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A Phylogeny of the Sea Snakes (Hydrophiidae)

HAROLD K. VORIS
ASSISTANT CURATOR, DIVISION OF AMPHIBIANS & REPTILES
FIELD MUSEUM OF NATURAL HISTORY

ABSTRACT

The purpose of this study has been to derive in an explicit fashion a phylogeny of the sea snakes (Hydrophiidae). In all, 632 specimens representing 50 nominal species of sea snakes, were examined. A total of 153 quantitative and qualitative characters were collected from specimens representing most of the species. The size of the overall data set was reduced on the basis of redundancy among the characters and missing data among some species, resulting in a data matrix of 40 species by 43 characters. Character state trees were constructed for the 43 characters.

The combinatorial method of Sharrock and Felsenstein (1976) was used in a unique way to organize the species into groups sharing the same set of character states. Character states were grouped together according to their degree of derivativeness (i.e., character state tree layer) and the 40 species were analyzed one character state tree layer at a time. The combinations generated at each character state tree layer were surveyed using several operational criteria and certain combinations were selected for further consideration. The selected combinations were related in a flow-chart diagram from which the relationships of the snakes were extracted. A phenetic analysis using the simple matching coefficient and single linkage is included for purposes of orientation and comparison.

The sea snakes consist of three major stocks: 1) the *Laticauda,* 2) the *Aipysurus* and *Emydocephalus,* and 3) all other species. The data suggest that these groups may have independent origins among the elapids or a single origin with a very early separation. The relationships within the three stocks are discussed in detail.

INTRODUCTION

The Hydrophiidae is a group of marine snakes which have anterior non-rotatable fangs, neurotoxic venom, and flattened oar-like tails. They occur from the east coast of Africa to the western coast of Central America with most species found in tropical and subtropical Asian seas (Minton, 1968; see also fig. 7). They are chiefly neritic

and frequent mangrove swamps, estuaries, bays, river mouths, coral reefs, and coastal water situations (Voris, 1972).

The Hydrophiidae were recognized as a cohesive group of 40 species of snakes by Boulenger in 1896. Since that time new species have been discovered but no species have been moved in or out of the family.[1] Malcolm Smith published two major taxonomic works on this family. In 1920 he described 23 species of sea snakes in a paper which included a complete list of the specimens he examined and the data he collected from them. A brief introduction was concerned with miscellaneous notes on natural history, zoogeography and methods of character collection. Smith's *Monograph of the Sea Snakes (Hydrophiidae),* published in 1926, included descriptions of nearly every species currently known, about 50. Many skulls and some heads were figured. Individual specimens examined were listed with some of the data collected from them. Smith also included introductory remarks on the evolution of the sea snakes and on the "Cranial characters," "External characters," and the "Hemipenis," and a section on the habitat and zoogeography. Keys to both the genera and species were given.

Since Smith's work of 1926, studies on the sea snakes have been limited in scope. There have been cursory studies on the ecology (e.g., Saint Girons, 1964; Kropach, 1971) or on the anatomy and physiology of a few selected species (e.g., Bal and Nawathe, 1949; Dunson and Ehlert, 1971). Taxonomic studies have also been limited, either to geographic areas (e.g., Volsøe, 1939; Wang, 1962) or to small sample sizes and/or only a relatively few consistently applied taxonomic characters (e.g., Underwood, 1967; McDowell, 1972). None of the classifications has been based on more than a few selected "key" characters and taxonomic procedures have remained obscure.

The purpose of this study has been to derive in an explicit fashion, a highly tenable phylogeny of the Hydrophiidae. My aim is not to defend exhaustively the methods used to derive the phylogeny, but rather to assure that the methods utilized are procedurally and logically defined, repeatable and therefore open to testing and criticism. This work is an offshoot of a much larger study (Voris, 1969) which included the comparison and evaluation of several numerical and orthodox phylogenetic methods. The methods used here were in part selected from the larger study.

[1]McDowell (1972), however, has put all sea snakes within the Elapidae. See p. 123 for comments on classification.

MATERIALS AND DATA COLLECTION

Data on external anatomy were collected from 632 preserved sea snakes representing 50 of the 52 nominal species. The average number of specimens examined per species was 10.9; the median was 7. In addition, 134 skulls representing all 16 genera and 42 of the species, 88 tail x-rays representing all the genera and 46 species, and 90 whole body x-rays representing all the genera and 44 species were studied. A list of species and a summary of specimens examined is given in Table 1. A total of 153 characters was collected from the above material. Table 2 lists the characters and arranges them into several categories related to the nature of the characters and their location on the snakes.

The characters selected for study were chosen on the basis of one of four criteria. First, some characters were chosen because they were previously in wide use in taxonomic literature. Second, characters were chosen simply on the basis of accessibility. That is, if a character showed variation within the family and was easily observed, it was included. Third, characters were chosen for special attention because they were related to specific aspects of the biology (such as behavior or development) of the organisms. Fourth, an effort was made to obtain a sample of characters that would reflect as large a proportion of the phenotype as practical (see table 2).

Traditional techniques were usually employed in the examination of the various types of characters. Modifications of these techniques, problems encountered, and further details concerning the materials examined (including a complete list of specimens) and character selection are presented elsewhere (Voris, 1969).

ADDITIONAL SOURCES OF DATA

Occasionally, when samples were small and when Smith had seen specimens not available to me, it seemed desirable to pool his and my data to make the delineation of some species more reliable. Prior to doing this, comparisons were made between my observations and Smith's (1920) on several series of the same specimens. Comparisons of statistics on Smith's and my data were also made. When Smith and I had examined the same specimen, I included the data from that specimen in my data set and excluded it from his when making the calculations. In the majority of samples, Smith's and my observations appeared to be fully comparable and pooling of data in these species was judged to be permissible (see Voris, 1969, pp. 16-17 for statistical comparisons).

DESIGNATION OF CHARACTER STATES

Several of the numerical approaches utilized in this study required discrete character states for each Operational Taxonomic Unit (OTU). In this study, all OTU's were species. Also, after states were initially designated, some pooling of states occurred because the computer programs used accommodated only characters with nine or fewer states.

Character states were designated as follows. For qualitative characters, states were defined and designated as the different states were encountered. In cases in which a species showed two or more discrete states or a gradation between states, intermediate states were designated.

Quantitative data were treated more extensively. Although sample sizes were small, several basic statistics (range, mean, and standard deviation) were calculated wherever possible. For each character the mean value of the specimens comprising the sample was chosen to represent that species.

The boundaries of quantitative character states were defined in two ways. First, the species' means were plotted in ascending order and the resulting curve examined. The following criteria were used to decide where character state boundaries would be designated:

1. State boundaries were set at sharp changes in the slope.

2. Boundaries were set at gaps in the distribution of points along the curve.

3. When the values over all species spanned a narrow range, and there were no sharp changes in the slope, nor breaks in the curve, states of about equal size range were established. (Those characters with wide ranging values were treated using arithmetic incrementation (see below)).

4. Additional states were designated for uncertain cases. Thus, similar character states would be oversplit but rarely would distinct states or groups be consolidated.

A second method of defining states using successive incrementation was applied to the characters whose states spanned a wide range (referred to in number 3 above). There are several different methods of incrementation that are designed to take into account the observation that with larger measurements an increase in variation is frequently noted (Kendrick, 1964). In many such situations a specific method of incrementation is justifiable, however, all cases

do not fit a single scheme. Also, there are a few species in which higher values are not accompanied by increases in variation. For example, in *Kolphophis annandalei* the number of ventrals is great yet variation is low. In this study arithmetic (fixed) incrementation was employed. In arithmetic incrementation, the number of data points included in a state is increased by a constant value as successive states are designated. For example, if one is incrementing by two, as was done in this study, and has data values running from 1 to 25, the following five states would result:

Data values	1;	2,3,4;	5,6,7,8,9;	10,11,12,13,14,15,16;	17,18...24,25
Number of data points included in each state	1	3	5	7	9

The character states designated for all 153 characters are described in Voris, 1969, Table 2.

PHYLOGENETIC ANALYSIS

Phylogenetic studies are composed of three general processes. Primary data collection is the first, consisting of the collection of data from the organisms and the designation of character states. The second process is the manipulation of these data, including all operations performed on the data through the formation of a phylogeny. The third process is the construction of a classification consistent with the phylogeny and preferably based directly on the data analysis.

This study is mainly concerned with the second of these three processes. It deals with the recognition of species and procedures for determining relationships among them.

SPECIES DETERMINATION AND RECOGNITION

The first task after data collection was to designate species. As a theoretical basis for delimiting species, the biological species definition of Mayr (1942) and Dobzhansky (1951) was accepted. However, in this study, everything concerning reproductive isolation and community gene pools was inferred from data other than breeding tests. That is, two sympatric populations represented by adults of both sexes collected over a several month period and having phenetic differences that could not be attributed to polymorphism (i.e., there were two or more characters which were complex, and showed

no intergradation) were interpreted as having genetic differences that have resulted from reproductive isolation of the populations.

In the case of populations that are not sympatric, or for which certain samples were unavailable, i.e., certain age classes, one sex, or some ecotypes were missing, I estimated whether or not the populations were reproductively isolated from the degree of difference observed between them as compared to the differences observed between well established sympatric species.

Specimens were first roughly grouped according to the above criteria. Next, these groups were compared to Smith's (1926) species and usually were found to correspond with them. For example, Smith's and my data show that bisexual adult samples of the sympatric species *Aipysurus eydouxi* (Smith, 19 specimens; Voris, 6 specimens) and *A. laevis* (Smith, 15 specimens; Voris, 4 specimens) differ by non-overlapping states in characters 4, 73, 77, 82, 84-88 (see table 2). *Microcephalophis gracilis* (Smith, 10 specimens; Voris, 13 specimens) and *M. cantoris* (Smith, 4 specimens; Voris, 5 specimens), also sympatric species, differ in the number of ventral body scales and in the relationship of the prefrontal to the third supralabial scale.

In three pairs of species my data, and Smith's data where applicable, indicated that the character states of two species overlapped broadly. The pairs were: *Laticauda laticaudata* (1) and *L. crockeri* (5); *Emydocephalus annulatus* (13) and *E. ijimae* (14); and *Lapemis curtus* (26) and *L. hardwickii* (25). The first two pairs have been left separate because the available sample was very small in one species of each pair. The third pair is thought to represent conspecific populations (Voris, 1969, Appendix B). However, these nominal species were retained as individual units in this study for practical purposes and it will become evident that doing so did not significantly affect the results. In sum, the absence of intergradation between sympatric forms was the operational basis for recognition of the 50 species of sea snakes included in this work (table 1).

REDUCTION OF THE DATA SET

For several compelling reasons, the entire data set was not used in all aspects of this study, i.e., a subset of the 153 characters was prepared for certain analyses beyond the species level. Thus, it is appropriate to consider the logic and procedures used to reduce the size of the data set.

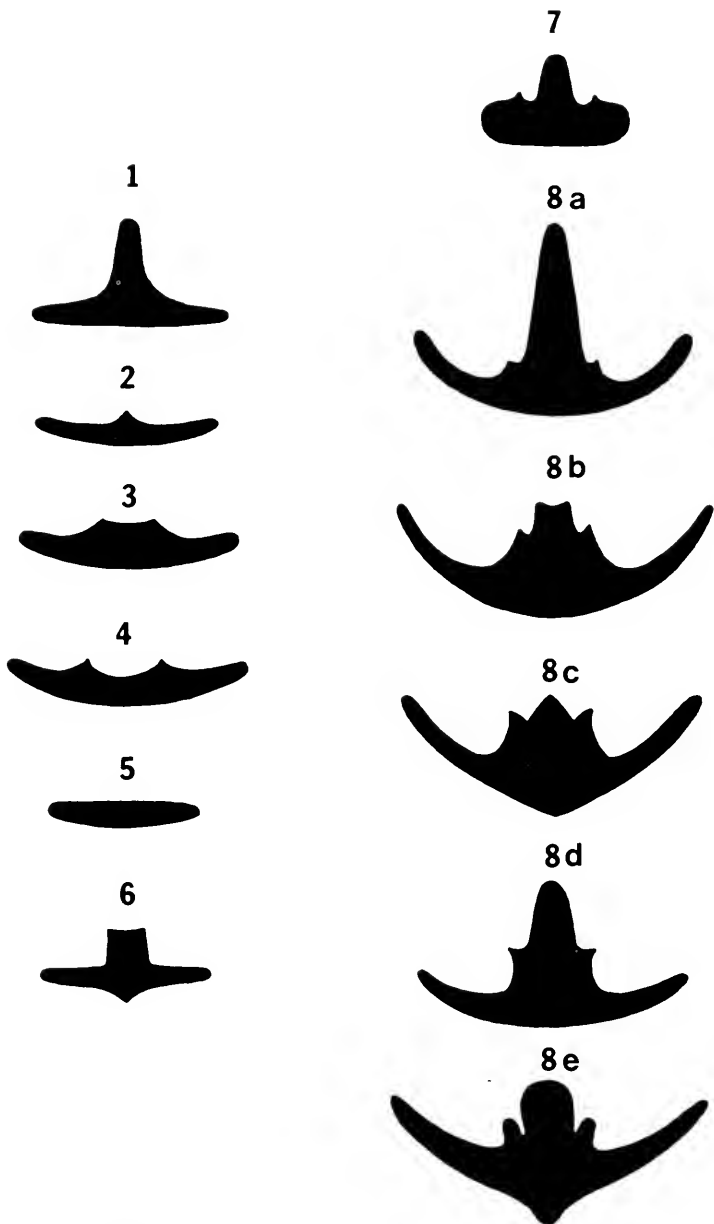A number of characters are obviously repetitious and introduce

FIG. 1. Outlines of the major types of premaxillary bones found in the Hydrophiidae (character 137). Numbers refer to designated character states (table 3).

undue weight to one or another aspect of the phenotype. The task of detecting and documenting character redundancy was approached systematically through an analysis of character association. Characters may be correlated for many reasons, one of which is redundancy. Correlations were measured using the chi-square statistic (Voris, 1971) and in the event that two characters showed high correlation the following possibilities of redundancy were investigated.

Redundancy due to physical factors of measurement.—This type of redundancy occurs when two or more measurements or character states describe the same feature (Davis and Heywood, 1963, p. 130). It is a simple matter to detect characters which are 100 per cent redundant for this reason. For example, it is redundant to use both the measurements of surangular (character number 119) and dentary length (120) and total jaw length, because in sea snakes, the jaw length equals the surangular length plus dentary length. This relationship may not necessarily hold true for newly discovered species and thus character relationships must always be re-evaluated when new organisms are added to a study. That is, 100 per cent correlation between characters in a small set of data does not justify assuming the same correlation in a larger data set.

Redundancy due to character repetition.—These associations are a result of characters being descriptions of the same type of feature. There are examples of complete and partial repetition of characters in the sea snakes. For example, in most species of sea snakes the number of scale rows around the body varies along the length of the body. However, in some species of *Laticauda* the scale row count remains nearly constant throughout the length of the snake so that all five counts are identical and effectively 100 per cent repetitious after character coding. When changes in number of scale rows occur they generally take place gradually. Smith (1926) made a scale-row count at the neck and in several places around the mid-body to find the maximum row, and was able to separate some species on this basis. After making survey counts I found that if counts were made at the neck, one-fourth, one-half, and three-fourths the number of ventral scales from the neck, and at 10 ventrals anterior to the vent (character numbers 84-88), a few additional bases for species separation were found. Thus it is conceivable that one might want to make scale row counts at every tenth ventral to study the scale row increases more thoroughly or even count every row. However, the latter procedure would add 300 to 400 characters to the study and effectively "swamp" the other characters.
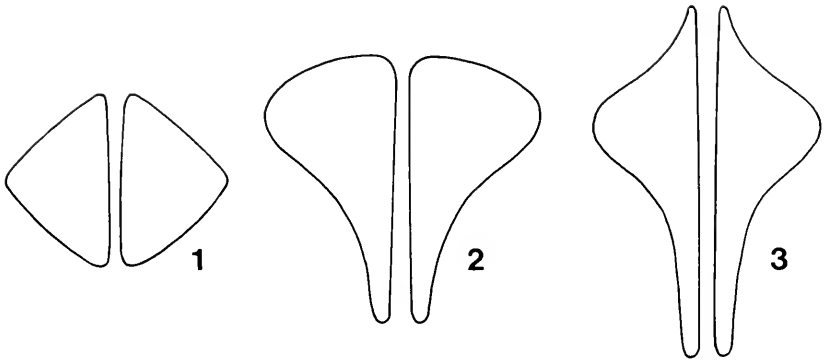
FIG. 2. Outlines of the three major types of nasal bones (character 138) found in the Hydrophiidae. Numbers refer to designated character states (table 3).

The choice as to how many characters of this type and which ones are retained remains for the moment with the judgement of the individual taxonomist. In this study redundancy of this type was minimized in the reduced data set.

Redundancy due to mechanical relationships.—This type of redundancy has been called necessary correlation (Cain and Harrison, 1960) and refers to characters that are mechanically related to one another. An obvious example in the sea snakes would be the two characters, number of pairs of enlarged chin shields (81), and the number of enlarged chin shields touching (82). In character 81, zero pairs of chin shields is necessarily 100 per cent correlated with zero pairs touching in character 82. One pair of shields will also be associated with one or zero pairs touching. An example in this study of character association where redundancy is not certain but a possible factor would be the association between the position of the nostril (2) and the presence or absence of the internasal scale (1).

In instances in which a group of characters was found to be redundant for one of the above reasons all but one of the characters were removed from the data set. The question of which character was retained in each case is not crucial but the decision was based on an evaluation of the reliability and completeness of the data on the characters. Character redundancy was the principal and first criterion applied to reduce the character set.
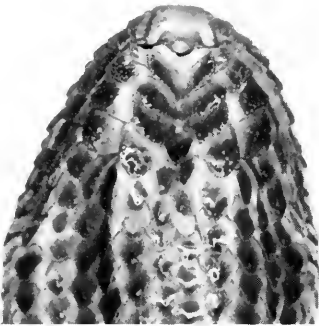
Two state characters which have one state almost universally distributed and the other state highly restricted in distribution, are not helpful in a study of most species' relationships. This is true irre-
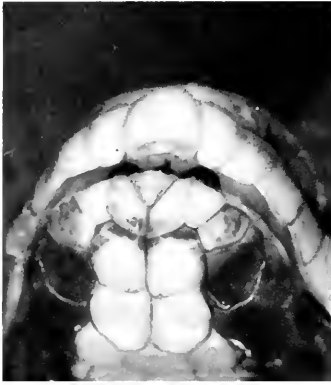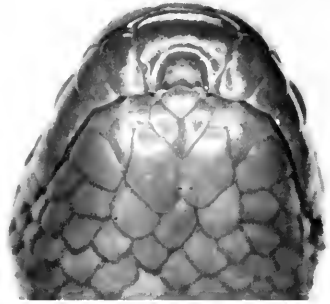
FIG. 3. Four major types of rostral grooves found among the Hydrophiidae. State 1 as in *Laticauda colubrina* (FMNH 13817); State 2 as in *Laticauda semifasciata* (FMNH 75169); State 3 as in *Aipysurus duboisii* (British Museum 1926.5.28.26); State 4 as in *Lapemis curtus* (Universitetets Zoologiske Museum R 66149).

gardless of which state, the common one or the rare one, is derivative. Character number 6, gular azygous scale present or absent, and number 7, anterior prefrontal azygous scale present or absent, are examples of these kinds of characters in that only one species of sea snake exhibits the presence state of each of the two characters. These characters were removed from the data set because they lend no relational information about the taxa.

Some characters and some species were removed from the data set in order to obtain a nearly complete data matrix. This was necessary because it has been learned in the process of these studies, that even an apparently small amount of missing data could have a significant impact on the results. Thus it was decided on the basis of experience that no species should have more than one missing data point. Species for which skull preparations were not possible could not be retained without eliminating all skull characters. In addition some characters, particularly hemipenis characters and measurement characters, were uncollected in some species. Thus 10 species were removed from further consideration in the study (species nos. 5, 16, 29, 32, 35, 37, 38, 39, 43, 52; recall also that species 8 and 42 were not initially included, see table 1).

Practical reasons such as computer program restrictions might necessitate further reduction of the data set in some studies, but in this one the reductions made on the other grounds were sufficient to avoid making reductions on this basis alone.

The data set which remained after applying these various criteria consisted of 43 characters on 40 species (table 3). It is worth noting that all characters not eliminated for a specific reason were retained. Thus the process of reduction of the data set was one of elimination and not selection. Some characters from every area and portion of the snakes' morphology were retained and are represented in the reduced data matrix (table 4).

RELATIONSHIPS AMONG THE SEA SNAKES

All methods employed to deduce relationships of organisms use phenetic data. However, the methods which have been developed to manipulate these data vary drastically procedurally and philosophically.

