PRINCIPLES AND METHODS

OF

PHYLOGENETIC SYSTEMATICS:

A CLADISTICS WORKBOOK

DANIEL R. BROOKS
JANINE N. CAIRA
THOMAS R. PLATT
MARY R. PRITCHARD

THE UNIVERSITY OF KANSAS
MUSEUM OF NATURAL HISTORY

PRINCIPLES AND METHODS OF PHYLOGENETIC SYSTEMATICS:

A CLADISTICS WORKBOOK

By

Daniel R. Brooks
Department of Zoology
University of British Columbia
2075 Wesbrook Mall
Vancouver, British Columbia V6T 2A9
Canada

Janine N. Caira
School of Life Sciences and
Harold W. Manter Laboratory
Division of Parasitology
University of Nebraska State Museum
University of Nebraska
Lincoln, Nebraska 68488 USA

Thomas R. Platt
Department of Biology
University of Richmond
Richmond, Virginia 23173 USA

Mary H. Pritchard
Harold W. Manter Laboratory
Division of Parasitology
University of Nebraska State Museum
University of Nebraska
Lincoln, Nebraska 68488 USA

PREFACE

This booklet is designed as a practical introduction to the principles and methods of CLADISTIC ANALYSIS. Cladistics has emerged as a powerful analytical tool in comparative Biology. Developed by Hennig (1966) as an aid to reconstructing PHYLOGENIES and subsequently refined by recent workers (see Pertinent Literature), cladistics provides the most informative summation of any set of biological observations. The results are displayed in a consistent, testable and reproducible framework. Use of the techniques by systematists and extension of the principles to other comparative areas of Biology has been hampered by the lack of an easily-understood account of the procedures involved. This workbook represents an attempt to acquaint interested biologists with the mechanics of non-quantitative and quantitative approaches in cladistics, provide a representative sampling of literature concerning the principles and techniques, and supply a summary of the main principles involved. It was first compiled as a teaching aid for a workshop on cladistic methods sponsored by the American Society of Parasitologists. Thus, the hypothetical taxa have been deemed parasites, but the methods and principles are generally applicable.

There are five main sections in this workbook. The first section contains an essay delimiting the goals and principles of cladistic analysis. The second section contains a simple example demonstrating the use of cladistics in examining the relationships among three natural taxa: a California Quail, a Ruffed Grouse, and a Sharp-Tailed Grouse. The next section deals with the actual mechanics of cladistics, it comprises a) descriptions and explanations of CHARACTERS for eight hypothetical taxa, seven to be classified and one to serve as the OUT-GROUP, b) a step-by-step cladistic analysis of the taxa using a non-quantitative technique and c) a step-by-step quantitative analysis using the Wagner algorithm developed by Dr. James S. Farris, State University of New York, Stony Brook. Section four contains a glossary of the terms capitalized in this workbook. And finally, we have included a representative list of recent literature concerning cladistics, including a summary of all pertinent literature published in Systematic Zoology from 1959 to 1981. For a more in-depth study, we recommend Phylogenetics- The Theory and Practice of Phylogenetic Systematics by E.O. Wiley (see literature section).

CONTENTS

PART 1:   CLADISTICS- A BRIEF REVIEW*

This essay will be an attempt to present a brief review of the assumptions of phylogenetic systematics, and examine the construction of classifications based on cladistic analyses. There is little original information in this presentation. I have relied heavily on material published in <u>Systematic Zoology</u> during the past decade, and particularly the work of Dr. E. O. Wiley of the University of Kansas. Errors of interpretation, however, rest soley with me.

The past decade has seen a revolution in Biological Systematics. This is generally regarded as a highly conservative discipline, hardly fraught with controversy (at least regarding methodology) since the publication of Darwin's (1859) <u>Origin of the Species</u>, some 120 years ago. The publication of the <u>Origin</u> represented a major shift in systematic thought, from the cataloguing of the plan of the Creator to the realization that all life is related on the basis of genealogical descent from a common ancestor.

The philosopher-historian Thomas Kuhn, in his book <u>The Structure of Scientific Revolutions</u>, established four criteria for detecting revolutions in science, which are outlined below:

1. An accumulation of observations that cannot be explained on the basis of existing theories or paradigms.
2. Expression of discontent by individuals working in the area.
3. A proliferation of competing hypotheses.
4. A recourse to philosophical examinations of the fundamental nature of the discipline.

These are all symptoms of a transition from what Kuhn termed "normal" to "extrodinary" research. A brief review of the papers included in the bibliography of this volume will

---

provide ample evidence to support the existence of a revolution in systematics. The transition was prompted, in my opinion, by a perceived lack of objectivity in systematics. Descriptions of the discipline as a combination of "art and science" by such luminaries as G.G. Simpson and E. Mayr have led to the desire for a more objective approach to systematics and the establishment of an objective science of comparative biology. The revolution has encompassed several competing approaches to systematics. It is not, however, my intention to review them here. The remainder of this presentation will be devoted to phylogenetic systematics, or cladistics.

The assumptions of phylogenetic systematics, as outlined by Wiley (1975) are as follows:

1. Evolution occurs.
2. There exists a single phylogeny of life and it is the result of genealogical descent.
3. Characters are passed from generation to generation, modified or unmodified, during genealogical descent.

The emphasis encompassed by these assumptions is clearly on genealogical descent. This is considered the only necessary and sufficient criterion for the establishment of a natural taxon. Genealogical relationships, however, cannot be observed. They must be inferred. Characters (morphological, biochemical, behavioral, etc.) can be observed and can be used to infer genealogical relationships.

Characters can be divided into two categories: 1) those that infer genealogical relationships, i.e., homologies; and 2) those that do not infer genealogical relationships, i.e., non-homologies (convergences and parallelisms). Bridge principles, in the sense of Hempel (1965), are required in order to use observable characters to infer genealogical relationships. The following bridge principles were proposed by Wiley (1979):

1. The hypothesized ..... set characters of a proposed taxon may be used as justification for the naturalness of that taxon if it is also hypothesized that these characters indicate that the members of the taxon are genealogically more closely related to each other than to any other organism outside the taxon.

2. The hypothesized .... set characters of a hypothesized natural taxon may be present only in certain stages of ontogeny or modified during subsequent evolution in members of subsets of the taxon.

Therefore, characters hypothesized to be homologous are sufficient to infer a natural taxon.

In a phylogenetic system, all taxa must be monophyletic. Monophyly, as defined by Hennig (1966), indicates that all members of a taxon are descended from a single stem species, which includes all members of the stem. In the figure below, taxa A, B and C are contained in taxon X and constitute a monophyletic group (on the left). In the figure on the right, taxa A and B are contained in taxon X, while C is placed in Y. As all descendents of the stem (Q) are not contained in a single taxon, both groups are paraphyletic and do not constitute natural taxa.
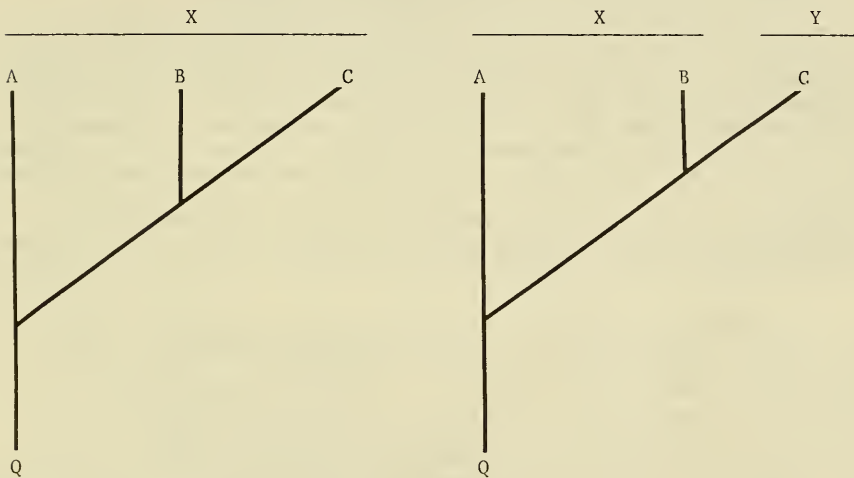
Only monophyletic taxa are considered natural and the goal of phylogenetic systematics is the identification of such taxa.

Two types of homologies are recognized in cladistic analysis. Plesiomorphies are the general or more primitive state of a character. The subsequent modification of the plesiomorphic state is regarded as derived and termed apomorphic. An apomorphic character shared by two or more taxa is termed a synapomorphy. Monophyletic taxa can only

be identified on the basis of synapomorphies, which are
assumed to have been inherited from a most recent common
ancestor.

Hennig (1966) proposed four methods for analyzing the
direction of change in a series of homologous characters,
termed a transformation series. These are outlined below:

    1. Holomorphological analysis via out-group comparison.
    2. Ontogenetic analysis.
    3. Geological precedence.
    4. Chorological (biogeographic) analysis.

Out-group comparison consists of comparing character states
in members of a proposed monophyletic taxon with species not
included in that taxon. Ideally, the comparison is made with
the sister-group, if known. However, all species not included
in the proposed taxon comprise the out-group. A character-
state present in the proposed monophyletic taxon that is not
present in the out-group is considered derived or apomorphic.
A character-state that is present in both the proposed mono-
phyletic taxon and the out-group is considered plesiomorphic.
For example, in the hypothetical taxa used in Part 3 of this
manual, all the organisms under consideration possess anchoring
devices. A comparison with the out-group, represented by X,
reveals that the out-group lacks anchors. Therefore, the
presence of these structures is considered apomorphic at the
level of the group in question.

Ontogenetic analysis is based on the Biogenetic Law of
von Baer. More general characters appear earlier in ontogeny
than more specialized characters (see Nelson, 1978, for a
detailed review of this topic). Geological precedence states
that characters found in organisms in older fossil strata are
plesiomorphic compared to those found in more recent strata.
The chorological method involves the implied progression of
organisms in space as a criterion for determining the direction
of evolution. The latter two methods are not widely accepted
at the present time.

Once character analysis is complete, a data matrix is
constructed. The constructions and evaluation of data
matrices will be   thoroughly discussed in Part 3 of
this manual and will not be dealt with further at this time.
The resulting cladogram (e.g., see figure opposite Step 13
in part 2) is an unambiguous hypothesis of the relationships
of the members of a monophyletic taxon. This hypothesis
can be tested by the discovery of new members hypothesized
to belong to that taxon and/or the identification of new
characters. This rigorous testing of phylogenetic hypotheses
is a primary function of the hypothetico-deductive method.

In many cases more than one possible hypothesis may be produced. In situations where more than one cladogram results (see the figure opposite step 8 in part 2) the most parsimonious set of relationships (i.e., requiring the fewest convergences) is chosen.

The methods that have been described to this point result in the relative ranking of taxa. Note that the branch angles and branch lengths of the cladograms in Part 3 do not impart subjective information regarding the degree of divergence or "adaptiogenesis" of the taxa.

Classification is the process of assigning absolute rank to monophyletic groups inferred from the cladogram. A requirement of phylogenetic systematics is that all taxa are monophyletic and that there is direct correspondence between the cladogram and the classification derived from it. The result is a classification that consists of monophyletic taxa based on genealogical relationships. Anagenesis or adaptiogenesis of evolutionary systematics are considered subjective and result in paraphyletic taxa (grades) rather than monophyletic taxa (clades) and are not considered. Such decisions are based on opinion or authoritarianism, not objective criteria.

Absolute ranking in a phylogenetic system was originally based on the time of origin of the group. Hennig (1966) proposed the following time scale for the establishment of supraspecific taxa:

Geological Age	Category
Pre-Cambrian	Phylum or Sub-Phylum
Cambrian-Devonian	Class
Carboniferous	Order
Triassic-Early Cretaceous	Family
Late Cretaceous-Oligocene	Tribe
Miocene	Genus

The timing of geological events, the chorological method, can also be used to determine the minimum age for monophyletic taxa. Absolute ranking is considered by many individuals to be the weakest part of Hennig's theory. It does, however, have the advantage of separating the ranking process from attempts to determine the degree of divergence which, as mentioned earlier, is a subjective process.

Wiley (1979) has set forth a formal framework for the presentation of phylogenetic classifications utilizing the

Linnaean Hierarchy. He formalized the following criteria:

    1. Taxa classified without restriction are mono-
        phyletic groups (sensu Hennig, 1966).
    2. The relationships of sister-taxa within the
        classification must be expressed exactly.

Cladistic classifications have often been criticized as
being too complex to be useful as a general reference system
in biology. Wiley (1979) has proposed a series of conventions
to be applied to the Linnaean System aimed at economy in
classification, integration of fossil and recent classifi-
cations and the expression of reticulate evolution in a
phylogenetic system. I will discuss only those conventions
that directly affect the classification of parasitic organisms.

The first convention states that, "The Linnaean Hierarchy
will be used, with certain other conventions, to classify
organisms." The second convention advocates the use of mini-
mum-length classifications. Only the five mandatory cate-
gories (genus, family, order, class and phylum) may be re-
dundant. In addition, where possible and when consistent
with phylogenetic relationships, taxa of "essential impor-
tance" will be retained at the traditional rank.

The third convention, the sequencing convention, is a
powerful tool in reducing the number of redundant categories
and names of taxa. This convention permits the placement
of taxa forming an asymmetrical part of a cladogram at the
same categorical rank and sequenced in the classification
in order of origin. In the example on the facing page, the
cladogram illustrates the relationships between taxa A-E.
Taxa C-E form an asymmetrical branch of the cladogram. The
non-sequenced classification includes two additional taxa
(Taxon C and D+E), erected to contain C-E and retain the
sister-group relationships demonstrated in the cladogram.
The sequenced classification eliminates two category names
and the arrangement of C, D and E, in order of their
branching pattern represents a minimum classification,
while retaining the sister-group relationships.
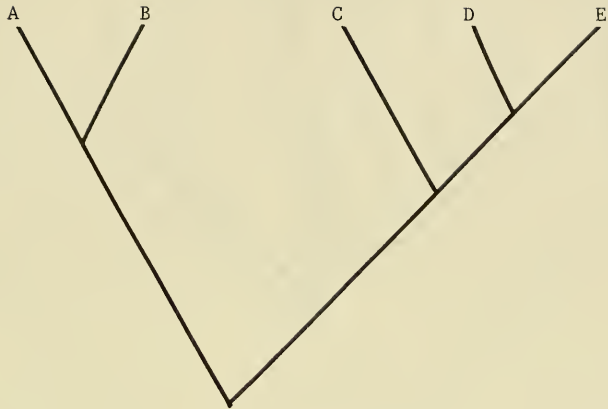
| NOT SEQUENCED	SEQUENCED
TAXON A+B+C+D+E	TAXON A+B+C+D+E
TAXON A+B	TAXON A+B
A	A
B	B
TAXON C+D+E	TAXON C+D+E
TAXON C	C
C	D
TAXON D+E	E
D	
E	

The fourth convention is the use of the term *sedis mutablis* (L. - of changeable position) (Wiley, 1979). This term is used in classifying trichotomous or poly-otomous relationships within monophyletic group. In the example below taxon A+B+C has been erected to accomodate taxa A, B and C. Using this convention

```
      A                    B                    C
```
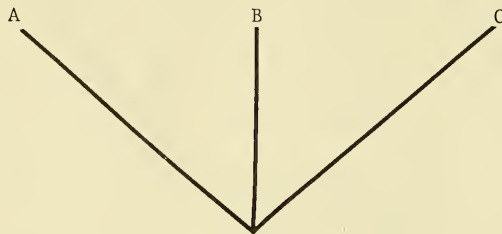
TAXON A+B+C

A

B

C

each is given equivalent rank and identified as *sedis mutablis*, clearly acknowledging the unresolved nature of the relationship.

