protractor laryngeus* absent (or fibres possibly corresponding to the true *protractor laryngeus*, entirely, or mostly, joining the *geniotrachealis*); all taxa except Caenophidia.

State 2. *protractor laryngeus* present, its fibres separate from the *geniotrachealis*; Caenophidia.

Regarding the distribution of states of Character A (divisions of the *ima*), the groups of taxa so produced are of interest firstly in purely phenetic terms. The taxa possessing a thin *pars anterior* only are those included by McDowell (1975) in his superfamily Anilioidea, apparently defined on a largely phenetic basis. True pythons, a phenetically well defined group (see Underwood 1976), share a similar condition of the *pars anterior*, in that it is more distinctly developed than in the 'anilioids' (*sensu* McDowell 1975).

The phenetic difference between pythons and *Calabaria*, and the resemblance of the latter to boas, would give independent support to Underwood's recent classification of boids (1976), based largely on a numerical phenetic approach, in which *Calabaria* is separated from the Pythoninae. This difference is also consistent with Underwood's cladistic arrangement (1976, p. 168) in which *Calabaria* is placed intermediate between pythons (primitive) and boas (more derived); and with the present author's study of the superficial palate (Groombridge 1979) in which respect *Calabaria* differs from pythons and resembles *Eryx* and *Charina* among boas.

Interest would be further enhanced, for those concerned with snake phylogeny, were a cladistic arrangement of these character states possible. This requires making a decision on the primitive to derived polarity of the character state transformations; this must be a matter for some debate, but I suggest that a reasonable initial hypothesis can be put forward.

One proposal, apparently supported by Langebartel (1968, pp. 76, 77), would be that the caenophidian condition (State 3), which occurs in the greatest number of species, is the most primitive. I suggest that the opposite conclusion may be better supported by available evidence, namely that State 1, (presence of a thin undivided *ima*), is the primitive state, while the caenophidian state is the most derived.

Scolecophidia seem primitive to other extant snakes in possessing a common foramen for the maxillary and mandibular branches of the trigeminal, in lacking an antero-median pillar of the frontals between the olfactory tracts (McDowell 1967), and in lacking an anterior toothed ramus of the palatine. The intermandibular muscles of Scolecophidia differ from those of all other snakes, and in general are more lizard-like (Langebartel 1968, p. 86, McDowell 1972, personal observation). They do however possess a very small muscle somewhat similar in its course to the undivided *ima* of lower Henophidia such as *Anilius* and *Cylindrophis*. It is very deep in position, and overlain by the superficial transverse *intermandibularis* slips. I am uncertain at present if it is the 'same' muscle (further work on scolecophidian throat muscles is in progress). Perhaps the subsequent joint ancestry of Henophidia and Caenophidia passed through a phase in which the anterior parts of the superficial *intermandibularis* were lost (assuming they were present in the ancestry of snakes as a whole), possibly in connection with burrowing. The extant henophidians that lack very distinct intermandibular kinesis are also those with a very thin individed *ima* (e.g. *Anilius, Cylindrophis, Melanophidium*), and are adapted to a varying degree to burrowing habits. The *ima* of Henophidia and Caenophidia may have been progressively developed during subsequent aboveground radiations with emphasis on the ingestion of large size prey items.

The suggestion that the presence of a thin undivided *ima* is primitive for Henophidia and Caenophidia is based largely on the fact that *Anilius, Cylindrophis, Loxocemus, Xenopeltis*, and uropeltids, between them also show various states of other characters that are frequently interpreted as primitive (Bellairs and Underwood 1951, Haas 1955, Rieppel 1977, Underwood 1967), and which in some cases resemble states seen in the late Cretaceous fossil *Dinilysia* (Estes, Frazzetta, and Williams 1970). Boas are more derived in respect of several characters (Frazzetta 1975, Underwood 1976), including the superficial palate (Groombridge 1979); this suggests that possession of a *pars posterior* may be a derived state also. Pythons are intermediate in the balance of several characters, and appear to be intermediate also in respect of the *ima*.

There is no evidence to suggest that a *pars posterior* has appeared in more than one lineage; the presence of an *ima, pars posterior* would thus qualify as a synapomorphy demonstrating the monophyly of the group composed of *Calabaria*, boas, acrochordids, and Caenophidia.

At least two major alternatives to this proposal are possible if it is suggested that the caenophidian state (State 3) is actually the most primitive. This would imply either that those taxa lacking the *pars posterior* are monophyletic (*sensu* Hennig 1966), if the loss occurred only once; or that multiple losses have occurred in different lineages. The former alternative is not supported by other evidence, although it is most parsimonious in respect of the *ima*; the latter appears to be the strongest opponent to the proposed scheme.

Those taxa with both portions of the *ima* also typically show distinct or very pronounced intermandibular kinesis (although this is seen in pythons also). McDowell (1972) has termed "... the X-shaped figure ... formed by the partes mediales (= *intermandibularis anterior, pars posterior*) and partes posteriores" (= *intermandibularis posterior, pars anterior*), the 'intermandibular chiasma'. He has made the interesting suggestion that the intermandibular chiasma is of functional significance, in connection with the presence of intermandibular kinesis, in unilateral prey ingestion (Gans 1961). However, this particular formation of the intermandibular chiasma cannot, as he suggests (p. 254), be diagnostic of Alethinophidia (= Henophidia plus Caenophidia) since in *Loxocemus*, pythons, and other taxa lacking a *pars posterior*, the anterior part of the chiasma is formed solely by the *transversus branchialis*.

With regard to Character B (insertion of the *ima, pars anterior*), the suggested polarity of the character state transformations is based on the same kind of argument as for Character A. Acrochordids share with Caenophidia the insertion of the *ima, pars anterior* onto an intermandibular ligament. I suggest that this is the derived state on the grounds that this particular configuration of the anterior intermandibular muscles is found nowhere else among Squamata, and derived states of several other characters also occur in Caenophidia (Underwood 1967, McDowell 1975, Hardaway and Williams 1976). The largely paired condition of the intermandibular ligament in acrochordids has probably arisen secondarily in association with specializations of the mental and rostral regions, and related aquatic habits; it may alternatively be a precursor of the caenophidian single ligament. However the significant feature that acrochordids and Caenophidia share is the shift in the insertion of the *pars anterior*. There is no evidence to indicate that this has occurred twice; the shift in insertion of the *pars anterior* off the oral mucosa, onto the intermandibular ligament, would thus be a synapomorphy demonstrating the monophyly of acrochordids and Caenophidia. As noted above, *Acrochordus* lacks the true *M. protractor laryngeus*. The *M. protractor quadrati* is also absent (Haas 1931), this muscle is likewise absent in all other Henophidia that have been examined. It is present in all Caenophidia examined (including xenodermatines, personal observation, and other lower Caenophidia); this point has also been noted by McDowell (1975, p. 19). Acrochordids have a simple form of costal cartilage like Scolecophidia and other Henophidia; all Caenophidia examined show a derived state (Hardaway and Williams 1976, Persky, Smith and Williams 1976). Thus in lacking the *M. protractor laryngeus* and *M. protractor quadrati*, in having simple costal cartilages, and primitive states of several other characters (Underwood 1967), *Acrochordus* retains a henophidian grade of organization. Many aspects of its anatomy are unique and peculiar, and provide no information on affinities (e.g. throat muscles, Langebartel 1968; superficial palate, Groombridge 1979; mobile frontal-parietal joint, McDowell 1975, p. 41, confirmed in BMNH 1966.12).

The synapomorphy suggested above (shift in *pars anterior* insertion) is thus of some significance in indicating the cladistic position of acrochordids, namely, monophyly with Caenophidia. Two other apparently derived conditions shared with Caenophidia may be noted. Firstly, the presence of spines on the hemipenis, absent for all Henophidia other than acrochordids (but absent, probably secondarily, from scattered caenophidian taxa, and present in a very few Scolecophidia). Secondly, the form of the hyoid apparatus, with closely parallel cornua and adpressed *M. hyoglossi* found only in acrochordids, Caenophidia, and two of the 'tropidophiine' boas (*Trachyboa* and *Tropidophis*, see addendum in Groombridge 1979).

The cladistic relationship of tropidophiines and Caenophidia is an area of considerable interest (McDowell 1975, p. 15, Underwood 1976, p. 172), both these workers suggest that, despite many points of resemblance, the two groups do not share an immediate common ancestry. The reduction (*Tropidophis*), or apparent loss (*Trachyboa*), of the *ima, pars anterior*, is not inconsistent with this view. This would indicate that the shared, and almost certainly derived, resemblance in the hyoid apparatus of these two groups, although detailed, is a parallelism. If this interpretation is correct, then the form of the hyoid apparatus may be of somewhat less significance in arguing for acrochordid–Caenophidia affinities. If, as suggested here, acrochordids and Caenophidia form a monophyletic (*sensu* Hennig 1966) group, the high proportion of primitive character states retained in acrochordids would indicate that these snakes diverged very early from the common ancestry of the group. Underwood (1967, p. 67) has previously raised the possibility that acrochordids "... may have some relation to the origin of the Caenophidia from Henophidian ancestors". In contrast, McDowell (1975) suggests that acrochordids and his 'anilioids' are closely related, while Dowling (1975, p. 169) suggests that the group are really natricine caenophidians. Although the former proposal appears to deserve consideration, the latter is not supported by any significant evidence.

A possible additional derived character state (in the trunk musculature), shared by acrochordids and Caenophidia was noted by Malnate (1974, p. 229), "with the exception of *Chersydrus* (Acrochordidae) presence of the *M. transversohypapophyseus* appears to be restricted to the advanced snakes". However, the differing interpretations of Auffenberg (1966, p. 158), and Gasc (1974, pp. 109, 110), suggests that this character (homology, presence/absence, and relationships of the *M. transversophypapophyseus*) requires critical re-examination.

A fifth derived state shared by acrochordids and Caenophidia, is the absence of pelvic vestiges. This is a 'loss' state and so cannot be given great significance, and is seen elsewhere among Henophidia in uropeltids (*s.s.*), *Xenopeltis*, and Bolyeriinae. However, the hypothesis of acrochordid–Caenophidia monophyly would have the virtue of parsimony in requiring one less loss of pelvic vestiges during snake evolution.

With regard to Character C (*M. protractor laryngeus*), this muscle, in its typical form, occurs only in Caenophidia. The acrochordids make perhaps the closest approach to the caenophidian condition; as in several boids, fibres apparently homologous to the *protractor laryngeus* of Caenophidia join the geniotrachealis posteriorly, but in acrochordids many fibres also insert slightly more anteriorly, on the oral mucosa and trachea. In the Caenophidia examined, the muscle inserts more anteriorly still, on the larnyx (and frequently on adjacent portions of the trachea and oral mucosa). The presence of this muscle is rather surely a derived state, and a probably synapomorphy of the various caenophidian lineages. Only a small sample of Caenophidia have been checked for this muscle, and some variations are to be expected in such a large and diverse group, but the species examined are taxonomically widespread enough to suggest that the absence of the muscle in any caenophidian is likely to be secondary.