Phenetic and phylogenetic methods can most easily be distinguished on the basis of objectives. Phenetic methods are largely concerned with estimating "overall similarity" (Sokal and Sneath,

1963, p. 3). Phylogenetic methods on the other hand, are concerned with estimating geneological relationships (Throckmorton, 1968). Generally, methods associated with phylogenetic studies involve many more implicit and/or explicit assumptions.

A Phenetic Treatment as a Point of Reference

Today the taxonomist has a vast number of phenetic methods from which he can choose (see Sneath and Sokal, 1973; or Jardine and Sibson, 1971). Numerous comparative studies have been conducted (e.g., Sokal and Michener, 1967; Boyce, 1969; Voris, 1969), and from them one generality has seemed to emerge: there is no single phenetic method that has general enough properties to satisfy more than a few of the practitioners. Rather, the tendency has been to recognize that each method supplies a distinct "window" into the nature of the relationships. Sneath and Sokal (1973, p. 147) after a lengthy discussion of estimations of taxonomic distances, came up with only one recommendation regarding the choice of methods, "of each type of coefficient considered, the simplest one should be chosen out of consideration for ease of interpretation."

The results of a phenetic analysis, using the simple matching coefficient (Sokal and Michener, 1958) with single linkage or nearest neighbor clustering (Sneath, 1957) are presented here to give the reader a relatively assumption-free view of the phenetic relationships of the sea snakes.

The simple matching coefficient (S.C.) is calculated for each pair of species as follows:

$$\text{S.C.} = \frac{\text{Number of character states shared}}{\text{Total number of characters}}$$

Descriptions of single linkage clustering are given elsewhere (Voris, 1969, Appendix D; or Sneath and Sokal, 1973).

These procedures were selected for two reasons. First, both the simple matching coefficient and the single linkage clustering method have been used widely since the late 1950's (see Sneath and Sokal, 1973, p. 132). Thus, from an *intuitive* standpoint, few methods have been more widely tested and evaluated. Second, these methods are among the simplest of all numerical taxonomic methods and thus the interpretation of the results is relatively straightforward.

The data matrix presented in Table 4 was used in the phenetic analysis. The relationships which resulted are presented in the form
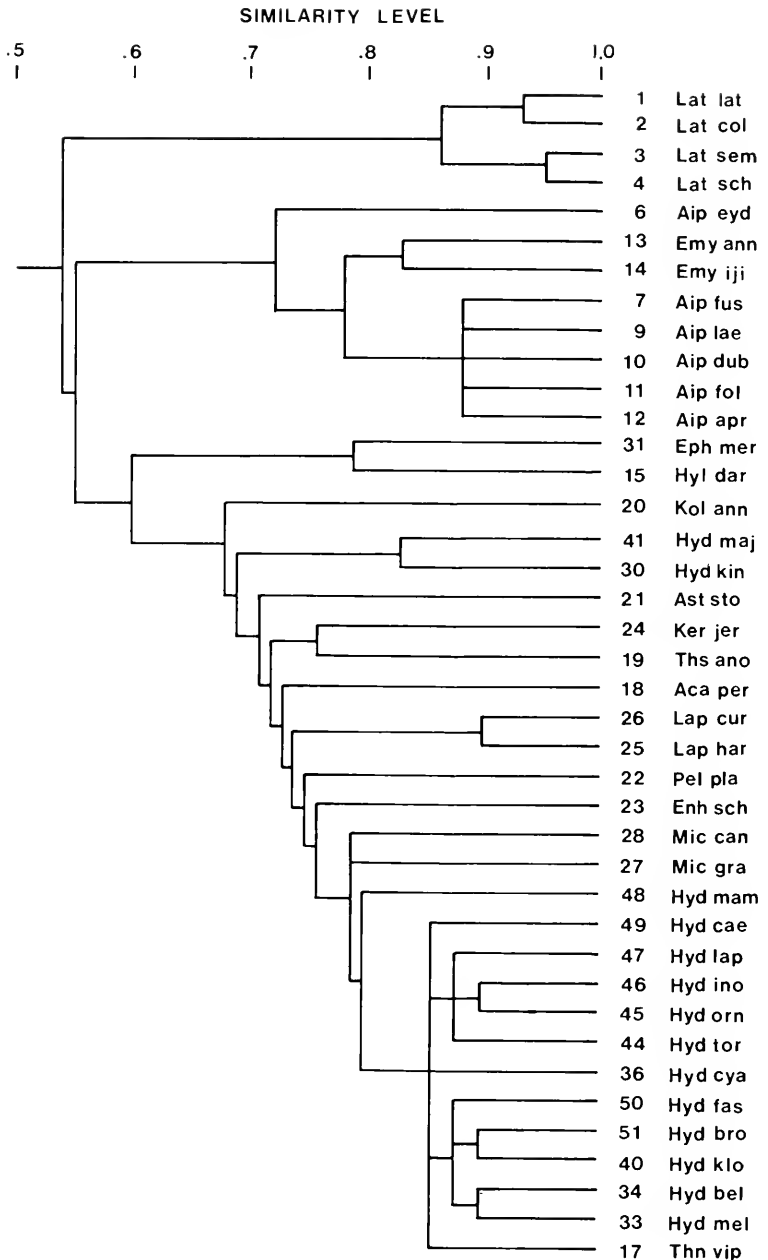
FIG. 4. Dendrogram of the phenetic relationships among 40 species of Hydrophiidae, based on 43 characters (table 4), using the simple matching coefficient and single linkage clustering.

of a dendrogram (fig. 4). The *Laticauda* separate from all others at a relatively low level of similarity and have high similarity among themselves. The *Aipysurus* and *Emydocephalus* also separate early. The similarity among the species of *Aipysurus* and *Emydocephalus* is less than that observed among the *Laticauda* species and, although the two *Emydocephalus* are depicted as nearest neighbors to each other, they are among the *Aipysurus* species. The remaining species form almost a continuum on the similarity scale. Within this group, *Ephalophis mertoni* and *Hydrelaps darwiniensis* are the first to separate. Several monotypic genera and two Australian *Hydrophis* branch off in rapid succession, until finally the majority of the genus *Hydrophis* joins at relatively high similarity levels. In summary, three major groups are indicated: *Laticauda, Aipysurus-Emydocephalus,* and all others.

A Phylogenetic Treatment

Both logically and procedurally the derivation of a phylogeny is complex and problematic. It necessitates making inferences concerning connectedness, direction of evolution, and evolutionary distance. The method which has been developed in this study to accomplish this and which is discussed in the following paragraphs, is not set forth as *the* method of deriving phylogeny, but as one attempt to utilize objectively defined and repeatable procedures to this end.

Character Selection: A Phylogenetic Perspective

Characters that are phylogenetically useful are those whose states are associated with one another for reasons of common evolutionary history (Davis and Heywood, 1963; Blackwelder, 1967; Voris, 1971). The task is first to detect those characters that are highly associated with other characters and then to evaluate the basis for the observed associations. Although historically important characters show high association, the converse is not necessarily true. Characters may show a high degree of association with one another for reasons other than common history, e.g., the various types of redundancy described on p. 86. High associations due to functional relationships (adaptive or convergent association) of characters are also possible, but difficult to detect *a priori*.

By removing from the data set those characters which could be shown to be highly associated due to various types of redundancy, a process which constituted residual weighting, I arrived at a data set which represented many aspects of the phenotype and which I think has a high probability of containing valid historical information.

Character State Trees

The methods used in this study to determine the evolutionary connectedness of OTU's, direction of evolution among the OTU's, and the evolutionary distances between the OTU's, utilized character state trees. Character state trees depict the primitive state and the sequence and direction of change for the character states. The character state tree concept is not a new one. The terms used in this study—"character state tree," "primitive state," "sequence and direction of change,"—correspond to Maslin's (1952, p. 51) terms "morpho-cline" and "polarity"; Hennig's (1966, p. 95) "character phylogeny," "transformation series," and "plesimorphous" (primitive) and "apomorphous" (derived) conditions; Throckmorton's (1962, p. 309) "stepwise sequence," "primitive characteristics," and "derivative characteristics"; and Camin and Sokal's (1965, p. 312) "presumed evolutionary sequences."

Primitive state information is obviously critical to the formation of character state trees. In this study, the primitive state information was derived from the contemporary group most closely related to the hydrophiids, which in the view of the majority of herpetologists is the Elapidae (Bellairs and Underwood, 1951; McDowell, 1972). The Hydrophiidae is considered to be the most recent group to be derived from the elapid stock, and thus the Elapidae is in a "pregroup" position. The evidence can be summarized as follows: because of certain derived character states common to the Elapidae and Hydrophiidae (e.g., anterior nonrotatable fang and neurotoxic venom) the Hydrophiidae are considered to be phylogenetically more closely related to the elapids than to any other contemporary group of snakes; and because the Hydrophiidae are highly specialized in their way of life, they are considered the more derivative of the two groups. The elapids have remained terrestrial for the most part as were their presumed ancestors, a stock common to the Xenopeltidae, Boidae, and Pythonidae (Bellairs and Underwood, 1951).

Returning to the specific problem of the determination of primitive states, I determined which of the hydrophiid states were primitive on the basis of their distribution among the elapids and the number of times a hydrophiid state appeared in the elapids. My primary criterion was that a hydrophiid state was designated as primitive if it appeared throughout the elapids, i.e., in many diverse groups. The reasoning behind this was that it is more logical to postulate that a widely distributed state is primitive and has been retained throughout the various lineages, than to postulate numerous

independent origins of it. A secondary criterion was invoked when the appropriate data were available. If the alternative states were rare and limited in their distribution to highly specialized elapids, I took this as an indication of derivativeness and a confirmation of the designation of the primitive state. If a hydrophiid state did not appear at all among the elapids, there was no basis for considering it anything but derivative among the hydrophiids. A qualification of this would be needed if the sea snakes were known to have separated from the elapid stock very early in their history, and in that sense would be as primitive as the elapids themselves. However, the possibility of this having occurred is not supported by evidence currently available. It should be noted that assumptions regarding the absolute occurrence or absence of character state reversal, the unique derivation of states, or multiple origins of states are not required here. Rather the logic is based on Occam's razor. Although multiple origins and reversals of character states as well as unique origins do occur, *most* character states have not originated many times, reversed many times or originated only once, and we thus assume that when a state is widely distributed *throughout* various linages of a group the simplest explanation is that it is a retained primitive state rather than a derivitive state with *many* independent origins.

Once the primitive state was designated, the rest of the character states were ordered in a logical numerical or phenetic sequence. For example, for character 95, number of maxillary teeth, the states in the sea snakes were designated as: state 1, 0-1 teeth; state 2, 2-4 teeth; state 3, 5-7 teeth; state 4, 8-10 teeth. State 2 was designated as primitive. Therefore the logical sequence is as follows: $1 \leftarrow \textcircled{2} \rightarrow 3 \rightarrow 4$. Character 41, sulcus shape, describes the shape of the sulcus and has four designated states.
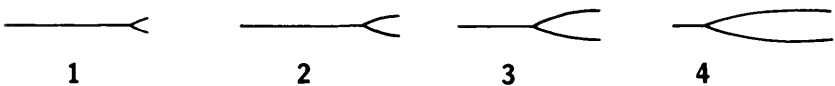
| 1 | 2 | 3 | 4 |

State 1 was designated as primitive and the phenetic sequence designated as $\textcircled{1} \rightarrow 2 \rightarrow 3 \rightarrow 4$. Clearly, these sequences are not the only possible ones, but sequences are necessary and these examples demonstrate how I proceeded with this task.
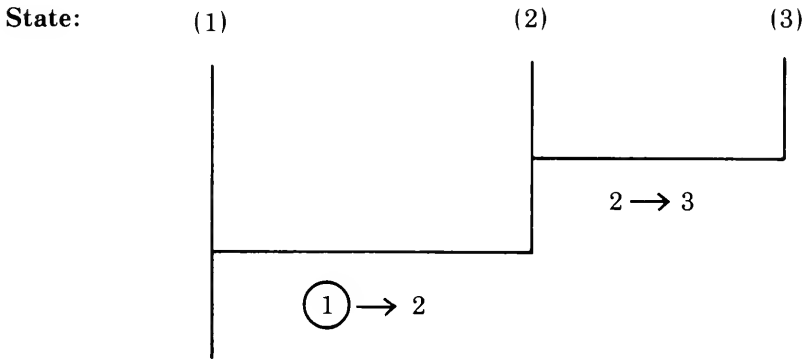
The elapid data used came from three sources: Marx and Rabb, 1972; Marx and Rabb, personal communications; and a survey of 24 skull characters on 28 species representing 22 genera of elapids

(Voris, 1969, Appendix C). The character state trees for the 43 characters used in this study are given in Table 3.

Arriving at a Consensus of Character State Trees

At this point we have 43 characters, represented by 146 states. Each of the 40 species of sea snakes has been assigned one state for each character. For each character a primitive state, connectedness of states, and direction of evolution, i.e., a character state tree, has been designated. Thus each character designates its own phylogeny of the 40 species. For example, character number 4 (parietal fragmentation) designates the following relationships (see tables 3 and 4 for the character state tree and the states for each species respectively).

Species:	1, 2, 3, 4, 5, 13, 15, 17, 19, 21, 24, 27, 28, 30, 31, 33, 34, 36, 40, 41, 44, 45, 46, 47, 49, 50, 51	12, 14, 20, 22, 23, 25, 26	7, 9, 10, 11, 18
State:	(1)	(2)	(3)

$2 \rightarrow 3$

$(1) \rightarrow 2$

Since the character state trees represent the only phylogenetic information available, it may be argued that a consensus of character state trees would provide the closest approximation to the actual phylogeny. However, all character state trees do not designate the same or even compatible arrangements of species, as may be seen from a comparison of just two characters, the tree above and the one given below (Character 46, relation of frontal bone to orbit). The problem of integrating character state trees to derive a consensus thus presents itself.

	1, 2, 3, 4, 5, 6, 7, 10,	9, 36, 50	15, 17, 18, 19, 20, 21,
Species:	11, 12, 13, 14, 22		23, 24, 25, 26, 27, 28,
			30, 31, 33, 34, 40, 41,
			44, 46, 47, 48, 49, 51

State: (1)   (2)   (3)

$2 \longrightarrow 3$

$\textcircled{1} \longrightarrow 2$
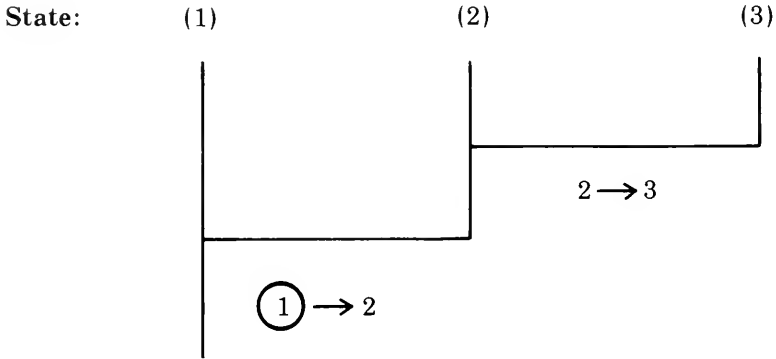
Several diverse approaches have been applied to use character state trees to derive phylogenies (e.g., Camin and Sokal, 1965; Throckmorton, 1965; Inger, 1972; Heyer, 1974). Some of these studies have dealt with the integration of character state trees through the manipulation of character-state reversals and the multiple origin of character states. This study utilizes the Sharrock and Felsenstein (1976) combinatorial method in a novel way as part of an attempt to build a consensus phylogeny. This method allows data on which the phylogeny is based, to be retrieved in their original form. The combinatorial method has been described and/or used previously (Liem, 1970; Inger, 1972; Heyer, 1974; Zehren, 1974; Sharrock and Felsenstein, 1976). However, because the original manuscript describes the method in somewhat abstract terms and because other workers have simply cited the later paper a synopsis of the method is included here.

Sharrock and Felsenstein Combinatorial Method

The computer programmed combinatorial method, as it has most commonly been used, operates on a binary data matrix of species by character states. Each species is coded as having (1) or not having (0) *each* character state. This binary matrix can be constructed in numerous ways. For example, all primitive states can be eliminated and/or species can be coded as possessing all states which they actually possess plus all those states which are designated by the char-

acter state trees as primitive to those states. In phylogenetic studies assumptions are routinely incorporated when the binary matrix is prepared and when the combinations generated are analyzed. A manuscript on the variety of options available and their application is in preparation (Marx et al., MS in prep.).

The criterion of similarity in the Sharrock and Felsenstein combinatorial method is not a similarity coefficient, but rather it is based on the actual number of the *same* character states held in common by all species in a group. These groups of species are called the nonredundant, monothetic combinations. Specifically, a non-redundant monothetic combination is the largest group of species sharing a given set of character states.

An example will help clarify the procedure. Below, the presence (1) or absence (0) of eight character states[1] is presented for three hypothetical species.

				Character States				
Species	1	2	3	4	5	6	7	8
A	0	1	1	1	1	1	1	1
B	1	0	0	0	0	1	1	1
C	0	0	0	0	1	0	1	1

The computer output for this data set would give the following information:

Combination Number	Number of Shared States	Group Size (Number of Species)	Members of Combination or Group (Species)	Shared Character States
1	7	1	A	2,3,4,5,6,7,8
2	4	1	B	1,6,7,8
3	3	2	AB	6,7,8
4	3	2	AC	5,7,8
5	2	3	ABC	7,8

In the output the nonredundant monothetic combinations are listed in descending order based on the number of shared character states. For each combination the number of members within the combination is listed, the members are listed and the character states shared

[1]This might represent data from one to four characters depending on the number of states per character.

by all the members are given. The first combinations usually (as in this example) are simply single species with unique combinations of character states. In this example, the third combination reveals that species A and B share three characters (numbers 6, 7, and 8). The fourth combination shows that species A and C also share three states (numbers 5, 7, and 8). Note that the latter suite of characters is distinct from the suite of characters shared by species A and B. All three species form a combination sharing character states 7 and 8.

It should be emphasized that the combinatorial method is a tool to derive groups of taxa with specified characteristics and the method itself assumes nothing. Its striking advantage is that the actual characters designating a group of species remain known, since they are listed with the combination they form, and are not obscured as in the calculation of a similarity coefficient. This is of particular significance in that the combinatorial method has the potential to satisfy one of the criteria set forth earlier: that the data on which the final phylogeny is based be known. How the combinatorial method is used to arrive at a consensus of character state trees follows.
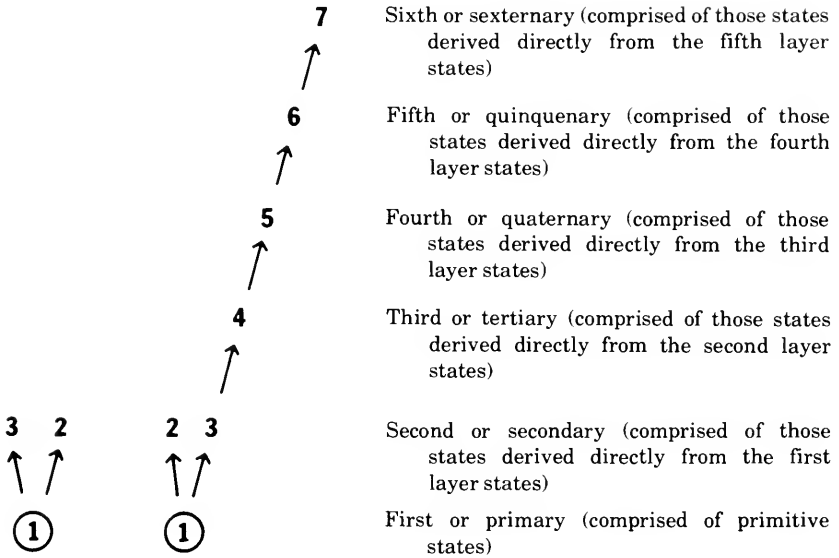
Approach to Combinatorial Method Computer Output

In this study the combinatorial method has been applied to the 40 species of sea snakes six separate times, once at each character state tree layer, each time independent of the states at other layers in the character state trees. The character state tree layers are defined as on p. 99, with two character state trees used as examples.

The most common way of coding data for use with the combinatorial method was briefly mentioned earlier, namely coding the data to imply that all states primitive to the state actually exhibited by a species were also possessed by it. While this allows the character state tree to be incorporated into the coded data to some extent, it has a significant disadvantage in that in effect it differentially weights those characters which have the greatest number of states, giving them more influence on the results on that basis alone (Heyer, 1974; Zehren, 1974). Another possibility, investigated at one point by me, is to code each state as present or absent in a straightforward way, but this is purely phenetic and effectively eliminates the phyletic information provided by the character state tree. The approach used in this study overcomes both of these objections in that each state is used once and only once, and it also allows incorporation of tree information in that the character state tree

Character State Trees *(2 different characters)*
Layer

7 ↑	Sixth or sexternary (comprised of those states derived directly from the fifth layer states)
6 ↑	Fifth or quinquenary (comprised of those states derived directly from the fourth layer states)
5 ↑	Fourth or quaternary (comprised of those states derived directly from the third layer states)
4 ↑	Third or tertiary (comprised of those states derived directly from the second layer states)
3 2 2 3 ↖ ↗ ↑ ↗ ① ①	Second or secondary (comprised of those states derived directly from the first layer states) First or primary (comprised of primitive states)

layers are considered sequentially. It may also be argued, that for a given species, the least advanced character state tree layer(s) (most primitive) will tend to designate largely phenetic relationships while more advanced layers (more derivative) tend to reveal its phyletic relationships (Hennig, 1966).