The remaining conventions proposed by Wiley (1979) fall into three categories: 1) the placement of mono-phyletic as well as para- and polyphyletic groups of uncertain origin in phylogenetic classifications, 2) the integration of fossil and recent classifications and, 3) the classification of reticulate evolution. Although these conventions will undoubtedly prove useful in con-structing parasite classifications, their general use-fulness at the present time is limited and they will not be discussed further.

I have chosen an analysis of the cestode order Proteocephalata proposed by Brooks (1978) as an example of a parasite classification using the conventions described above. Rather than presenting the complete cladogram for discussion, I will concentrate on the superfamily Monticelloidea (see the facing page).
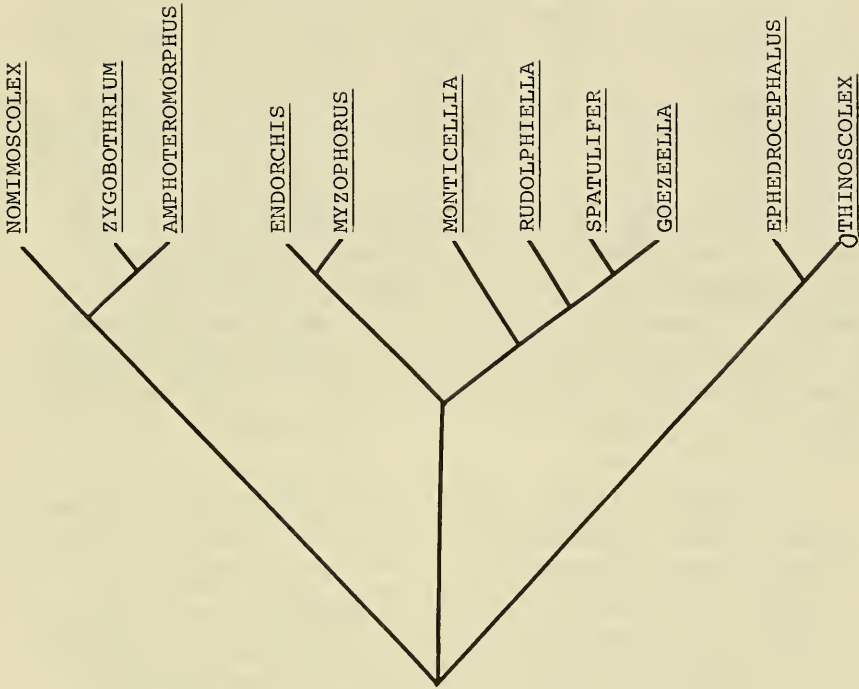
```
SUPERFAMILY MONTICELLOIDEA
   FAMILY ZYGOBOTHRIIDAE S.M.
            NOMIMOSCOLEX
            ZYGOBOTHRIUM
            AMPHOTEROMORPHUS
   FAMILY MONTICELLIDAE S.M.
      SUBFAMILY ENDORCHIINAE
            ENDORCHIS
            MYZOPHORUS
      SUBFAMILY MONTICELLINAE
            MONTICELLIA
            RUDOLPHIELLA
            SPATULIFER
            GOEZEELLA
   FAMILY EPHEDROCEPHALIDAE S.M.
            EPHEDROCEPHALUS
            THINOSCOLEX
```

The superfamily consists of an unresolved trichotomy. The branches are designated as the families Zygobotriidae, Monticellidae and Ephedrocephalidae, respectively. As the sister-group relationships of these families are not known, these taxa are designated as *sedis mutablis* in the accompanying classification. Note that when the sister-group relationships are established for these families, the sequencing convention will permit the retention of familial status, hence adding to nomenclatural stability and accuracy.

The family Monticellidae (middle branch) is composed of two subfamilies, Endorchiinae and Monticellinae. The Monticellinae is composed of four taxa: Monticellia, Rudolphiella, Spatulifer and Goezeella. The use of the sequencing convention permits these taxa to be given the same rank (genus) and they are listed in the classification in order of the branching sequence, an exact representation of the sister-group relationships expressed in the cladogram. There is also an economy of names. Use of the sequencing convention eliminates five supra-generic taxa at two category levels.

A comparison of the complete classification of the Proteocephalata, modified from Brooks (1978), with the previous classification of Freze (1965) is presented on the facing page. The purpose of making this comparison is to demonstrate that the cladistic classification is no more complex than the previous classification, prepared using what are deemed "conventional" methods. It should be noted that Brooks' classification requires one less supra-generic category than that of Freze, while accurately representing the sister-group relationships proposed by cladistic analysis.

A cladistic classification should be minimally re-dundant, minimally novel (although this is not the case in the example cited) and maximally informative (Farris, 1976 and Wiley, 1979). A classification constructed using the tenets of phylogenetic systematics, using the conventions of Wiley (1979) ably fulfills these criteria. Therefore, a classification based on cladistic principles is considered the best general reference system for systematic biology.

In closing I wish to make a personal observation regarding the status of systematics in Parasitology. Although new taxa are constantly being described in the literature, there appears to be little impetus, particularly in North America, to deal with major problems of phylogeny recon-struction and classification of parasitic taxa. The "CIH Keys to the Nematode Parasites of Vertebrates" are a notable

ORDER PROTEOCEPHALATA

FREZE, 1965	BROOKS, 1978

SUPERFAMILY PROTEOCEPHALOIDEA
  FAMILY PROTEOCEPHALIDAE
    SUBFAMILY PROTEOCEPHALINAE
    SUBFAMILY CORALLOBOTHRIINAE
    SUBFAMILY PARAPROTEOCEPHALINAE
    SUBFAMILY GANGESIINAE
    SUBFAMILY SANDONELLINAE
    SUBFAMILY ZYGOBOTHRIINAE
  FAMILY OPHIOTAENIIDAE
    SUBFAMILY OPHIOTAENIIDAE
    SUBFAMILY ACANTHOTAENIINAE
SUPERFAMILY MONTICELLOIDEA
  FAMILY MONTICELLIDAE
    SUBFAMILY MONTICELLINAE
    SUBFAMILY RUDOLPHIELLINAE
    SUBFAMILY MARSIPOCEPHALINAE
    SUBFAMILY ENDORCHIINAE
    SUBFAMILY EPHEDROCEPHALINAE
    SUBFAMILY ORTHINOSCOLICINAE

SUPERFAMILY PROTEOCEPHALOIDEA
  FAMILY PROTEOCEPHALIDAE S.M.*
    SUBFAMILY PROTEOCEPHALINAE S.M.
    SUBFAMILY ACANTHOTAENINAE S.M.
     TRIBE ACANTHOTAENINI
     TRIBE GANGESINI
    SUBFAMILY CREPIDOBOTHRINAE S.M.
  FAMILY CORALLOBOTHRIIDAE S.M.
    SUBFAMILY CORALLOBOTHRIINAE S.M.
    SUBFAMILY MARSIPOCEPHALINAE S.M.
    SUBFAMILY CORALLOTIINAE S.M.
  FAMILY SANDONELLIDAE S.M.
SUPERFAMILY MONTICELLOIDEA
  FAMILY MONTICELLIDAE S.M.
    SUBFAMILY ENDORCHIINAE
    SUBFAMILY MONTICELLINAE
  FAMILY ZYGOBOTHRIIDAE S.M.
  FAMILY EPHEDROCEPHALIDAE S.M.

---

* Sedis Mutablis

exception in terms of revised classifications, yet they give little or no indication of the evolutionary relation- ships of these organisms, and in all fairness they were not intended to serve this purpose. Dr. Franklin Sogandares- Bernal (1980) noted that a comparison of the years 1960 and 1980 revealed a 45% reduction in papers presented at the annual meeting by individuals trained primarily in systematics. He suggested that economic concerns (i.e., inability to find jobs, lack of funding for research, etc.) may have played a primary role in this decline. The final two sentences of his editorial accurately convey his concern, "Some measure of encouragement should be extended to those members in the esoteric disciplines lest one day we wake up and no one is left to train students, identify parasites, or interpret the phylogeny of the different taxa. We would be the poorer for it, and it would reflect in an inferior manner upon our sense of values as scholars." While economic concerns may be a part of the problem, the lack of a rigorous method in systematics may have taken its toll as well. The advent of a more objective approach to the discipline may encourage a resurgence in systematics, which lies at the heart of an understanding of Parasitology.

LITERATURE CITED

Anderson, R.C., A.G. Chabaud and S. Wilmott (eds.). 1974—. CIH Keys to the Nematode Parasites of Vertebrates. Nos. 1— . Commonwealth Agricultural Bureaux, England.

Brooks, D.R. 1978. Evolutionary history of the cestode order Proteocephalata. Syst. Zool. 27: 312-323.

Darwin, C. 1859. On the Origin of Species. First ed. London.

Farris, J.S. 1976. Phylogenetic classification of fossils with Recent groups. Syst. Zool. 25: 271-282.

Freze, V.I. 1965. Proteocephalata in fish, amphibians, and reptiles. In: Skrjabin, K.I. (ed.), Essentials of cestodology, Vol. 5, 597 pp. (ISPT English translation.)

Hempel, C.G. 1965. Aspects of scientific explanation. The Free Press. New York.

Hennig, W. 1966. Phylogenetic systematics. University of Illinois Press. Urbana, Illinois. 263 pp.

Kuhn, T.S. 1970. The structure of scientific revolutions. 2nd ed. University of Chicago Press. Chicago. 210 pp.

LITERATURE CITED, continued

Nelson, G. 1978. Ontogeny, phylogeny and the biogenetic
    law. Syst. Zool. 324-345.

Sogandares-Bernal, F. 1980. The changing face of the
    society. ASP Newsletter 2: 11-12.

Wiley, E.O. 1975. Karl R. Popper, systematics and classi-
    fication: a reply to Walter Bock and other evolution-
    ary taxonomists. Syst. Zool. 24: 233-242.

_____. 1979. An annotated Linnaean Hierarchy, with comments
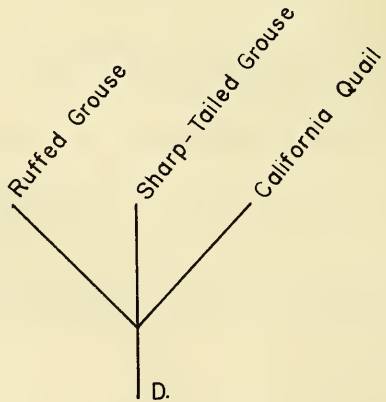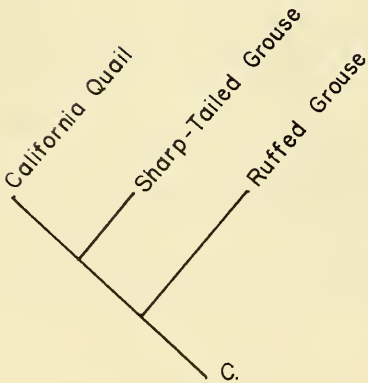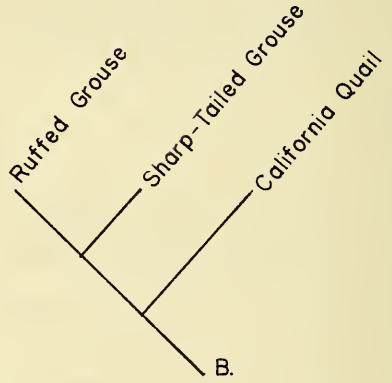   on natural taxa and competing systems. Syst. Zool. 27:
    308-337.

14
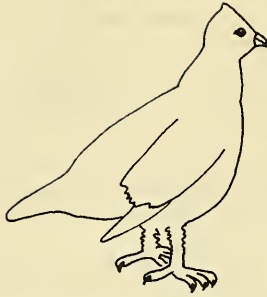
Ruffed Grouse   Sharp-Tailed Grouse   California Quail
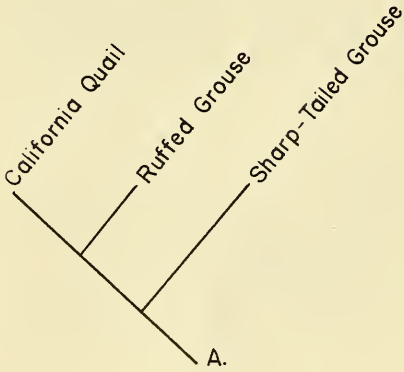
PART 2: A SIMPLE PRACTICAL EXAMPLE

In this section we shall demonstrate the use of cladistics in determining the phylogenetic relationships among three real TAXA. Consider the following organisms: a Ruffed Grouse, a Sharp-Tailed Grouse and a California Quail which are illustrated at the top of the facing page. Only four patterns of phylogenetic relationship are possible among any three taxa. These are diagrammed on the bottom of the opposite page for the above three taxa. Cladistic analysis is a method of PARSIMONY analysis which allows us to determine which one of these four hypotheses of phylogeny is most consistent with the pattern of character states exhibited by the taxa.

In order to perform the cladistic analysis we shall examine the taxa for any characters that are exhibited among them in more than one STATE. The obvious characters in this case are : (1) Head Plumage: present or absent; (2) Leg Feathering: present or absent; (3) Wing Shape: pointed wings or not; and (4) Tail Shape: fan-shaped or not. Additional characters (skeletal, anatomical, biochemical, etc.) might also be considered, but for the sake of simplicity in this example, we will restrict our analysis to the four morphological characters listed above.

Our next concern is with the POLARIZATION of these characters; in other words, we wish to determine which state of each character is PLESIOMORPHIC. In order to do this we require an out-group. Ideally the out-group should be the SISTER GROUP of the taxa being examined; but, as the actual sister group of the taxa may not be known at the time of analysis, the choice of an out-group should at least satisfy two main criteria. First, the taxa of the out-group should be close enough in relation to the study taxa to allow a comparison of the characters. Second, the taxa of the out-group should be a MONOPHYLETIC LINEAGE outside of the study taxa. In our example, then, the choice of a Prairie Lizard as the out-group would be inappropriate as this organism possesses no feathers or wings and consequently would not allow us to determine which state of each of our four characters is plesiomorphic. The Prairie Lizard, although outside of our group of study taxa, is too distant a relative to be useful. A more appropriate out-group for our study taxa would be some type of bird. Caution should be exercised, however, as some birds such as the Spruce Grouse would also be inappropriate. This taxon is very similar to our study taxa, and may in fact be a member of the monophyletic lineage under investigation. Polarization of the characters with the Spruce Grouse in this case would be a form of IN-GROUP COMPARISON and could lead to incorrect polarization of the characters. In our example a White Pelican will serve well as an out-group.