On the presence of a *M. geniomyoideus* in snakes

The *M. geniomyoideus* was defined by Camp (1923, p. 373) as "a cutaneous attachment of the forward part of the *genioglossus*." This muscle typically originates at the mandibular symphysis and shortly has a median insertion on the skin near the tip of the lower jaw. It may not be clearly separate from the deeper *genioglossus* near the origin. Upon contraction, the *geniomyoideus* would presumably tend to draw the soft tissues of the interramal region antero-dorsally. How this muscle acts in coordination with other throat muscles is unknown, as is its adaptive significance. The presence of this muscle was one of the features used by Camp (1923, p. 326) to characterize his superfamily Anguioidea. Haas (1960) describes a *geniomyoideus* in the anguimorph *Shinisaurus*. McDowell (1972, p. 224) suggests that a muscle described by Sondhi (1953, p. 172) in *Varanus monitor* (= *V. bengalensis*) may be a *geniomyoideus*; McDowell (p. 217) also describes a *geniomyoideus* in *Lanthanotus borneensis*. The presence of a *geniomyoideus* may thus be characteristic, not only of anguioids, but all Anguimorpha. Camp (1923, pp. 302, 454) raises the possibility that his *geniomyoideus* is the same as the 'intermaxillaris' of snakes; the latter muscle, in some Caenophidia at least, corresponds to the *ima, pars anterior* of the present paper. McDowell (1972) goes further than Camp and specifically identifies a *geniomyoideus* in snakes. The presence of this muscle in snakes, otherwise known only in anguimorph lizards, would have interesting phylogenetic implications.

Work in progress on the throat muscles of Scolecophidia indicates that the 'geniomyoideus' described by McDowell in *Anomalepis aspinosus* and *Leptotyphlops humilis* is probably the *M. transversus branchialis*. In my specimens (*Anomalepis* *mexicana*, *Helminthophis flavoterminatus*, *Liotyphlops ternetzii*, *Leptotyphlops humilis*, *L. macrolepis*, *L. maximus*, *L. melanotermus*) the muscle in question does *not* have an anterior origin from the mandibular symphysis (as McDowell indicates 1972, pp. 234, 239), but arises more deeply, from the lateral sublingual gland. The *Anomalepis aspinosus* examined by McDowell may be atypical in this respect. I would identify this muscle as the *transversus branchialis*. The muscle in Scolecophidia differs from that of other snakes only in that it passes lateral to the *genioglossus* but medial to the *geniotrachealis*, instead of lateral to both; also the insertion (although varying among the Scolecophidia) is not usually in the ventral mid-line, but somewhat more lateral, most fibres apparently terminating freely, in the fascia around the other throat muscles, and with some diffuse cutaneous connections. The 'geniomyoideus' of McDowell in *Typhlops* he states is the 'intermaxillaris' figured by Camp in *T. congestus* (= *T. punctatus congestus*). Neither the origin or insertion of this muscle correspond with those of an anguimorph *geniomyoideus*, the only points of resemblance are that both muscles are short and occur in the region of the mandibular symphysis. I can see no firm grounds for concluding that the muscle in *Typhlops* is a *geniomyoideus*. *Typhlops* also has a *transversus branchialis* like that of other Scolecophidia.

McDowell (1972, p. 252) describes a muscle in *Loxocemus bicolor*, initially called the 'intermaxillaris', but then identified as the 'geniomyoideus', and labelled as such ('GMY') in his fig. 21. This muscle could not be found in the three specimens of *Loxocemus bicolor* examined in the present study (fig. 2.). There is no muscle present whose fibres originate "... at the extreme tip of the jaw ... cover the ventromedial surface of the genioglossus medialis" (the major, lateral, head of the *genioglossus* of snakes), and run "longitudinally to an insertion on the skin in the vicinity of the mental groove". There is a band of tendinous connective tissues linking the tip of each dentary with the skin of the lower jaw, with a somewhat similar course, but this is hardly to be confused with muscle fibres, and is of virtually constant occurrence in snakes.

McDowell also figures a muscle labelled 'GMY', for *geniomyoideus*, in the caenophidian *Diadophis punctatus* (his fig. 22). In this case there is no question about the existence of the muscle, it is the muscle herein termed the *ima*, *pars anterior*, in its typical caenophidian form (e.g. *Xenochrophis*, fig. 6.). It would appear from the text of Sondhi (1958, p. 184) that this is the muscle he terms 'intermaxillaris', but his figures are difficult to match. The 'intermaxillaris' of Camp, in *Typhlops*, has a superficial resemblance to the 'intermaxillaris' in Caenophidia. This slip is not present in other Scolecophidia. I do not consider this muscle to be homologous to the caenophidian *ima*, *pars anterior*, this is evident from the suggestions made in the previous section. The lateral attachment, in the specimens examined here, is not to the mandible, but to the oral mucosa lateral to the lateral sublingual gland, partly concealed by the mandible. In Caenophidia the *ima*, *pars anterior* arises from the mandible. The medial attachment also differs in detail from that of Caenophidia. There are several other major differences in the throat musculature, and, in general, *Typhlops* and Caenophidia stand at opposite extremes of the range of snake morphology.

In summary, the 'geniomyoideus' of McDowell (1972), as reported in snakes, appears to be represented by the *transversus branchialis* in *Anomalepis* and *Leptotyphlops*; by the 'intermaxillaris' in *Typhlops* (probably not the homologue of the 'intermaxillaris', or *ima*, *pars anterior*, of Caenophidia); to be absent in

Loxocemus bicolor (where it is supposedly present in additjon to the undivided *ima* reported herein): and to be represented by the *ima, pars anterior* in Caenophidia.

If my interpretations are correct, McDowell is proposing the elaborate hypothesis that the anguimorph *geniomyoideus* is represented by at least three different individual muscles in different groups of snakes. I would suggest that unless *a priori* committed to an anguimorph origin of snakes (which remains a theory for consideration), there is no reason at present to accept that *any* muscle found in snakes is homologous to the *geniomyoideus*. I do not wish to imply that any given muscle of snakes is definitely *not* homologous to the *geniomyoideus*, but simply that a more objective nomenclature may aid further investigation by not giving the impression that muscle homologies are already well-established. Cundall (1974, p. 172) has previously expressed some reservations about McDowell's interpretation of these muscles.

It would be desirable to determine the innervation of the *geniomyoideus*, and its homologues as suggested by McDowell in snakes. A problem, as McDowell points out (1972, p. 226), is that his 'geniomyoideus', in some Caenophidia at least, is innervated distal to an anastomosis between a ramus of the trigeminal emerging from the mandible, and the hypoglossal. Thus innervation cannot be determined by gross dissection. Quite possibly this anastomosis is not present in all cases. Until such information is available, interpretations (as given here) must be based primarily on the topographical relationships of the muscle slips concerned.

Perhaps giving some support to one of McDowell's candidates for a snake 'geniomyoideus', is the observation that the 'genioglossus portio minor' of Sondhi (1958, p. 172) in *Varanus bengalensis*, identified by McDowell (1972, p. 224) as a *geniomyoideus*, is very similar in its course to the undivided *ima* of pythons and lower Henophidia reported above. The muscle (presence confirmed in *V. bengalensis* and *V. exanthematicus*) arises from the dentary immediately antero-medial to the 'major' portion of the *genioglossus* and passes postero-medially to insert on the oral mucosa just anterior to a point ventral to the oral opening of the outer tongue sheath. The insertion is thus not primarily cutaneous as in other anguimorphs, but deeper, and in fact closely resembles that of the *ima* of pythons and lower Henophidia. Other close similarities between *Varanus* in particular (among anguimorphs), and snakes, include the morphology of the tongue (McDowell 1972), and the presence of a tracheal protractor muscle (*geniotrachealis* of snakes). However, McDowell himself states (p. 265) that "*Varanus* is not so close to the true ancestry of snakes as is *Lanthanotus*". This would suggest that the 'genioglossus portio minor' or 'geniomyoideus' is not homologous to the snake *ima*. The argument of Underwood (1970, p. 90), that snakes diverged from the basal Squamata before any extant lizard group, would imply that any such similarities, not primitive to Squamata in general, are developed in parallel in snakes and the lizard group in question.

Sondhi (1958, p. 186, and fig. 11) also describes a 'portio minor' in '*Natrix*' (= *Xenochrophis*) *piscator*; in this case it appears to be the typical lateral head of the *genioglossus*.

It may also be noted here that a *geniomyoideus*-like muscle is present in the apparently non-anguimorph lizard *Dibamus novaeguinea*. This was not reported by Gasc (1968). It is present in both specimens examined here. The muscle arises close to the mandibular symphysis, just superficial to the *genioglossus*, and runs posteriorly for a very short distance before inserting, superficial to the anterior-most *intermandibularis* fibres, on the skin of the lower jaw. This muscle thus conforms to

Camp's original usage of the term *geniomyoideus*. The presence of this muscle may indicate that *Dibamus* has affinities with the anguimorph lizards. As a rather more probable alternative, if the muscle in *Dibamus* is not homologous to the anguimorph *geniomyoideus*, it would tend to diminish the significance of a somewhat *geniomyoideus*-like muscle in some snakes.

Conclusions

The major conclusions to be drawn from the above observations and discussion are the following.

(1) The muscle occurring in *Cylindrophis maculatus* and *C. rufus*, identified by Langebartel (1968) as the *ima* (*intermandibularis anterior*), is actually the *transversus branchialis* (*sensu* Cowan and Hick 1951).

(2) The muscle occurring in *Loxocemus*, identified by McDowell (1972) as the 'pars medialis' of the *ima* (= *ima, pars posterior*), is actually the *transversus branchialis*.

(3) The presence of caenophidian-type *ima* fibres in *Cylindrophis maculatus*, as figured by Lubosch (1933, fig. 26), could not be confirmed in the four specimens examined.

(4) *Anilius, Cylindrophis, Loxocemus, Melanophidium, Platyplectrurus*, and *Xenopeltis*, possess a relatively thin muscle with a deep insertion, here considered to represent the *ima*, on the grounds of its very close resemblance to the *ima* of pythons and the anterior portion of the *ima* of boas.

(5) Pythons possess a similar muscle, also identified as the *ima*, but it is typically better developed, more distinct, and more exposed superficially.

(6) The *ima* is divided into two portions in the remaining Henophidia (*Calabaria*, boas, acrochordids) and Caenophidia. In *Calabaria* and boas, the anterior portion (*ima, pars anterior*) retains the same course as the entire undivided *ima* of pythons and lower Henophidia. The posterior portion (*ima, pars posterior*) has a more superficial insertion in the ventral mid-line with other elements of the intermandibular musculature, many fibres here attaching to the skin. In some Caenophidia the two portions are more or less fused, but always retain the two areas of insertion (except in *Dasypeltis*, where a single muscle resembling the *ima, pars posterior*) is present.

(7) In acrochordids and Caenophidia, the *ima, pars anterior* is relatively bulky, and inserts on a median longitudinal intermandibular ligament, not on the oral mucosa (as in Henophidia except acrochordids). This ligament is typically divided posteriorly into two parasagittal portions in acrochordids.