The first character state tree layer, composed of all primitive states[1], consisted of a total of 43 states, that is one state for each character. The second layer consisted of 65 states. This value exceeds the number of characters because bifurcating and trifurcating character state trees contribute two and three states respectively to this layer (as in the example given above). The third, fourth, fifth, and sixth layers contained 23, 10, 3, and 1 character states respectively. Since each species is represented by only one state per character, the maximum number of states which any single species could

[1]This study differs from many previous ones in that primitive states are included and used in the data analysis rather than eliminated. The argument for including the primitive states is that the concept of primitive states is a relative one. This approach is in part an outgrowth of Hennig's (1966) discussion of the relative nature of character states to each other, and Throckmorton's (1968) "operational primitive" concept. The full argument for the use of primitive states is presented in much greater detail in a forthcoming study (Marx et al., MS in prep.).

possess is 43 (less if the species is missing data on a character). The number and percentage of states each species possesses at the various character state tree layers is of some interest and value in later aspects of the analysis (table 5).

Applying the combinatorial method to each layer of the character state trees resulted in the generation of 688 combinations of species at the first layer, 1,661 combinations at the second layer, 182 combinations at the third layer, 17 combinations at the fourth layer, 4 combinations at the fifth layer, and 1 combination at the sixth layer.

When the combinations generated by the combinatorial method are surveyed, two types of combinations may be observed: first, there are combinations of species whose members are not parts of any other combination at the same number of shared states. In this data set, a second type of combination is also often observed: these are combinations in which some members are found in one or more other combinations formed at the same level of shared character states. The existence of these two types of combinations suggests that there are some groups of species which are quite distinct from the others at a given character state tree layer, and other groups which are diffuse and whose species form more or less a continuum of phenotypes. Groups of species which are distinct in this sense from other groups and formed with high numbers of shared character states, are likely valid phyletic units. The "contested" combinations are also important because they illustrate the degree and way in which various groups are inter-related.

A set of systematic procedures has been developed to be applied to the computer output of the combinatorial method for each character state tree layer to detect this kind of structure in the data set. The result is a "flow-chart" of species relationships at each character state tree layer. The procedures were developed in accord with two general principles: they must be consistent and repeatable, and they must expose the relationships of the species as represented by the sometimes large number of possible combinations, as completely as possible without incorporating obfuscating redundancy. The procedures used to accomplish this are described below:

1. At each character state tree layer the combinations of species generated by the combinatorial method are scanned beginning at the highest number of shared states and proceeding level by level down through the lowest level of shared states, detecting and diagrammatically representing structure among the species according to the following criteria:

2. A single species or a combination of species is considered to have formed an *uncontested* group at a given level of shared states, if none of those species are found in any other group at that same level of shared states.

3. A group or combination is considered to be *contested* if one or more of the species in that group are also found in one or more other groups at that same level of shared states.

4. As groupings at lower levels of shared characters are considered, groups once formed are never broken up, whether they were first formed as contested or uncontested groups (although the contested-uncontested status itself may change, see below). That is, as lower levels of shared states in common are considered, groups designated at higher levels may enlarge to form new groups by joining one another, or new species may appear and/or be added on to an existing group, but once a species has been placed in a group or groups, it is never linked to another species or group of species to form a new group unless all members of at least one of its groups are linked to that new species or group of species. Thus, contested groups may resolve into a single, larger, uncontested group at a lower level of shared states if all members of the two or more contested groups are found within a single group at that level. Also, uncontested groups may become parts of contested groups if a whole uncontested group is found in two or more combinations containing different species as their additional group members at a lower level.

5. A previously formed group or groups (which may consist of one or more species and be contested or uncontested) may be detected at a lower level of shared states within a combination which also contains some but not all species from one or more other previously formed groups. According to number 4 above, the whole combination cannot constitute a new group without breaking up a previously formed group. However, the information provided by such a relationship is an important aspect of the data set, and so those extraneous species which are parts of previously formed groups, are listed as *neighbors* to whatever whole group exists within the larger combination at that level, or whatever new group is formed within that combination. The first time, i.e., the highest level, at which this occurs for each group, the neighbors are referred to as *near* or *nearest neighbors*.

As mentioned previously, the structure detected by the procedure outlined above was originally recorded in the form of a flow-chart. Although highly informative, the flow-charts are extensive and complex and cannot be reduced to the size of the standard printed page. Thus each flow-chart was converted to a punctuation representation. A sample flow-chart for the first few levels of shared states for the first character state tree layer is presented in Figure 5. The punctuation representation of the data (explained in the table heading) is given in Table 6 for the first character state tree layer, in Table 7 for the second layer, in Table 8 for the third layer, and in Table 9 for the fourth, fifth, and sixth layers. Comparison of Figure 5 with the beginning of Table 6 will clarify how each representation may be converted to the other.
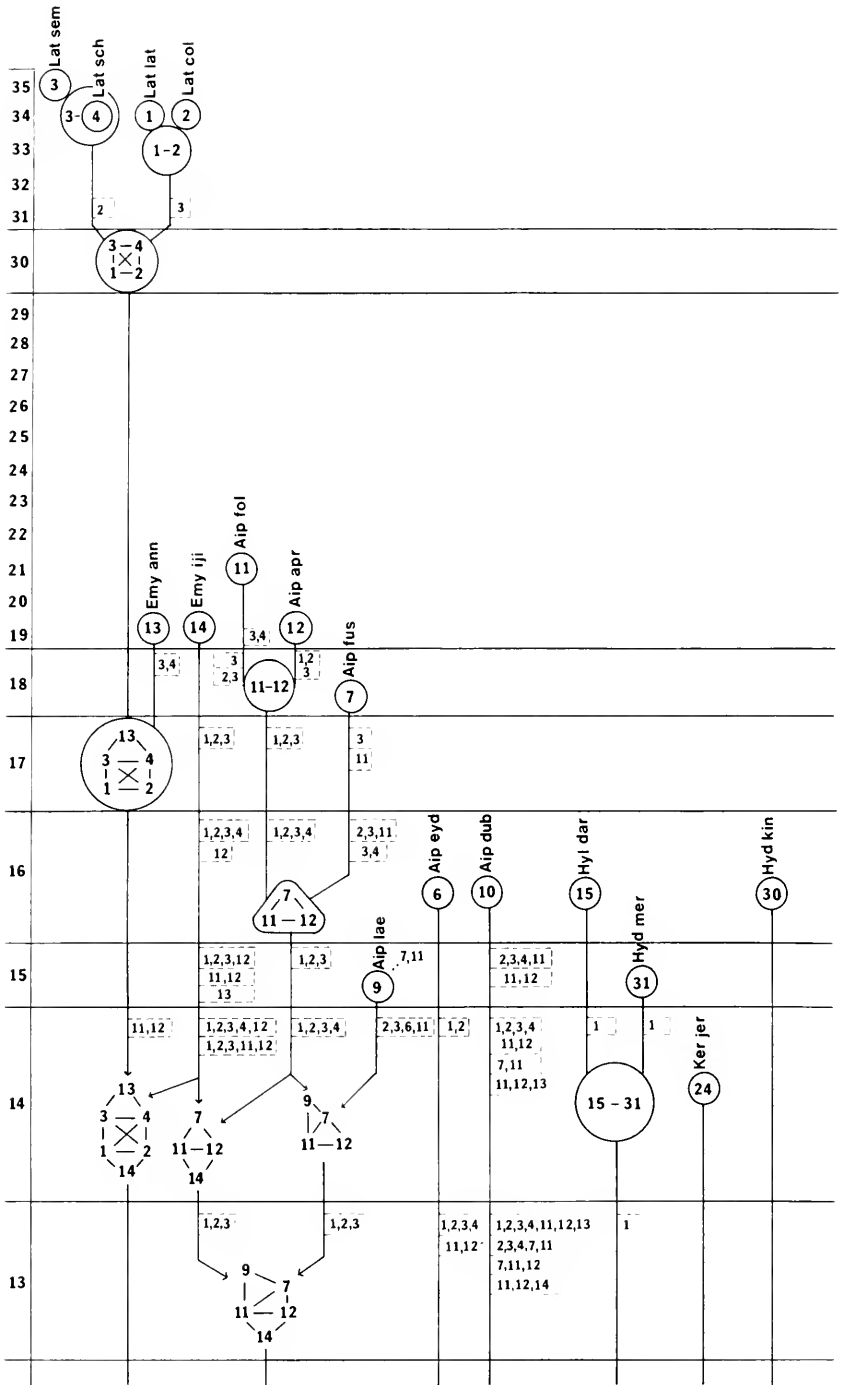
Since one of the goals of these procedures was to present the species relationships as completely as possible without redundancy, it is of interest to consider what proportion of the total combinations generated by the combinatorial method at each character state tree layer, were included (either as uncontested or contested groups or near neighbors to groups) in the final representation of the structure at each level. Of the 688 first-layer combinations, 287 (42 per cent) are represented in Table 6. Of 1,661 second-layer combinations, 575 (35 per cent) are represented in Table 7. Of 182 third-layer combinations, 158 (87 per cent) are represented in Table 8. Of 24 fourth-layer combinations, all 24 (100 per cent) are depicted in Table 9, and similarly 4 out of 4 (100 per cent) fifth-layer combinations, and 1 out of 1 (100 per cent) sixth-layer combinations are included in Table 9.

The next task, the integration of the structure from each of the character state tree layers (Tables 6-9) into a final consensus phylogeny, was approached by first placing species into one of several groups based on the relative percentage of character states exhibited at each of the character state tree layers (see table 5 and below). These groups were formulated only to facilitate discussion, and whether or not manageable groups of species would be designated by this procedure in another study is dependent on the data

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Opposite:

Fɪɢ. 5. Flow-chart representation of selected combinations of Hydrophiidae species to shared state level 13. For all levels see Table 6. Selection was from those combinations generated by the Felsenstein and Sharrock combinatorial method at the first character state tree layer.

Lat sem Lat sch Lat lat Lat col

35 (3)
34 (3—4) (1) (2)
33 (1—2)
32
31 [2] [3]
30 3—4 ⊠ 1—2
29
28
27
26
25
24
23 Aip fol
22
21 (11)
20 Emy ann Emy iji Aip apr
19 (13) (14) (12) [3,4]
18 [3,4] [3 2,3] 11—12 [1,2 3] Aip fus
     (7)
17 13 3 ⊠ 4 1   2 [1,2,3] [1,2,3] [3 11]
16 [1,2,3,4 12] [1,2,3,4] [2,3,11 3,4] Aip eyd Aip dub Hyl dar Hyd kin
     7 11—12 (6) (10) (15) (30)
15 [1,2,3,12 11,12 13] [1,2,3] Aip lae [7,11] [2,3,4,11 11,12] Hyd mer
     (9) (31)
14 [11,12] [1,2,3,4,12 1,2,3,11,12] [1,2,3,4] [2,3,6,11] [1,2] [1,2,3,4 11,12 7,11 11,12,13] [1] [1] Ker jer
     13 3 ⊠ 4 1   2 14   7 11—12 14   9   7 11—12 14   15—31   (24)
13 [1,2,3] [1,2,3] [1,2,3,4 11,12] [1,2,3,4,11,12,13 2,3,4,7,11 7,11,12 11,12,14] [1]
     9   7 11—12 14

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set. For example, a data set with all two-state characters would obviously require a different scheme or criteria in order to separate the data set into groups small enough for efficient discussion. However, in this study, in addition to providing small enough groups for efficient discussion, this basis for grouping species had two further advantages: it separated species into groups with similar distributions of amounts of information (character states), and, it directed attention to the character state tree layer(s) at which each species' relationships should be best resolved and most reliable.

The following groups have been designated in this study, with respect to the relative percentages of states at each character state tree level.[1]

I. 1st. layer > 2nd. layer > 3rd. layer > 4th., 5th., or 6th. layer

    1) *Laticauda laticaudata*
    2) *Laticauda colubrina*
    3) *Laticauda semifasciata*
    4) *Laticauda schistorhynchus*

II. 1st. layer ≅ 2nd. layer > 3rd. layer > 4th., 5th., or 6th. layer

    11) *Aipysurus foliosquama*

III. 2nd. layer > 1st. layer > 3rd. > 4th., 5th. or 6th. layer.

    6) *Aipysurus eydouxi*
    7) *Aipysurus fuscus*
    9) *Aipysurus laevis*
    10) *Aipysurus duboisii*
    12) *Aipysurus apraefrontalis*
    13) *Emydocephalus annulatus*
    14) *Emydocephalus ijimae*
    15) *Hydrelaps darwiniensis*
    19) *Thalassophis anomalous*
    24) *Kerilia jerdoni*
    25) *Lapemis hardwickii*
    26) *Lapemis curtus*
    30) *Hydrophis kingi*
    31) *Ephalophis mertoni*

IV. 2nd. layer > 1st. ≅ 3rd. layer > 4th., 5th. or 6th. layer

    18) *Acalyptophis peronii*
    21) *Astrotia stokesii*
    23) *Enhydrina schistosa*
    27) *Microcephalophis gracilis*
    28) *Microcephalophis cantoris*
    33) *Hydrophis melanosoma*

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[1]Percentage values were considered to be about equal (≅) when they differed by five or fewer percentage points.

34) *Hydrophis belcheri*
36) *Hydrophis cyanocinctus*
40) *Hydrophis klossi*
41) *Hydrophis major*
45) *Hydrophis ornatus*
46) *Hydrophis inornatus*
50) *Hydrophis fasciatus*
51) *Hydrophis brookii*

V. 2nd. layer > 3rd. layer > 1st. layer > 4th., 5th., or 6th. layer.

17) *Thalassophina viperina*
20) *Kolpophis annandalei*
22) *Pelamis platurus*
44) *Hydrophis torquatus*
47) *Hydrophis lapemoides*
48) *Hydrophis mamillaris*
49) *Hydrophis caerulescens*

The structure at each of the character state tree layers is discussed below for each group of species.

Results of Analysis of Combinatorial Method Computer Output

Group I Species

Four species all of the genus *Laticauda* (*laticaudata* (1), *colubrina* (2), *semifasciata* (3), and *schistorhynchus* (4)) have over 75 per cent of their states at the primary or first character state tree layer (table 5). Of the 34 or 35 states which each of these species possesses, 30(88 per cent) are shared by all four species (table 6; fig. 5). There is a gap of 13 character states between this group and the character-state level at which the next species, *Emydocephalus annulatus* (13), joins the group. On the basis of the bulk of the phenotype measured, the genus *Laticauda* is a tight cluster of species very distinct from all other taxa.

These species of *Laticauda* have eight or nine states (about 20 per cent) at the second character state tree layer (table 5). The relationships designated by these more derived states are compatible with the relationship designated by the first layer (table 7). However, at the second character state tree layer, the combination including all four species of *Laticauda* does not occur .until the level of three shared states; and, at the level of three and four shared states, both species pairs (1, 2 and 3, 4) have near neighbors from the genera *Aipysurus* and *Emydocephalus*. The *Laticauda* have very little information above the second character state tree layer (table 5).

Conclusions on Group I Species.—The genus *Laticauda* is a phenetically tight group of closely related species. On the basis of a few

derived states, it appears to have weak phyletic relationships with several *Aipysurus* and *Emydocephalus* species, leaving open the possibility that these groups are monophyletic. However, at the same time, because of the weakness of the phyletic relationship, a very early separation of the groups or even polyphyly is implicated.

Group II and Group III Species

Because only one species fell into the group II category, group II and group III species were considered together. At the first character state tree layer these species have from 21 states (49 per cent) in *Aipysurus foliosquama* (11) to eight states (19 per cent) in *Lapemis hardwickii* (25) (table 5). With two exceptions (*Lapemis hardwickii* (25) and *Lapemis curtus* (26)), at this character state tree layer the neighbors to each of the group II and group III species are one or more species of the genus *Laticauda* (fig. 5; table 6). This phenomenon is a function of the fact that the *Laticauda* possess a very high proportion of primitive states and the group II and group III species possess the same primitive states, although not as many. The *Lapemis* species do not share these states and in this respect they are more like species in groups IV and V. At this layer the relationships among the group II and group III species are, for the most part, complex. Looking beyond the fact that neighbors are predominantly among the *Laticauda,* it is evident that some of these species are very similar to each other. *Aipysurus foliosquama* (11) and *A. apraefrontalis* (12) have 45-49 per cent of their states at this level and they share most of them, namely 18. *Aipysurus fuscus* (7) is similar to both these forms at the level of 16 shared states, but it is a bit closer to *A. foliosquama* (11) which is a near neighbor at 17 shared states. It is crucial to note that both *A. duboisii* (10) and *A. laevis* (9) do not have as many states at this level as the previously mentioned species of *Aipysurus,* but when they first appear they are in contested combinations with *A. foliosquama* (11) and/or *A. fuscus* (7). That is, all the primitive states that *A. laevis* (9) and *A. duboisii* (10) have are also possessed by *A. foliosquama* (11) and/or *A. fuscus* (7). *Aipysurus eydouxi* (6) stands slightly away from all other *Aipysurus* at this level and the fact that it forms an uncontested combination with *A. duboisii* (10) at the level of 12 shared states is clearly an artifact of the combination selection procedures. That is, both these species are clearly closest individually (see shared states levels 16, 15, 14) and as a group (see shared states level 12) to *A. foliosquama* (11), *A. fuscus* (7), and *A. apraefrontalis* (12). *Emydocephalus ijimae* (14) has relatively high affinities with the *Laticauda,*

the various *Aipysurus,* and *E. annulatus* (13). Because of these affinities and because *E. annulatus* (13) shares 17 states with all four *Laticauda* forming an uncontested group with them, several contested groups are generated at and below the level of 14 shared states. Without exception, contested groups and their neighbors are species of *Aipysurus, Emydocephalus,* or *Laticauda* down to the level of six shared states.

Hydrelaps darwiniensis (15) and *Ephalophis mertoni* (31) form an uncontested group with 14 shared states and have neighbors with only the *Laticauda* until the level of 10 shared states. *Kerilia jerdoni* (24) and *Hydrophis kingi* (30) do not share more than 12 primitive states (about 30 per cent) with any species, but at 11, 10, and 9 shared states they are linked with species of *Laticauda* (1, 2, 3, 4), *Aipysurus* (11), *Emydocephalus* (13, 14), *Hydrelaps darwiniensis* (15), *Thalassophis anomalus* (19) and *Hydrophis major* (41). Both species of *Lapemis* (25, 26) have only eight or nine primitive states, of which they share seven with *Hydrophis belcheri* (34). At six shared states, *Lapemis* (25, 26) clusters with several species found in groups IV and V.

At the second character state tree layer, most group II and group III species have the bulk of their states, with the range from 18 (42 per cent) in *Hydrophis kingi* (30) to 29 states (67 per cent) in *Lapemis hardwickii* (25) (table 5). In terms of secondary character states, the genus *Aipysurus* (species 6, 7, 9, 10, 11, 12) is relatively compact (table 7). These species have between 26 and 22 secondary states. Although two uncontested combinations occur, *Aipysurus fuscus* (7) with *A. laevis* (9) at 21 shared states, and *A. duboisii* (10) with *A. foliosquama* (11) at 20 shared states, the near neighbor relationships indicate the compactness of the genus. For example, although *A. fuscus* (7) and *A. laevis* (9) form an uncontested combination at 21 shared states, both these species and *A. foliosquama* (11) are near neighbors to *A. duboisii* (10) at the level of 20 shared states. Although *A. eydouxii* (6) does not share as many states with the other *Aipysurus* (its first near neighbors occur at 18 shared states) it demonstrates the same general pattern—numerous combinations with other *Aipysurus,* with no species of other genera joining until the level at which it joins all other *Aipysurus,* namely 14 shared states. At this level it also shares overlapping sets of character states with both species of *Emydocephalus* (13, 14). The two species of *Emydocephalus* possess 21 and 22 secondary states and they share 18 of them. No near neighbors to this combination occur

until level 14 where it has a group of four species of *Aipysurus* (9, 10, 11, 12) as its nearest neighbor. All the *Aipysurus* and *Emydocephalus* share 12 secondary states and form an uncontested combination at this level (species 6, 7, 9, 10, 11, 12, 13, 14).