White Pelican

California Quail

Sharp-Tailed Grouse

Ruffed Grouse

Head Plume

Pointed Tail

Feathers on Legs

Fan-shaped Tail
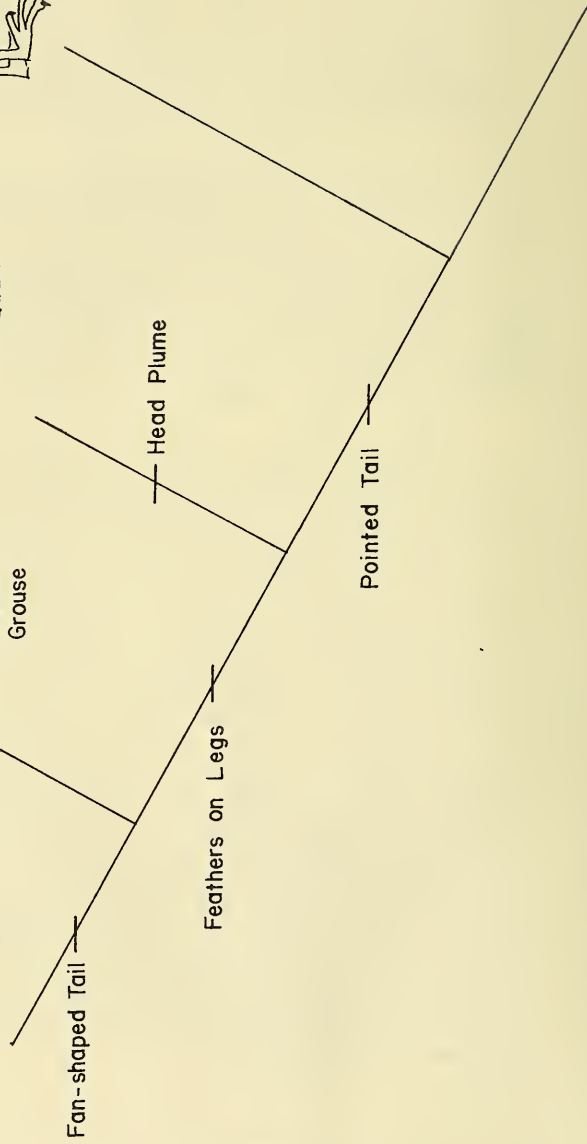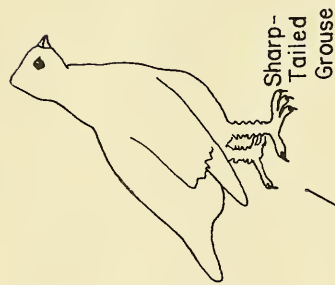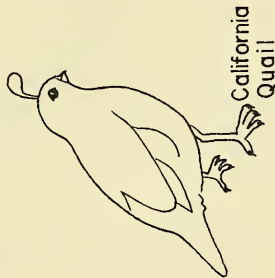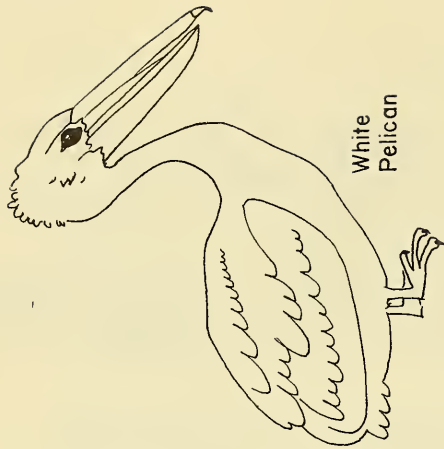
The plesiomorphic state of each character is that state exhibited by the White Pelican. Thus, for the character Head Plumage, absence of a head plume is the plesiomorphic state. Consequently the alternate state, presence of head plume, is the APOMORPHIC state. It follows then, that the plesiomorphic state for each of the characters Leg Feathering, Wing Shape, and Tail Shape are: leg feathers absent, wings not pointed, and tail not fan-shaped respectively. The apomorphic states for these characters would thus be: feathers present on feet, wings pointed, and tail fan-shaped.

Now that the characters are polarized we are ready to perform either the non-quantitative or the quantitative method of cladistic analysis. As sections three and four of this workbook deal with the mechanics of each of these procedures in detail, we will not elaborate on them here. However, the CLADOGRAM produced from analysis of our taxa with either method is given on the facing page. Note that this cladogram is identical to our second hypothesis of phylogeny for our taxa (B). From our analysis then, it appears that the Sharp-Tailed Grouse and the Ruffed Grouse are more closely related to each other than they are to the California Quail.

PART 3:   THE MECHANICS OF CLADISTICS

A: Taxa and Characters

The eight hypothetical taxa which we will examine and attempt to produce a cladogram for are shown on the next page. The seven taxa to be classified are numbered 1-7. Taxon "X" will serve as the out-group, or member of a closely related group which will aid in polarizing the characteristics used in the analysis.

We will use 12 characters to classify these taxa. On the four pages following the next page, each character has been listed and the various attributes exhibited by each taxon for each character have been illustrated. Compare these depictions with the taxa shown on the next page to gain some comfort with the notion of treating taxa as collections of observations or traits. For example, we have chosen character 1 to be anchor arm length. If you look at the taxa you will notice that all of them exhibit one of two attributes, or CHARACTER-STATES, for this character, namely, anchor arms elongate or anchor arms reduced. Become familiar with the twelve characters and their respective character-states.

You should also notice that character 1, along with characters 2-6, 11, and 12 exhibit only two different states. Such two-state characters are termed BINARY CHARACTERS. However, not all characters may occur in this form. Characters 7-10 occur in 3-5 variable forms among taxa. Such complex characters are called MULTI-STATE CHARACTERS.
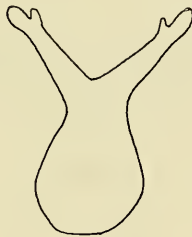
CHARACTER 1 - Anchor Arm Length
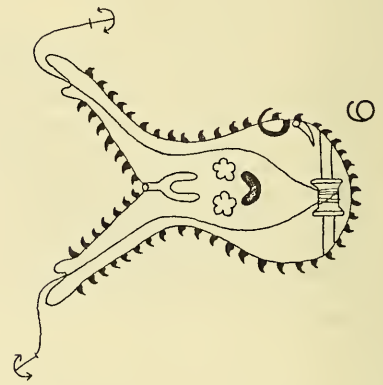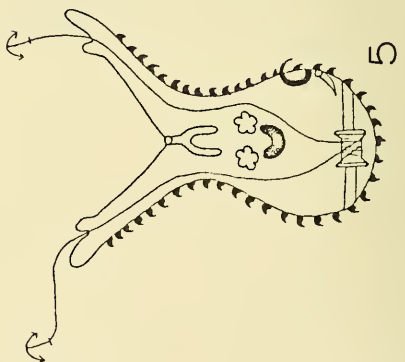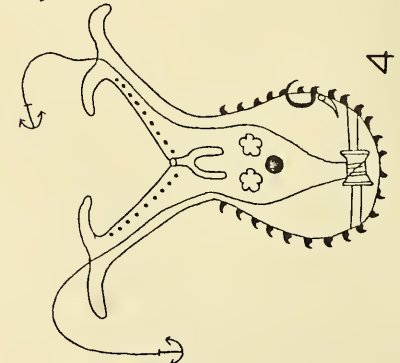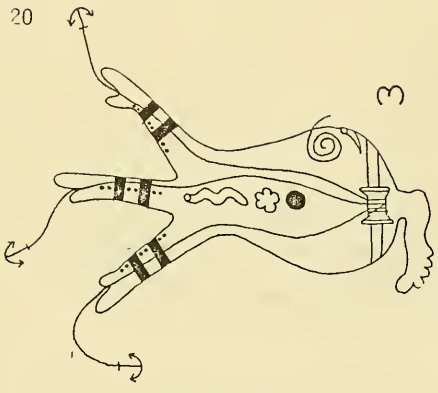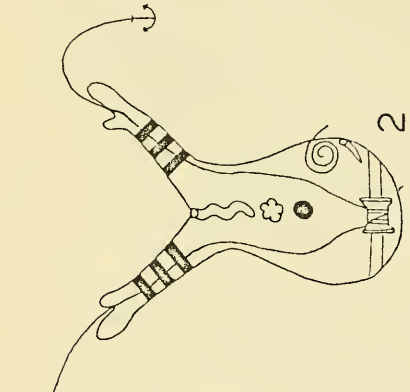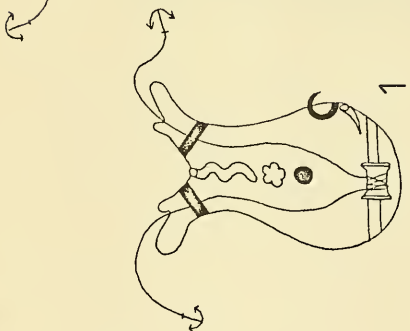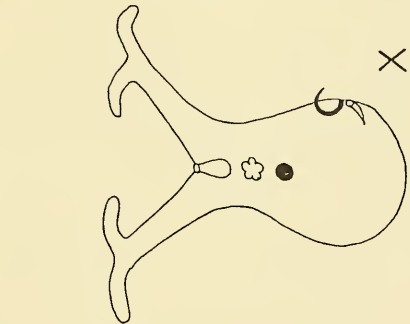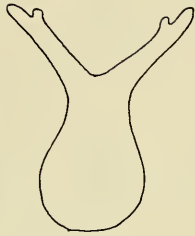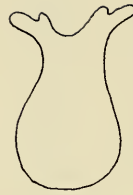
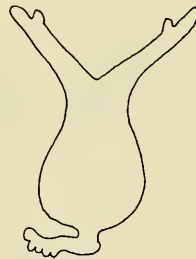Anchor Arms Long   Anchor Arms Reduced

CHARACTER 2 - Presence of Accessory 'Foot'
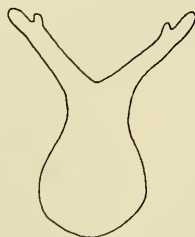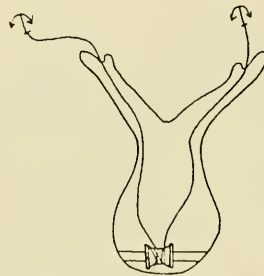

Accessory 'Foot' Absent   Accessory 'Foot' Present

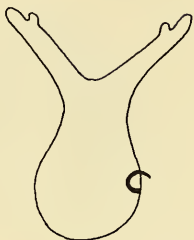# CHARACTER 3 - Presence of Anchor Spool & Anchors

Anchor Spool &   Anchor Spool &
Anchors Absent   Anchors Present

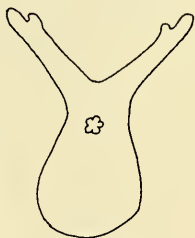CHARACTER 4 - Cirrus Shape

Cirrus Short and
Uncoiled

Cirrus Long and
Coiled

CHARACTER 5 - Ovary Number

1 Ovary
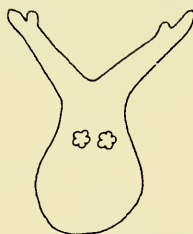
2 Ovaries

CHARACTER 6 - Testes Shape
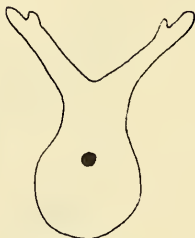
Testis Oval

Testis U-shaped

CHARACTER 7 - Spine Location
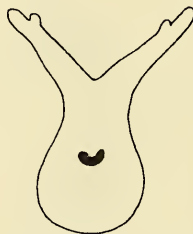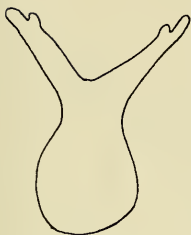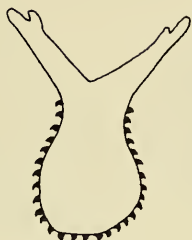
| No Spines | Spines on Body Only | Spines on Body & Lower Surface of Arms | Spines on Body & Both Surfaces of Arms | Spines on Arms Only |
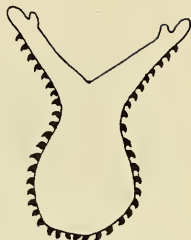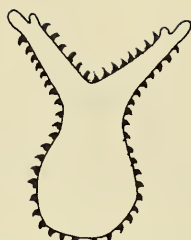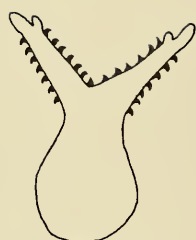
CHARACTER 8 - Stripe Number on Anchor Arms
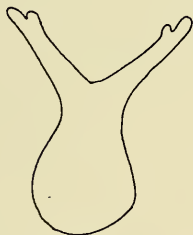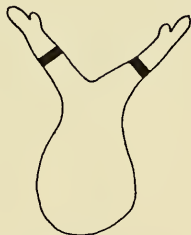
| No Stripes | 1 Stripe/Arm | 2 Stripes/Arm | 3 Stripes/Arm |
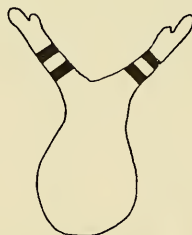
CHARACTER 9 - Anchor Arm Number
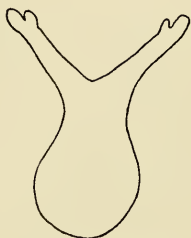
| 1 Anchor Arm | 2 Anchor Arms | 3 Anchor Arms |

CHARACTER 10 - Gut Shape
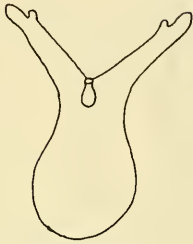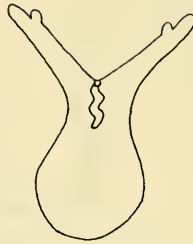
Saccate Gut   Sinuous Gut   Bifurcate Gut
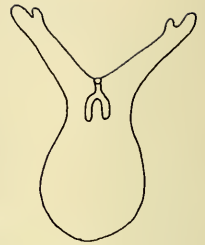
CHARACTER 11 - Spot Presence
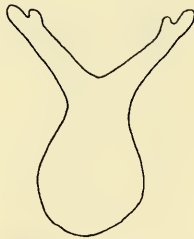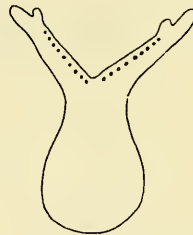
Spots Absent   Spots Present

CHARACTER 12 - Extension of Distal Portion of Anchor Arms
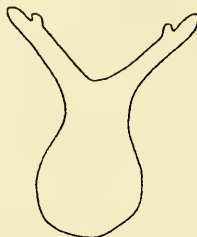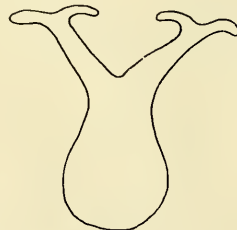
Reduced   Broadly Extended

B: Non-quantitative approach (Hennigs's Argumentation Scheme,

Step 1: Polarize all characters as much as possible using the out-group. You should be able to determine the generalized, or plesiomorphic, states for all characters. List below the taxa which exhibit the plesiomorphic trait found in the out-group for each character.