(8) It is suggested that (*a*), the presence of an *ima, pars posterior*, and (*b*), the insertion of the *ima, pars anterior* onto an intermandibular ligament, may be synapomorphies indicating the monophyly (*a*), of the group composed of *Calabaria*, boas (*s.l.*), acrochordids, and Caenophidia, and (*b*), of the group composed of acrochordids and Caenophidia.

(9) A typical *M. protractor laryngeus* (not joining the *geniotrachealis* posteriorly) is found only in Caenophidia. Similar fibres occur in many Henophidia (prominent in acrochordids, and present in many boids), but become more or less confluent with the *geniotrachealis* posteriorly. The presence of a true *protractor laryngeus* may well be a synapomorphy of the various caenophidian lineages.

(10) Three apparent innovations, the division of the *ima* into a *pars anterior* and *pars posterior*, the shift in insertion of the *ima, pars anterior* onto an intermandibular

ligament, and the differentiation of a *protractor laryngeus*, may constitute progressive improvements to the typical snake mode of 'unilateral' feeding. The first two of these modifications appear to be functionally correlated with the development of intermandibular kinesis, and may serve to enhance control over the position of each ramus of the mandible, relative to the other, during prey ingestion.

(11) The proposal of McDowell (1972), that an anguimorph *M. geniomyoideus* is present in snakes, is not adequately supported by available evidence.

(12) A small *geniomyoideus*-like muscle is present in the non-anguimorph lizard *Dibamus novaeguinea*.

Summary

Some new observations and interpretations are made concerning certain intermandibular muscles in snakes.

A muscle occurring in *Cylindrophis* and *Loxocemus*, previously identified as part of the *M. intermandibularis anterior* (herein abbreviated to *ima*), is actually the *M. transversus branchialis* (*sensu* Cowan and Hick, 1951). A deeper muscle found in these taxa is here considered to represent the *ima*; this muscle is also present in *Anilius*, *Xenopeltis*, and uropeltids (*Melanophidium*, *Platyplectrurus*), where the *ima* had been reported as absent. The *ima* has a similar course, but is typically larger, in pythons. In *Calabaria*, boas, acrochordids, and Caenophidia, the *ima* is typically divided into two portions, the *pars anterior* and *pars posterior*. It is proposed that this condition is a synapomorphy of these four groups. In acrochordids and Caenophidia (except *Dasypeltis*), the *pars anterior* is fully developed and inserts more anteriorly, onto an intermandibular ligament. It is proposed that this condition is a synapomorphy of these two groups. In acrochordids the ligament is deeply bifurcate posteriorly.

The *M. protractor laryngeus* is absent from all Henophidia examined, but present in all Caenophidia. It is suggested that insufficient evidence is available to accept the proposal that a *M. geniomyoideus*, homologous to that found in anguimorph lizards, is present in snakes. A *geniomyoideus*-like muscle is present in the non-anguimorph lizard *Dibamus novaeguinea*.

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Appendix: Specimens Examined

SCOLECOPHIDIA

Anomalepis mexicana, 1929.6.1.41.
Helminthophis flavoterminatus, 65.10.6.1.
Leptotyphlops macrolepis, 1904.6.30.5.
L. maximus, 1906.6.1.242.
L. melanotermus, 89.11.20.13.
L. humilis, 82.11.15.20.
Liotyphlops ternetzii, 1956.1.16.34.
Typhlops angolensis, 1959.1.4.76.
T. bibronii, 95.4.4.1.
T. punctatus, 1975.568, and unregistered specimen.
T. schlegelii, 1965.35, 96.9.7.2.

HENOPHIDIA

Acrochordus javanicus, 1913.10.31.186, 1974.3865, 11.13.1.2, 1974.3860, 1966.12.
Anilius scytale, 95.2.29.4, and unregistered specimen.
Aspidites melanocephalus, 1931.12.2.2.
Boa constrictor, 1904.10.29.31.
Bolyeria multocarinata, 96.3.25.2.
Calabaria reinhardti, 1967.115, 1969.515.
Candoia asper, 99.7.24.3.
Charina bottae, 94.3.4.5.
Chersydrus granulatus, 1974.3863.
Cylindrophis maculatus, 1931.5.31.1, 1905.3.25.76, 97.10.20.18, 52.9.13.266.
C. rufus, 1933.12.5.3, 1938.9.8.1.
Epicrates cenchria, 89.8.23.1.
Eryx jaculus, 97.10.28.539.
Eunectes murinus, 97.7.23.26.
Exiliboa placata, 1977.209.
Liasis amethistinus, 1969.2630.
Lichanura roseofusca, 1901.5.14.2, 1902.3.3.1.
Loxocemus bicolor, 82.8.17.17, 1914.1.28.124, 61.11.18.11.
Melanophidium punctatus, 97.7.19.9.
Platyplectrurus madurensis, 1923.10.13.29.
Pseudotyphlops philippinus, 1951.1.6.17.
Python reticulatus, unregistered specimen.
P. sebae, 1959.1.6.65, 1968.1220, 1975.581.
Sanzinia madagascariensis, 51.6.1.17.
Trachyboa boulengeri, 1913.11.12.37.
Tropidophis caymanensis, 1939.2.3.71.
T. haetianus, 1948.1.6.67.
Uropeltis arcticepts, 93.4.18.4.
Xenopeltis unicolor, 97.10.8.19, 1925.5.25.6, and unregistered specimen.

CAENOPHIDIA

Agkistrodon piscivorus, 60.9.30.6.
Ahaetullua nasuta, 97.10.20.5.
Amphiesma stolata, 97.10.20.7.
Aspidura trachyprocta, 94.9.11.11.
Causus maculatus, 1975.675.
Coluber viridiflavus, personal collection.
Dasypeltis fasciata, 1975.610, 1948.1.2.80.
Elaphe obsoleta, 87.5.14.24.
Miodon collaris, 1907.5.22.59.
Naja naja, unregistered specimen.
Opheodrys vernalis, 1933.9.11.108.
Pareas monticola, 1940.3.9.15.
Pseudoboa neuwiedi, 63.6.18.6.
Xenochrophis piscator, 1974.896, and unregistered Ceylon specimen.
Xenodermus javanicus, 1939.1.4.5.

SAURIA

Dibamus novaeguineae, 1966.15, 87.1.20.2.
Gerrhonotus caerulus, 8.5.12.32.
Varanus bengalensis, 50.5.19.17.
V. exanthematicus, 1975.103.

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A previously unreported throat muscle in Scolecophidia (Reptilia: Serpentes), with comments on other scolecophidian throat muscles

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Introduction

A recent investigation of certain anterior throat muscles in henophidian and caenophidian snakes revealed some variation of possible phyletic significance (Groombridge 1979 b). This study was extended to the Scolecophidia, where observations were made on several species (see Appendix: material examined).

The primary purpose of this paper is to report the presence of a throat muscle in scolecophidian snakes, that appears to be absent from all other extant snakes (although a possible homologue is present in diverse lizards). This finding further widens the already considerable morphological gap between Scolecophidia and other snakes (Henophidia plus Caenophidia of Underwood (1967); Alethinophidia of Hoffstetter (1955) and McDowell (1967, 1972, 1974)). The possible cladistic significance of the presence of this muscle in Scolecophidia is discussed. In a subsidiary section, some differences are noted between my observations, and reports in the literature, regarding certain other scolecophidian throat muscles. Langebartel (1968) may be consulted for a generally useful account of snake throat muscles.

A previously unreported throat muscle in Scolecophidia

Observations

For the purposes of discussion the new muscle is here termed the *geniomucosalis*. Although there must be some reluctance to add a further name to the myological literature, the problem of homology remains unsettled and it thus seems advisable to use a new and purely descriptive term for the muscle in Scolecophidia. The present name is derived from the fact that the muscle arises from the genial region of the lower jaw, and inserts on the ventral surface of the mucosa of the floor of the oral cavity.

The *geniomucosalis* is present in all Scolecophidia examined, and arises in most cases directly from the posterior ventro-medial region of the dentary (and adjacent angular and/or splenial), see fig. 1 (*Leptotyphlops melanotermus*; the *geniomucosalis*, 'GM' in figure, passes anteriorly deep to the angular), and fig. 3 (*Helminthophis flavoterminatus*). In the *Typhlops* species examined (fig. 2, *T. punctatus*), it arises mainly from the anterior portion of the compound bone. The relatively wider origin of the *geniomucosalis* is always immediately posterior to that of the *geniotrachealis*. In some cases (*H. flavoterminatus*) these two sets of muscle fibres appear to be continuous with each other just at their origin along the mandible, in other cases (*Liotyphlops ternetzii*, *Leptotyphlops melanotermus*) there is a clear division between the two, while in others (*Anomalepis mexicana*, *T. punctatus*) there is a distinct gap

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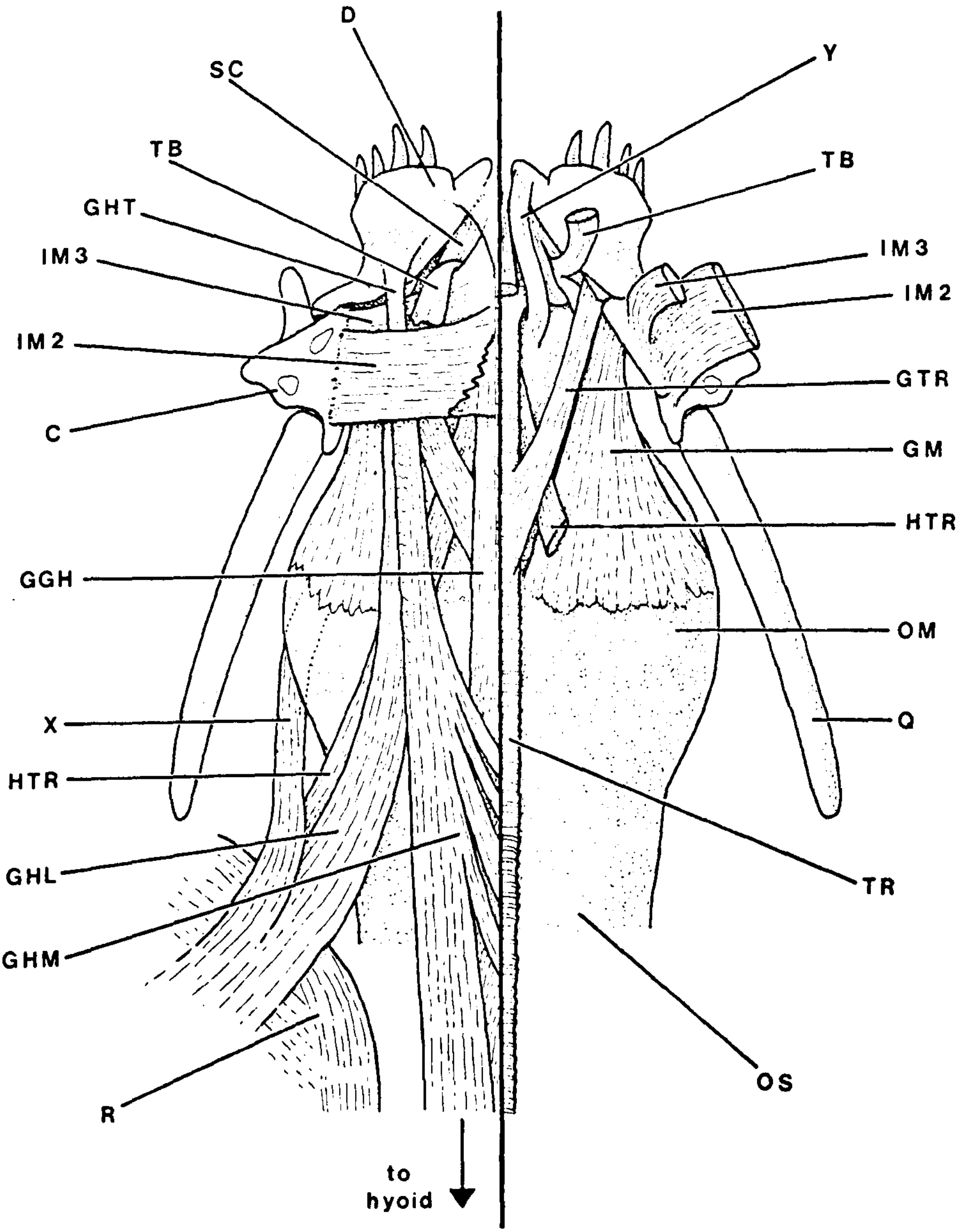