Hydrelaps darwiniensis (15) has 22 secondary states. It has only one neighbor, *Lapemis hardwickii* (25) at 17 shared states prior to forming an uncontested combination with *Ephalophis mertoni* (31) at the same level. *Ephalophis mertoni* (31) has 20 secondary states and no near neighbors prior to combining with *H. darwiniensis* (15) at level 17. At 14 shared states, *H. darwiniensis* (15) and *E. mertoni* (31) have the two *Lapemis* (25, 26) as near neighbors and at 13 shared states, *Hydrophis torquatus* (44) (see group V) is their neighbor. At 12 shared states, many neighbors are designated from several genera including *Aipysurus*.

The two species of *Lapemis* (25, 26) share 26 secondary states and have *Thalassophina viperina* (17) as a near neighbor at 20 shared states. *Thalassophis anomalus* (19) has as its nearest neighbors at 19 shared states, *Thalassophina viperina* (17) and *Hydrophis inornatus* (46). At this same level of shared states *Thalassophis anomalus* (19) and *K. jerdoni* (24) form a contested combination. *Hydrophis kingi* (30) initially comes in at 18 states and its nearest neighbor is another Australian *Hydrophis, H. major* (41), at level 17. Relationships of these species below 18 or 19 shared states are complex and involve many of the group IV and group V species. Species of *Laticauda, Aipysurus,* and *Emydocephalus* do not combine with these species here.

The group-II-and-III species have relatively few tertiary states. The range is from one state (2 per cent) in *Aipysurus eydouxii* (16) and *A. apraefrontalis* (12) to seven states (16 per cent) in *Hydrophis kingi* (30) (table 5). *Aipysurus duboisii* (10) first comes in with four tertiary states, and at the level of two shared states is a member of two contested combinations, one of which contains three other *Aipysurus* (species 7, 9, and 11), and the other of which contains the two *Emydocephalus* species (13, 14) (table 8). These are all the *Aipysurus* and *Emydocephalus* which have come in prior to or at this level of shared states. At this same level of two shared states, the two states shared in the combination containing the *Emydocephalus* are also present in *Hydrelaps darwiniensis* (15) and *Kolpophis annandalei* (20), that is, species 15 and 20 are near neighbors to the group *A. duboisii* (10), *E. annulatus* (13), *E. ijimae* (14) at this level. At one shared state, two contested combinations of *Aipysurus* and

Emydocephalus (3, 7, 9, 10, 11) and (6, 7, 9, 10, 11, 12, 13, 14) have neighbors from numerous other combinations. At five shared states *Hydrelaps darwiniensis* (15) and *Ephalophis mertoni* (31) are separate but have near neighbors. *Hydrelaps darwiniensis* (15) is closest to *Kolpophis annandalei* (20), while *Ephalophis mertoni* (31) shares five states with three species of *Hydrophis* (44, 45, 46).

Thalassophis anomalus (19) has six tertiary states and shares five of them with several group IV and group V species. *Kerilia jerdoni* (24) has only four tertiary states and shares these with six species from group IV and group V. The *Lapemis* (25, 26) share five states with each other, and *L. curtus* (26) has a near neighbor of three other species at the same level. *Hydrophis kingi* (30) shares all seven of its tertiary states with *H. major* (41). Several of the above relationships will be encountered and discussed in more detail under the section on group IV and group V species.

Of the group II and group III species, only *Kerilia jerdoni* (24), *H. kingi* (30), and *E. mertoni* (31) have more than 1 per cent of their character states at the fourth, fifth, or sixth character state tree layer. These species will be discussed with the group IV and group V species with respect to their relationships at these layers.

Conclusions on Group II and Group III Species.—Analysis of the first layer states shows that the *Emydocephalus* and *Aipysurus* share a very large proportion of their primitive states with the *Laticauda*. This is not surprising because *Laticauda* has such a great proportion of primitive states. On the other hand, *Lapemis* fails to overlap the *Laticauda* in primitive states to nearly the same extent. The phenomenon of a very large proportion of shared primitive states is considered to be weak evidence of monophyly for the *Laticauda, Emydocephalus,* and *Aipysurus.* Further examination of the primary state data show the *Aipysurus* species to be close to each other; *Hydrelaps darwiniensis* and *Ephalophis mertoni* closely linked; and the *Emydocephalus* separated and in a sense bridging a gap between the *Laticauda* and *Aipysurus. Thalassophis anomalus, Kerilia jerdoni,* and *Hydrophis kingi* show ties with the *Laticauda, Aipysurus, Emydocephalus,* among themselves, and to some group IV and group V species. The *Lapemis* are clearly associated with the group IV and group V species.

The secondary and tertiary state data reinforce and clarify the above relationships. *Aipysurus* is a compact, monophyletic group of species. *Aipysurus eydouxi,* a slightly more generalized species, is on the periphery. The *Emydocephalus* species are also monophyletic

and arose out of the early *Aipysurus* stock. *Hydrelaps darwiniensis* and *Ephalophis mertoni* are separate from all others and have their closest relationships with the two *Lapemis* species. *Thalassophis anomalus, Kerilia jerdoni,* and *Hydrophis kingi* are related to group IV and group V species through *Thalasophina viperina* and the two *Lapemis* species. These relationships will be more fully discussed in the following pages.

Group IV and Group V Species

The species in groups IV and V are discussed together because both groups lack a large proportion of primary states and because they show many relationships with each other. These species are the most derivative, with the proportion of primary states being small, ranging from 12 states (28 per cent) in *Microcephalophis gracilis* (27) to five states (12 per cent) in *Astrotia stokesi* (21) (table 5).

Microcephalophis gracilis (27) with 12 primary or first layer states, has two *Laticauda* (3, 4) as near neighbors at the level of 10 shared states, and all four *Laticauda* (1, 2, 3, 4) at level 9 (table 6). *Hydrophis major* (41) has 10 primary states which it shares with *H. kingi* (30), and nine of which it shares with *Kerilia jerdoni* (24). These three species share eight states with *Hydrelaps darwiniensis* (15) and *Thalassophis anomalus* (19), and at the level of seven shared states, *Ephalophis mertoni* (31) joins this group to form an uncontested combination. All these species except *Hydrophis major* (41) are group III species and have a relatively large proportion of primary states compared to most group IV and group V species. It is interesting to note that at the level of six shared states, *Laticauda colubrina* (2) is the only near neighbor to this group, and all four species of *Laticauda* (1, 2, 3, 4) among some others, are near neighbors to this group at the level of five shared states.

At the level of eight shared states, two species of *Microcephalophis* (26, 27) independently form combinations with *Hydrophis belcheri* (34), and the latter is in another combination with *Hydrophis melanosoma* (33) and *Hydrophis fasciatus* (50) at the same level of shared states. At seven shared states, *Acalyptophis peroni* (18) forms separate groups with two *Laticauda* (3, 4); *Hydrelaps darwiniensis* (15); *Kerilia jerdoni* (24); and *Microcephalophis gracilis* (27). At this level of shared states and below, the relationship of the group IV and group V species becomes very complex. The number of contested groups directly reflects the degree to which the species are inter-related with one another in terms of primary states. For exam-

ple, *Hydrophis melanosoma* (33) and *Hydrophis belcheri* (34) share a suite of seven characters with *M. gracilis* (27) and *H. fasciatus* (50), and a different suite of characters with *Hydrophis klossi* (40) and *Hydrophis brookii* (51) at the same level; and a third combination contains two species which occur for the first time at level seven: *Hydrophis ornatus* (45) and *Hydrophis lapemoides* (47), as well as *Hydrophis fasciatus* (50). It is worth noting that most of the combinations containing group IV and group V species, and sharing six or fewer states, do not have *Laticauda* species as near neighbors as did many of the earlier combinations.

Most of the group IV and group V species have about 50 per cent of their states at the second character state tree layer (table 5). *Microcephalophis gracilis* (27) has the fewest with 20 states (47 per cent) and *Astrotia stokesi* (21) has the most with 30 states (71 per cent) at the secondary layer.

Within the six levels between the levels of 27 shared states and 22 shared states, 14 of the group IV and group V species appear for the first time (table 7). The relationships among these species become complex almost immediately. *Thalassophina viperina* (17) with 27 secondary states, joins *Hydrophis inornatus* (46) at 24 shared states. *Hydrophis ornatus* (45) and *Hydrophis lapemoides* (47) each with 24 secondary states, form an uncontested combination with 23 shared states. However, at this same level, *Hydrophis ornatus* (45) has a second near neighbor, *Hydrophis inornatus* (46). Thus, although in terms of uncontested combinations, *H. ornatus* (45) and *H. inornatus* (46) do not appear close, in fact *H. inornatus* (46) is a near neighbor to *H. ornatus* (45). At the level of 22 shared states, the inter-relationship between these two uncontested groups (species 17, 47, and 45, 47) is further substantiated by the fact that each group has as its nearest neighbor, a species from the other group. *Hydrophis torquatus* (44) and *Hydrophis fasciatus* (50) each with 23 secondary states, have nearest neighbors to *Hydrophis inornatus* (46) and *Hydrophis lapemoides* (47) of these two groups at the level of 22 shared states. At 21 shared states, four contested combinations exist involving the above species, and including *Astrotia stokesi* (21). In addition, *Hydrophis cyanocinctus* (36), *Hydrophis brookii* (51), and *Hydrophis klossi* (40) form two contested combinations at level 23. *Hydrophis melanosoma* (33) and *Hydrophis belcheri* (34) both come in for the first time at 22 shared secondary states in a combination including *H. cyanocinctus* (36) and *H. brookii* (51). At 21 shared states, *H. klossi* (40) becomes part of the latter group and forms an

uncontested combination. Although this is unquestionably a close knit group of species, it is also crucial to point out that the combination of *H. melanosoma* (33), *H. belcheri* (34), *H. cyanocinctus* (36), and *H. brookii* (51) has two separate near neighbors at the same level that it combines with *H. klossi* (40), namely *T. viperina* (17) and *H. lapemoides* (47). In fact, the nearest neighbors to this entire group of five *Hydrophis* (species 33, 34, 36, 40, 51) occur at level 20 and are *T. viperina* (17) and *H. lapemoides* (47). It is also true that one of *H. fasciatus'* (50) near neighbors is *H. cyanocinctus* (36) at level 22, and at level 20, three of the four combinations containing the species *T. viperina* (17), *H. torquatus* (44), *H. ornatus* (45), *H. inornatus* (46), *H. lapemoides* (47), and *H. fasciatus* (50) have the near neighbor *H. cyanocinctus* (36). Thus it is clear that these two clusters of species which appear in separate series of combinations are inter-related with one another.

It is critical to note the near neighbors of the various groups of species at the levels of 21, 20, and 19 shared states. Because groups of species have formed relatively large combinations of four to five species by level 21, a species such as *Microcephalophis gracilis* (27), *M. cantoris* (28), *Hydrophis mamillaris* (48), or *Hydrophis caerulescens* (49) which have only 20, 22, 21, and 21 secondary states respectively, are unlikely to share all their states with a large series of species and, in fact, do not. Thus, *H. caerulescens* (49) at level 20, has as its nearest neighbor *H. torquatus* (44), and at level 19 has neighbors of *Astrotia stokesi* (21); *Lapemis hardwickii* (25); *H. torquatus* (44) and *H. inornatus* (46); and *H. cyanocinctus* (36), *H. klossi* (40), and *H. brookii* (51). Eventually at a level of 18 shared states *H. caerulescens* (49) joins the two *Lapemis* (25, 26) to form a contested combination. At the same level it also joins the group *H. melanosoma* (33), *H. belcheri* (34), *H. cyanocinctus* (36), *H. klossi* (40), and *H. brookii* (51).

At 18 shared states *Microcephalophis gracilis* (27) and *M. cantoris* (28) form a contested combination, with *M. cantoris* (28) also appearing in a combination with *H. melanosoma* (33), *H. belcheri* (34), *H. cyanocinctus* (36), *H. klossi* (40), and *H. brookii* (51). At this same level *M. gracilis* (27) has a near neighbor, *H. brookii* (51); and *M. cantoris* (28) has three rather large groups of species as neighbors. At the level of 17 shared states, the group of the two *Microcephalophis* (27, 28) has a near neighbor of *H. melanosoma* (33), *H. belcheri* (34), *H. cyanocinctus* (36), and *H. brookii* (51).

Several genera, *Acalyptophis* (18), *Enhydrina* (23), and *Pelamis*

(22), do not enter combinations including the other species mentioned above, but have near neighbors at relatively low levels with species within those combinations. For example, at level 20 *Enhydrina schistosa* (23) which forms an uncontested group with *Acalyptophis peroni* (18), has the near-neighbor *Astrotia stokesi* (21); and *Pelamis* (22) has the near-neighbor *Thalassophina viperina* (17). The genera *Acalyptophis* (18), *Enhydrina* (23), *Astrotia* (21), *Pelamis* (22), and *Lapemis* (25, 26) (the *Lapemis* being from group III) can be characterized as having their nearest neighbors several levels below the maximum level of 24 states which they possess. Although these monotypic genera do tend to stand off, it is also true that they are linked to the central groups of IV and V species through *Thalassophina viperina* (17).

To illustrate the complexity of the inter-relationships that exist at or below level 19, we can look specifically at the four contested combinations including *Thalassophina viperina* (17) at 19 shared states. As mentioned earlier, two of these combinations actually include *H. cyanocinctus* (36) as a near neighbor at this same level. The parent combination (*T. viperina* (17), *H. ornatus* (45), *H. inornatus* (46), and *H. lapemoides* (47)) which was formed at the level of 20 shared states, has near neighbors at level 19 which include *Lapemis hardwicki* (25); *H. melanosoma* (33), *H. belcheri* (34), *H. cyanocinctus* (36), *H. brooki* (51); and separately, *H. klossi* (40). These near neighbors are parts of two uncontested groups (*L. hardwicki* (25), *L. curtus* (26); and *H. melanosoma* (33), *H. belcheri* (34), *H. cyanocinctus* (36), *H. klossi* (40), *H. brookii* (51)), which occur at level 19. Both of these uncontested groups have as near neighbors at the same level, *T. viperina* (17) and other species from the four contested groups.

Unlike the group II and III species, the group IV and V species have a significant number of their states at the tertiary character state tree level. *Astrotia stokesi* (21) and *Kerilia jerdoni* (24) have the fewest tertiary states, four, while *Kolpophis annandalei* (20) and *Hydrophis mamilaris* (48) each have 11 or 26-27 per cent of their total states at the tertiary level (table 5).

The tertiary states depict relationships of group IV and V species that are effectively identical to those depicted by the secondary states (table 8). Between the levels of 11 and 9 shared states, 16 of the group IV and group V species occur for the first time. At the level of eight shared states, there are already 10 contested combinations. Again, as for the secondary states, the near neighbors to spe-

cies and groups of species are crucial to a clear picture of the relationships. For example, *Microcephalis gracilis* (27) and *M. cantoris* (28) each contain 10 tertiary states. *M. cantoris* (28) shares nine states forming a contested combination with *H. klossi* (40) which has only these nine states; *M. gracilis* (27) has no near neighbors at this level. However, at the level of eight shared states, the nearest neighbor to *M. gracilis* (27) is *M. cantoris* (28) (which it can't combine with since, as indicated, *M. gracilis* (27) already formed two groups at a higher level), and *H. belcheri* (34) with which it forms a contested group. At this same level of eight shared states, *M. cantoris* (28) forms a contested combination with *H. belcheri* (34), *H. klossi* (40), and *H. lapemoides* (47). Also, at the level of eight shared states, the two *Microcephalophis* (27, 28) and *H. belcheri* (34) are involved in four contested combinations, and *H. torquatus* (44) and *H. ornatus* (45), and *H. inornatus* (46) are involved in three contested combinations. These series of combinations are not mutually exclusive, for example, the contested combination at eight shared states, of *H. belcheri* (34) and *H. caerulescens* (49) overlaps the two groups of combinations (27, 34) (28, 38, 40, 47) (28, 40, 48) and (44, 45, 46) (44, 46, 47) (45, 47) (47, 49) and, in addition, each of these species individually has *H. torquatus* (44) as a near neighbor at the same level. At the level of seven shared states these groups of combinations overlap broadly in contested combinations (e.g., the combination *M. cantoris* (28), *H. belcheri* (34), *H. klossi* (40), *H. lapemoides* (47), *H. mamilaris* (48), and *H. caerulescens* (49)).

At the tertiary level the monotypic genera *Acalyptophis peroni* (18), *Kolpophis annandalei* (20), *Pelamis platurus* (22), and *Enhydrina schistosa* (23) as at the secondary level, are somewhat separated from the central core of species which have been discussed above. *Thalassophina viperina* (17) and *K. annandalei* (20) share eight states with each other and they share seven states with several of the group IV and group V species involved in contested combinations at that level. Although *H. fasciatus* (50) does not occur in a contested or uncontested combination until level six, at level seven it has three near neighbors which designate its affinity to other group IV and group V species. *Hydrophis kingi* (30) and *H. major* (41) form an uncontested combination at seven shared states, but the affinity of these two species to the group IV and group V species is clear. For example, at this same level of seven shared states, *H. major* (41) is found with *K. annandalei* (20) and *H. lapemoides* (47), and both species *H. kingi* (30) and *H. major* (41) share a set of six characters with *K. annandalei* (20) and another set of six characters

with *H. mamilaris* (48). An examination of the combinations and neighbors of the combinations occurring at level six and below, reiterates the pattern of inter-relationships described above.

Group IV and group V species have between 0 and 7 per cent of their character states at the fourth character state tree layer. Thus the maximum number of states present is three, as in *Enhydrina schistosa* (23), *H. kingi* (30), and *H. melanosoma* (33). At the level of two shared states, eight species come in by themselves for the first time and six come in for the first time in combination with other species. With so few character states involved, the relationships designated are of limited value. It is possibly worth noting that *H. kingi* (30) and *H. major* (41) form an uncontested combination at two shared states. This repeats the relationships observed between these two species at previous character state tree layers. In addition, at this level there are combinations of other *Hydrophis* species with each other and with three of the monotypic genera. At the level of one shared state, nine contested combinations occur. These contested combinations are a product of the fact that every species or combination of species which occurs at the level of two shared states (with the exception of one, *K. annandalei* (20)) occurs in two separate combinations at the level of one shared state. At the level of one shared state, some of the combinations contain species from groups I and III. The six largest combinations at this level depict relationships among the species similar to those of previous layers in that they contain overlapping sets of species, several of which are species of *Hydrophis*. *Astrotia stokesi* (21) and *Pelamis platurus* (22) share one state at this level and share 18 states in common at the second character state tree layer. However, at neither the second nor the third layers are these two species near neighbors.

Three species, *H. klossi* (40), *H. fasciatus* (50), and *H. brookii* (51), have two character states at the fifth character state tree layer which they all share. These three species are all microcephalic *Hydrophis* species and at the level of one shared state they share a state with *M. cantoris* (28), another microcephalic species. In addition, at the level of one shared state, *Hydrophis* species form a contested combination which also contains the three microcephalic *Hydrophis* species 40, 50, and 51.

At the sixth character state tree layer, no species contains more than one character state and most species contain none at all.

Conclusions on Group IV and Group V Species.—Several conclusions seem to emerge from an analysis of the group IV and group V

species. First, these species are related to *Thalassophis anomalus* and *Lapemis* of group III. The bulk of the species in group IV and group V appears to represent the result of a rapid period of speciation in that the species show a pattern of complex inter-relationships.

Within this group there are some consistent patterns which confirm certain perviously recognized genera or species clusters, (e.g., *Lapemis, Microcephalophis,* and some clusters of *Hydrophis* species), but these species as well as the majority of the others show complex relationships among one another. A few monotypic genera, for example, *Pelamis, Enhydrina,* and *Acalyptophis,* have clearly diverged from the central stock of group IV and group V species but this does not necessarily make them significantly earlier lineages. They show no greater affinity to the early lineage of this group, e.g., *Hydrelaps,* than do other species in the group.

In summary, the complex inter-relationships among group IV and group V species designated by the character states at all levels reflect a rapid radiation of species which is not resolvable by the character states under consideration.

Summary Statement of Phylogeny

Figure 6 is a diagram summarizing the relationships of the sea snakes. The relationships depicted in this figure are based on the interpretations of the combinations of species at each character state tree layer. Several species which are omitted from the data matrix and the subsequent analysis due to missing information are placed in the summary phylogeny where they are thought to belong.

The *Laticauda* are clearly a group of very closely related species. They are very distinct from all other sea snakes and either represent an independent evolutionary line or a very early separation from all other sea snakes. They are by far the most primitive stock of sea snakes and they possess many elapid character states.

The *Aipysurus* are a group of closely related species. *Aipysurus eydouxi* is the most generalized of the *Aipysurus* species and it is phenetically on the periphery of the central group of five. However, its eventual combining with several *Aipysurus* and *Emydocephalus*

Opposite:

Fɪɢ. 6. Diagram of the major phylogenetic relationships among the Hydrophiidae drawn from the detailed account starting on p. 105.