Listings of Plesiomorphic States

```
Character 1:    Long anchor arms
Character 2:    No accessory "foot"
Character 3:    No anchors or anchor spool
Character 4:    Cirrus  short and uncoiled
Character 5:    One ovary
Character 6:    Oval testes
Character 7:    No spines on body
Character 8:    No stripes on arms
Character 9:    Two anchor arms
Character 10:   Saccate gut
Character 11:   Spots absent
Character 12:   Distal portion of anchor arms broadly extended
```

Step 2: Determine all binary (two-state) transformation-
         series. You should be able to determine the
         plesiomorphic and apomorphic traits for
         characters 1-6 and 11-12. List groupings of
         taxa as determined by the apomorphic trait for
         each character.

Groupings for binary transformation-series

        Character 1: plesiomorphic taxa 2-7, "X"
                      apomorphic taxa   1
        Character 2: plesiomorphic taxa 1-2,4-7, "X"
                      apomorphic taxa   3
        Character 3: plesiomorphic taxa "X"
                      apomorphic taxa   1-7
        Character 4: plesiomorphic taxa 1, 4-7, "X"
                      apomorphic taxa   2-3
        Character 5: plesiomorphic taxa 1-3, "X"
                      apomorphic taxa   4-7
        Character 6: plesiomorphic taxa 1-4, "X"
                      apomorphic taxa   5-7
        Character 11: plesiomoprhic taxa 1-2,5-7, "X"
                      apomorphic taxa   3-4
        Character 12: plesiomorphic taxa 4, "X"
                      apomorphic taxa   1-3,5-7

Step 3: Classify all taxa based on character 3. One may begin
         with any character but for the sake of clarity we
         will add characters in a manner designed to give the
         most parsimonious solution in the fewest steps. You
         may want to experiment on your own by beginning with
         other characters and proceeding in a different sequence.

anchor spool + anchors (3)
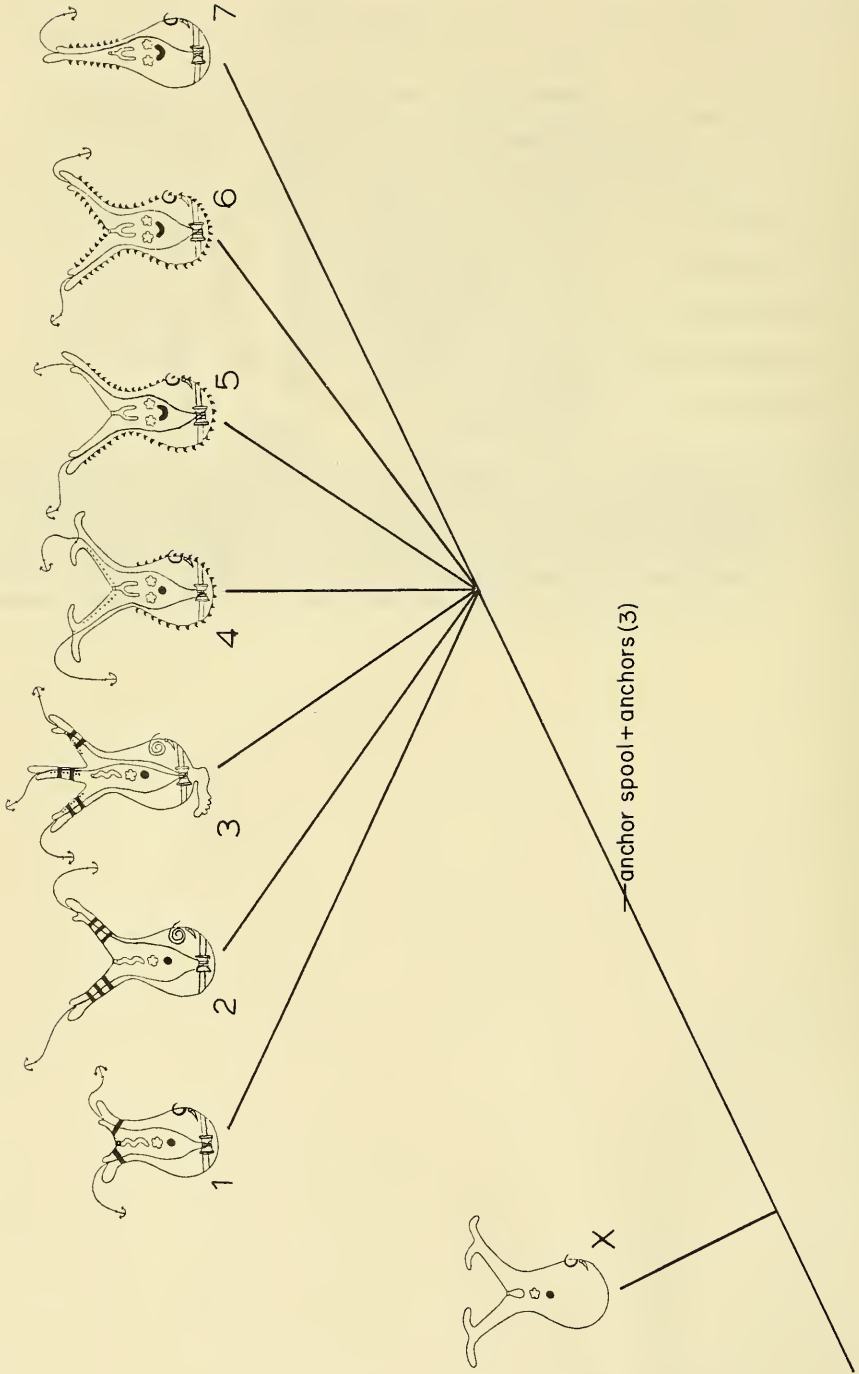
You should have a diagram which looks like the one on the facing page. Character 3 therefore, is a shared derived trait, or SYNAPOMORPHY, for taxa 1-7 with respect to the out-group, "X".

Step 4:   Add character 5 to the cladogram and produce a new cladogram. You have now distinguished three groups, or clusters. The clusters are "X", 1+2+3, and 4+5+6+7.

X

anchor spool + anchors (3)

2 ovaries (5)

1 2 3 4 5 6 7
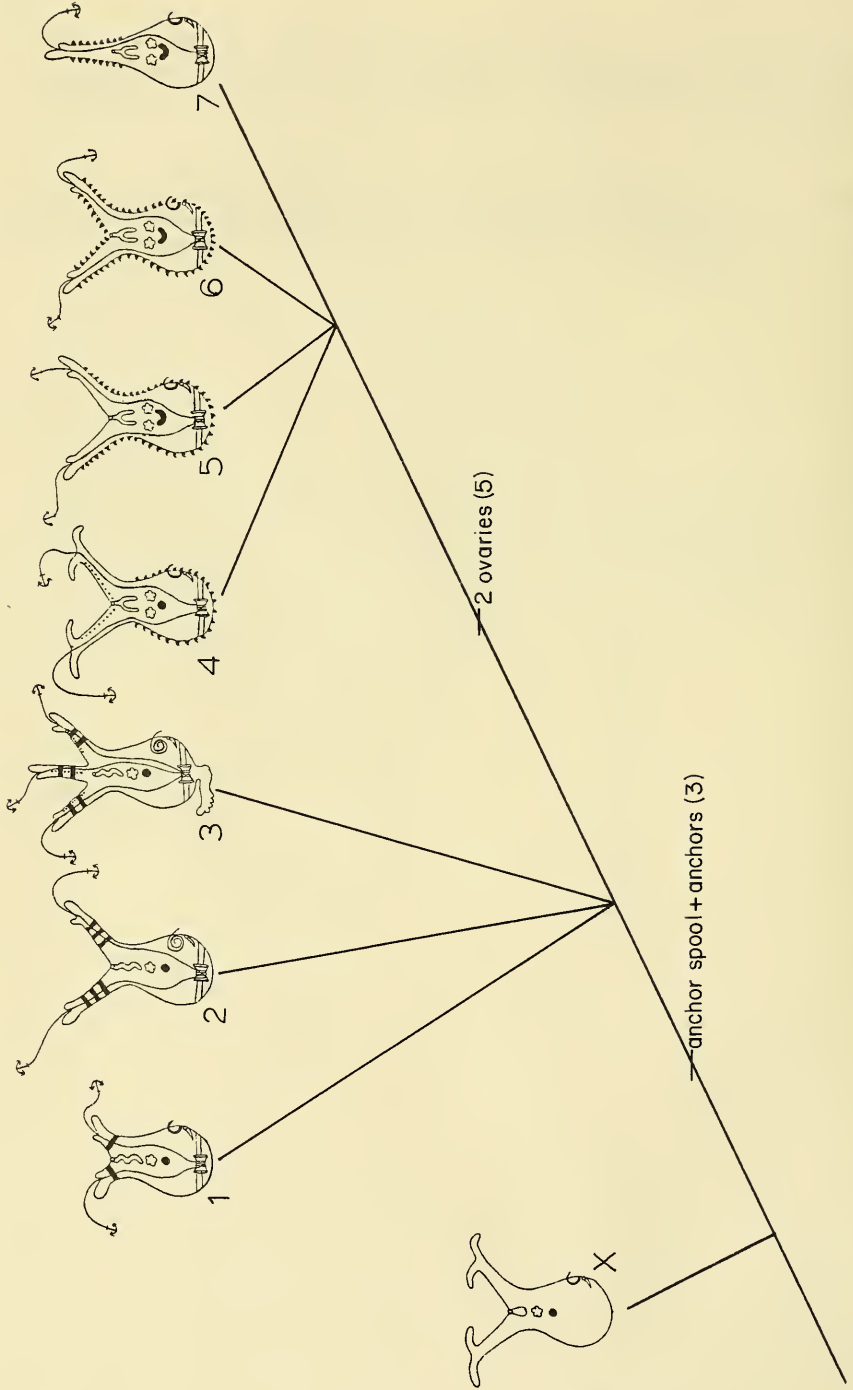
Your cladogram should look lide the one on the facing page.

Step 5: Add character 6 to the above cladogram and produce
        a new cladogram. There are now four clusters
        indicated or resolved. Only completely DICHOTOMOUS
        sequences may be termed FULLY-RESOLVED.
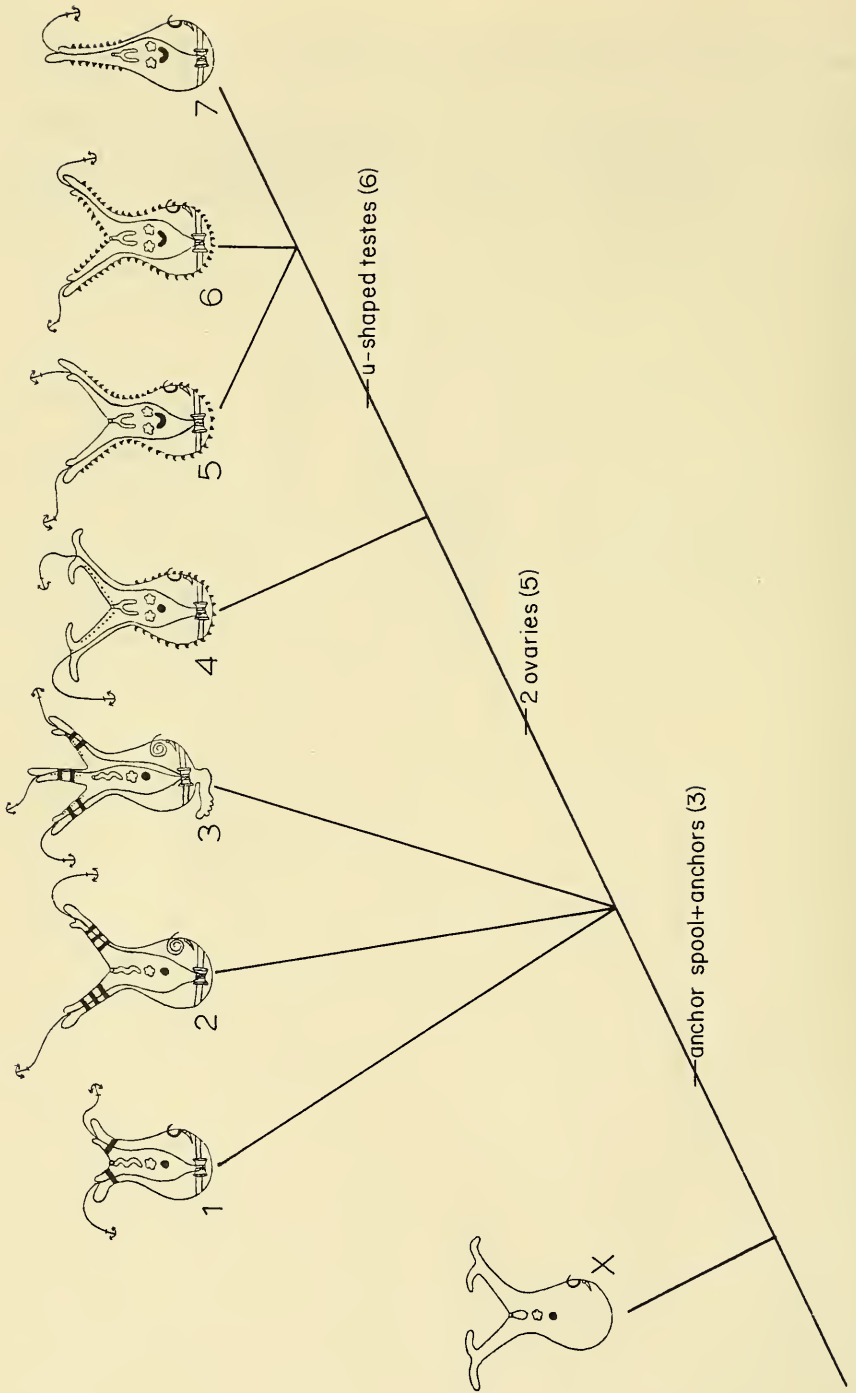
Your cladogram should look like the one on the facing page.