FIG. 1. *Leptotyphlops melanotermus*. All figures are semi-diagrammatic. The mandible, oral mucosa. and muscles of the throat region are shown in ventral view, after removal of the skin and other structures. Anterior is toward the top of the page. The portion of the figure to the left of the median line (the animal's right side) is a more superficial view, the portion to the left of the median line is a deeper view. with overlying muscles removed or cut and reflected. Note: Certain muscles appearing in the figures are referred to in the text. but are not formally named therein. and are not listed in the abbreviations below; these are muscles A. B. L. M. X. Y. Abbreviations for all figures: C, compound bone: D. dentary; GG, *genioglossus*; GGH, hyoid portion of *genioglossus*; GH1, GH2, GH3. superficial, middle, deep, slips of *geniohyoideus*; GHL, lateral head of *geniohyoideus*; GHM, medial head of *geniohyoideus*; GHT, tendon of attachment of *geniohyoideus*; GTR, *geniotrachealis*; H, hyoid; HTR, *hyotrachealis*; IM1, IM2, IM3, IM4, portions of the *intermandibularis*: OM, ventral surface of oral mucosa of mouth floor; OS, oesophagus; Q, quadrate; R, ribs and associated muscles; SC, lateral sublingual gland, enclosed in constrictor muscles; TB, *transversus branchialis*; TR, trachea.

between the two muscles. Whatever the degree of separation between the *geniotrachealis* and *geniomucosalis* on the mandible, the two muscles subsequently diverge from each other. As in all snakes, the *geniotrachealis* runs postero-medially to insert on the anteriormost part of the trachea. In all snakes other than Scolecophidia, there is no muscle immediately postero-lateral to the *geniotrachealis*; in Scolecophidia the *geniomucosalis* occurs in this position, and forms a broad, but thin, sheet of near-parallel muscle fibres fanning out to insert over the lateral portion of the mucosa of the floor of the oral cavity. This lateral region of the oral cavity has a somewhat pouch-like form. The *Leptotyphlops* species examined here had an additional muscle inserting on the lateral and dorsal (i.e., immediately ventral to the base of the braincase) surfaces of this lateral portion of the oral cavity. This additional muscle takes origin, with fibres of the lateral (costal) head of the lateral portion of the *geniohyoideus*, and occasionally some posterior fibres of the *hyotrachealis*, from the lateral surface of the anterior extremity of the rib cage (see muscle 'X' in fig. 1).

In *Typhlops* and *Leptotyphlops*, the anterior part of the *hyotrachealis* passes diagonally between the posterior portions of the *geniomucosalis* and *geniotrachealis*, superficial to the former and deep to the latter (figs. 1 and 2). In the anomalepidids examined, the *hyotrachealis* passes superficial to the *geniomucosalis*, but appears to interweave with the *geniotrachealis* at their dual insertion on the trachea, or (*Helminthophis flavoterminatus*) passes mostly superficial to the insertion of the *geniotrachealis*. In *Typhlops punctatus*, a prominent blood vessel was also seen to pass between the *geniomucosalis* and *geniotrachealis*, superficial to the former and deep to the latter.

In *Typhlops* the *geniomucosalis* is innervated by a twig of the same branch of the XIIth cranial nerve that also innervates the *geniotrachealis* and *genioglossus* (details of innervation could not be determined with certainty in the other, much smaller, Scolecophidia examined). The *geniomucosalis* can thus be assigned to the hypobranchial-spinal group of throat muscles (Edgeworth 1935, Langebartel 1968). This group also includes, among others, the *geniotrachealis*, *genioglossus* and *geniohyoideus* ('mandibulohyoideus' of McDowell (1972), and including the 'cerato-mandibularis' of Langebartel (1968)).

Both Langebartel (1968, 120, for *Liotyphlops albirostris*), and McDowell (1972, 235, for *Anomalepis aspinosus*), state that the *geniotrachealis* (the 'mandibulotrachealis' or 'genioglossus lateralis' of McDowell (1972)) is unusually well-developed. This was not the case in the specimens examined here, the *geniotrachealis* is a rather slender strap-like muscle, as in other snakes; perhaps these authors noted the wide adjacent origins of the *geniotrachealis* and *geniomucosalis* on the mandible, but did not trace the separate insertion of the latter muscle. Certainly, the *geniomucosalis* is thin and rather easy to overlook, unless first seen in one of the larger *Typhlops* species, for example.

Discussion

In order to assess the possible systematic significance of the presence of the *geniomucosalis* in Scolecophidia, some introductory remarks on the relationships of, and within, the group are necessary.

The three families of scolecophidian snakes (Anomalepididae, Typhlopidae, Leptotyphlopidae), are clearly distinguished from all other extant snakes by many character states (that are not found in the same combination, and usually not at all, in other snakes). These states include the following: small to minute adult size (relative to the size range of other snakes), cylindrical body form (head not distinct from trunk), tail extremely short, absence of enlarged ventral scales, mouth short and ventral in position (countersunk behind snout), eye extremely reduced, brille absent (eye beneath head scales), single type of visual cell (rod) in retina (Underwood 1967), general construction of braincase (McDowell 1967), lack of kinesis between bones of snout and frontals, lack of lachrymal foramen (McDowell 1974, 5), quadrate slanting antero-ventrally from its proximal articulation (as opposed to vertical or postero-ventrally), squamosal (also termed tabular or supratemporal) vestigial or absent, no teeth on palatine or pterygoid, one thymus body (usually two in other snakes) on each side anterior to heart (Underwood 1967), right and left systemic arches join anterior to tip of ventricle (Brongersma 1958), liver divided into several or many lobes (Underwood 1967), lack of left oviduct (except *Liotyphlops* and *Typhlophis*, Robb and Smith (1966)), lack of neural spines.

In addition, members of the group are unusual among snakes in that they specialize in small soft-bodied arthropods as a food source, frequently ants (including larvae and pupae) or termites (see, e.g., Punzo 1974).

The presence of the *geniomucosalis* in Scolecophidia clearly contributes further to the already considerable morphological gap between Scolecophidia and other snakes.

Despite the fairly strong general phenetic resemblance, there are some fundamental differences between the three scolecophidian families. These differences involve, in particular, the form of the upper and lower jaw apparatus and their dentition (Haas 1930, 1964, 1968, List 1966), the form of the hyoid apparatus and associated muscles (Langebartel 1968, McDowell 1972), and the morphology of the pituitary gland (Saint Girons 1970, 181, 194). These differences, combined with the observation that several of the features shared by Scolecophidia (e.g. consolidation of certain skull elements, short tail, lack of neural spines) can be interpreted as parallel adaptive modifications for burrowing (and when seen in other snakes, are usually seen in burrowers, e.g. uropeltids), have led several workers to question whether the Scolecophidia do in fact represent a strictly monophyletic group (*sensu* Hennig 1966).

List (1966, 55) suggests that two basic lineages can be discerned in snake phylogeny, a group formed of anomalepidids and typhlopids, on one hand, and a group formed of leptotyphlopids and remaining snakes, on the other. By this interpretation, the Scolecophidia do not form a monophyletic group. This division is based primarily on the nature of the jaw apparatus in the different scolecophidian families.

In both typhlopids and anomalepidids the compound bone is rather elongated, with a long retro-articular process. The dentary is much reduced, extremely so in typhlopids. The anomalepidids typically retain a very few dentary teeth, these are absent in typhlopids. There may be a trace of intra-mandibular kinesis in some anomalepidids, but the mandible is rigid in typhlopids. By contrast, in leptotyphlopids the compound bone is very much reduced, but the quadrate is extremely elongate (the distal portion is inclined anteriorly in all Scolecophidia). The dentary is short but deep and provided with several teeth, arranged in a near transverse row at the front of the lower jaw. Intra-mandibular kinesis is extremely well developed in leptotyphlopids.

Although the palato-maxillary arch differs in detail in typhlopids and anomalepidids, in both the maxilla is of a similar form, and is highly kinetic. Somewhat similar to the dentary teeth in leptotyphlopids, the short tooth row is in a near transverse position. By contrast, in leptotyphlopids the maxilla is reduced, immobile, and without teeth.

To summarize, in all groups of Scolecophidia one element of either the upper or lower jaw is highly kinetic, with a short and near transverse row of teeth. In typhlopids and anomalepidids this element is the maxilla, in leptotyphlopids it is the dentary. In all groups the opposing element in the other jaw (the dentary in typhlopids and anomalepidids, the maxilla in leptotyphlopids) is immobile, or nearly so, and without teeth, or with very few teeth (anomalepidids). Haas (1930, 1964, 1968) and List (1966) may be consulted for further details.

These two types of jaw morphology would appear to suggest alternative divergent strategies for the intake of small invertebrate prey items. The significant point is that it seems rather implausible to derive the leptotyphlopid type of jaw apparatus from the typhlopid-anomalepidid type (or vice versa). It is difficult to conceive of a possible selective force to drive such a shift. While both types appear to be derived states, relative to other Squamata, they seem to be derived in different directions from a hypothetical less-modified ancestral form. Indeed, Haas (1968, 129) states, "the mandibular characters alone exclude any relationship between Typhlopids (Haas included anomalepidids in this taxon) and Leptotyphlopids".

By contrast, Langebartel (1968, fig. 19) has proposed, primarily on the basis of the hyoid apparatus and associated muscles, that the initial dichotomy in snake phylogeny was between anomalepidids, on the one hand, and a group formed of all other snakes, on the other. The next dichotomy was between the common ancestry of typhlopids and leptotyphlopids, and that of the remaining snakes. By this interpretation also, the Scolecophidia are not monophyletic (*sensu* Hennig 1966), but the different character complex suggests a different grouping of the scolecophidian families.