ELAPIDAE

1 Lat lat
2 Lat col
5 Lat cro
3 Lat sem
4 Lat sch

13 Emy ann
14 Emy iji
6 Aip eyd
7 Aip fus
9 Aip lae
10 Aip dub
11 Aip fol
12 Aip apr

15 Hyl dar
16 Eph gre
31 Eph mer
30 Hyd kin
41 Hyd maj
24 Ker jer
17 Thn vip
18 Aca per
19 Ths ano
20 Kol ann
21 Ast sto
22 Pel pla
23 Enh sch
25 Lap har
26 Lap cur
27 Mic gra
28 Mic can
29 Hyd nig
32 Hyd spi
33 Hyd mel
34 Hyd bel
35 Hyd ele
36 Hyd cya
37 Hyd sem
38 Hyd mec
39 Hyd obs
40 Hyd klo
43 Hyd str
44 Hyd tor
45 Hyd orn
46 Hyd ino
47 Hyd lap
48 Hyd mam
49 Hyd cae
50 Hyd fas
51 Hyd bro

seems to indicate that it is, in a phylogenetic sense, a stem species. The two *Emydocephalus* species are very closely related to each other and emerged from *Aipysurus* stock. The *Aipysurus* stock (including *Emydocephalus*) shows weak affinity with both the *Laticauda* and the other sea snakes and like the *Laticauda* has either an independent origin among the elapids or a very early separation from ancestral sea snakes.

Hydrelaps darwiniensis, Ephalophis greyi, and *Ephalophis mertoni* represent early lines from the stock of remaining sea snakes which includes the *Hydrophis* and several other genera. Although these three species are relatively primitive, they have clear ties to this stock.

Hydrophis kingi and *H. major* along with the monotypic genera, *Kerilia jerdoni* and *Thalassophis anomalus* are relatively primitive and may have diverged from the main *Hydrophis* stock just prior to the radiation which produced the majority of sea snake species. In Figure 6 these species with few exceptions are given in numerical order since branching details within the group are not resolved and since the relationships of the species are too complex to be represented in a two or three dimensional diagram.

An Amplification of the Phylogeny

The previous sections of this paper are an attempt to explore the phylogeny of the sea snakes with explicit methods. Here a few interpretive comments are added.

Evolutionary trends within the Hydrophiidae: Within the sea snakes I have found no evidence for a single unifying adaptive trend reflected by a sequence of related morphological conditions. Grade levels do exist. The *Laticauda* are amphibious (feed largely on eels, lay eggs on land, and locomote terrestrially) while all other sea snakes are fully aquatic (bear live young at sea and have poor terrestrial locomotion). However, the *Laticauda* do not stand on a character-by-character basis between the terrestrial elapids and the other sea snakes. In fact, the *Laticauda* share very few character states with the other sea snakes which do not clearly show by their distribution within the family a tendency toward multiple origin and/or character state reversal.

The *Aipysurus* and *Emydocephalus* share many characters which reflect their overall phenetic similarity and the common adaptive zone which these species have exploited. Most of these species are

associated with coral reefs. In addition, the habit of eating demersal fish eggs is wide spread in this group and does not occur among other sea snakes (Voris, 1972). Trends in skull morphology associated with egg eating are a dominant theme among these species, with the most derived conditions occurring in the *Emydocephalus*. Like the *Laticauda*, the *Aipysurus* and *Emydocephalus* do not have many character states which are intermediate between states found in elapids and the advanced sea snakes.

Within the other sea snakes, including several monotypic or bi-typic genera and the genus *Hydrophis*, trends in body form have occurred but there is some evidence which indicates that these trends are recurring themes. For example, the reduction of head and neck size occurs to different degrees in several species and is an adaptation to nook and cranny feeding behavior and the consumption of eels (Voris, 1972). It reaches a rather extreme condition in the two species of *Microcephalophis, Hydrophis brookii,* and *H. klossi* (two very similar species), as well as in *Hydrophis torquatus, H. caerulescens,* and *H. mamilaris.* There are no other morphological or geographical data which support a hypothesis of monophyly for this assemblage and thus the microcephalic condition appears to be a recurring adaptation.

A complex of characters including the number and size of ventral scales, the number of vertebrae, the costo-cutaneous muscle system and the overall body form have been directly involved in the shift from a terrestrial to an aquatic existence (Voris, 1975). The adaptations involved are complex and have not followed the same path of change in all lineages of sea snakes. However, the overall trends are clear. For example, there is a general tendency toward a proliferation of ventral scutes, and to a lesser extent a proliferation of vertebrae with the consequent loss of correspondence between the vertebrae and ventrals. Ventral scales have tended either to become sharply keeled medially or reduced in size. In addition, within the framework of each of the various body forms the posterior part of the body has tended to become laterally flattened.

Uniquely derived states: Only a very few of the character states studied here are likely to be uniquely derived within the sea snakes. Several character states which are *restricted* in distribution to single species are possible examples of uniquely derived states. Characters 6 (gular azygous scale) and 7 (anterior prefrontal azygous scale) are examples. If one assumes that these are uniquely derived states they necessarily become states of little importance to

interspecies relationships because they are states which arose after all branching involving the species possessing the trait had taken place.

An even smaller number of characters have states which are *widely* distributed and are likely to be uniquely derived. A possible example of such a state for which much data is available, is the loss of correspondence between the number of ventral scales and the number of body vertebrae. However, although a single origin interpretation is compatible with the phylogeny in Figure 6, a detailed analysis of this character (Voris, 1975) has revealed intraspecific variation in one species and patterns of variation in the relationship of ventrals and vertebrae along the length of the body which suggest some experimentation and more than one mode of change for this character.

Age and distribution of the Hydrophiidae: The age of the Hydrophiidae is indefinite since no fossil record of the group has been discovered. During the Mesozoic and up through the Miocene of the Cenozoic, the Tethys Sea formed a large variable marine environment from Southeast Asia to Eastern Europe (Darlington, 1957). Since Hydrophiidae are not found in the Mediterranean Sea nor the tropical Atlantic Ocean, it is possible that the snakes are more recent than the Miocene (Tethys Sea). On the other hand, the current distribution of the Hydrophiidae might also indicate that sea snakes cannot live in the Mediterranean Sea or the Atlantic Ocean for ecological reasons. One might argue that the former hypothesis is more likely because the Persian Gulf (with 11 species of sea snakes) has habitats very similar to those found in parts of the Mediterranean. Concurring with this hypothesis is the observation that of the species that appear in the Persian Gulf, and their close relatives *Pelamis platurus* ranges as far south as the Cape of Good Hope, South Africa, and *Hydrophis cyanocinctus* ranges as far east and north as the Sea of Japan, and *Hydrophis semperi* (very similar to *H. cyanocinctus*) is found in a fresh-water lake, Lake Taal, in the Philippines. It may be argued that if the Persian Gulf species are so wide ranging, it is unlikely that they are excluded from the Mediterranean for ecological reasons. This argument fails to be completely convincing, however, because ecological data on the Hydrophiidae are so lacking that even the most tentative hypothesis on this subject seems premature.

Zoogeographic data have been collected from the literature and from the specimens. The major literature sources were the fol-
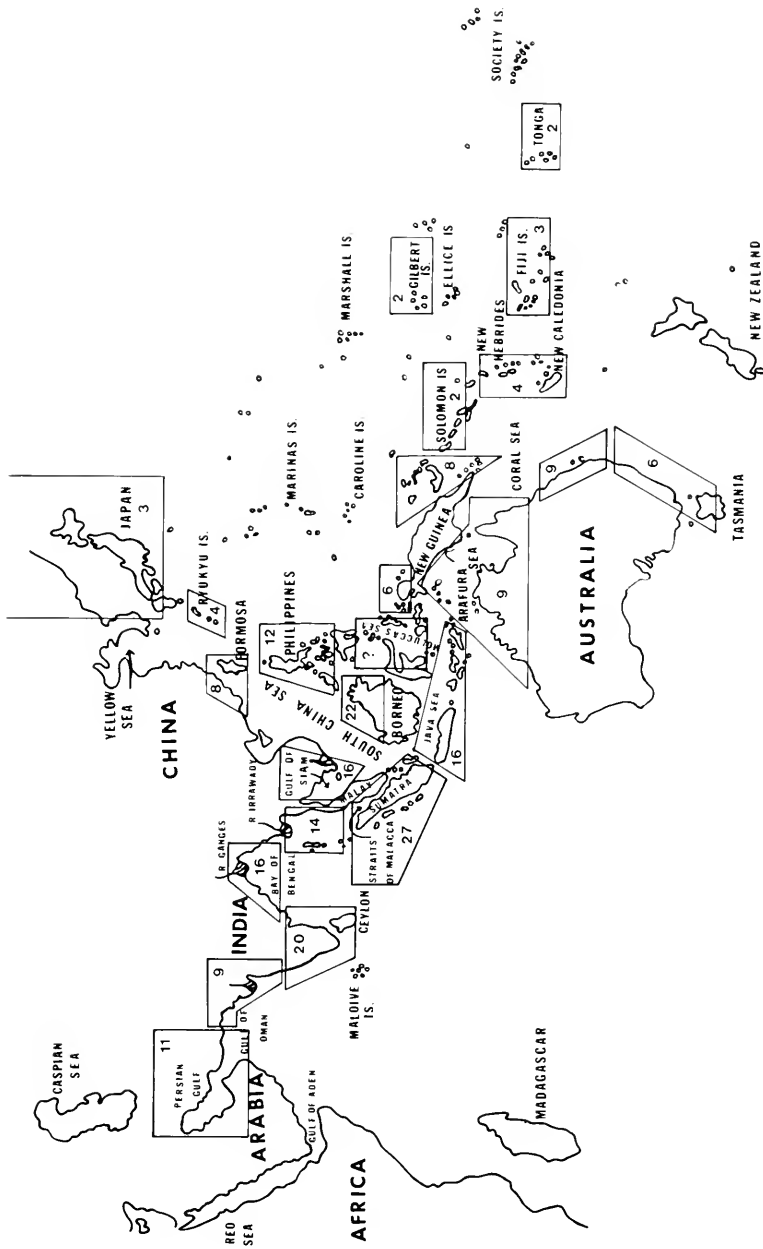
Fig. 7. Frequency distribution of Hydrophiidae species, with the exception of the pelagic sea snake *Pelamis platurus*. The number of species is indicated within each sector. Data are from the literature (see p. 122), and preserved specimens (Voris, 1969).

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lowing: Wall, 1909; Smith, 1920, 1926, 1935; Taylor, 1922; Bourret, 1936; Volsøe, 1939; De Haas, 1950; Suvatti, 1950; Wang, 1962; and Worrell, 1963. (The detailed distribution data are available and discussed in Voris, 1969.) The species frequency distributions are given in Figure 7 and are subject to considerable error. There is a decrease in the numbers of species along the coasts (the habitat of most species) going from the Straits of Malacca to the Persian Gulf. This decrease is rather erratic and is probably in large part due to a sampling error. Generally, the areas with large numbers of species, the Straits of Malacca and the Gulf of Siam (Smith, 1920), Ceylon (Wall, 1909), and the Persian Gulf (Volsøe, 1939), are areas which have been collected and studied. The other areas, mouths of the Irrawady, Ganges, and Indus Rivers, have been given less attention and thus appear to be depauperate.

Taking into account the limitations of the available data, I consider the center of distribution in terms of both number of species and of genera to be the in shore areas of the Straits of Malacca, the Gulf of Siam, and the southern end of the South China Sea. As one travels outward from this region, fewer species are found with increasing distance.

Genera from every major lineage depicted in Figure 6 are found in and/or between the Gulf of Siam and Northern Australia. In fact, several *Aipysurus, Hydrelaps,* and *Ephalophis* are endemic to this region. Thus it is likely that the large number of *Hydrophis* species (23) and associated genera (10) is the product of a relatively recent radiation in northern Australian and Southeast Asian waters. The fluctuating borders of the South China Sea during the Pleistocene and possibly up to recent times (Darlington, 1957) placed the Sunda Shelf (Straits of Malacca, the Gulf of Siam, the south end of the South China Sea, and the Java Sea) above sea level, making Sumatra, Java, and Borneo part of the Asian continent. One can easily imagine that at the time this barrier was forming, early representatives of *Aipysurus eydouxi, Emydocephalus ijimae,* and numerous populations of *Hydrophis* were separated to the north of the main populations and isolated there for various lengths of time. There is some evidence that the sea level rose and fell more than once (Darlington, 1957) and this alone may have caused the splitting of populations which gave rise to the numerous species of *Hydrophis*.

COMMENTARY

Certain procedural and philosophical aspects of this study require further clarification or comment.

Nomenclature.—The nomenclature used here is, with few exceptions, that of Malcolm Smith (1925). *Laticauda crockeri* is from Sleven (1934) and *Hydrophis parviceps* is from Smith (1935). The designation for *Ephalophis mertoni* is from McDowell (1969). McDowell (1972) and Burger and Natsuno (1974) have suggested extensive nomenclature changes among the sea snakes, some of which in my opinion, are unwarranted and will require modification when substantial samples are evaluated. The Linnean system of nomenclature can carry only a limited amount of phyletic information and when relationships are largely speculation a conservative position on the nomenclature has been taken and nomenclature changes have not been proposed in this study. Thus, because Smith's (1926) work has served as the standard reference for many years and is by far the best known in the field, I have used its nomenclature for the most part.

Character Analysis and Weighting, and Equivalency of States.—The process of character analysis is a rapidly developing area (see issues of *Systematic Zoology,* 1971, 1973), but its role and mode of application in the process of derivation of phylogeny is not yet clear. In this study it has been assumed or implied that the process of character selection and elimination has resulted in a group of characters containing a substantial amount of historical information. Thus, character weighting was considered unnecessary. However, it is generally agreed that characters are not historically equivalent in any exact sense. This point extends to the character states also and the procedure of classifying states into a few character state tree layers is not justifiable in a purely theoretical sense in that the states of different characters have, in general, evolved independently. The grading of states as was done in this study, is in the process of further exploration and refinement. Also underway is an extensive, in-depth analysis of ways of handling all data simultaneously to derive a consensus of the character state trees using the combinatorial method (Marx et al., MS in prep.).

Resolution and Precision.—The data matrix of 40 species by 43 characters on which most of the conclusions are based is limited in the following sense. Most characters have relatively few states (two or three) and thus their "partitioning power" is limited. This study deals with 50 species. Many of the characters designate the same or similar partitions or major groups and do not vary within these groups. Thus there is not much information bearing on the "micro-relationships" of species. In short, a detailed study using many more

characters (including some of those removed from this data set due to restricted distribution) would definitely add resolution to the intra-group relationships of some of the *Aipysurus* and *Hydrophis*.

Phenetic and Phyletic Results.—In my opinion it is not surprising that the dendrogram (fig. 4) and the phylogeny (fig. 6) presented do not differ from each other greatly or for that matter from Malcolm Smith's (1926) overall view as reflected by his classification. This has likely occurred because data used in the different approaches overlap extensively, and because in many groups of organisms, estimates of overall similarity (phenetics) are highly congruent with the history of the group.

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Table 1 -- List of Hydrophiidae materials utilized in this study. The species are those recognized by Smith (1926, 1935) and Slevin (1934). The number preceeding each species name is the code for that species. The species abbreviations follow each name in parentheses.

No.	Species	Spec-imens	Skulls	Tail X-rays	Whole Body X-rays
1	Laticauda laticaudata (Lat lat)	7	4	1	1
2	Laticauda colubrina (Lat col)	35	6	6	5
3	Laticauda semifasciata (Lat sem)	4	5	1	1
4	Laticauda schistorhynchus (Lat sch)	19	2	3	2
5	Laticauda crockeri (Lat cro)	1	0	0	0
6	Aipysurus eydouxi (Aip eyd)	12	1	1	3
7	Aipysurus fuscus (Aip fus)	9	1	2	1
8	Aipysurus tenuis (Aip ten)	0	0	0	0
9	Aipysurus laevis (Aip lae)	4	2	1	1
10	Aipysurus duboisii (Aip dub)	4	1	1	1
11	Aipysurus foliosquama (Aip fol)	11	1	4	1
12	Aipysurus apraefrontalis (Aip apr)	3	1	1	1
13	Emydocephalus annulatus (Emy ann)	5	2	2	0
14	Emydocephalus ijimae (Emy iji)	6	2	2	1
15	Hydrelaps darwiniensis (Hyl dar)	8	1	3	2
16	Ephalophis greyi (Eph gre)	2	1	1	1
17	Thalassophina viperina (Thn vip)	13	4	2	2
18	Acalyptophis peronii (Aca per)	6	1	2	2
19	Thalassophis anomalous (Ths ano)	13	1	2	4
20	Kolpophis annandalei (Kol ann)	6	1	2	3
21	Astrotia stokesii (Ast sto)	6	2	1	1
22	Pelamis platurus (Pel pla)	17	15	4	4
23	Enhydrina schistosa (Enh sch)	27	10	2	2

TABLE 1 -- Continued

No.	Species	Spec-imens	Skulls	Tail X-rays	Whole Body X-rays
24	Kerilia jerdoni (Ker jer)	7	1	2	1
25	Lapemis hardwickii (Lap har)	37	14	4	9
26	Lapemis curtus (Lap cur)	9	1	2	0
27	Microcephalophis gracilis (Mic gra)	13	1	1	4
28	Microcephalophis cantoris (Mic can)	5	1	2	0
29	Hydrophis nigrocinctus (Hyd nig)	3	0	1	2
30	Hydrophis kingi (Hyd kin)	1	1	1	1
31	Ephalophis mertoni (Eph mer)	1	1	1	1
32	Hydrophis spiralis (Hyd spi)	6	0	1	1
33	Hydrophis melanosoma (Hyd mel)	7	1	1	1
34	Hydrophis belcheri (Hyd bel)	14	3	1	6
35	Hydrophis elegans (Hyd ele)	1	0	1	1
36	Hydrophis cyanocinctus (Hyd cya)	45	11	5	6
37	Hydrophis semperi (Hyd sem)	1	0	0	0
38	Hydrophis melanocephalus (Hyd mec)	8	1	0	1
39	Hydrophis obscurus (Hyd obs)	2	0	1	2
40	Hydrophis klossi (Hyd klo)	17	1	2	3
41	Hydrophis major (Hyd maj)	1	1	1	1
42	Hydrophis bituberculatus (Hyd bit)	0	0	0	0
43	Hydrophis stricticollis (Hyd str)	5	0	1	1
44	Hydrophis torquatus (Hyd tor)	23	7	2	6
45	Hydrophis ornatus (Hyd orn)	14	2	1	3
46	Hydrophis inornatus (Hyd ino)	16	2	1	1
47	Hydrophis lapemoides (Hyd lap)	15	3	2	2
48	Hydrophis mamillaris (Hyd mam)	1	1	1	1

Table 1 -- <u>Continued</u>

No.	Species	Spec-imens	Skulls	Tail X-rays	Whole Body X-rays
49	Hydrophis caerulescens (Hyd cae)	26	5	2	4
50	Hydrophis fasciatus (Hyd fas)	36	6	3	5
51	Hydrophis brookii (Hyd bro)	13	6	4	7
52	Hydrophis parviceps (Hyd par)	1	0	0	0
	Total	546	134	88	90

TABLE 2 is located on the back cover.