Step 6: Add character 4. There will now be five resolved
         clusters.

anchor spool+anchors (3)

2 ovaries (5)

cirrus long, coiled (4)

u-shaped testes (6)

1 2 3 4 5 6 7
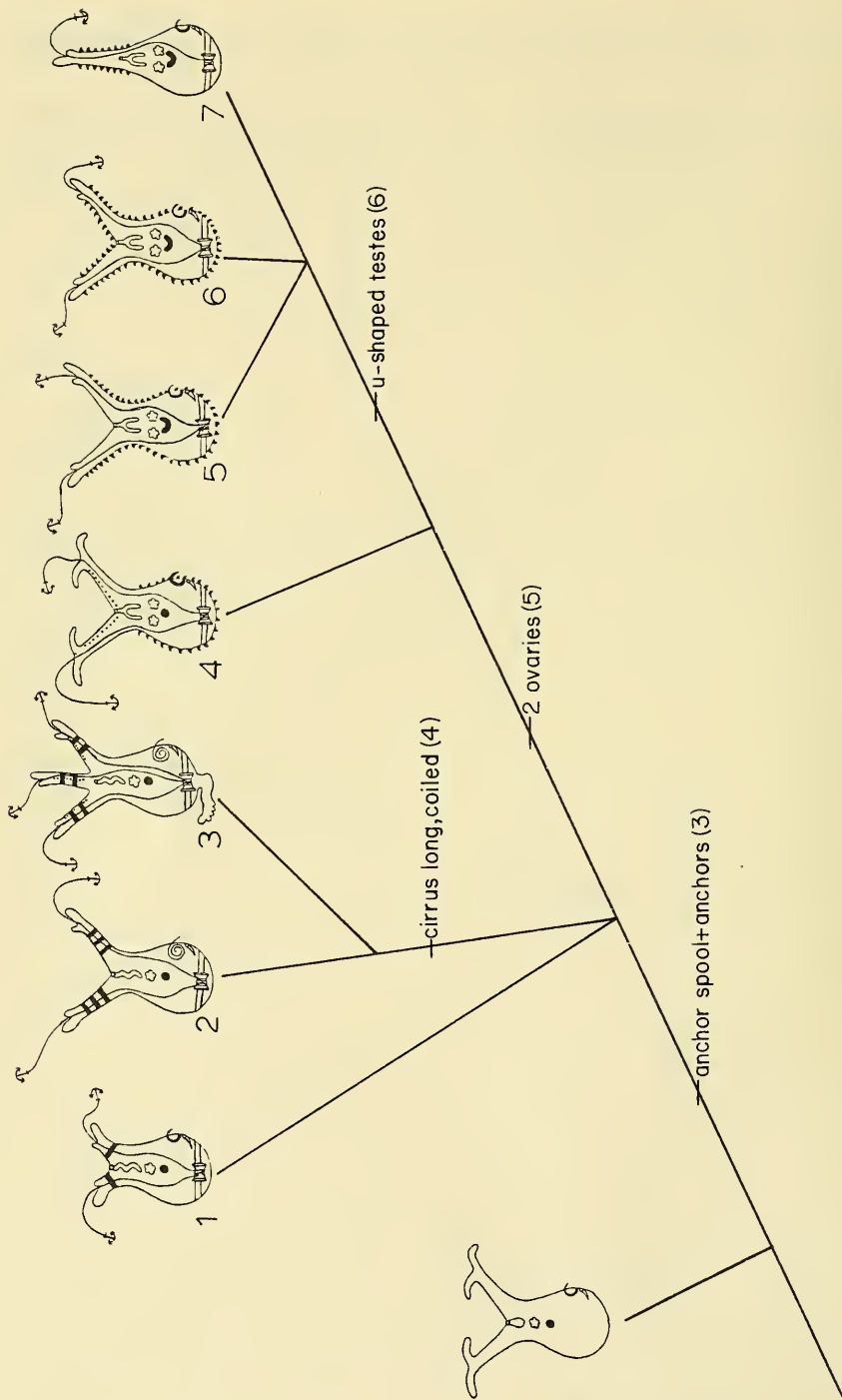
Your cladogram should look like the one on the facing page.

Step 7:   Add characters 1 and 2.   The same five clusters as
          indicated in step 6 will be resolved.   Thus,
          characters 1 and 2 agree with the previous cladogram
          and are said to be CONGRUENT with it.

short arms (1)

accessory "foot" (2)

cirrus long, coiled (4)

u-shaped testes (6)

2 ovaries (5)

anchor spool + anchors (3)
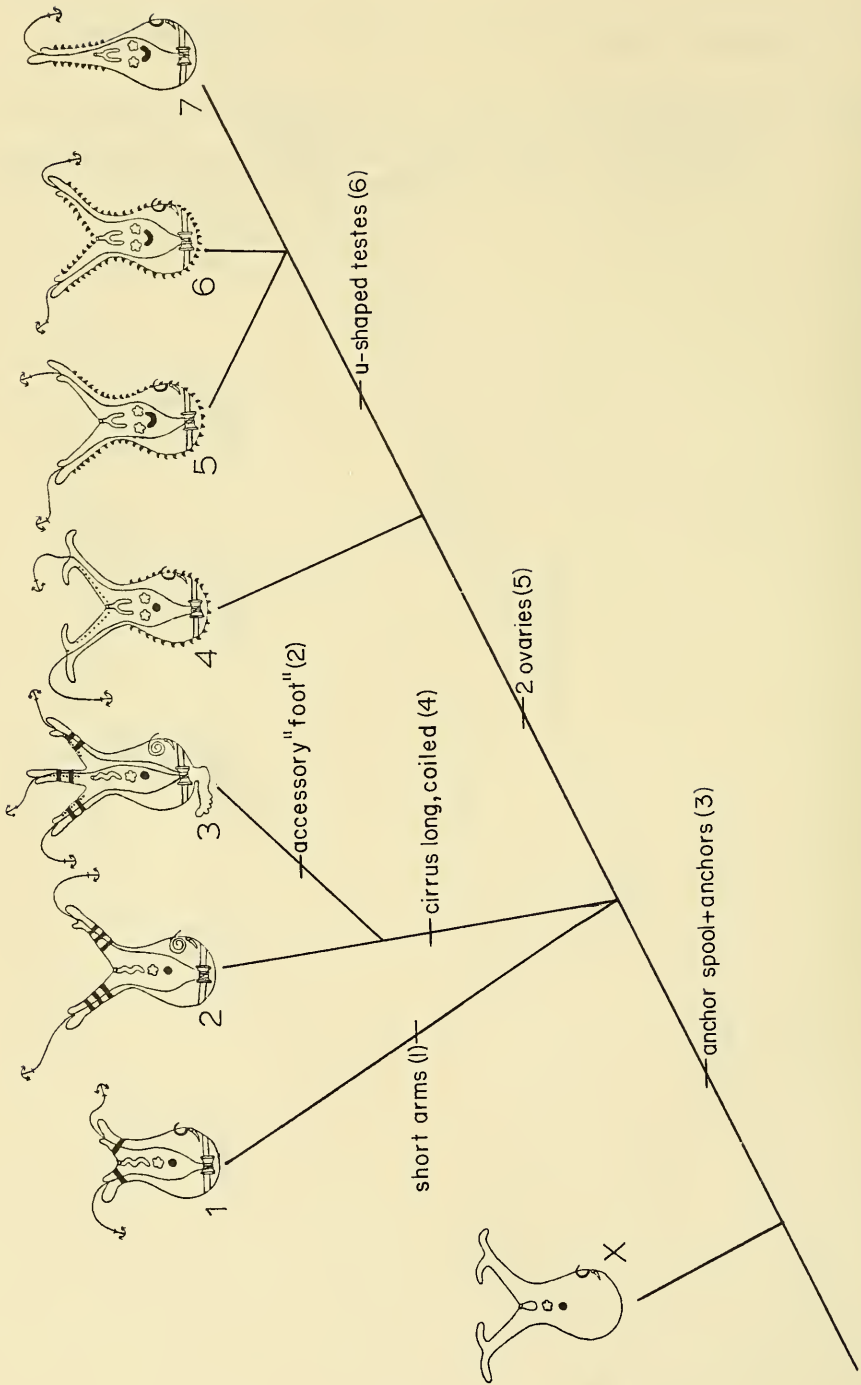
Your cladogram should look like the one on the facing page.
Note that character 2 is found only in taxon 3. In this
case character 2 is said to be an AUTAPOMORPHY for taxon 3.
Note also that character 3, which was synapomorphic for the
group 1+2+3+4+5+6+7 with respect to the taxon "X", is
SYMPLESIOMORPHIC for taxon 3 with respect to taxa 1,2,4,5,
6 and 7.

Step 8:   Add character 11. Notice that the apomorphic trait
          occurs twice, once in taxon 3 and once in taxon 4.
          Thus, character 11 is incongruent with the previous
          cladogram. Now construct a cladogram which is
          congruent with character 11. Notice that although
          the apomorphic trait for character 11 occurs only
          once, the apomorphic traits for characters 4 and
          5 now occur twice. Such a formulation is more
          ambiguous, or less parsimonious than one which
          depicts the apomorphic trait for 11 twice.
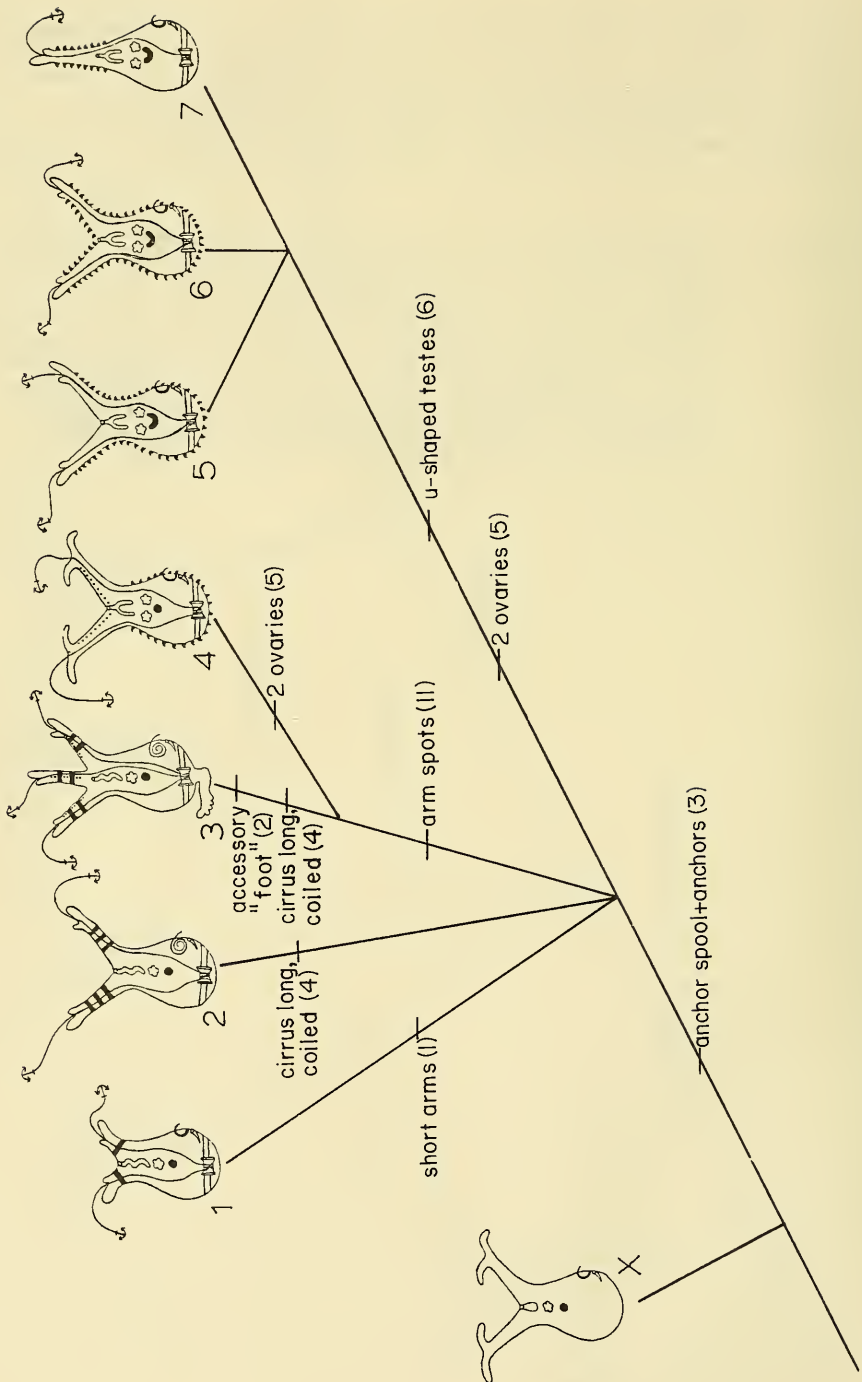
Your most parsimonious cladogram should look like the one
constructed in step 7 with the addition of character 11.
The cladogram depicting no ambiguities for character 11
should look like the one on the facing page.

Step 9:   Add character 12 to the most parsimonious solution
          (from step 7). Notice that the apomorphic trait
          for 12 occurs twice, indicating still more
          incongruence. Formulate a cladogram which is
          congruent with character 12. Notice that the
          apomorphic trait for character 5 now occurs twice.
          Thus, each cladogram depicts one ambiguity and
          each is thus equally parsimonious. We must
          consider additional characters before we choose
          either solution.
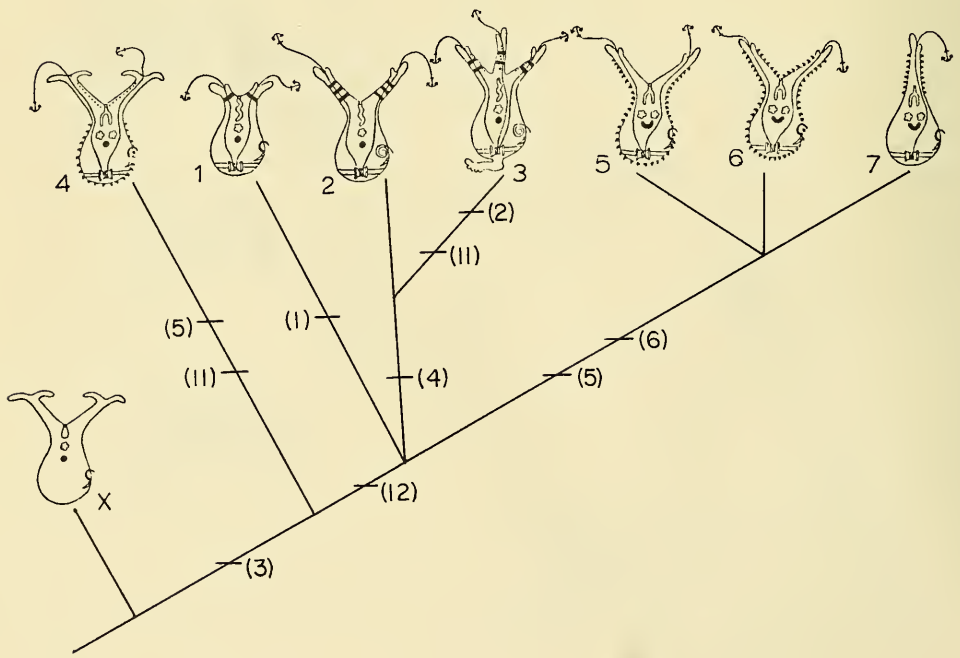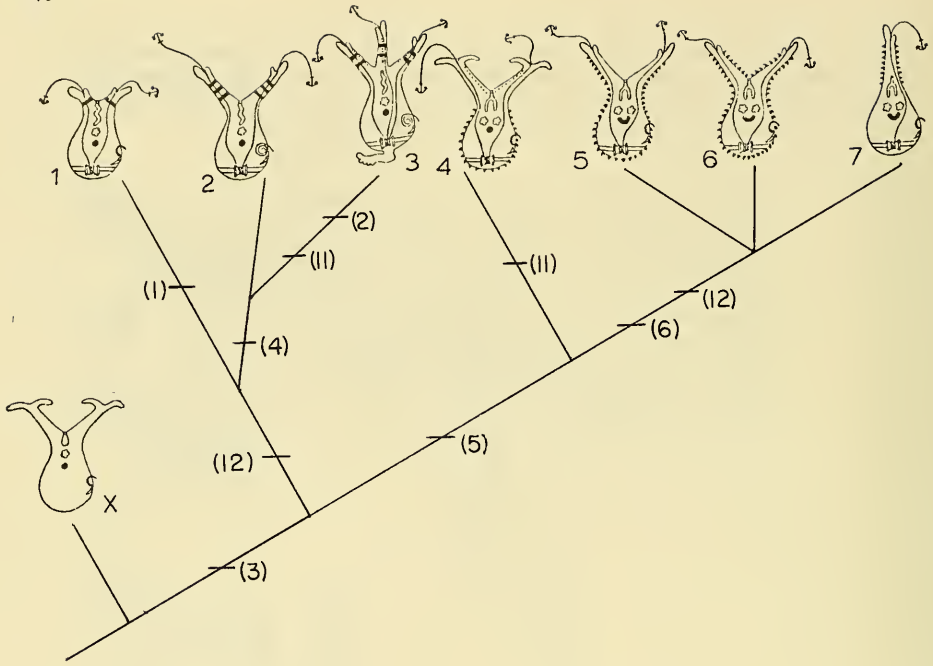
The cladogram incongruent with character 12 should look like the upper tree on the facing page. The tree congruent with character 12 should look like the lower tree on the facing page.