The differences in the hyoid apparatus between typhlopids-leptotyphlopids, and anomalepidids, may not be quite as fundamental as Langebartel suggested. He proposed that the hyoid apparatus is derived from different visceral arches in different groups of snakes; either the hyoid arch, the first branchial, or second branchial, being represented. Typhlopids-leptotyphlopids (first branchial), and anomalepidids (hyoid arch), were said to differ in this respect. McDowell (1972, 232–4) pointed out that the composition of the hyoid apparatus should not be decided solely on the basis of its shape (considered in isolation), and that the muscle attachments in both groups are those of the first branchial arch in other Squamata. He concluded that the hyoid apparatus most probably includes first branchial arch derivatives in both groups (Langebartel includes the jaw and hyoid arches in his 'branchial' series, i.e. the entire visceral arch series, so the second branchial arch of Langebartel is the hyoid arch of McDowell and the present paper).

Despite this re-interpretation of the composition of the hyoid in typhlopids-leptotyphlopids, and anomalepidids, some striking differences remain between the two groups in its form, position, and musculature (Langebartel 1968, List 1966). For example, unique to typhlopids-leptotyphlopids among snakes (and probably unique among all the jawed vertebrates), is the relatively far posterior location of the hyoid, and the consequent slender and elongate form of the *geniohyoideus*, with its tendinous origin on the mandible. According to current criteria for determining the polarity of a transformation series (Kluge 1976, 21–25), this is rather certainly a derived state. The problem is whether the state was uniquely derived (a synapomorphy), or derived in parallel in typhlopids and in leptotyphlopids.

This problem could perhaps be resolved more readily if the unique typhlopid-leptotyphlopid hyoid and musculature could be seen to have some clear adaptive significance. Possibly the important morphological character is actually not the posterior position of the hyoid itself, but the fact that the *hyoglossi*, arising from the hyoid cornua (and forming most of the body of the tongue), are thereby considerably lengthened. The *hyoglossi* are about twice as long, in relative terms, as those of anomalepidids. If the assumption is made that a longer gross muscle means longer individual muscle fibres, then given the same proportion of shortening during contraction as an absolutely shorter muscle (and if other parameters remain constant), the longer muscle can both shorten faster and shorten over a greater absolute distance (Bock 1974, 174–180). If these two properties are adaptively involved in tongue function in typhlopids and leptotyphlopids, there may be a greater probability that their unique hyoid apparatus and musculature has indeed evolved in parallel in the two groups. However, this is speculation, there is little evidence currently available on feeding methods and tongue function in Scolecophidia. Typically in snakes the tongue has a role only in olfaction, via Jacobson's organ, and it is difficult to suggest the significance of longer *hyoglossi* in these circumstances. Possibly they would facilitate greater tongue protraction, a longer arc of movement of the tongue tips through the air, and more rapid retraction, bearing the collected scent particles. It may be significant for this suggestion that certain higher snakes, with a 'parallel type' hyoid, also appear to have relatively long *hyoglossi*; however, in this case the anterior portion of the hyoid remains in the standard position, but the origins of the *hyoglossi* have been extended posteriorly by the relatively long parallel hyoid cornua.

The hyoid apparatus of anomalepidids is of a very different form ('M' type of Langebartel (1968, 8)), that is also unique among snakes. It is in the usual squamate position, not displaced posteriorly. This form of hyoid would also seem to be a derived state, if McDowell is correct in rejecting Langebartel's suggestion that the anomalepidid hyoid apparatus is formed solely of hyoid arch derivatives. When a lizard hyoid includes an 'M' shape component, this appears to be formed from the hyoid arch; if the anomalepidid 'M' shape hyoid apparatus is formed from first branchial arch derivatives, it cannot be a primitive state retained from a lizard ancestry.

Also present in typhlopids-leptotyphlopids is a muscle running anteriorly from the ventral midline (anterior to the heart) to the hyoid. Langebartel identifies this muscle as the *sternohyoideus*. If this is the correct homology, then the presence of this muscle, found in lizards and other vertebrates, but in no other snakes (Langebartel 1968), would be a shared primitive state (a symplesiomorphy), having no bearing on the question of typhlopid-leptotyphlopid monophyly. However, since the presence of this muscle is correlated with other, almost certainly derived, states of the hyoid and its musculature (noted above), the possibility may be raised that the 'sternohyoideus' in this group is not strictly homologous to the muscle of the same name in lizards, and is a derived state. This is a matter that requires further comparative study.

Certain other apparently derived character states indicate the same grouping (typhlopids plus leptotyphlopids) as the evidence of the hyoid apparatus and its musculature. By itself the latter complex should perhaps be given less weight in a cladistic analysis than the evidence of the jaw apparatus, noted above. These characters include, loss of the *levator pterygoidei* muscle (Haas 1973), and loss of a free ectopterygoid (List 1966, 14–16 notes a possibility that the ectopterygoid has become fused in different positions in typhlopids and in leptotyphlopids).

As does Langebartel, McDowell (1974, 6) also suggests that typhlopids and leptotyphlopids share a common ancestry not itself shared with anomalepidids, primarily based on his interpretation of the hyoid and its musculature (McDowell 1972, 1974). In contrast to Langebartel (also to List, and Haas) he appears to imply (e.g. 1967, 690) that the Scolecophidia are a strictly monophyletic group.

In respect of the hyoid apparatus and associated muscles, both typhlopids-leptotyphlopids and anomalepidids appear to show derived states, in relation to other Squamata, but derived in different directions. It seems implausible to derive one condition from the other, rather than from hypothetical less modified primitive forms.

The situation thus emerges that the two major character complexes among Scolecophidia, that appear amenable to cladistic interpretation, indicate different groupings: a monophyletic group formed of Typhlopidae plus Anomalepididae (jaw apparatus), or a monophyletic group formed of Typhlopidae plus Leptotyphlopidae (hyoid and its musculature). The transformation series proposed for one character is not congruent with that proposed for the other.

If the polarity of the transformations in these character complexes is interpreted correctly, two solutions are possible; either the resemblance in the jaw apparatus, or in the hyoid and its musculature, was derived in parallel (in typhlopids and anomalepidids, or in typhlopids and leptotyphlopids, respectively). If parallelism is rejected, the two major alternatives imply either that the leptotyphlopid type of jaw apparatus was derived from the typhlopid-anomalepidid type, or that the anomalepidid hyoid was derived from the typhlopid-leptotyphlopid condition. There seems to be no basis on which to prefer one of these alternatives to the others. Various subsidiary characters do not appear to resolve this conflict. Therefore either new characters or new interpretations are required to clarify the problem of the cladistic relationships among the families of Scolecophidia.

This problem is closely associated with the fact that, despite a rather striking general phenetic resemblance, there is no strong evidence, subject to an unambiguous cladistic interpretation, that the Scolecophidia form a monophyletic group (*sensu* Hennig 1966). Most character states occurring frequently or consistently within Scolecophidia are either probably primitive for all snakes (rectal caecum present, *M. intermandibularis* portions transverse in position, lack of frontal processes between the olfactory tracts, undivided trigeminal foramen), or are of uncertain polarity (the *geniomucosalis*, see below; short systemic arches), or their cladistic significance is somewhat compromised since similar states occur sporadically in other snakes (single rod-like visual cells also in the uropeltid *Rhinophis* (Baumeister 1908); left oviduct also vestigial in the caenophidian *Tantilla* (Clark 1970); two thymus bodies instead of four in several non-scolecophidian taxa (Bockman 1970). Also, certain apparently significant characters are found to vary within the Scolecophidia (left oviduct not vestigial or absent, but normally developed, in some anomalepidids (Robb and Smith 1966). However, a probably derived state, the multilobed condition of the liver, has been found in all Scolecophidia examined (Underwood 1967, Robb and Smith 1966).

McDowell (1967, 690) suggests that the ventral enclosure of the braincase was completed independently and in different ways, in the Scolecophidia on one hand, and in remaining snakes on the other. However, it seems equally possible that both general types of braincase construction were derived from a common ancestry, with a completely enclosed braincase, among the earliest snakes. While in some respects the scolecophidian braincase is very probably primitive to that of other snakes, the position of the optic foramen within the frontal may be a secondary state, derived within the group (as is almost certainly the case in uropeltids (Underwood 1967, 64)).

Overall, although there may not be even one character that can, with confidence, be proposed as a synapomorphy of the families of Scolecophidia, the phenetic resemblance is strong enough over several characters (Robb and Smith 1966, 6–7; Underwood 1967, 58–60), to support the distinct suspicion that the Scolecophidia are in fact a monophyletic group. The combination of primitive with unique or unusual character states, suggests early divergence from a basal snake stock.

It should be noted that if the Scolecophidia are not monophyletic, but comprise two lineages of separate immediate ancestry (whatever combination of families), one of which is more closely related to other snakes, then either all the resemblances between these two lineages (that are not primitive for snakes in general) must have been derived in parallel, or, the common ancestry of all snakes passed through a 'scolecophidian' grade of organization. The problem of the cladistic relationship of the families of Scolecophidia to each other, and to other snakes, is thus a most fundamental one in the investigation of snake phylogeny.

Unfortunately, the character 'presence/absence of the *geniomucosalis*', does not contribute any unambiguous evidence toward the solution of this problem. In phenetic terms, the character clearly distinguishes Scolecophidia (muscle present), from other snakes (muscle absent). In cladistic terms, the polarity of the character states is subject to some uncertainty.

This uncertainty arises from doubt about the homology of the muscle. There are two major hypotheses to be considered. Firstly: was the *geniomucosalis* derived, within snakes, from the closely adjacent and near parallel *geniotrachealis*? The *geniotrachealis* is a muscle unique to snakes, and was itself very probably derived from a portion of the *genioglossus* of other squamates (among the latter, *Varanus* alone has a *geniotrachealis*-like muscle, almost certainly a parallelism). If the *geniomucosalis* is regarded as a division of the *geniotrachealis*, then the *geniomucosalis* must have been derived within snakes. Secondly: does the *geniomucosalis* represent a lateral portion of the *genioglossus* (of lizards), inserting on the mucosa of the floor of the oral cavity, such as is found in diverse lizards? The snake *geniotrachealis* would then represent a further division of the ancestral form of *genioglossus*.

The former alternative would imply that the Scolecophidia are a monophyletic group, if the *geniomucosalis* was uniquely derived (a synapomorphy) in their immediate common ancestry. The latter alternative would imply that the *geniomucosalis* is a retained primitive feature (a symplesiomorphy), not providing any information on whether the Scolecophidia are monophyletic or not, and that other snakes share a derived state, the absence (loss) of the muscle.

Present evidence suggests that the latter hypothesis is somewhat more likely to be correct

Gnanamuthu (1937) recorded a lateral portion of the *genioglossus*, with an oral insertion, in several genera of lizards; *Anolis* (Iguanidae), *Sitana*, *Calotes*, and *Draco* (Agamidae), *Cabrita* (now referred to *Ophisops*; Lacertidae), and *Varanus*

(Varanidae). McDowell (1972) found a similar condition in *Gerrhonotus gadovi* (Anguidae), and *Heloderma* (Helodermatidae). Rieppel (pers. comm.) found such an insertion in most of many anguimorph species examined. A similar oral insertion of a portion of the *genioglossus* also occurs in the amphisbaenian *Bipes canaliculatus* (Renous 1977, 486). This condition is thus found within both ascalabotan and autarchoglossan lizards, and within amphisbaenians.