Table 3 -- Character states and character state trees for 43 sea snake characters

Character Number	Character Name	Character State	Character State Name	Character State Tree
1	Internasal scales	1	Internasals present	(1)→2→3
		2	Internasals absent	
		3	Present via fragmentation of all head plates	
2	Position of nostril	1	Lateral	(1)→2
		2	Dorsal	
3	Postocular relationship to parietal	1	Touching	(1)→2→3
		2	Variable	
		3	Not touching	
4	Parietal fragmentation	1	Complete	(1)→2→3
		2	Partially fragmented	
		3	Fragmented	
5	Texture of dorsal head scales	1	Smooth	(1)→2→3→4
		2	Mostly smooth	
		3	Mostly rough	
		4	Rough	
12	Ventral keeling at 1/4 S-V length	1	No keels	2←(1)→3
		2	Paired keels	
		3	Central keels	
14	Ventral keeling at 3/4 S-V length	1	No keels	2←(1)→3
		2	Paired keels	
		3	Central keels	
17	Ventral tuberosities at 3/4 S-V length	1	No tuberosities	5←(1)→2→3→4
		2	Two paired tuberosities +/-	
		3	Two or more paired tuberosities	
		4	More than 2 paired tuberosities	
		5	One median tuberosity	

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Table 3 -- continued

Character Number	Character Name	Character State	Character State Name	Character State Tree
22	Relative width of ventrals in relation to adjacent scales at 2/3 S-V length	1	Ventral width 3-4 of adjacent scales	①→2→3→4
		2	" 2-3 " " "	
		3	" 1-2 " " "	
		4	" 1 +/- " " "	
23	Relative width of ventrals 10th to one at 2/3 S-V length	1	10th ventral smaller than at 2/3	①→2→3
		2	10th ventral about equal to at 2/3	
		3	10th ventral larger than at 2/3	
28	Relationship of lateral body scales at 2/3 number of ventrals	1	Imbricate	①→2→3
		2	Intermediate	
		3	Justaposed	
30	Body shape at 1/4 S-V length	1	Cylindrical	①→2→3
		2	Slightly compressed	
		3	Compressed laterally	
34	Anterior ventral scales split or entire	1	Ventrals entire	①→2→3
		2	Variation	
		3	Ventrals split	
35	Posterior ventral scales split or entire	1	Ventrals entire	①→2→3
		2	Variation	
		3	Ventrals split	
36	Subcaudal scales single or paired	1	Paired subcaudals	①→2→3
		2	Variable	
		3	Single subcaudals	

Table 3 -- continued

Character Number	Character Name	Character State	Character State Name	Character State Tree
46	Relation of frontal bone to orbit	1 2 3	Enters orbit Variable Not enter orbit	1 — 2 — 3
48	Postorbital shape	1 2	"Spoon" shaped "L" shaped	1 — 2
52	Maxillary-palatine relationship, degree of anterior extension	1 2 3	Maxillary extends = palatine Maxillary extends > palatine Maxillary extends < palatine	2 — 1 — 3
57	Angular splenial length relationship	1 2	Angular = splenial Angular > splenial	1 — 2
58	Posterior-lateral aspect of maxillary	1 2	Projection absent Projection present	1 — 2
59	Maxillary-ectopterygoid articulation	1 2	Abutt Overlap	1 — 2
60	Ectopterygoid lateral projection	1 2	Projection absent Projection present	1 — 2
77	Number of supralabial scales	1 2 3	5-8 1-4 9 or more	2 — 1 — 3
82	Number of pairs enlarged chin shields touching at midline	1 2 3 4 5 6	1-2 pairs 0-1 2 2-3 3 highly variable	2 — 6 — 3 — 4 — 5, with 1 below 3

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Table 3 -- continued

Character Number	Character Name	Character State	Character State Name	Character State Tree
83	Number of ventral scales	1	176-220	
		2	135-175	
		3	221-260	
		4	261-310	
		5	311-360	
		6	361-425	
84	Number of scale rows at neck	1	16-24	
		2	25-34	
		3	35-40	
		4	41-55	
		5	56-67	
87	Number of scale rows at 3/4 number of ventral scales	1	17-25	
		2	26-37	
		3	38-45	
		4	46-55	
		5	56-66	
		6	> 66	
90	Number of scales on posterior margin of vent	1	5-7	
		2	8-11	
		3	12-14	
		4	15	
92	Number of subcaudal scales	1	22-38	
		2	39-46	
		3	47-55	
		4	56-63	

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Table 3 -- continued

Character Number	Character Name	Character State	Character State Name	Character State Tree
93	Number of lateral caudal scales	1 2 3 4	6-8 2-5 9-12 13-16	2←③→3→4
95	Number of maxillary teeth	1 2 3 4	0-4 5-7 8-10 11-16	①→2→3→4
98	Number of dentary teeth	1 2 3 4	9-15 0-8 16-18 19-23	2←③→3→4
137	Premaxillary bone shape	1 2 3 4 5 6 7 8	see Figure 1	5, 4←①→6→7, 3←①, 2→8
138	Nasal bone shape	1 2 3	see Figure 2	2←①→3
139	Nasal bone position relative to frontal bone	1 2 3	Nasal not in contact with frontal Nasal adjacent but not in close contact Nasal in broad contact with frontal	2←①→3

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Table 3 -- continued

Character Number	Character Name	Character State	Character State Name	Character State Tree
142	Pterygoid flange	1 2	Present Absent	
143	Vertebra-ventral correspondence	1 2	Correspondence No correspondence	
144	Neck-body scale row correspondence	1 2 3	Correspondence Correspondence ± 4 scales No correspondence	
145	Nasal valve position	1 2	Posterior & squeeze-type valve Anterior & trapdoor-like valve (includes many variations)	
146	Rostral groove	1 2 3 4	see Figure 3	
148	Mode of reproduction	1 2	Oviparous Ovoviviparous	
149	Prefrontal-frontal articulation	1 2 3 4	Anterior & lateral (square) Anterior Lateral Anterior & lateral (round)	
153	Neural spine height	1 2 3	Low Medium High	

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TABLE 4. Matrix of the character states of 43 characters for 40 species of sea snake. See Table 3 for the names of the characters and character states.

Character Number

Spec. No.	Species	01	02	03	04	05	12	14	17	22	23	28	30	34	35	36	46	48	52	57	58	59	60	77
1	Lat lat	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	2	2	1	1	1	1
2	Lat col	1	1	1	1	1	2	2	1	1	1	1	1	1	1	1	1	1	2	2	1	1	1	1
3	Lat sem	1	1	1	1	1	2	2	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1
4	Lat sch	1	1	1	1	2	2	3	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1
6	Aip eyd	2	2	2	1	2	3	3	5	2	1	1	2	1	1	3	1	2	1	2	2	1	1	1
7	Aip fus	2	2	1	3	1	3	3	1	2	1	1	2	1	1	3	1	1	2	2	2	1	1	1
9	Aip lae	2	2	1	3	1	3	3	1	2	1	1	2	1	1	3	2	2	2	2	2	1	1	1
10	Aip dub	2	2	1	3	3	3	3	4	2	1	1	2	1	1	3	1	1	2	2	1	1	1	3
11	Aip fol	2	2	1	3	1	3	3	1	2	1	1	2	1	1	3	1	1	2	1	1	1	1	1
12	Aip apr	2	2	1	2	1	3	3	1	2	1	1	1	1	1	3	1	1	9	2	1	1	1	1
13	Emy ann	2	2	1	1	2	3	3	1	2	1	1	2	1	1	3	1	1	2	1	1	1	1	2
14	Emy iji	2	2	1	2	1	3	3	1	2	1	1	1	1	1	3	1	2	1	2	1	1	1	2
15	Hyl dar	2	2	1	1	1	1	1	1	3	1	2	1	1	1	3	3	2	3	1	2	2	1	1
17	Thn vip	2	2	1	1	3	1	1	2	3	3	2	2	2	2	2	3	2	3	1	2	2	2	1
18	Aca per	3	2	1	3	2	1	1	1	4	2	3	2	2	2	2	3	2	3	1	2	2	2	1
19	Ths ano	1	2	1	1	2	1	1	2	4	2	3	1	1	1	2	3	2	3	1	2	2	2	1
20	Kol ann	1	2	2	2	1	1	1	1	3	3	2	2	2	2	3	3	2	1	1	2	2	2	3
21	Ast sto	2	2	2	1	2	1	1	2	2	3	1	2	2	2	2	3	2	3	1	2	2	2	3
22	Pel pla	2	2	2	2	1	1	1	3	3	3	2	2	3	3	2	1	2	3	1	2	2	2	1
23	Enh sch	3	2	1	2	4	1	1	3	4	2	3	2	2	2	2	3	2	3	1	2	2	2	1
24	Ker jer	2	2	1	1	2	1	1	2	4	2	1	1	1	1	2	3	2	1	1	2	2	2	1

Table 4. *continued.*

Character Number

Spec. No.	Species	82	83	84	87	90	92	93	95	98	137	138	139	142	143	144	145	146	148	149	153
1	Lat lat	5	3	1	2	1	1	2	1	3	1	1	1	1	1	1	1	1	1	2	1
2	Lat col	6	3	1	2	1	1	2	1	1	1	1	1	1	1	1	1	1	1	2	1
3	Lat sem	3	1	1	2	1	1	2	1	1	1	1	1	1	1	1	1	2	1	1	2
4	Lat sch	3	1	1	2	1	1	2	1	1	1	1	1	1	1	1	1	2	1	1	2
6	Aip eyd	3	2	1	1	1	1	2	4	4	3	2	3	2	1	2	2	3	2	2	1
7	Aip fus	3	2	1	1	2	1	2	2	1	5	2	3	2	1	2	2	3	2	1	2
9	Aip lae	2	2	1	1	2	1	2	2	1	2	2	3	2	1	2	2	3	2	3	2
10	Aip dub	4	2	1	1	1	1	2	2	1	5	2	3	2	1	2	2	3	3	3	2
11	Aip fol	1	2	1	1	1	1	2	2	1	5	2	3	2	1	2	2	3	2	3	2
12	Aip apr	3	2	1	1	1	1	2	2	3	5	2	3	2	1	2	2	3	2	3	2
13	Emy ann	4	2	1	1	1	1	2	1	2	6	2	1	2	9	2	2	4	2	3	2
14	Emy iji	4	2	1	1	2	1	2	1	2	6	2	1	2	1	2	2	4	2	3	2
15	Hyl dar	4	2	2	2	2	1	2	2	3	7	2	1	2	1	2	2	4	2	4	1
17	Thn vip	4	3	2	6	3	2	3	2	3	8	3	2	2	2	3	2	4	2	4	3
18	Aca per	5	1	1	3	2	1	3	3	4	9	2	2	2	2	3	2	4	2	4	3
19	Ths ano	3	3	2	3	3	1	3	1	3	4	3	2	9	2	2	2	4	2	4	3
20	Kol ann	4	5	5	6	3	4	4	2	1	9	2	2	2	2	3	2	4	2	4	3
21	Ast sto	2	3	4	6	4	2	3	2	4	8	2	3	9	2	3	2	4	2	4	2
22	Pel pla	2	5	4	6	3	3	3	2	3	9	3	2	2	2	3	3	4	2	4	3
23	Enh sch	2	4	4	6	2	3	3	1	1	8	2	9	2	2	3	2	4	2	4	2
24	Ker jer	5	3	1	2	2	1	1	3	4	4	3	2	2	2	2	2	4	2	4	3

<div align="center">Character Number</div>

Spec. No.	Species	01	02	03	04	05	12	14	17	22	23	28	30	34	35	36	46	48	52	57	58	59	60	77
25	Lap har	2	2	2	2	2	1	1	2	4	3	2	2	2	2	2	3	2	1	1	2	2	2	1
26	Lap cur	2	2	2	2	1	1	1	2	3	3	2	2	2	2	2	3	2	1	1	2	2	2	1
27	Mic gra	2	2	1	1	2	1	1	3	3	2	2	1	2	3	2	3	2	2	2	1	2	2	1
28	Mic can	2	2	2	1	1	1	1	4	3	2	3	1	2	3	2	3	2	2	1	2	2	1	1
30	Hyd kin	2	2	1	1	1	1	1	2	3	1	1	3	1	1	3	3	2	1	2	1	1	2	3
31	Eph mer	2	2	1	1	1	1	1	1	2	1	3	1	1	1	3	3	2	3	1	2	2	2	1
33	Hyd mel	2	2	1	1	4	1	1	3	4	2	3	2	2	2	2	3	2	1	1	2	2	2	1
34	Hyd bel	2	2	1	1	1	1	1	3	3	2	3	2	2	2	2	3	2	1	1	2	2	2	1
36	Hyd cya	2	2	2	1	4	1	1	3	3	2	3	2	2	2	2	2	2	1	1	2	2	2	1
40	Hyd klo	2	2	2	1	2	1	1	2	3	2	3	2	1	2	2	3	2	1	1	2	2	2	1
41	Hyd maj	2	2	1	1	2	1	1	2	3	1	1	3	1	1	3	3	2	3	1	2	2	2	3
44	Hyd tor	2	2	1	1	4	1	1	3	4	2	3	2	2	2	2	3	2	3	1	2	2	2	1
45	Hyd orn	2	2	1	1	2	1	1	2	4	2	3	2	2	2	2	3	2	1	1	2	2	2	1
46	Hyd ino	2	2	1	1	1	1	1	2	4	2	3	2	2	2	2	3	2	3	1	2	2	2	1
47	Hyd lap	2	2	1	1	2	1	1	2	3	2	3	2	2	2	2	3	2	1	1	2	2	2	1
48	Hyd mam	2	2	1	9	1	1	1	2	3	3	3	3	2	3	2	3	2	3	1	2	2	2	1
49	Hyd cae	2	2	2	1	4	1	1	3	3	2	3	2	1	2	2	3	2	3	1	2	2	2	1
50	Hyd fas	2	2	1	1	2	1	1	3	4	2	3	2	2	2	2	2	2	1	1	2	2	2	1
51	Hyd bro	2	2	2	1	2	1	1	3	4	2	3	2	2	2	2	3	2	1	1	2	2	2	1

TABLE 4. *continued.*

Character Number

Spec. No.	Species	82	83	84	87	90	92	93	95	98	137	138	139	142	143	144	145	146	148	149	153
25	Lap har	1	2	2	3	2	1	3	2	1	8	2	2	2	2	2	2	4	2	4	3
26	Lap cur	2	2	2	3	2	1	3	1	1	8	2	2	2	9	2	2	4	2	4	3
27	Mic gra	4	4	1	4	3	1	3	2	1	8	3	2	2	2	3	2	4	2	4	3
28	Mic can	4	6	1	4	3	3	3	2	1	8	3	2	2	2	3	2	4	2	4	3
30	Hyd kin	3	5	2	4	4	1	3	1	3	8	3	2	2	2	3	2	4	2	4	3
31	Eph mer	5	2	3	4	2	1	2	3	3	1	2	2	2	1	2	2	4	2	4	1
33	Hyd mel	4	4	2	5	4	3	3	2	1	8	3	2	2	2	3	2	4	2	4	3
34	Hyd bel	4	4	2	5	3	1	3	2	1	8	3	2	2	2	3	2	4	2	4	3
36	Hyd cya	4	5	2	5	3	2	3	2	3	8	3	2	2	2	3	2	4	2	4	3
40	Hyd klo	4	6	2	5	3	3	3	2	1	8	3	2	2	2	3	2	4	2	4	3
41	Hyd maj	3	3	2	4	4	1	3	2	4	8	3	2	2	2	3	2	4	2	4	3
44	Hyd tor	4	4	3	5	3	2	3	3	3	8	2	2	2	2	3	2	4	2	4	3
45	Hyd orn	4	3	3	6	4	2	3	3	4	8	3	2	2	2	3	2	4	2	4	3
46	Hyd ino	4	3	3	6	3	2	3	3	3	8	3	2	2	2	3	2	4	2	4	3
47	Hyd lap	4	5	2	5	3	2	3	3	4	8	3	2	2	2	3	2	4	2	4	3
48	Hyd mam	5	5	2	5	3	3	3	3	3	8	3	2	2	2	3	2	4	2	4	3
49	Hyd cae	1	4	3	5	3	2	3	4	4	8	2	2	2	2	3	2	4	2	4	3
50	Hyd fas	4	6	2	5	3	3	4	1	1	8	3	2	2	2	3	2	4	2	4	3
51	Hyd bro	5	6	2	5	3	3	3	2	1	8	3	2	2	2	3	2	4	2	4	3

Table 5 -- For each species the number and percentage of character states at each character state tree layer is given. The first layer corresponds to the primitive states. See the text for a further explanation.

	Species	First		Second		Third		Fourth		Fifth		Sixth	
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
1	Lat lat	34	79	8	19	0	00	1	02	0	00	0	00
2	Lat col	34	79	9	21	0	00	0	00	0	00	0	00
3	Lat sem	35	81	8	19	0	00	0	00	0	00	0	00
4	Lat sch	34	76	9	20	1	02	1	02	0	00	0	45
6	Aip eyd	16	39	24	58	1	02	0	00	0	00	0	41
7	Aip fus	18	41	23	54	2	05	0	00	0	00	0	00
9	Aip lae	15	35	26	61	2	05	0	00	0	00	0	00
10	Aip dub	16	37	22	51	4	09	1	02	0	00	0	00
11	Aip fol	21	49	20	47	2	05	0	00	0	00	0	00
12	Aip apr	19	45	22	52	1	02	0	00	0	00	0	00
13	Emy ann	19	45	21	50	2	05	0	00	0	00	0	00
14	Emy iji	19	44	22	51	2	05	0	00	0	00	0	00
15	Hyl dar	16	37	22	51	5	12	0	00	0	00	0	00
17	Thn vip	6	14	27	63	9	21	0	00	0	00	1	02
18	Aca per	9	21	22	52	9	21	2	05	0	00	0	00
19	Ths ano	12	29	24	57	6	14	1	02	0	00	0	00
20	Kol ann	8	19	20	48	11	26	2	05	1	02	1	02
21	Ast sto	5	12	30	71	4	10	2	05	0	00	1	02
22	Pel pla	6	14	23	55	10	24	2	05	0	00	1	02
23	Eah sch	7	17	24	57	8	19	3	07	0	00	1	02
24	Ker jer	14	33	22	51	4	09	2	05	0	00	0	00
25	Lap har	8	19	29	67	5	12	1	02	0	00	0	00
26	Lap cur	9	21	27	64	6	14	0	00	0	00	0	00
27	Mic gra	12	28	20	47	10	23	1	02	0	00	0	00
28	Mic can	8	19	22	51	10	23	2	05	1	02	0	00
30	Hyd kin	16	37	18	42	7	16	3	07	0	00	0	00
31	Eph mer	15	35	20	47	6	14	2	05	0	00	0	00
33	Hyd mel	8	19	22	51	8	19	3	07	1	02	0	00

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Table 5 --

Species	Character State Tree Layers											
	First		Second		Third		Fourth		Fifth		Sixth	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
34 Hyd bel	10	24	22	52	9	21	0	00	1	02	0	00
36 Hyd cya	6	14	26	61	7	16	2	05	1	02	0	00
40 Hyd klo	8	19	24	56	9	21	0	00	2	05	0	00
41 Hyd maj	10	23	23	52	9	21	2	05	0	00	0	44
44 Hyd tor	6	14	23	54	10	23	2	05	1	02	0	00
45 Hyd orn	7	16	24	56	9	21	2	05	0	00	1	02
46 Hyd ino	7	16	25	58	9	21	1	02	0	00	1	02
47 Hyd lap	7	16	24	56	10	23	1	02	1	02	0	00
48 Hyd mam	6	15	21	51	11	27	2	05	1	02	0	41
49 Hyd cae	7	17	21	51	10	24	2	05	1	02	0	41
50 Hyd fas	9	20	23	52	9	20	1	02	2	05	0	44
51 Hyd bro	7	16	24	56	7	16	2	05	2	05	0	00

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Table 6 -- Combinations of species selected from those generated by the combinatorial method from 40 species and the 43 character states at the first character state tree layer (see text for selection procedures). The following punctuation system is used in Tables 6,7,8, and 9 (examples are taken from Table 6): A species is circled at the level of shared states at which it first appears (e.g., species 3 has 35 character states at the first character state tree layer, see also Fig. 5). An asterisk denotes the formation of a new combination (e.g., species 3 and 4 form a combination at the level of 34 shared character states). A combination is solidly underlined if it is uncontested, that is none of its members are found in another group at that level of shared states (e.g., the group 1,2 is uncontested at the level of 33 shared states, and at level 14, the species 1,2,3,4,13 within the group 1,2,3,4,13,14 are underlined individually because they formed an uncontested group at level 17). The neighbors of species or combinations of species are given in parentheses (e.g., species 11 is a near neighbor to species 10 at level 16, and species 2,3,4,11 and 11,12 are neighbors to species 10 at the level of 15 shared states). Brackets denote the neighbors of combinations which merge to form a new combination at that level of shared states (e.g., the combination 7,11,12 formed at the level of 16 shared states. At the same level species 7 has neighbors 2,3,11 and 3,4; and the combination 11,12 has the neighbors 1,2,3,4).