Step 10:   Select one of the cladograms from step 9. We suggest the one incongruent with characters 11 and 12 but either one will work. Add character 8 to it and formulate a new cladogram.

short arms (1)

3 arm stripes (8)

2 arm stripes (8)

accessory "foot" (2)

arm spots (11)

cirrus long, coiled (4)

distal portion arms reduced (12)

1 arm stripe (8)

arm spots (11)

u-shaped testes (6)

distal portion arms reduced (12)

2 ovaries (5)

anchor spool + anchors (3)
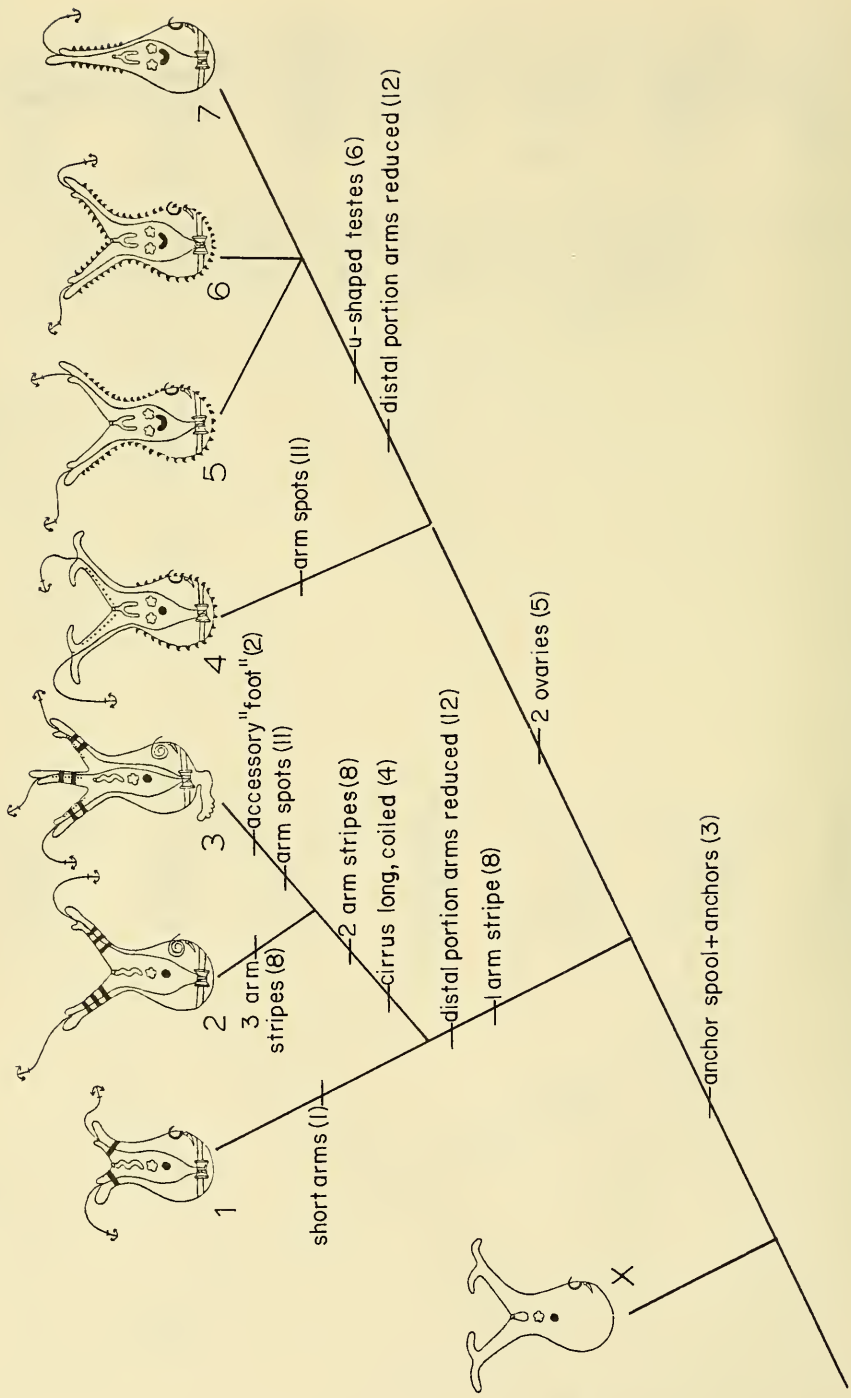
If you chose the cladogram from step 9, your new cladogram should look like the one on the facing page.

Step 11: Add character 7 and formulate a new cladogram.
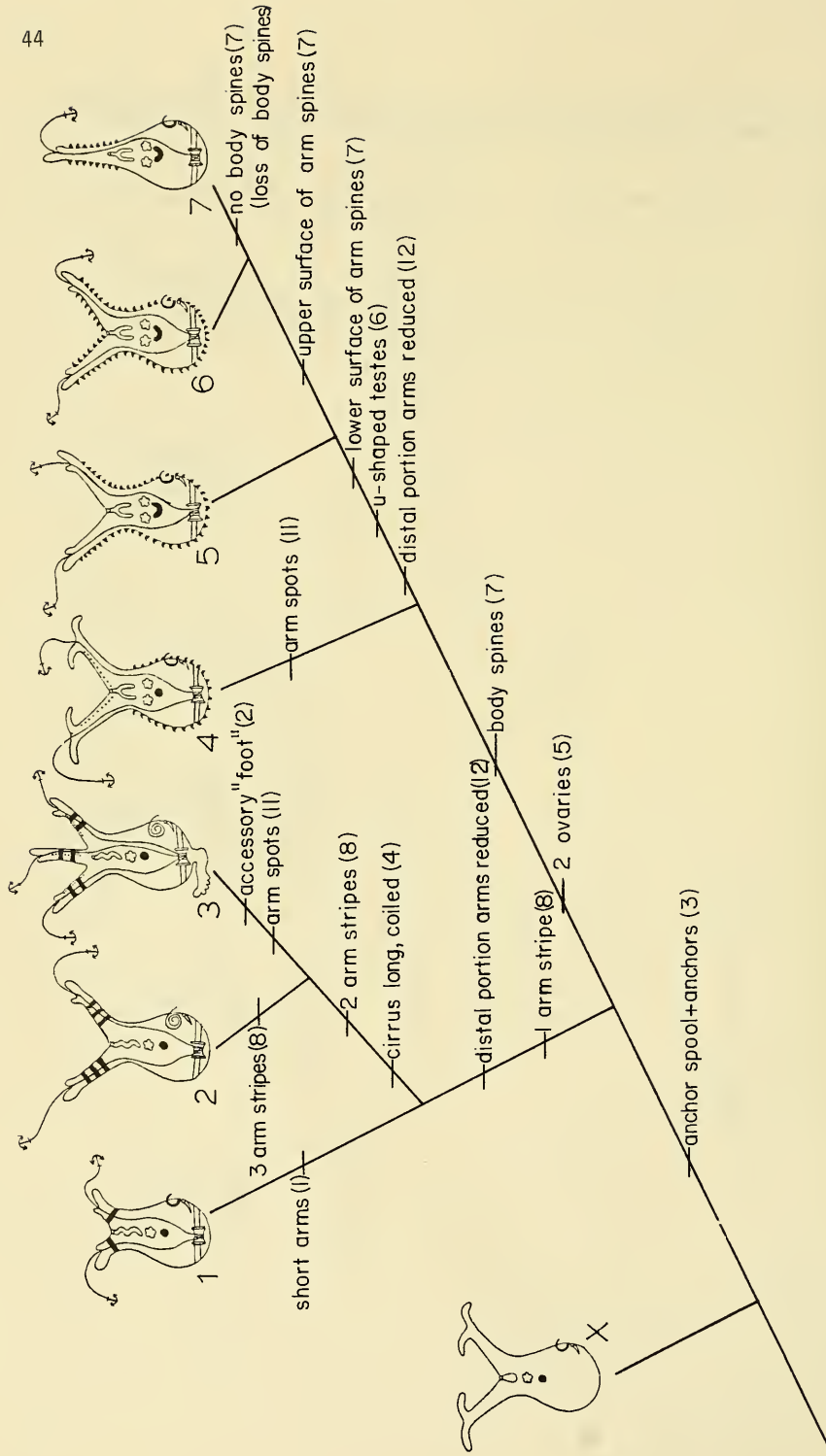
Your new cladogram should look like the one on the facing page.

Step 12: Add characters 9 and 10 and formulate a new cladogram.
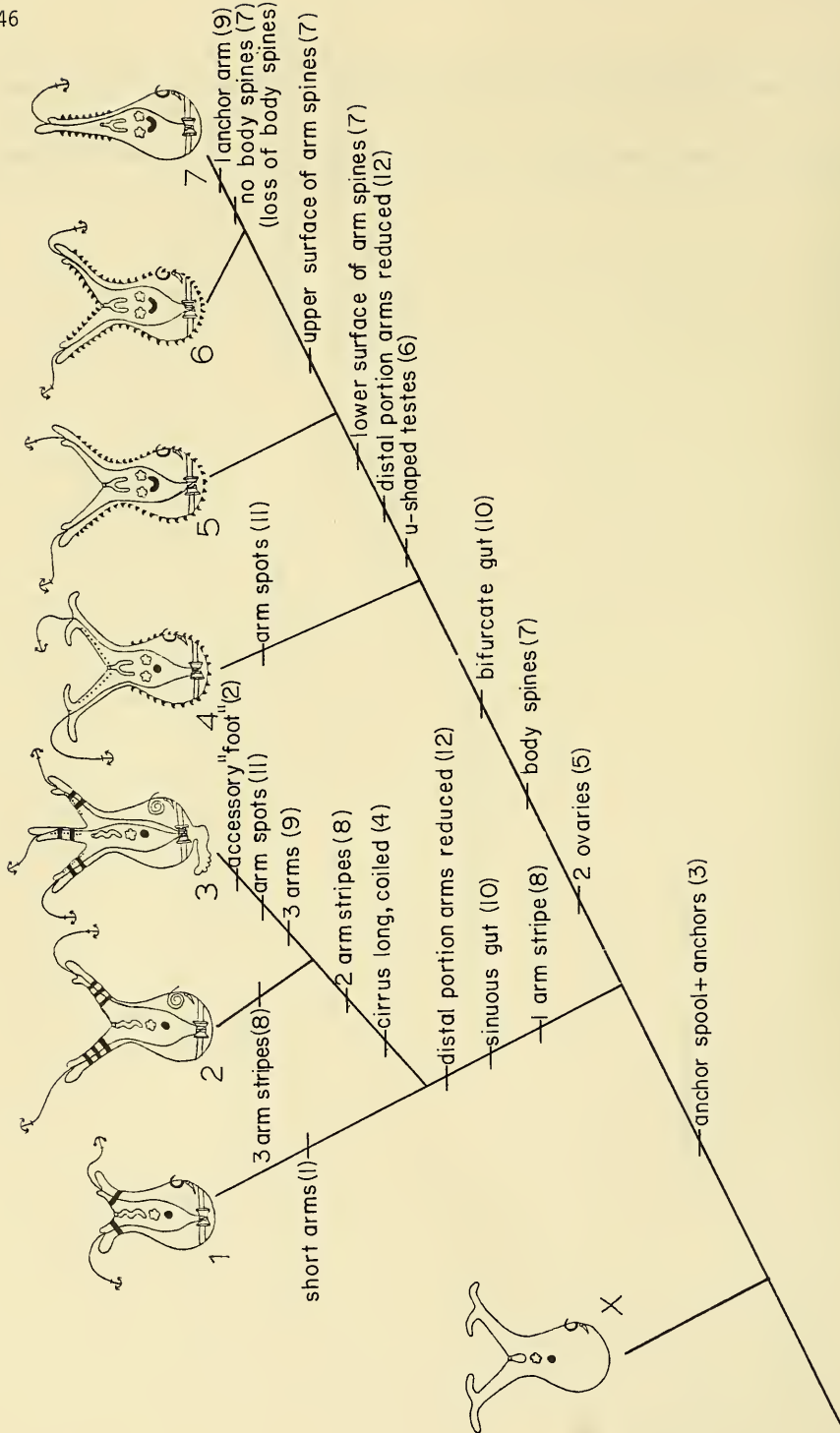
Your new cladogram should look like the one on the facing page.

Step 13:   If you chose the suggested cladogram in step 10, your
            cladogram should now be fully resolved (completely
            dichotomous), and apomorphic traits for characters
            11 and 12 should appear twice. If you chose the
            opposite cladogram in step 10, your cladogram will
            also be fully resolved, but apomorphic traits
            for characters 5,7,10 and 11 will appear twice.
            The first formulation is thus more parsimonious
            and is preferred. Note that character 11 is
            incongruent with either formulation. Note also
            that a single most parsimonious cladogram is
            detectable even when there are mutually
            contradictory characters in the data set. Such
            contradictions are due to HOMOPLASY (CONVERGENCE
            and PARALLELISM) and are considered a major problem
            by many systematists as far as reconstructing
            phylogenies is concerned. In this example,
            however, 2/12 or 16.6% of the characters exhibit
            homoplasy and the "correct" answer can still be
            discerned. In addition, those characters producing
            ambiguity are clearly pointed out.

C: Quantitative Approach (Farris' Wagner Analysis)

Step 1:   Construct a data matrix. Identify each taxon and each character. Fill in with numerical notations for each trait for each character, called the character-states. Plesiomorphic states, as determined by out-group comparisons, are traditionally labeled "0" but any coding convention is feasible so long as the same character-state in any taxon is given the same number each time.