On the other hand, no such insertion was reported in *Sphenodon* by Haas (1973, 310), in *Ctenosaura* (Iguanidae) by Oelrich (1956), or in *Hemidactylus* (Gekkonidae) by Gnanamuthu (1937).

Overall, it thus seems possible that an oral insertion of a lateral portion of the *genioglossus* is a primitive state for lizards. This is on the grounds that it is of widespread occurrence among the sample available. Consequently, it is most parsimonious on present evidence to suggest that the *geniomucosalis* of Scolecophidia represents a lateral portion of the ancestral squamate *genioglossus*, with an oral insertion. By this interpretation, the *geniomucosalis* is primitively present in snakes.

This suggestion carries several implications: that other evidence is still required to demonstrate the monophyly of Scolecophidia; that snakes other than Scolecophidia share a derived state, loss of the *geniomucosalis* (in addition to those already proposed, see fig. 10 in (Groombridge, 1979a): and that the *genioglossus* of lizards would have been represented in the earliest snakes by three distinct portions, the *genioglossus* (of snakes), the *geniotrachealis*, and the *geniomucosalis*.

However, it should be evident from the above considerations that the decision as to whether the presence of the *geniomucosalis* is a primitive or derived state for snakes, remains very finely balanced.

Even though the presence of the *geniomucosalis* may possibly be a primitive state for snakes, its retention in Scolecophidia may be associated with the specialized feeding habits of the group. As noted above, these snakes feed largely or entirely on small arthropods, such as ants and termites. Certain authors have suggested an apparent 'suction' component in the feeding process, either in draining the abdominal contents of termites (*Leptotyphlops phenops* (Smith 1957)), or in swallowing whole prey items (*Typhlops* (Haas 1964, 46)). Perhaps the *geniomucosalis* is somehow involved in production of this suction action, the muscle 'X' in *Leptotyphlops* (see Observations, and fig. 1, this paper) may also be involved here. Alternatively, the *geniomucosalis* may act to pull the oral mucosa anteriorly over the prey, in conjunction with highly mobile jaw elements (maxilla in anomalepidids-typhlopids, dentary in leptotyphlopids) simultaneously pushing the prey posteriorly into the mouth and pharynx.

Comments on other throat muscles in Scolecophidia

During the course of this study, several differences have emerged between my findings regarding certain throat muscles, and published descriptions (in some cases of other scolecophidian species). These differences are set out below, with associated discussion, with the object of gaining a broader view of conditions within Scolecophidia.

(1) Contrary to Langebartel (1968, 79–80), in the anomalepidids examined here the *hyotrachealis* does not arise from the floor of the oral cavity; the fibres of this muscle, although closely applied to the oral mucosa, continue posteriorly to attach to the

distal portion of the recurrent arm of the hyoid (fig. 3, 'HTR').

An origin on the hyoid is the most usual, and probably primitive, pattern in snakes; the anomalepidids have this typical pattern, even though the hyoid itself is of a unique form.

In *Leptotyphlops* the posterior portion of the *hyotrachealis* is attached to the floor of the oral cavity, as Langebartel reported. It is joined here by fibres of the lateral head of the *geniohyoideus* (fig. 1, 'HTR' and 'GHL'). There is an indistinct tendinous raphe at this junction. A band of muscle fibres continues posteriorly from this point, to overlie the lateral surface of the ribs; this muscle is composed largely of *geniohyoideus* fibres, but in some cases (as in the specimen figured), some *hyotrachealis* fibres also appear to continue onto the ribs. Because of this intermixing of the two muscles, it was not always possible to determine whether the *hyotrachealis* actually terminated on the oral mucosa, or over the ribs.

In *Typhlops* the origin of the *hyotrachealis*, as noted by Langebartel (1968, 80), lies over the lateral surface of the anterior rib cage.

With regard to the origin of the *hyotrachealis*, both *Leptotyphlops* and *Typhlops* appear derived in relation to anomalepidids and other snakes, but show different derived states (although the *Typhlops* state could be derived from a *Leptotyphlops*-like precursor).

(2) McDowell (1972, 236) found three separate slips of the *geniohyoideus* (his 'mandibulohyoideus') to run between the hyoid and the mandible in *Anomalepis aspinosus*, interdigitating with three transverse slips of the *intermandibularis* (all passing between the most superficial and the second slips of the *geniohyoideus*). By contrast, in all the anomalepidids examined here, although there are three distinct muscle slips attaching to the hyoid posteriorly, anteriorly there are only two regions of attachment. The second and third *geniohyoideus* slips (fig. 3, 'GH2' and 'GH3') converge onto a common tendon ('GHT') inserting on the mandible. A further difference in my material is that the anteriormost of the three *intermandibularis* slips (fig. 3, 'IM3') was certainly deep to the entire *geniohyoideus*.

These apparently trivial points are noted here only because the homologies that McDowell suggests for the *intermandibularis* slips, and the resulting terminology, are largely dependent on the nature of the interdigitation of the *intermandibularis* with the *geniohyoideus*. This interdigitation does not appear to be of a constant pattern in all anomalepidids. There may also be intrageneric or intraspecific variation in this pattern. On the right side only of the *Anomalepis* examined here (*A. mexicana*), a very thin tendinous cord (no muscle fibres) was found to diverge from the combined 'GH2' plus 'GH3' tendon and pass deep to 'IM3' onto the dentary. This condition thus makes some approach to that described by McDowell for *A. aspinosus*.

In the accompanying figures, I have numbered the *intermandibularis* slips in posterior–anterior sequence ('IM1, 2, 3, 4'), without making a definite commitment on their homology to those in lizards and other snakes. Of these slips in Scolecophidia, 'IM1' is unique to anomalepidids, 'IM4' is unique to typhlopids, but 'IM2' and 'IM3' occur throughout.

It is appropriate to note here that muscle 'Y' in Scolecophidia (figs. 1, 2 and 3) is virtually identical, and probably homologous, to the *intermandibularis anterior* of other snakes; in particular, as it occurs in anilioids (*sensu* Reippel 1977) and pythons (see Groombridge 1979b, for discussion of this muscle in snakes other than Scolecophidia). By this interpretation, the portions 'IM2' and 'IM3' of the scolecophidian *intermandibularis* are probably homologous to the *intermandibularis posterior, pars posterior* and *pars anterior*, respectively, of other snakes.

Scolecophidia appear primitive to other snakes in respect of several character states, one of which is the presence in Scolecophidia (as in remaining Squamata) of relatively broad portions of the *intermandibularis*, nearly transverse in position. If Scolecophidia are primitive to other snakes, and if (as suggested here) muscle 'Y' is actually homologous to the *intermandibularis anterior* of Alethinophidia, this would imply that some portions of the *intermandibularis* of Scolecophidia ('IM1, IM4') have been lost in other snakes (if either are actually primitively present in Scolecophidia), some portions ('IM2, IM3') have become reduced and diagonal in position, while a further portion ('Y') has been enlarged and modified within Alethinophidia.

These modifications may well have occurred during a shift to the 'unilateral' prey ingestion mechanism (Gans 1961), characteristic of most Alethinophidia, with the correlated formation by the intermandibular muscles of the 'intermandibular chiasma' (McDowell 1972, 254; Groombridge 1979b).

(3) McDowell (1972, 242) states that "... in both *Typhlops* and *Leptotyphlops*", the *geniohyoideus* (his 'mandibulohyoideus'), if traced posteriorly from its attachment on the mandible is found to divide into "... a dorsolateral head, arising from the lateral surface of trunk muscles, and a ventromedial head, that extends back to the region of the hyobranchium".

There was actually no such 'dorsolateral head' in any of the typhlopids examined here, nor in those reported by Langebartel. The muscle in *Typhlops* with a posterior attachment similar in position to that of the lateral head of the *geniohyoideus* in *Leptotyphlops*, is in fact the *hyotrachealis* (compare *Typhlops*, fig. 2, 'HTR', with *Leptotyphlops*, fig. 1, 'GHL'). The *geniohyoideus* in *Typhlops* is a very slender muscle, free of the adjacent muscles, that runs directly posterior to attach to the hyoid (itself far back from the head).

As noted by McDowell (1972), anomalepidids appear primitive among snakes (and in general terms, resemble lizards) in having more than one separate slip of the *geniohyoideus* arising from the hyoid. The most superficial of these (fig. 3, 'GH1') was found to attach largely by a very thin aponeurosis over the lateral jaw musculature in my material, rather than directly to the mandible. As noted above, in my specimens the second and third portions of the *geniohyoideus* were found to join a common tendon inserting on the mandible. There is a strong resemblance to *Typhlops* and *Leptotyphlops* in respect of this form of insertion, in particular to the latter in that the medial (typical) and lateral (costal) heads of the *geniohyoideus* in *Leptotyphlops* have a similar relation to each other as do the second and third portions of the *geniohyoideus* in anomalepidids (fig. 3, 'GH2, GH3'). Perhaps the 'GH3' was left behind, with posterior migration of the hyoid, to form the lateral head of the *geniohyoideus* in *Leptotyphlops* (fig. 1, 'GHL'), but was lost in *Typhlops* (regardless of whether *Typhlops* and *Leptotyphlops* are strictly monophyletic).

Snakes other than anomalepidids show a derived state in having only a single portion of the *geniohyoideus* (with a lateral head in *Leptotyphlops*). The differences between *Typhlops* and *Leptotyphlops* on the one hand (having the hyoid far posterior, with the *geniohyoideus* very elongate and slender, and inserting on the mandible by a narrow tendon), and the remaining snakes, on the other (having the hyoid in the standard squamate position, with the *geniohyoideus* short and broad, occasionally