Table 6 --

SHARED STATES	SELECTED COMBINATIONS		SHARED STATES	SELECTED COMBINATIONS
35	③		19	1,2,3,4
				11(3)
34	①			⑫
	②			⑬
	* 3④			⑭
33	* 1,2		18	1,2,3,4
	3,4			⑦
32	no changes			* 11,12 [11(2,3)(3,4) 12(1,2,3)]
				13(3,4)
31	1,2(3)			14
	3,4(2)		17	* 1,2,3,4,13 [1,2,3,4(12)]
30	* 1,2,3,4			7(3)(11)
				11,12(1,2,3)
29	no changes			14(1,2,3)
28	no changes		16	1,2,3,4,13
27	no changes			⑥
26	no changes			* 7,11,12 [7(2,3,11)(3,4) 11,12
25	no changes			(1,2,3,4)]
				⑩(11)
24	no changes			14(1,2,3,4)(12)
23	no changes			⑮
				㉚
22	no changes		15	1,2,3,4,13
21	1,2,3,4			6
	⑪			7,11,12(1,2,3)
20	no changes			⑨(7,11)
				10(2,3,4,11)(11,12)
				14(1,2,3,12)(11,12)(13)
				15
				30
				㉛

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Table 6 -- continued

SHARED
STATES   SELECTED COMBINATIONS

14   * 1,2,3,4,13,14   [1,2,3,4,13(11,12)   14(1,2,3,4,12)(1,2,3,11,12)]
           6(1,2)
        * 7,9,11,12   [7,11,12(1,2,3,4)   9(2,3,7,11)]
        * 7,11,12,14   [7,11,12(1,2,3,4)   14(1,2,3,4,12)(1,2,3,11,12)]
           10(1,2,3,4,11,12)(7,11)(11,12,13)
        * 15,31   [15(1)   31(1)]
           ㉔
           30

13   1,2,3,4,13,14
           6(1,2,3,4)(11,12)
        * 7,9,11,12,14   [7,9,11,12(1,2,3)   7,11,12,14(1,2,3)]
           10(1,2,3,4,11,12,13)(2,3,4,7,11)(7,11,12)(11,12,14)
           15,31(1)
           24
           30

12   1,2,3,4,13,14(11,12)
        * 6,10(11,12)   [6(1,2,3,4,11,12)(7,11,12)(13)(14)   10(1,2,3,4,7,11,12)(1,2,
              3,4,11,12,14)(7,9,11)(7,9,12,13)(7,11,12,14)(11,12,13,14)]
           7,9,11,12,14(1,2,3)
           15,31(1,2)
           ⑲
           24
           ㉗
           30(1)(3)

11   1,2,3,4,13,14(7,11,12)(10,11,12)
           6,10(1,2,3,4,11,12)(7,11,12)(11,12,13)
           7,9,11,12,14(1,2,3,4)(10)(13)
           15,31(1,2,3)
           19
           24(1)(3,4)
           27
           30(1,2,3)(3,4,13)(11)(14)

Table 6 -- continued

10   * 1,2,3,4,7,9,11,12,13,14   [1,2,3,4,13,14(7,10,11,12)   7,9,11,12,14
            (1,2,3,4,10)(10,13)]

      * 6,7,9,10,11,12,14   [6,10(1,2,3,4,7,11,12,14)(1,2,3,4,11,12,13)(7,11,
            12,13,14)   7,9,11,12,14(1,2,3,4,10)(10,13)]

         15,31(1,2,3,4)(1,2,3,12)

      * 19,24(15)   [19(1)(3,4)   24(1,2,3,4)]

      * 24,30   [24(1,2,3,4)   30(1,2,3,4,13)(1,2,3,14)(3,11)(15)]

         27(3,4)

      * 30,㊶   [30(1,2,3,4,13)(1,2,3,4,14)(3,11)(15)]

         ㉞

9   1,2,3,4,7,9,11,12,13,14(10)

         6,7,9,10,11,12,14(1,2,3,4)(11)

      * 15,19,24,31   [15,31(1,2,3,4,7,9,11,12)(1,2,3,4,12)(1,2,3,12,14)
            (30)]

         ⑱

         24,30,41   [30,41(15)]

         ㉖

         27(1)(2,3,4)

         34

         ㊿

8   * 1,2,3,4,6,7,9,10,11,12,13,14

         15,19,24,31(1)

         18

         ⑳

         24,30,41(15,19)

         ㉕

      * 26,34   [34(15)(24)(30)]

      * 27,34   [27(1,2,3,4)(3,4,11)(24)   34(15)(24)(30)]

         ㉘

      * �33,34,50   [34(15)(24)(30)]

         ㊵

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Table 6 -- continued

SHARED STATES	SELECTED COMBINATIONS

7 <u>1,2,3,4,6,7,9,10,11,12,13,14</u>

 * <u>15,19,24,30,31,41</u> [15,19,24,31(1,2,3,4) 30,31,41(1)(3,4,13)]

  18(3,4,)(15)(24,27)

  20

  ㉓(50)

 * 25,26,34

 * 27,33,34,50

  28(27)

 * 33,34,40,�51

 * 33,34,㊺,㊼,50

  ㊻(15,34)

  4̃9̃

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6 <u>1,2,3,4,6,7,9,10,11,12,13,14</u>(30)

  <u>15,19,24,30,31,41</u>(1)

 * ⑰,27,33,34,㊹,45,46,47,50(15,19,24) [33,34,45,47,50(24,30) 46(15,30,34)

   (15,31,34)]

  18(1)(3,4,11)(15,19,24,27,34)(15,31)

  20(26,34)

  ㉒

 * 23,27,33,34,50 [23(19,50)(26,50)]

 * 25,26,33,34,40,51(50) [25,26,34(24)(27)]

 * 27,33,34,40,50,51

  28(1)(2,3)(34)

 * 33,34,㊱,40,45,47,50,51(24) [33,34,45,47,50(24,30)]

 * 46,㊽(15,34) [46(15,30,34)(15,31,34)]

  49(15,19,24,40)(30)

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5 <u>1,2,3,4,6,7,9,10,11,12,13,14</u>(24)(30,41)

  <u>15,19,24,30,31,41</u>(1,2,3,4,13)(27,34)

 * 17,18,23,27,33,34,44,45,46,47,48,50(15,19,24) [17,27,33,34,44,45,46,

   47,50(15,19,24,30,41)(15,19,24,31) 18(1,2,3,4,7,9,11,12)(1,15,31)

   (1,24,27)(3,4,11,13)(3,4,11,15)(3,4,11,24,27)(15,19,24,25,26,27,34)

   (15,19,24,27,30,34,41)(15,19,24,27,34) 46,48(15,30,34)(15,31,34)]

 * 17,27,33,34,36,40,44,45,46,47,49,50,51(15,19,24) [17,27,33,34,44,45,

   46,47,50(15,19,24,30,41)(15,19,24,31) 33,34,36,40,45,47,50,51(24,

   30) 49(15,19,24,30,40,41)(15,19,24,31,40)(25)]

 * 20,25,26,33,34,40,51(50) [20(3)(15)(26,30,34)]

  ㉑(24,30,41)

 * 22,46,48(15,26,34) [46,48(15,30,34)(15,31,34)]

 * 23,25,26,27,33,34,40,50,51

 * 25,26,33,34,36,40,45,47,50,51(24) [33,34,36,40,45,47,50,51(24,30)]

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Table 6 -- continued

* 27,28,33,34,40,50,51   [28(1,2,3)(1,27)(2,3,4,27)(15,31,34,46)(24,27)
(26,34)]

---

4   1,2,3,4,6,7,9,10,11,12,13,14(15,30,31,41)(24,30,41)
15,19,24,30,31,41(1,2,3,4,6,13)(1,2,3,4,7,9,10,11,12,13,14)(1,27,34)
(17,27,33,34,44,45,46,47,50)(18,27,34)(40,49)

* 17,18,22,23,25,26,27,33,34,36,40,44,45,46,47,48,49,50,51(15,19,24)   [17,
18,23,27,33,34,44,45,46,47,48,50(15,19,24,30,41)(15,19,24,31)   22,
46,48(15,20,26,30,34)(15,26,28,31,34)]

* 17,21,27,33,34,36,40,44,45,46,47,49,50,51(15,19,24,30,41)

* 17,27,28,33,34,36,40,44,45,46,47,49,50,51(15,19,24,31)

* 20,23,25,26,27,33,34,40,50,51

* 20,25,26,33,34,36,40,45,47,50,51(24,30)

* 23,25,26,27,28,33,34,40,50,51

---

3   * 1,2,3,4,6,7,9,10,11,12,13,14,15,19,24,30,31,41   [1,2,3,4,6,7,9,10,11,12,
13,14(27)   15,19,24,30,31,41(1,2,3,4,13,27,34)(1,17,27,33,34,44,45,
46,47,50)(1,18,27,34)(1,40,49)(17,18,23,27,33,34,44,45,46,47,48,50)
(18,25,26,27,34)]

* 15,17,19,21,24,27,28,30,31,33,34,36,40,41,44,45,46,47,49,50,51   [15,19,24,
30,31,41(1,2,3,4,13,27,34)(1,17,27,33,34,44,45,46,47,50)(1,18,27,34)(1,
40,49)(17,18,23,27,33,34,44,45,46,47,48,50)(18,25,26,27,34)   17,27,
28,33,34,36,40,44,45,46,47,49,50,51(1,15,19,24,31)]

* 17,18,20,21,22,23,25,26,27,33,34,36,40,44,45,46,47,48,49,50,51(15,19,24,
30,41)

* 17,18,22,23,25,26,27,28,33,34,36,40,44,45,46,47,48,49,50,51(15,19,24,31)
[17,27,28,33,34,36,40,44,45,46,47,49,50,51(1,15,19,24,31)]

* 20,23,25,26,27,28,33,34,40,50,51

---

2   1,2,3,4,6,7,9,10,11,12,13,14,15,19,24,30,31,41
* 15,17,18,19,20,21,22,23,24,25,26,27,28,30,31,33,34,36,40,41,44,45,46,
47,48,49,50,51   [15,17,19,21,24,27,28,30,31,33,34,36,40,41,44,45,
46,47,49,50,51(1)   17,18,22,23,25,26,27,28,33,34,36,40,44,45,46,
47,48,49,50,51(1,15,19,24,31)]

---

1   1,2,3,4,6,7,9,10,11,12,13,14,15,19,24,30,31,41(18,25,26,27,34)(40,49)
15,17,18,19,20,21,22,23,24,25,26,27,28,30,31,33,34,36,40,41,44,45,46,47,
48,49,50,51(1)

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Table 7 -- Combinations of species selected from those generated by the combinatorial method from 40 species and the 65 character states at the second character state tree layer (see text for selection procedures, and see heading for Table 6 for an explanation of the punctuation system used).

SHARED STATES	SELECTED COMBINATIONS	SHARED STATES	SELECTED COMBINATIONS
30	21	23	6
			⑦
29	21		9
	②5		17,46
			19
28	21		21
	25		㉒
			23
27	⑰		25,26
	21		* 36,51
	25		* 40,51
	㉖		㊶
			㊹
26	⑨		* 45,47 [45(46)]
	17		50
	21		
	* 25,26	22	6
	㊱		7
			9
25	9		⑩
	17		⑫
	21		⑭
	25,26		⑮
	36		17,46(45)
	㊻		⑱
			19
24	⑥		21(17)(25)
	9		22
	* 17,46		23
	⑲		㉔
	21		25,26
	㉓		㉘
	25,26		* �33,�34,36,51
	36		* 36,40,51
	㊵		41
	㊺		44(46)
	㊼		45,47(46)
	㊱		50(36)(47)

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Table 7 -- continued

SHARED
STATES   SELECTED COMBINATIONS

21   6

            7,9

            10

            12

            ⑬

            14

            15

        *   17,21,46   [17,46(36)   21(45)]

        *   17,44,46   [17,46(36)   44(36,46)]

        *   17,45,46,47   [17,46(36)   45,47(36,46)(40)(51)]

            18

            19

            22

            23

            24

            25,26

            28

        *   33,34,36,40,51   [33,34,36,51(17)(47)]

            41

        *   45,47,50   [45,47(36,46)(40)(51)   50(36,47)(47,51)]

            ④⑧(17)

            ④⑨

---

20   6

            7,9

        *   10,⑪   [10(7,9)]

            12

            13

            14

            15

            17,21,46(45)

            17,44,46(36)

            17,45,46,47(36)

        *   18,23   [23(21)]

            19

            ⑳   .

            22(17)

            24

            25,26(17)

            ㉗

            28(36,51)

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Table 7 -- continued

SHARED
STATES   SELECTED COMBINATIONS

              ③1
              33,34,36,40,51(17)(47)
              41(17)
              45,47,50(36,46)(51)
              48(17,46)
              49(44)

───

19   6
              7,9(10)
              10,11(7)(9)
              12(7)(10)
              13
              14
              15
        *   17,21,44,46
        *   17,21,45,46,47   [17,45,46,47(25)(33,34,36,51)(40)]
        *   17,44,45,46,47(36)   [17,45,46,47(25)(33,34,36,51)(40)]
        *   17,45,46,47,50(36)   [17,45,46,47(25)(33,34,36,51)(40)   45,47,50(33,34,36,
                 46,51)(36,44,46)(40,51)]
              18,23
        *   19,24   [19(17)(46)]
        *   19,41   [19(17)(46)   41(21)(40)]
              20(25)
              22(25)(36)
              25,26(17,47)(21)(36,51)(40)
              27
              28(33,34,36,51)(36,40,51)
              31
              33,34,36,40,51(17,25)(17,47)(45,46,47)(47,50)
              48(17,36)(17,47)
              49(21)(25)(36,40,51)(44,46)

───

18   6(7)(9)
              7,9,10,11
        *   10,11,12   [12(7,10)(9,10)]
        *   13,14
              15
        *   17,21,44,45,46,47(36)   [17,21,45,46,47(25)   17,44,45,46,47(25,33,34,36,51)]
        *   17,44,45,46,47,50   [17,44,45,46,47(25,33,34,36,51)   17,45,46,47,50(33,34,
                 36,51)]
              18,23(44)

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Table 7 -- continued

SHARED
STATES   SELECTED COMBINATIONS

      19,24

      19,41

      20

      22(17,36) (17,46) (21) (26) (36,40,51)

* 25,26,49   [25,26(17,33,34,36,47,51) (17,40,47) (17,45,46,47) (23) (36,40,51) (44)
         49(17,44,46) (18,44) (21,25) (21,44) (23,44) (25,36,40,51) (25,44)]

* 27,28   [27(51)   28(17,33,34,36,51) (25,36,51) (33,34,36,45,46,47,51)]

* 28,33,34,36,40,51   [28(17,33,34,36,51) (25,36,51) (33,34,36,45,46,47,51)   33,
         34,36,40,51(17,25,47) (17,45,46,47) (17,47,50) (45,46,47,50)]

      ㉚

      31

* 33,34,36,40,49,51(44,45,46,47)   [33,34,36,40,51(17,25,47) (17,45,46,47) (17,
         47,50) (45,46,47,50)   49(17,44,46) (18,44) (21,25) (21,44) (23,44) (25,36,
         40,51) (25,44)]

      48(17,19) (17,36,46) (17,40,47) (17,41) (17,44,46) (17,45,46,47)

---

17   6(7,9)

      7,9,10,11

      10,11,12

      13,14

* 15,31   [15(25)]

* 17,21,44,45,46,47,50(36)   [17,21,44,45,46,47(25,33,34,36,51)   17,44,
         45,46,47,50(25,33,34,36,51)]

      18,23(21,44) (25) (44,46) (44,49)

      19,24(45)

      19,41(17)

      20(21) (25,26)

* 22,48(17,46)   [22(17,25) (17,33,34,36,40,51) (17,36,46) (17,44,46) (25,26) (25,
         36,40,51) (28,36,40,51)   48(17,19,46) (17,21,46) (17,25,26,47) (17,25,
         33,34,36,47,51) (17,25,40,47) (17,25,45,46) (17,28,33,34,36,45,46,47,51)
         (17,33,34,36,40,47,51) (17,33,34,36,47,50,51) (17,36,44,46) (17,40,41,
         47) (17,40,45,46,47) (17,41,46)]

      25,26,49(21) (36,40,51) (44)

      27,28(33,34,36,51)

      28,33,34,36,40,51(17) (45,46,47)

      30(41)

      33,34,36,40,49,51(17,25,44,45,46,47) (44,45,46,47,50)

Table 7 -- continued

16   6(7,9,10)(7,12)

   * 7,9,10,11,12

    13,14

    15,31

    17,21,44,45,46,47,50(25,33,34,36,51)

    18,23(17,21,44,46)(21,25,44)(21,44,49)(25,26)(33,34,36,44,45,46,47,51)(44,
      46,49)

    19,24(40,45,47)(45,46)(45)

    19,41(17,46)(17,48)(40,47)

    20(17,25)(21,25)(22,25)(25,36,51)

    22,48(17,19,46)(17,36,46)(17,44,46)

   * 25,26,33,34,36,40,49,51(17,44,45,46,47)　[25,26,49(21,36,40,51)(21,44)
      33,34,36,40,49,51(17,21,25,44,45,46,47)(17,25,44,45,46,47,50)(18,
      44,45,46,47)(23,44,45,46,47)

   * 27,28,33,34,36,40,51　[27,28(17,33,34,36,51)(33,34,36,45,46,47,51)　28,
      33,34,36,40,51(17,22)(17,25)(17,41)(17,45,46,47,48)(45,46,47,50)]

   * 28,33,34,36,40,49,51(44,45,46,47)　[28,33,34,36,40,51(17,22)(17,25)(17,41)
      (17,45,46,47,48)(45,46,47,50)　33,34,36,40,49,51(17,21,25,44,45,46,
      47)(17,25,44,45,46,47,50)(18,44,45,46,47)(23,44,45,46,47)]

    30(17,48)

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15   6(7,9,10,11)(7,9,10,12)

    7,9,10,11,12

    13,14

    15,31

    17,21,44,45,46,47,50(23,25,33,34,36,51)(25,26,33,34,36,51)(25,33,34,36,
      40,49,51)

    18,23(17,21,25,33,34,36,44,45,46,47,51)(17,21,44,46,49)(21,25,26,44)(21,
      25,44,49)(33,34,36,40,44,45,46,47,49,51)(33,34,36,44,45,46,47,50,51)

   * 19,24,41(45)　[19,24(17,45,46)(25)(40,45,46,47)(40,45,47,50,51)　19,41(17,
      40,47,48)(17,45,46)(17,46,48)(21)]

    20(17,25,33,34,36,51)(18,25,44)(21,25,36,51)(23,25)(25,49)(25,36,40,51)

    22,48(17,19,36,46)(17,19,44,46)(17,28,33,34,36,40,45,46,47,51)(17,36,44,
      46)(17,41,46)(17,44,46,49)

    25,26,33,34,36,40,49,51(17,21,44,45,46,47)(17,44,45,46,47,50)

    27,28,33,34,36,40,51(17)(45,46,47)

    28,33,34,36,40,49,51(17,25,44,45,46,47,48)(44,45,46,47)

    30(17,36,48)(17,40,41,47,48)(17,46,48)(19)

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Table 7 -- continued

Table 7 -- continued

SHARED
STATES   SELECTED COMBINATIONS

13   6,7,9,10,11,12

    13,14,(7,9,10,12)

    15,31(44)

  * 17,18,20,21,23,44,45,46,47,50 [17,18,21,23,44,45,46,47,50(25,26,33,34,
     36,51)(25,33,34,36,40,49,51) 18,20,23(21,25,26,44)(21,25,44,49)]

    17,21,25,26,33,34,36,40,44,45,46,47,49,50,51(23)

    19,24,41(17,40,45,46,47,48)(21,45)(25,40,45,47)(40,45,47,50,51)

  * 22,25,26,28,33,34,36,40,48,49,51(17,44,45,46,47) [22,28,33,34,36,40,48,
     49,51(17,18,19,25,44,45,46,47)(17,21,25,44,45,46,47)(17,24,25,44,45,
     46,47,50)(17,25,41,44,45,46,47) 25,26,28,33,34,36,40,49,51(17,21,
     44,45,46,47,48)(17,41,44,45,46,47,48)(17,44,45,46,47,48,50)

    27,28,33,34,36,40,49,51(17,25,44,45,46,47,48)(44,45,46,47,50)

    30(17,19,36,48)(17,19,40,41,47,48)(17,22,36,46,48)(17,25,26,40,41,47,48)
     (17,25,33,34,36,40,41,47,48,51)(17,25,40,41,45,46,47,48)(17,28,33,34,
     36,40,41,45,46,47,51)(17,33,34,36,40,41,47,48,50,51)(17,36,44,46,48)
     (21,41)

---

12 * 6,7,9,10,11,12,13,14

    15,31(9)(14)(17,22,44,46,48)(18,23)(19)(21,44,49)(24,25,26)

    17,18,20,21,23,44,45,46,47,50(25,26,33,34,36,51)(25,33,34,36,40,49,51)

    17,21,25,26,33,34,36,40,44,45,46,47,49,50,51(18,23)(22)(28,48)

    19,24,41(17,21,45,46)(17,22,28,33,34,36,40,45,46,47,48,50,51)(17,25,40,
     45,46,47,48)(18,25,40,45,47,50,51)(21,25,40,45,47)

    22,25,26,28,33,34,36,40,48,49,51(17,18,19,44,45,46,47)(17,21,44,45,46,47)
     (17,24,44,45,46,47,50)(17,41,44,45,46,47)

    27,28,33,34,36,40,49,51(17,21,25,44,45,46,47,48)(17,22,25,44,45,46,47,48)
     (17,25,26,44,45,46,47,48)(17,25,41,44,45,46,47,48)(17,25,44,45,46,47,
     48)(18,19,44,45,46,47)(23,44,45,46,47)(24,44,45,46,47,50)