		1	2	3	CHARACTERS 4	5	6	7	8	9	10	11	12
	X	0	0	0	0	0	0	0	0	0	0	0	0
	1	1	0	1	0	0	0	0	1	0	1	0	1
	2							0			1		
TAXA	3							0			1		
	4							1			2		
	5							2			2		
	6							3			2		
	7	0	0	1	0	1	1	4	0	-1	2	0	1

		CHARACTERS										
		1	2	3	4	5	6	7	8	9	10	11	12
	X	0	0	0	0	0	0	0	0	0	0	0	0
	1	1	0	1	0	0	0	0	1	0	1	0	1
	2	0	0	1	1	0	0	0	3	0	1	0	1
TAXA	3	0	1	1	1	0	0	0	2	1	1	1	1
	4	0	0	1	0	1	0	1	0	0	2	1	0
	5	0	0	1	0	1	1	2	0	0	2	0	1
	6	0	0	1	0	1	1	3	0	0	2	0	1
	7	0	0	1	0	1	1	4	0	-1	2	0	1

Your data matrix should look like the one on the facing page.

Step 2: Find a root (the out-group "X") and connect to it
any two taxa. This THREE-TAXON STATEMENT is called
a WAGNER NEIGHBORHOOD. All three taxa are joined
together at a single point called a NODE. For
any three taxa, there is only a single neighborhood
possible. The characteristics of the node are
defined as the majority state for each binary
character or the median state for multi-state
characters of all characters exhibited by the
three taxa surrounding the node. A starting
neighborhood with labeled node is produced below.

(101 000010101) 1   7 (00101140(-1)201)

(001000000101)

X(000000000000)
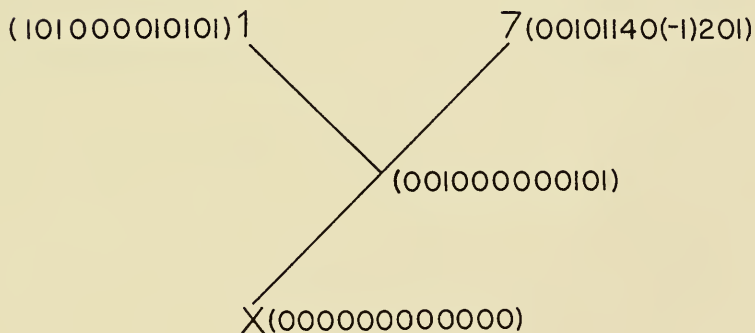
Step 3:   "The Connection Rule." Constructing a cladogram
using this method involves searching for the most
efficient pattern of shared departures, by taxa,
from common reference points, nodes. This is
accomplished by adding taxa one at a time and looking
for the most parsimonious connection to the cladogram.
This can be done by hand for large numbers of characters
and taxa, but can become laborious quickly if there
is much homoplasy in the data set. Dr. Farris
has developed a computer program to implement such
calculations.
Add taxon 2 to the original neighborhood. Try all
three possible connections, compute node character-
states, and choose the one which provides a reference
point for a unique shared departure by Taxon 2 and
one other taxon. The result will be the formulation
of a new neighborhood.

(101000010101) 1

(001100030101)
2

7 (00101140(-1)201)

(001000000101)

(001000000101)

X (000000000000)

(001100030101) 2

(101000010101)
1

7 (00101140(-1)201)

(001000000101)

(001000000101)

X (000000000000)

(00101140(-1)201) 7

(101000010101)
1

2 (001100030101)

(001000010101)

(001000000101)

X (000000000000)
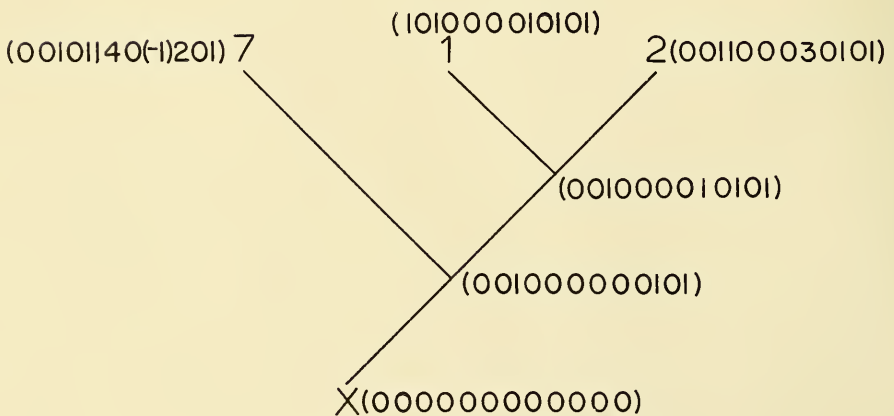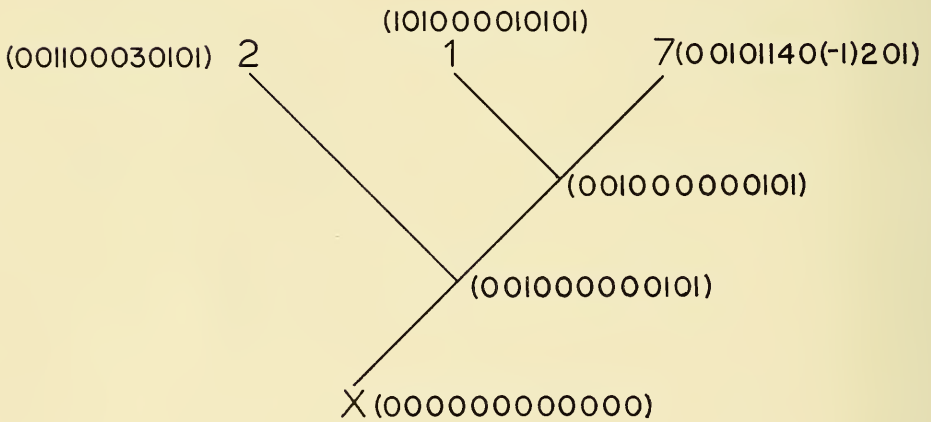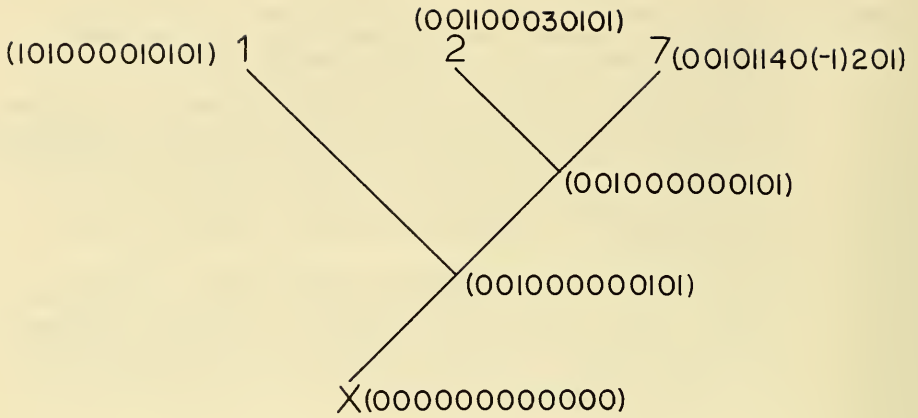
Your three postulated cladograms should look like the ones
on the facing page. The preferred one is the bottom one,
which postulates a new neighborhood. One would read the
three results in the following manner: 1) taxon 7 and taxon
1 do not share a unique departure from a reference point
which excludes taxon 2, 2) taxon 7 and taxon 2 do not share
a unique departure from a reference point which excludes
taxon 1, and 3) taxon 1 and taxon 2 share a unique departure
from a reference point which excludes taxon 7. For character
8 in calculating nodal values, take the median of three
different states; thus, for the bottom cladogram, the node
is the median of 0, 1, and 3, or 1.

     Step 4: Add taxon 3 by the same method. Place taxon 3
               as the sister-group of taxon 2 and calculate
               the value of the node.
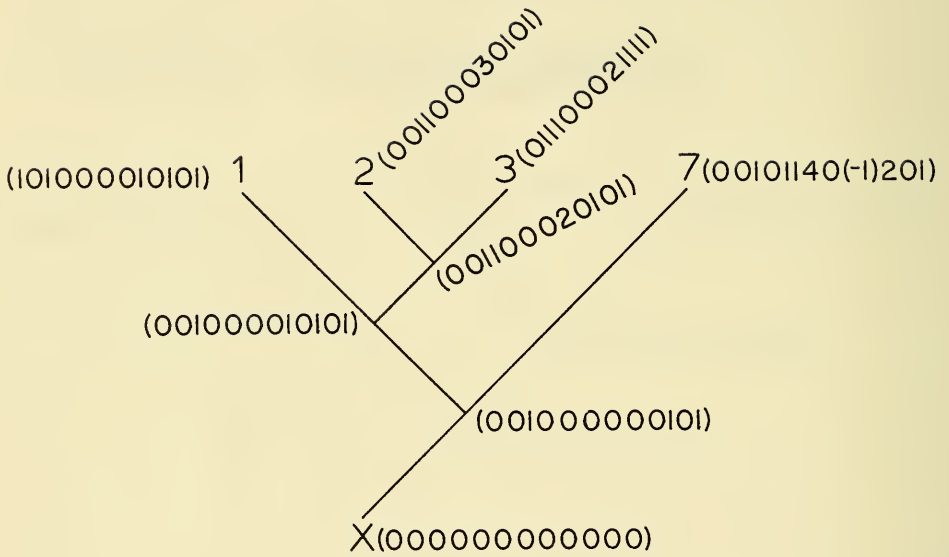
Your cladogram should look like the one on the facing page.

Step 5: Add taxon 4 by the same method. There are seven possible connections for taxon 4 to the cladogram. Five of them are distinct. Calculate all five possible distinct connections and their nodal values.
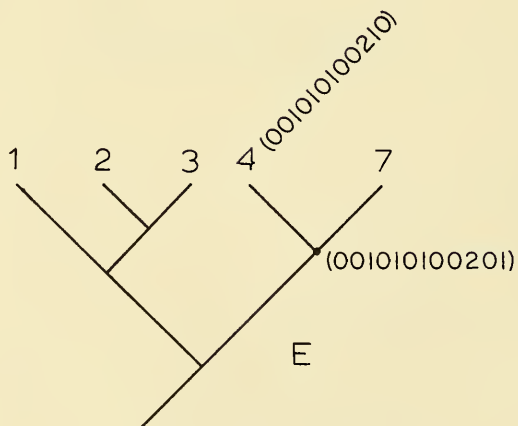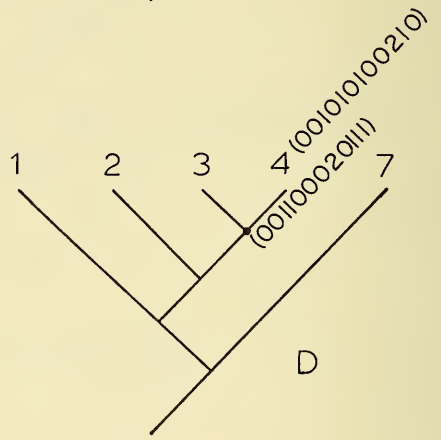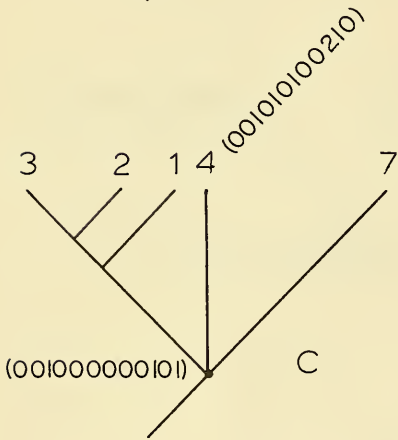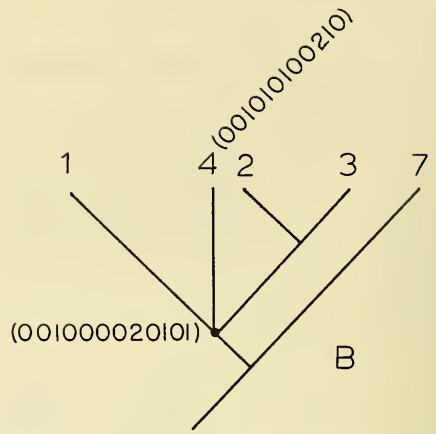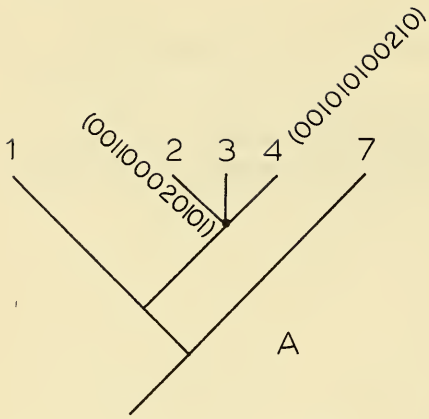
Your cladograms should look like the ones on the facing page. We can now invoke a parsimony criterion to choose the preferred cladogram. Notice that only two of the five postulated nodes actually represent new nodes, while the remaining three have been calculated previously for other taxa. If we add up the total number of differences in character-states between the node and taxon 4, we find that for cladogram A, there are 8 character-state changes postulated; for cladogram B there are 7 changes; for cladogram C there are 5 changes; for cladogram D there are 7 changes; and for cladogram E there are 2 changes. We prefer the nodal value which maximizes the number of shared departure points from the node, or which minimizes the number of postulated new character-state changes. Thus, in this case we prefer cladogram E. Cladogram E in this case postulates a new node. Cladogram D also postulates a new node, but requires 7 character-state changes rather than only 2. Cladogram C does not postulate a new node, but requires fewer changes than does cladogram D. Therefore, because there is a new node requiring only 2 changes, and because there is a previously-calculated node requiring only 5 changes, we postulate that the trait linking taxon 4 and taxon 3 (character-state 1 for character 11) is the result of convergence rather than common ancestry.

Step 6: Add taxon 5.