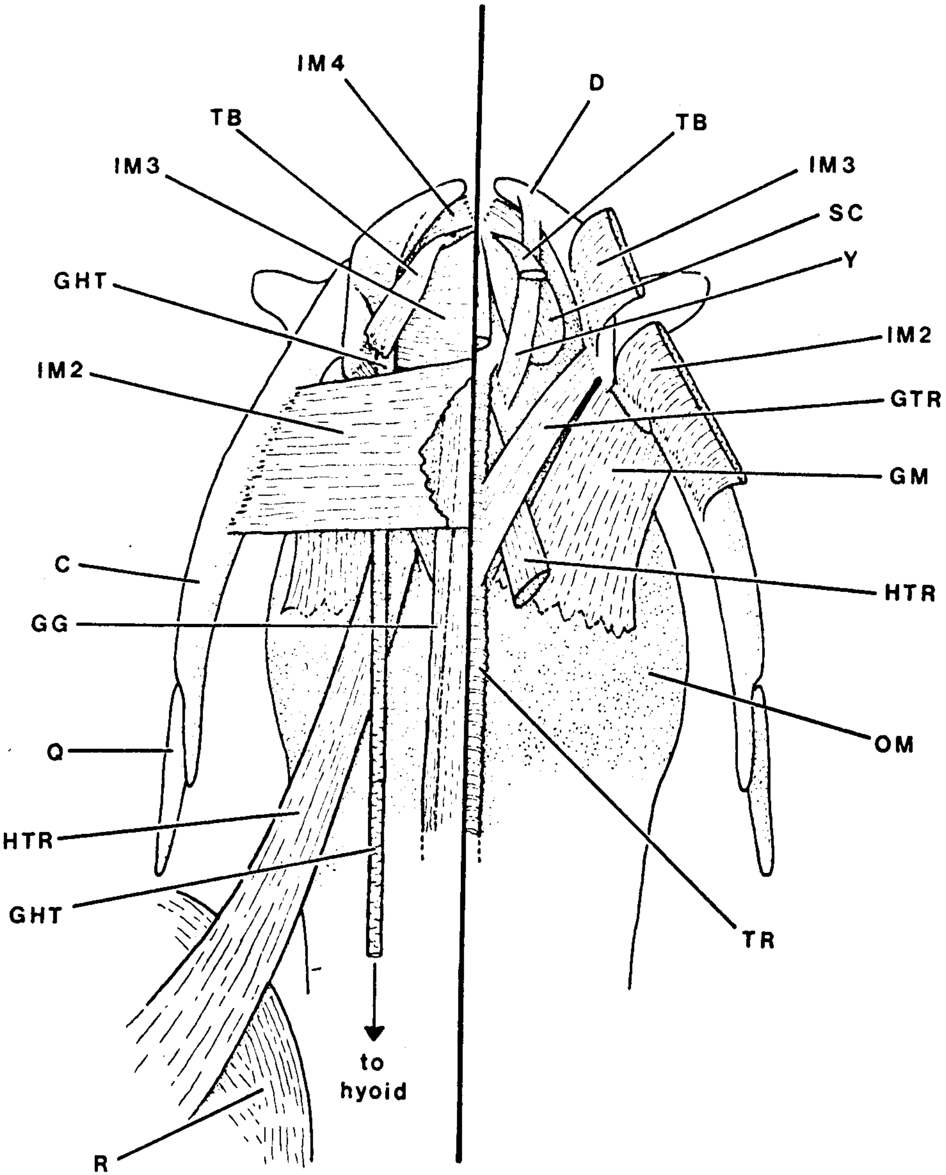

Fig. 2. *Typhlops punctatus*. For key to abbreviations see under fig. 1.

partially subdivided, with a wide fleshy insertion along the mandible), suggests the possibility of parallel simplification from the lizard-anomalepidid condition.

(4) Warner (1946, 3), describing a specimen of *Anomalepis aspinosus*, reported the presence of two muscles attaching to the posterior of the hyoid. One muscle, "...inserts on the posterior border of the horizontal portion and on the median surface of the posterior processes. It extends caudad to a cutaneous origin". Warner identified this muscle as the 'sternohyoideus', but Langebartel (1968, 66–69) quite convincingly interprets it as an extension of the *costocutaneous superior*. A second muscle, that Warner identifies as the *omohyoideus*, "...inserts on the posterior margin of the bend and runs posterolaterally to its cutaneous origin".

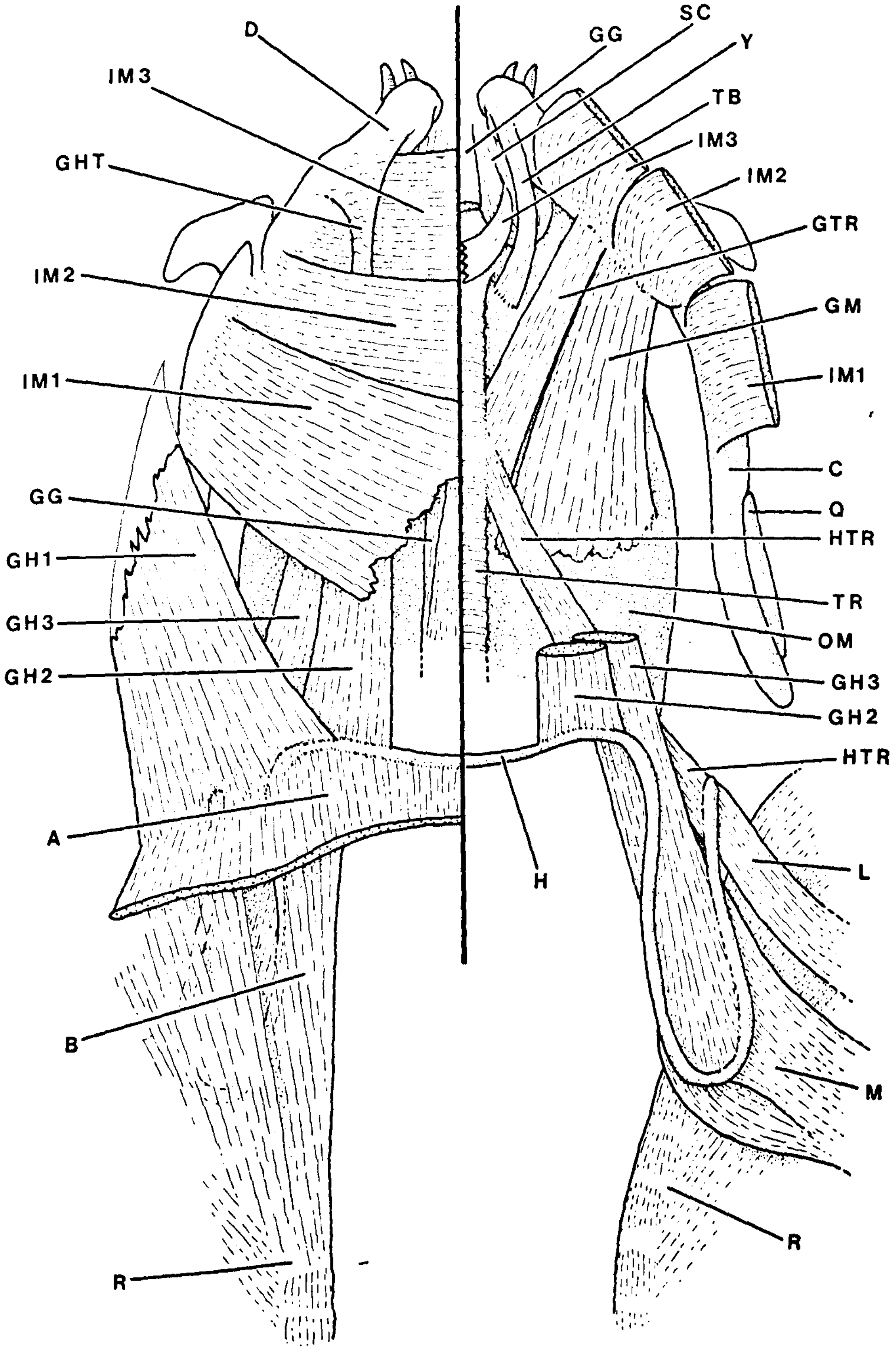

FIG. 3. *Helminthophis flavoterminatus*. For key to abbreviation see under fig. 1. Muscle A, shown transected here, extends posteriorly to a cutaneous origin.

On the other hand, McDowell (1972, 236), describing a specimen of the same species, reported two different layers of muscle (his 'omohyoideus-sternohyoideus complex') attaching to the posterior of the hyoid. "(1) the more superficial layer, much the broader, inserted along most of the length of the first ceratobranchial, originating from the surface of the muscles of the vertebrae (the dorsal head) and from the external surface of the muscles of the ribs (the ventral head); (2) a deeper and much narrower layer, originating on the skin of the belly near the midline and inserted on the medial portion of the first ceratobranchial".

The situation in the specimen of *Anomalepis* examined here (*A. mexicana*) is almost the same as that reported by Warner, and does not correspond to that reported by McDowell. The major difference from the account of Warner, is that her *omohyoideus* was represented by two distinct portions in my specimen.

A very similar situation was also found in *Helminthophis flavoterminatus*, *Typhlophis squamosus*, and *Liotyphlops ternetzii*, and is shown in fig. 3. Muscle 'A' is the 'sternohyoideus' of Warner, muscles 'L' and 'M' are the two portions in the position of the *omohyoideus* of Warner. However, in these species, an additional muscle ('B') was found to run between the hyoid (lateral part of the horizontal portion, and much of the rest of the cornua) and the region of the tips of the ribs. This muscle is very similar to the *costomandibularis* of Langebartel (1968, 63), as represented in those snakes lacking a *neurocostomandibularis* complex (of which it is a component). I could not positively distinguish this muscle in *Anomalepis mexicana*.

The apparently atypical condition reported for McDowell's specimen of *Anomalepis aspinosus* (combined with Langebartel's identification of the 'sternohyoideus' in anomalepidids as part of the *costocutaneous superior*), indicates that some doubts may be justified regarding McDowell's interpretation of these muscles.

(5) McDowell (1972, 242) states that the *neurocostomandibularis* complex (see Langebartel 1968, 93) is present in *Typhlops* and *Leptotyphlops*. Since the *neurocostomandibularis* is a composite muscle, an anterior component of which is the *geniohyoideus* (includes the 'ceratomandibularis' of Langebartel), I do not see how the *neurocostomandibularis* can logically be described as present in *Typhlops* when the *geniohyoideus* is actually entirely independent of adjacent muscle elements (as just noted above).

McDowell (1972, 242) suggests that the dorsolateral head of the *geniohyoideus* in *Typhlops* and *Leptotyphlops* (as stated above the 'dorsolateral head' is actually not present in *Typhlops*), "... appears quite homologous with the dorsolateral head of the omohyoideus-sternohyoideus complex of *Anomalepis*...". I have already suggested above that McDowell's concept of the 'omohyoideus-sternohyoideus complex' does not appear to be valid throughout anomalepidids (certainly not in the forms examined here, nor in *Anomalepis aspinosus* according to Warner's account). Accordingly, I do not accept that the 'dorsolateral head' of the *geniohyoideus* in *Leptotyphlops* (fig. 1, 'GHL') is homologous to the 'dorsolateral head' of the 'omohyoideus-sternohyoideus complex'. Furthermore the supposed 'neurocostomandibularis' that McDowell describes in these forms has no *costomandibularis* component, as occurs in the typical *neurocostomandibularis*.

I conclude that, contrary to McDowell (1972), the *neurocostomandibularis* is not present in either *Typhlops* or *Leptotyphlops*.

(6) McDowell (1972) has suggested that a muscle homologous to the *geniomyoideus* of anguimorph lizards is also to be found in snakes. I have expressed some

reservations about this proposal elsewhere (Groombridge 1979b). The figures provided in the present paper show that the 'geniomyoideus' of McDowell in *Leptotyphlops* and anomalepidids does not attach anteriorly to the dentary as McDowell indicates, but to the lateral sublingual gland (enclosed in constrictor muscles 'SC' in the figures), and is very probably identical to the *transversus branchialis* of other snakes. The 'geniomyoideus' of McDowell in *Typhlops* is the muscle here labelled 'IM4' (fig. 2).