    30(17,19,22,36,46,48)(17,19,25,40,41,47,48)(17,19,33,34,36,40,41,47,48,51)
     (17,19,40,41,45,46,47,48)(17,21,25,40,41,45,46,47,48)(17,22,28,33,34,
     36,40,41,45,46,47,48,51)(17,22,36,44,46,48)(17,24,40,41,45,46,47,48)
     (17,25,26,33,34,36,40,41,47,48,51)(17,25,26,40,41,45,46,47,48)(17,
     25,28,33,34,36,40,41,44,45,46,47,48,49,51)(17,25,33,34,36,40,41,47,
     48,50,51)(17,27,28,33,34,36,40,41,45,46,47,48,51)(17,28,33,34,36,40,
     41,45,46,47,48,50,51)

---

11   6,7,9,10,11,12,13,14

    15,31(6,9)(7,9)(9,14)(9,25,26)(14,25,26)(17,21,22,41,44,46,48,49)(17,22,36,
     44,46,48)(18,21,23,44,49)(18,23,25,26)(21,25,26,44,49)

  * 17,18,20,21,23,25,26,33,34,36,40,44,45,46,47,50,51 [17,18,20,21,23,44,

Table 7 -- continued

SHARED
STATES   SELECTED COMBINATIONS

45,46,47,50(22,25,33,34,36,40,49,51)(25,28,33,34,36,48,51) 17,21,
25,26,33,34,36,40,44,45,46,47,49,50,51(18,22,23)(23,48)(28,41,48)]

* 17,21,22,25,26,28,33,34,36,40,44,45,46,47,48,49,50,51(24) [17,21,25,26,33,
34,36,40,44,45,46,47,49,50,51(18,22,23)(23,48)(28,41,48) 22,25,26,
28,33,34,36,40,48,49,51(17,18,19,21,23,44,45,46,47)(17,18,19,24,44,
45,46,47,50)(17,18,19,41,44,45,46,47)(17,21,41,44,45,46,47)(17,24,
31,41,44,45,46,47,50)]

* 19,24,30,41(40,45,46,47,48 [19,24,41(17,18,20,22,25,28,33,34,36,40,44,
45,46,47,48,49,50,51)(17,21,25,40,45,46,47,48)(17,25,26,40,45,46,47,
48)(18,21,25,40,45,47,50,51)(27,40,45,47,50,51) 30(17,19,22,28,33,
34,36,40,41,45,46,47,48,51)(17,19,22,44,46,48)(17,19,25,26,40,41,47,
48)(17,19,25,33,34,36,40,41,47,48,51)(17,19,25,40,41,45,46,47,48)(17,
19,33,34,36,40,41,47,48,50,51)(17,21,25,26,40,41,45,46,47,48)(17,21,
25,28,33,34,36,40,41,44,45,46,47,48,49,51)(17,22,24,28,33,34,36,40,
41,45,46,47,48,50,51)(17,22,25,28,33,34,36,40,41,45,46,47,48,49,51)
(17,22,27,28,33,34,36,40,41,45,46,47,48,51)(17,24,25,40,41,45,46,47,
48)(17,25,26,28,33,34,36,40,41,44,45,46,47,48,49,51)(17,25,26,33,34,
36,40,41,47,48,50,51)(17,25,28,33,34,36,40,41,44,45,46,47,48,49,50,
51)(17,27,28,33,34,36,40,41,45,46,47,48,50,51)]

* 22,25,26,27,28,33,34,36,40,48,49,51(17,44,45,46,47) [22,25,26,28,33,34,
36,40,48,49,51(17,18,19,21,23,44,45,46,47)(17,18,19,24,44,45,46,47,
50)(17,18,19,41,44,45,46,47)(17,21,41,44,45,46,47)(17,24,31,41,44,45,
46,47,50) 27,28,33,34,36,40,49,51(17,18,19,22,25,44,45,46,47,48)
(17,21,22,25,44,45,46,47,48)(17,21,25,26,44,45,46,47,48)(17,21,25,
41,44,45,46,47,48)(17,21,25,44,45,46,47,48)(17,21,25,44,45,46,47,50)
(17,22,24,25,44,45,46,47,48,50)(17,22,25,41,44,45,46,47,48)(17,25,
26,41,44,45,46,47,48)(17,25,26,44,45,46,47,48,50)(17,25,41,44,45,46,
47,48,50)(18,19,23,44,45,46,47)(18,19,24,44,45,46,47,50)(23,44,45,
46,47,50)]

* 27,28,30,33,34,36,40,49,51(17,25,41,44,45,46,47,48) [27,28,33,34,36,
40,49,51(17,18,19,22,25,44,45,46,47,48)(17,21,22,25,44,45,46,47,48)
(17,21,25,26,44,45,46,47,48)(17,21,25,41,44,45,46,47,48)(17,21,25,
44,45,46,47,48)(17,21,25,44,45,46,47,50)(17,22,24,25,44,45,46,47,48,
50)(17,22,25,41,44,45,46,47,48)(17,25,26,41,44,45,46,47,48)(17,25,
26,44,45,46,47,48,50)(17,25,41,44,45,46,47,48,50)(18,19,23,44,45,
46,47)(18,19,24,44,45,46,47,50)(23,44,45,46,47,50) 30(17,19,22,28,
33,34,36,40,41,45,46,47,48,51)(17,19,22,44,46,48)(17,19,25,26,40,
41,47,48)(17,19,25,33,34,36,40,41,47,48,51)(17,19,25,40,41,45,46,47,
48)(17,19,33,34,36,40,41,47,48,50,51)(17,21,25,26,40,41,45,46,47,48)
(17,21,25,28,33,34,36,40,41,44,45,46,47,48,49,51)(17,22,24,28,33,34,
36,40,41,45,46,47,48,50,51)(17,22,25,28,33,34,36,40,41,45,46,47,48,

Table 7 -- continued

SHARED
STATES   SELECTED COMBINATIONS

          49,51) (17,22,27,28,33,34,36,40,41,45,46,47,48,51) (17,24,25,40,41,45,
          46,47,48) (17,25,26,28,33,34,36,40,41,44,45,46,47,48,49,51) (17,25,26,
          33,34,36,40,41,47,48,50,51) (17,25,28,33,34,36,40,41,44,45,46,47,48,
          49,50,51) (17,27,28,33,34,36,40,41,45,46,47,48,50,51)]

---

10   6,7,9,10,11,12,13,14(31)

    *   15,17,21,22,25,26,28,31,33,34,36,40,44,45,46,47,48,49,50,51(24,41)   [15,31
          (6,7,9) (6,9,14)(6,9,25,26) (7,9,14) (7,9,25,26) (9,14,25,26) (12) (13,14)
          (17,19,22,36,44,46,48) (18,20,21,23,25,26,44,49) (18,23,24,25,26)   17,
          21,22,25,26,28,33,34,36,40,44,45,46,47,48,49,50,51(18,19,23,24)]
          17,18,20,21,23,25,26,33,34,36,40,44,45,46,47,50,51(22,49)

          19,24,30,41(17,22,28,33,34,36,40,45,46,47,48,50,51) (17,25,40,45,46,47,48)
          22,25,26,27,28,33,34,36,48,49,51(17,18,19,20,31,41,44,45,46,47,50) (17,18,
          19,44,45,46,47) (17,21,44,45,46,47) (17,24,44,45,46,47,51) (17,41,44,45,
          46,47)
          27,28,30,33,34,36,40,49,51(17,21,25,41,44,45,46,47,48) (17,22,25,41,44,45,
          46,47,48) (17,25,26,41,44,45,46,47,48) (17,25,41,44,45,46,47,48,50)

---

9   ②
          ④
          6,7,9,10,11,12,13,14(15,31)

    *   15,17,18,20,21,22,23,25,26,28,31,33,34,36,40,44,45,46,47,48,49,50,51
          19,24,30,41(17,18,20,22,25,28,33,34,36,40,44,45,46,47,48,49,50,51) (17,
          21,25,40,45,46,47,48) (17,22,27,28,33,34,36,40,45,46,47,48,50,51) (17,
          25,26,40,45,46,47,48)

    *   22,25,26,27,28,30,33,34,36,40,48,49,51(17,41,44,45,46,47)   [22,25,26,27,28,
          33,34,36,40,48,49,51(17,18,19,21,23,44,45,46,47) (17,18,19,24,44,45,46,
          47,50) (17,18,19,41,44,45,46,47) (17,21,24,44,45,46,47,50) (17,21,41,44,
          45,46,47) (17,24,31,41,44,45,46,47,50)   27,28,30,33,34,36,40,49,
          51(17,18,19,22,25,41,44,45,46,47,48) (17,21,22,25,41,44,45,46,47,48)
          (17,21,23,25,41,44,45,46,47,48) (17,21,25,26,41,44,45,46,47,48) (17,
          21,25,41,44,45,46,47,48,50) (17,22,24,25,41,44,45,46,47,48,50(17,25,26,
          41,44,45,46,47,48,50)]

Table 7 -- continued

SHARED STATES	SELECTED COMBINATIONS

8   ①
    2
    ③
    4

6,7,9,10,11,12,13,14(15,25,26,31)

15,17,18,20,21,22,23,25,26,28,31,33,34,36,40,44,45,46,47,48,49,50,51

19,24,30,41(17,18,20,21,22,23,25,28,33,34,36,40,44,45,46,47,48,49,50,51) (17,18,20,22,25,27,28,33,34,36,40,44,45,46,47,48,49,50,51) (17,21,25, 26,40,45,46,47,48)

22,25,26,27,28,30,33,34,36,40,48,49,51(17,18,19,41,44,45,46,47) (17,21,41, 44,45,46,47) (17,24,31,41,44,45,46,47,50)

---

7   * 1,2

    * 3,4

6,7,9,10,11,12,13,14(15,25,26,31)

* 15,17,18,19,20,21,22,23,24,25,26,28,30,31,33,34,36,40,41,44,45,46,47,48, 49,50,51 [15,17,18,20,21,22,23,25,26,28,31,33,34,36,40,44,45,46,47, 48,49,50,51(19,24,27,41) 19,24,30,41(17,18,20,21,22,23,25,27,28,33, 34,36,40,44,45,46,47,48,49,50,51)]

* 19,22,24,25,26,27,28,30,33,34,36,40,41,48,49,51(17,18,20,31,44,45,46,47, 50) [19,24,30,41(17,18,20,21,22,23,25,27,28,33,34,36,40,44,45,46, 47,48,49,50,51) 22,25,26,27,28,30,33,34,36,40,48,49,51(14,15,17,21, 24,31,41,44,45,46,47,50) (17,18,19,21,23,41,44,45,46,47)]

---

6   1,2

    3,4

6,7,9,10,11,12,13,14(15,21,25,26,31,44,49) (15,24,25,26,31)

* 15,17,18,19,20,21,22,23,24,25,26,27,28,30,31,33,34,36,40,41,44,45,46,47, 48,49,50,51(14) [15,17,18,19,20,21,22,23,24,25,26,28,30,31,33,34, 36,40,41,44,45,46,47,48,49,50,51(6,9)]

---

5   1,2

    3,4

6,7,9,10,11,12,13,14(15,17,21,22,24,25,26,27,28,30,31,33,34,36,40,41,44,45, 46,47,48,49,50,51) (15,18,20,21,23,25,26,31,44,49) (15,19,24,25,26,31)

15,17,18,19,20,21,22,23,24,25,26,27,28,30,31,33,34,36,40,41,44,45,46,47, 48,49,50,51(6,9,14) (13,14)

---

4   1,2(3)

    3,4(7)(2)

* 6,7,9,10,11,12,13,14,15,17,18,19,20,21,22,23,24,25,26,27,28,30,31,33,34, 36,40,41,44,45,46,47,48,49,50,51

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Table 7 -- continued

3   * 1,2,3,4 [1,2(6)(7,9,10) 3,4(7,9,10,11,12,13)]
           6,7,9,10,11,12,13,14,15,17,18,19,20,21,22,23,24,25,26,27,28,30,31,33,34,
              36,40,41,44,45,46,47,48,49,50,51

2   1,2,3,4(6)(7,9,10,11,12,13)(15)
           6,7,9,10,11,12,13,14,15,17,18,19,20,21,22,23,24,25,26,27,28,30,31,33,34,
              36,40,41,44,45,46,47,48,49,50,51

1   1,2.3,4(6,7,9,10,11,12,13,14,15,31)(7,9,10,11,13,27,28)(15,24)
           6,7,9,10,11,12,13,14,15,17,18,19,20,21,22,23,24,25,26,27,28,30,31,33,34,
              36,40,41,44,45,46,47,48,49,50,51

Table 8 -- Combinations of species selected from those generated by the combinatorial method from 40 species and the 23 character states at the third character state tree layer (see text for selection procedures, and see heading of Table 6 for an explanation of the punctuation system used).

SHARED STATES	SELECTED COMBINATIONS
11	⑳
	㊽
10	20
	㉒
	㉗
	㉘
	㊹
	㊼
	48
	㊾
9	⑰
	⑱
	20
	22
	27
	* 28,㊵
	* 28,48
	㉞
	㊶
	* 44,㊻
	㊺
	47
	49
	㊿
8	* 17,20
	18
	* 20,47
	22(48)
	㉓
	* 27,34 [27(28) 34(44)]
	* 28,34,40,47 [34(44)]
	* 28,40,48
	㉝
	⸴ 34,49 [34(44) 49(44)]
	41
	* 44,45,46
	* 44,46,47

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Table 8 -- continued

SHARED STATES	SELECTED COMBINATIONS

```
               * 45,47
                 47,49   [49(44)]
                 50
```

```
7     * 17,20,27,28,34,40,47  [17,20,(48)  27,34(44)(49)]
      * 18,45,47
      * 20,47,49
        22(27)(28,48)
        23
      * 28,34,40,47,48,49  [34,49(44)]
      * 28,34,(36),40,47
      * 28,34,40,44,46,47
      * 28,40,48,(51)
      * (30),41   [41(20)(47)]
        33(28,40)(34,44)
      * 44,45,46,47
        50(20)(28,40)(47)
```

```
6       17,20,27,28,34,40,47(36)(44,46)(48,49)
      * 18,44,45,46,47  [18,45,47(41)]
        (19)
        20,47,49(41)
        22(17,20,48)(27,28,48)(28,40,48)
      * 23,33  [23(49)  33(27,34,44)(34,44,49)]
        (26)
      * 28,33,40,48,51  [33(27,34,44)(34,44,49)]
      * 28,33,34,40,44,45,46,47  [33(27,34,44)(34,44,49)]
      * 28,34,36,40,47,48,49
      * 28,34,36,40,44,46,47,50  [50(20,47)(45,47)(47,49)]
      * 28,34,40,44,46,47,48,49,51
        28,40,48,50,51  [50(20,47)(45,47)(47,49)]
        30,41(20)(48)
        (51)
      * 33,50  [33(27,34,44)(34,44,49)  50(20,47)(45,47)(47,49)]
```

Table 8 -- continued

5   ⑮(20)

          * 17,20,22,27,28,34,36,40,47,48,49   [20,47,49(18,41,45)(50)]

          * 17,20,27,28,30,34,40,41,47,49(48)   [20,47,49(18,41,45)(50)]

          * 17,20,27,28,33,34,40,44,45,46,47

          * 17,20,27,28,34,36,40,44,46,47,50

          * 17,20,27,28,34,40,44,46,47,48,49,51   [20,47,49(18,41,45)(50)]

          * 18,28,33,34,40,44,45,46,47,48,49,51   [18,44,45,46,47(41)]

          * 19,28,34,40,44,46,47,48,49,51   [19(18)]

          * 22,28,40,48,50,51

          * 23,28,33,40,46,51

          * ㉕,26   [26(17,20,48)]

          * 28,33,34,36,40,44,45,46,47,50

          * 28,33,40,48,50,51

          * 28,34,36,40,44,46,47,48,49,50,51

             31(44,45,46)

             33,50

4   ⑩

             15(18,20,27,28,34,40,47)(20,30,41)

          * 17,18,20,27,28,30,33,34,40,41,44,45,46,47,48,49,51   [17,20,27,28,30,34,40,
             41,47,49(26,48)]

          * 17,19,20,27,28,34,40,44,46,47,48,49,51

          * 17,20,22,27,28,30,34,36,40,41,47,48,49   [17,20,27,28,30,34,40,41,46,49(26,
             48)]

          * 17,20,22,27,28,34,36,40,44,46,47,48,49,50,51

          * 17,20,27,28,33,34,36,40,44,45,46,47,50

          * 18,19,28,33,34,40,44,45,46,47,48,49,51

          * 18,23,28,33,34,40,44,45,46,47,48,49,51

          * 18,28,33,34,36,40,44,45,46,47,48,49,50,51

          * 19,28,34,36,40,44,46,47,48,49,50,51

             ㉑(17,20,48)

          * 22,28,33,40,48,50,51

          * 23,28,33,40,48,50,51

             ㉔(18,41,44,45,46,47)

             25,26(17,20,48)(18,19)

             31(18,44,45,46,47)(41)(44,45,46,49)

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Table 8 -- continued

SHARED
STATES   SELECTED COMBINATIONS

3   10

    * 15,31(20,30,41)   [15(17,20,26,27,28,30,34,40,41,47,48,49)(17,20,27,28,33,
        34,40,44,45,46,47)(17,20,27,28,34,36,40,47)   31(18,24,41,44,45,46,47)]

    * 17,18,19,20,24,<u>25</u>,<u>26</u>,27,28,<u>30</u>,33,34,40,<u>41</u>,<u>44</u>,45,<u>46</u>,47,48,49,51   [25,26(17,
        20,22,48)]

    * 17,18,20,21,23,27,28,<u>30</u>,33,34,40,<u>41</u>,<u>44</u>,45,<u>46</u>,47,48,49,51   [21(17,20,22,48)]

    * 17,18,20,22,27,28,<u>30</u>,33,34,36,40,<u>41</u>,<u>44</u>,45,<u>46</u>,47,48,49,50,51   [17,20,22,27,
        28,30,34,36,40,41,47,48,49(26)]

    * 17,19,20,22,27,28,34,36,40,<u>44</u>,<u>46</u>,47,48,49,50,51

    * 18,19,23,28,31,33,34,40,<u>44</u>,45,<u>46</u>,47,48,49,51   [31(18,24,41,44,45,46,47)]

    * 18,19,28,33,34,36,40,<u>44</u>,45,<u>46</u>,47,48,49,50,51

    * 18,23,28,33,34,36,40,<u>44</u>,45,<u>46</u>,47,48,49,50,51

    * 21,<u>25</u>,<u>26</u>(17,20,48)   [21(17,20,22,48)   25,26(17,20,22,48)]

    * 22,23,28,33,40,48,50,51

---

2   *⑦⑨,10,⑪   [10(1)]

    * 10,⑬,⑭(15,20)   [10(17)]

    * 15,17,18,19,20,21,23,24,<u>25</u>,<u>26</u>,27,28,<u>30</u>,31,33,34,40,<u>41</u>,<u>44</u>,45,<u>46</u>,47,48,49,
        51   [21,25,26(17,20,22,48)]

    * 17,18,19,20,22,24,<u>25</u>,<u>26</u>,27,28,<u>30</u>,33,34,36,40,<u>41</u>,<u>44</u>,45,<u>46</u>,47,48,49,50,51

    * 17,18,20,21,22,23,27,28,<u>30</u>,33,34,36,40,<u>41</u>,<u>44</u>,45,<u>46</u>,47,48,49,50,51

    * 18,19,23,28,31,33,34,36,40,<u>44</u>,45,<u>46</u>,47,48,49,50,51

---

1   ④(18,20,23,41,45,47,49,50)

    *⑥,7,9,10,11,⑫,13,14(15,20,30,31,41)   [10,13,14(15,17,20,27,28,33,34,36,
        40,44,45,46,47,50)]

    7,9,10,11(18)

    * <u>15,17,18,19,20,21,22,23,24,25,26,27,28,30,31,33,34,36,40,41,44,45,46,47,</u>
        <u>48,49,50,51</u>

Table 9 -- Combinations of species selected from those generated by the combinatorial method from 40 species and the 10, 3, and 1 character states at the fourth, fifth and sixth character state tree layers respectively (see text for selection procedures, and see heading of Table 6 for an explanation of the punctuation system used).

SHARED STATES	SELECTED COMBINATIONS
FOURTH LAYER	
3	23
	30
	33
2	* 18,24,51
	20
	21
	22
	* 23,33,44
	28
	* 30,41
	31
	* 33,45
	36
	48
	49
1	* 1,18,24,31,48,51
	* 4,49
	* 10,28
	* 18,19,23,24,25,33,44,45,46,50,51
	* 20,22,36,47,48(30)
	* 21,22(23)
	* 21,30,33,41,45
	* 23,33,36,44,49
	* 27,28,30,31,41

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Table 9 -- continued

FIFTH LAYER

2   * ㊵,㊿,�51

1   ⑳

     * ㉘,40,50,51

     * ㉝,㉞,㊱,40,㊹,㊼,㊽,㊾,50,51

SIXTH LAYER

1   * ⑰,⑳,㉑,㉒,㉓,㊺,㊻

Table 2 -- One hundred fifty-three characters categorized according to their nature (qualitative or quantitative) and location on the snake.