McDowell shows the 'geniomyoideus' (*transversus branchialis*) in *Leptotyphlops* to have two regions of insertion (his fig. 17), one labelled 'GMY', the other labelled 'IMP'. In the *Leptotyphlops* examined here, the muscle (fig. 1, 'TB', *in situ* on animal's right, deflected anteriorly in deeper view of animal's left) does not divide posteriorly, and the insertion does not correspond to either of those indicated by McDowell. The muscle arises from the lateral sublingual gland, turns superficially (lateral to the *genioglossus* but medial to the *geniotrachealis*) over the 'IM3', to a diffuse cutaneous insertion. In other words the 'GMY' plus 'IMP' of McDowell correspond to the 'TB' or *transversus branchialis* of the present paper. Since the muscle does not attach to the dentary in *Leptotyphlops*, it is rather unlikely that it serves to flex the intramandibular hinge as McDowell suggests (1972: 239). I could not definitely identify any muscle fibres (as opposed to connective tissue) in the position of those labelled 'IMA 1' in McDowell's fig. 17.

In *Leptotyphlops maximus* and *L. melanotermus* (other *Leptotyphlops* species not checked), but not *Typhlops* or anomalepidids, the *transversus branchialis* appears to divide into two portions at its origin on the lateral sublingual gland. The major portion forms the typical *transversus branchialis*. The second portion remains deep in position and becomes applied to the oral mucosa, it then runs posteriorly and laterodorsally around the oral mucosa and comes to overlie the mucosal insertion of muscle 'X'. The origin of this deep portion is shown (unlabelled) in fig. 1, immediately posterior to the reflected *transversus branchialis* ('TB') on the animal's left side.

The *transversus branchialis* in *Typhlops* and anomalepidids differs from that in *Leptotyphlops* and all other snakes, in that (in the specimens examined) it passes medial to muscle 'Y' (see the figures, muscle 'Y' is probably homologous to the *intermandibularis anterior* of snakes other than Scolecophidia). This may possibly be a derived state.

In all snakes other than Scolecophidia, the *transversus branchialis* passes lateral to the *genioglossus* and its probable derivative, the *geniotrachealis*. The possible homologue of the *transversus branchialis* in some lizards ('mylohyoideus anterior superficialis' of Camp (1923)) also passes lateral to the *genioglossus* (the *geniotrachealis* is absent in lizards, although a probable analogue is present in *Varanus*). In Scolecophidia the *transversus branchialis* passes lateral to the *genioglossus*, but medial to the *geniotrachealis*. This may be a derived state.

(7) In *Leptotyphlops* there is a muscle that would seem, by its general position, to be a portion of the *genioglossus* (and is labelled 'GGH' in fig. 1). This muscle arises anteriorly from the same median tendon as the typical portion of the *genioglossus* (that inserts along the sides of the tongue), but just posterior to the origin of the latter muscle. It passes posteriorly, closely ensheathing the typical *genioglossi* and the *hyoglossi*, to three regions of insertion. A median portion attaches to the lingual process of the hyoid, and two lateral portions curve around the roots of the *hyoglossi* to attach to the hyoid cornua. Langebartel (1968, 51, and fig. 10) includes this muscle with the *genioglossus*. As noted by Langebartel, this muscle is unique to

Leptotyphlops among snakes. In *L. melanotermus* a few fibres of this muscle appeared to be continuous with those of the *sternohyoideus* (of Langebartel) around the distal tip of the hyoid cornua. This muscle is in the approximate position of that labelled 'NCM L' in McDowell's fig. 17. of *L. humilis* (and apparently identified with the *sternohyoideus* of Langebartel). I am uncertain if it is the same muscle because not only did the situation in the *Leptotyphlops* examined here not correspond with McDowell's description (1972, 242), but the muscle was certainly not present in the *Typhlops* specimens (McDowell states that his 'NCM L' is present in both genera). Although there may perhaps be some question as to the homology of the *sternohyoideus* of Langebartel, the specimens examined here were found to correspond quite closely with his description (1968, 69–70).

Conclusions

A throat muscle, present in Scolecophidia but absent in other snakes, is reported here for the first time. This muscle, the *geniomucosalis*, arises on the mandible immediately posterior to the *geniotrachealis* and passes posteriorly, nearly parallel with the latter muscle, to a broad and thin insertion over the mucosa of the lateral part of the floor of the oral cavity. This muscle is possibly homologous to a lateral portion of the *genioglossus* (of lizards), with an insertion on the oral mucosa, as is found in diverse lizards. By this interpretation it would be primitively present in snakes, and snakes other than Scolecophidia show a derived state, the absence (loss) of the *geniomucosalis*. An alternative proposal is that it is derived, within snakes, from the *geniotrachealis* (itself probably derived from the *genioglossus* of lizards; only *Varanus* among lizards has a *geniotrachealis*-like muscle). By this interpretation, that on present evidence appears less likely than the former, the Scolecophidia would share a derived state.

Even though the *geniomucosalis* may be a retained primitive state, it may have been retained in association with the unusual feeding habits, and mechanisms (as far as known), of the Scolecophidia.

If the *geniomucosalis* is a retained primitive state, its presence in Scolecophidia provides no information on the monophyly (*sensu* Hennig 1966), or otherwise, of the group. Current evidence (mostly based on phenetic simularities) indicates that the Scolecophidia are likely to be monophyletic, but a strictly cladistic approach to available characters does not allow a more definite conclusion.

The new observations and interpretations presented here indicate that, in respect of the throat muscles, the three families of Scolecophidia are about equally distinct from each other (in phenetic terms), each family having its own set of peculiarities. The precise arrangement of the *intermandibularis*, the *geniohyoideus*, and the *hyotrachealis*, is different in each family. This contrasts with a distinct impression of general uniformity in throat musculature throughout the Alethinophidia (with the exception of the *intermandibularis anterior*, Groombridge 1979b).

However, all Scolecophidia differ from Alethinophidia in several characters of the throat muscles: the *intermandibularis* muscles are broad and transverse in position, not forming an 'intermandibular chiasma'; the *geniohyoideus*, whether single, or having two or three portions, does not have a broad single (or partially divided) fleshy insertion along the mandible; the *neurocostomandibularis* is absent, but present in Alethinophidia (except anilioids, *sensu* Rieppel (1977)); the *geniomucosalis* is present; the *transversus branchialis* passes medial to the *geniotrachealis*. The first three of these are rather certainly primitive to the corresponding states in

Alethinophidia. It is more cautiously suggested above that the presence of a *geniomucosalis* is primitive. The last state may be derived, with Alethinophidia having the primitive state, '*transversus branchialis* passes lateral to *geniotrachealis*'.

Within Scolecophidia, *Leptotyphlops* is generally the most divergent form, with four unique derived character states: *genioglossus* with separate portion inserting on hyoid; presence of muscle 'X', passing from lateral surface of ribs (attachment shared with the lateral head of the *geniohyoideus*) to the lateral and dorsal surface of the oral mucosa; *transversus branchialis* with a deep portion also inserting on the oral mucosa; presence of a lateral (costal) head of the *geniohyoideus*.

With reference to the throat muscles and hyoid apparatus, the only clearly derived character states shared between only two of the three scolecophidian families (and thus cladistically significant within the group), are those shared by *Typhlops* and *Leptotyphlops*. Perhaps these are better treated as a single derived character complex, rather than as separate states. This complex involves the far posterior position of the hyoid, with consequently elongate *geniohyoideus* and *hyoglossus*. Also associated in this complex is the presence, unique among snakes, of a muscle termed the 'sternohyoideus' by Langebartel (1968, 69–70). If this is the correct homology, this is a retained primitive state, but the correlation with the other derived states raises the possibility that the 'sternohyoideus' is not homologous to that of the same name in lizards, and is itself a derived state. Another associated feature is that, according to Langebartel (1968, 54), the *hyoglossi* in these two genera are by far the bulkiest among snakes. It would be of great interest to have some experimental information on functional aspects of this character complex, or indeed on any aspect of scolecophidian feeding mechanisms.

The Anomalepididae appear to be generally primitive to other Scolecophidia in some characters of the throat musculature, as in certain other characters (e.g., teeth retained in both upper and lower jaws; *levator pterygoidei* retained; posterior extension of postorbital, probably representing a vestige of the jugal arch, retained in *Anomalepis*, Haas (1968)). The 'M'-shape hyoid is of a form unique among Squamata (if it includes first branchial arch elements, as appears probable after the argument of McDowell (1972, 234)), and is thus likely to be a derived state. This perhaps raises the question whether any of the muscles attaching to the hyoid have been modified in association with this transformation.

From a taxonomic viewpoint, it may be noted that a primary division of extant snakes into two taxa of equal rank, Scolecophidia and Alethinophidia (as currently used by McDowell, 1972, 1974), would not only reflect, in purely phenetic terms, the extent of the morphological gap between Scolecophidia and other snakes (based on the throat musculature, including the *geniomucosalis*, and on various characters noted above and by Robb and Smith, McDowell, and Underwood, op. cit.); but may also reflect, in cladistic terms, a basic dichotomy in snake phylogeny (as far as this can be determined on available evidence).

Summary

A throat muscle, present in Scolecophidia but absent in other snakes, is reported here for the first time. This muscle passes from the genial region of the lower jaw to the mucosa of the floor of the oral cavity. The precise homology of the muscle is uncertain. In *Typhlops* at least, it appears to receive hypoglossal innervation, and can thus be assigned to the hypobranchial-spinal muscle group. It may have been

derived from a lateral portion of the *genioglossus* that inserts on the floor of the oral cavity, as is found in diverse lizards, or it may have been derived from the snake *geniotrachealis*. Present evidence tends to favour the former hypothesis. While the evolutionary origin of the scolecophidian muscle remains unclear a new name is required, it is here termed the *geniomucosalis*, after the regions of origin and insertion.

Some major problems of scolecophidian phylogeny are discussed as a background to remarks on the possible cladistic implications of the presence of the *geniomucosalis* in Scolecophidia. The conclusion is reached that although the muscle further contributes to the considerable phenetic gap between Scolecophidia and other snakes, while its homology remains uncertain the *geniomucosalis* is of limited significance in a cladistic analysis.

Numerous points of difference are noted between my observations on various scolecophidian throat muscles, and observations reported in the literature.

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Appendix: Material examined

All specimens examined are in the collection of the British Museum (Natural History).

Anomalepididae
- *Anomalepis mexicana*, 1929.6.1.41
- *Helminthophis flavoterminatus*, 65.10.6.1
- *Liotyphlops ternetzii*, 1956.1.16.34
- *Typhlophis squamosus*, 95.5.7.1

Leptotyphlopidae
- *Leptotyphlops emini*, 1947.1.2.87
- *L. macrolepis*, 1904.6.30.5
- *L. maximus*, 1906.6.1.242
- *L. melanotermus*, 89.11.20.13
- *L. humilis*, 82.11.15.20

Typhlopidae
- *Ramphotyphlops australis*, 1974.750
- *R. bicolor*, 1904.10.7.61
- *Typhlops angolensis*, 1959.1.4.75
- *T. bibronii*, 95.4.4.1
- *T. lumbricalis*, 1932.11.11.21–22
- *T. punctatus*, 1975.568, & unreg.spec.
- *T. schlegelii*, 1965.35, 96.9.7.2

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