4(001010100210)

5(001011200201)

7(0010114 0(-1)201)

(001011200201)

(001010100201)

1 2 3 4 5 7

X
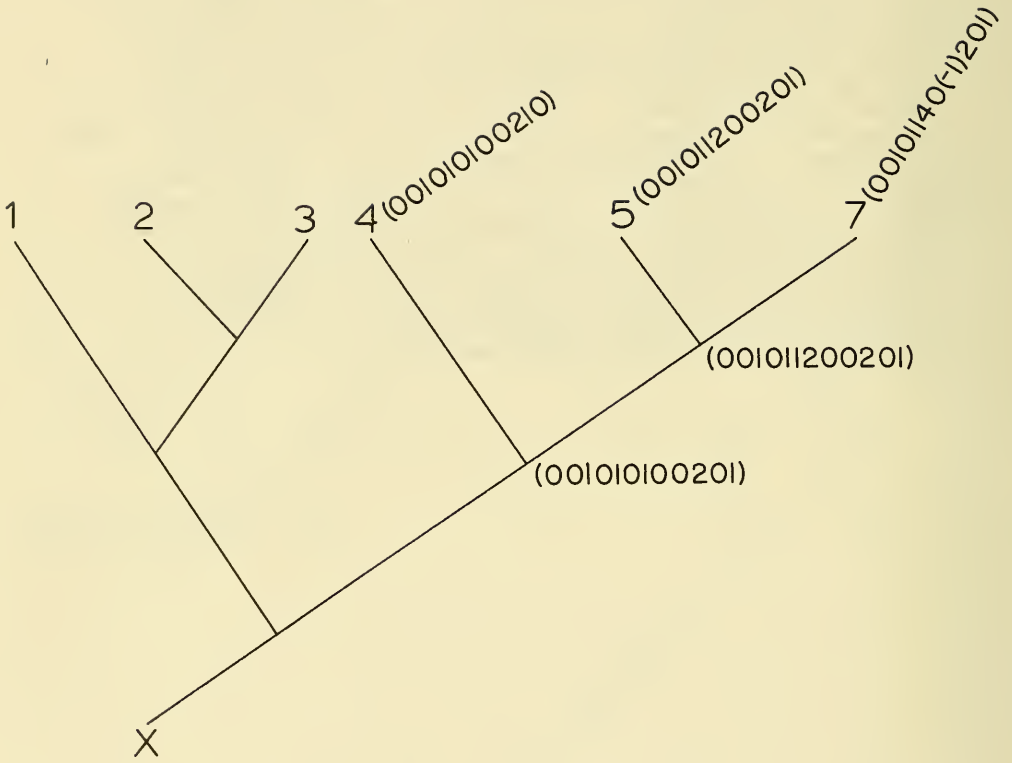
Your cladogram should look like the one on the facing page.

Step 7: Add taxon 6.

5(001011200201)

6(001011300201)

7(001011140(-1)201)

1 2 3 4 5

(001011300201)

(001011200201)

X
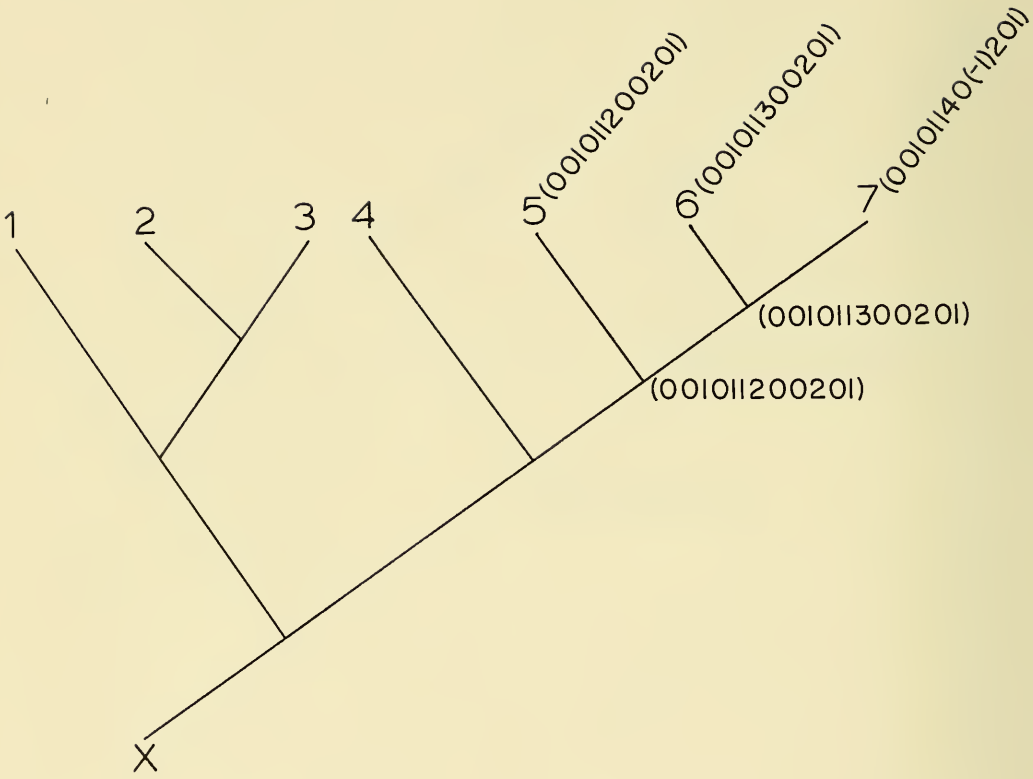
Your cladogram should look like the one on the facing page.

Step 8: Remove the root "X". Add numerical shorthand
notations indicating synapomorphies. Your
final cladogram should look like the one below.
Each slash mark indicates a shared apomorphic
trait for the character denoted by the accompany-
ing number; a cross indicates an apomorphic
trait indicated by a negative sign (-1 for
character 9); an asterisk indicates a postulated
reversal (0 for character 12 in taxon 4). Apo-
morphic traits for multistate characters are
determined by summing up slashes for a given
character from the bottom of the cladogram.
Thus, the "7 slash" on the branch leading to
the cluster taxon 6 + taxon 7 represents state
"3" for character 7.
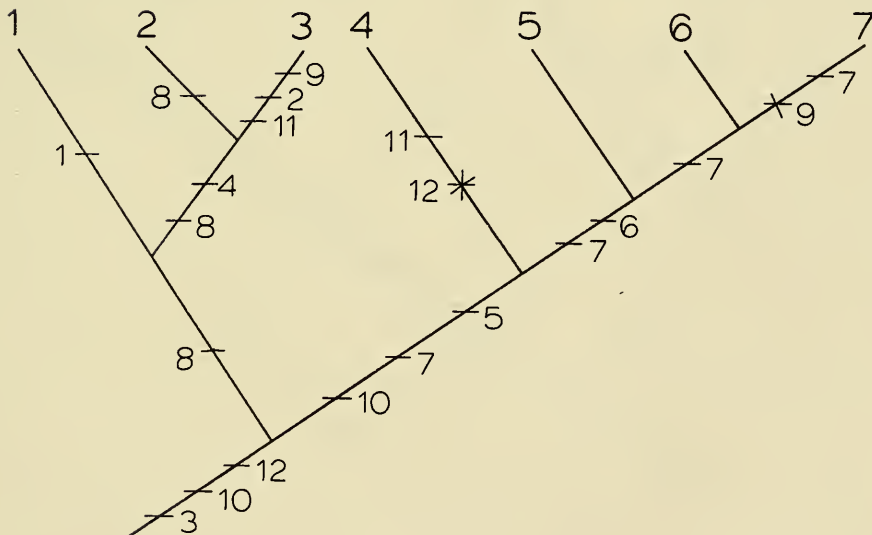
We are now able to compare the cladograms generated in Part 3 (previous page) and in Part 2 (below). Note that there is no difference in branching pattern. The only difference is the interpretation of the evolution of character 12. The Wagner solution postulates a single origin for state 1 with a reversal in taxon 4 to the plesiomorphic condition. The non-quantitative approach suggests two independent origins of state 1. In the first case, the "0" state found in taxon 4 and in the out-group would not be HOMOLOGOUS. In the second case, the "1" state found in taxa 1+2+3 would not be homologous with the "1" state found in taxa 5+6+7. Comparative developmental (ontogenetic) studies could resolve these alternatives.
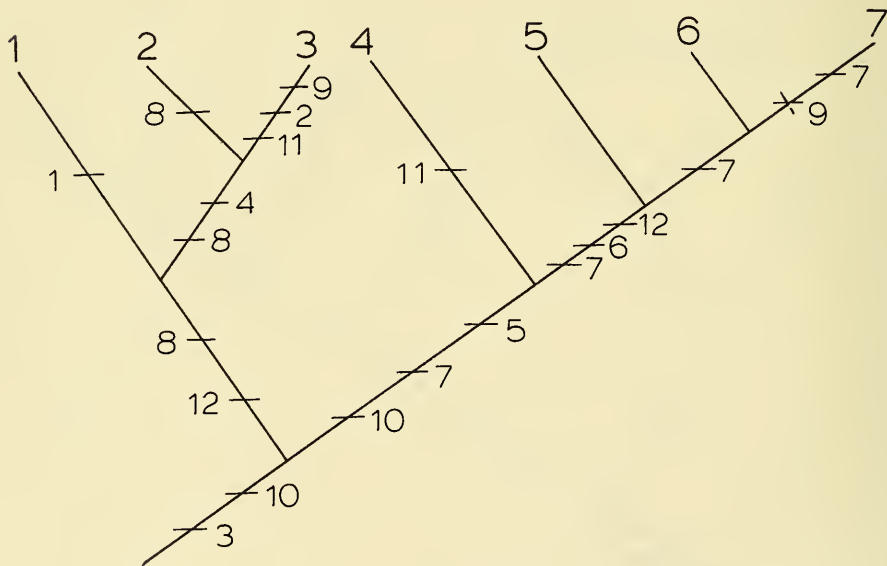
Step 9:   Standardizing your data-   Additive Binary Coding

      Multistate characters pose some particular
problems for cladistic analysis.   First, the
greater the number of character-states associated
with a character, the greater the likelihood that
we will be unable to polarize the states correctly.
Second, it has been suggested that one multistate
character will unduly influence the results of a
cladistic analysis based on data which are mostly
binary.   And thirdly, complex multistate characters
cannot be coded directly for computer-assisted
computations.   The first two objections may be
overcome by using the Wagner algorithm rather than
a more restrictive algorithm such as the Camin-
Sokal method.   All three problems may be overcome
if all multistate characters are converted into a
series of binary characters.   The technique for
such conversions is called ADDITIVE BINARY CODING.
We present an example first to demonstrate the
technique.   Consider the following multistate
character with nine states related in the pattern
shown below:
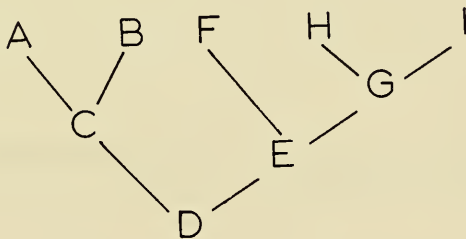
        To convert this CHARACTER STATE TREE into a set
of binary characters, set up a matrix labeled A-I X A-I.
Then, beginning with row "A", fill in "1" in each column
representing a state linking "A" to the basal "D", inclusive.
For "A" that would be "A", "C", and "D". For row "B",
"B", "C", and "D" would be scored "1". All slots in the
matrix not scored "1" would be scored "0". The final
matrix comrpises a set of columns each representing a
character-state from the original character-state tree
and a set of rows each corresponding to a new binary
character. The total data matrix is a binary represen-
tation of the entire character-state tree. The complete
matrix is given below.

Old Character-States

	A	B	C	D	E	F	G	H	I
A	1	0	1	1	0	0	0	0	0
B	0	1	1	1	0	0	0	0	0
C	0	0	1	1	0	0	0	0	0
D	0	0	0	1	0	0	0	0	0
E	0	0	0	1	1	0	0	0	0
F	0	0	0	1	1	1	0	0	0
G	0	0	0	1	1	0	1	0	0
H	0	0	0	1	1	0	1	1	0
I	0	0	0	1	1	0	1	0	1

New Binary Characters

Formulate character-state trees and binary characters
for characters 7, 8, 9, and 10.

Character 7:

	0	1	2	3	4
0	1	0	0	0	0
1	1	1	0	0	0
2	1	1	1	0	0
3	1	1	1	1	0
4	1	1	1	1	1
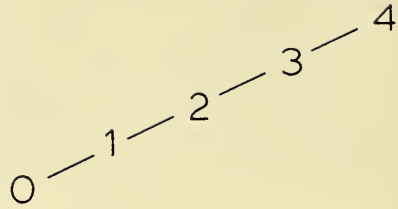
Character 8:

	0	1	2	3
0	1	0	0	0
1	1	1	0	0
2	1	1	1	0
3	1	1	1	1
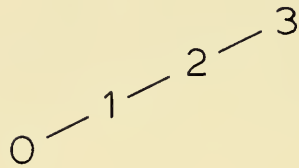
Character 9:

	0	1	-1
0	1	0	0
1	1	1	0
-1	1	0	1
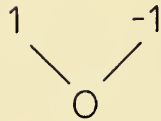
Character 10:

	0	1	2
0	1	0	0
1	1	1	0
2	1	1	1
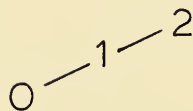
The four character-state trees and binary matrices should
look like the ones on the facing page. When these new binary
characters are substituted for the old multistate characters
(7, 8, 9, 10) in the data matrix on page 36, the new data
matrix looks like the one below.

CHARACTERS

```
         1 2 3 4 5 6     7         8       9       10  11 12
                       ┌─────┐  ┌─────┐ ┌─────┐ ┌─────┐
    X    0 0 0 0 0 0 1 0 0 0 0 1 0 0 0 1 0 0 1 0 0  0   0
    1    1 0 1 0 0 0 1 0 0 0 0 1 1 0 0 1 0 0 1 1 0  0   1
    2    0 0 1 1 0 0 1 0 0 0 0 1 1 1 1 0 0 1 1 0 0  0   1
    3    0 1 1 1 0 0 1 0 0 0 0 1 1 1 0 1 1 0 1 1 0  1   1
    4    0 0 1 0 1 0 1 1 0 0 0 1 0 0 0 1 0 0 1 1 1  1   0
    5    0 0 1 0 1 1 1 1 1 0 0 1 0 0 0 1 0 0 1 1 1  0   1
    6    0 0 1 0 1 1 1 1 1 1 0 1 0 0 0 1 0 0 1 1 1  0   1
    7    0 0 1 0 1 1 1 1 1 1 1 1 0 0 0 1 0 1 1 1 1  0   1
```


This technique of additive binary coding adds several
extra dimensions to cladistic analysis. First, it allows
precise formulations of median values for multistate characters.
As an example, consider the following Wagner neighborhood for
three taxa characterized by the states "A", "E", and "H" for
the sample multi-state character-state tree. What value do
we place at the node? The solution to the problem involves
designating "A", "E", and "H" with their binary coding and finding
the mean values of the binary characters just as in Step 3.
Calculate the node for the example just described.


```
      A
      |
      |────H
      |
      E
```

A(101100000)

H(00011011O)

(00011000O)

E(000110000)

4(11111)

1(11000)
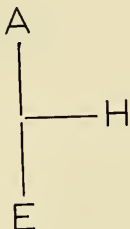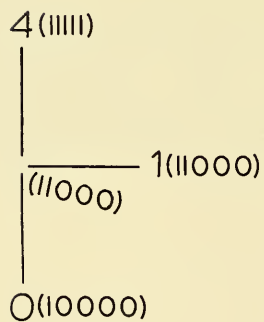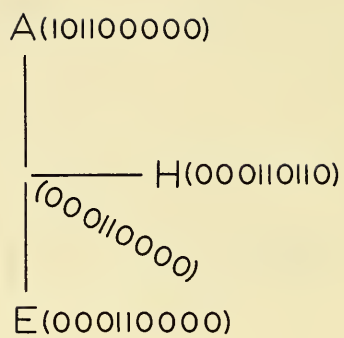
(11000)

O(10000)

Your calculated node should be (000110000) or "E", as given
in the upper diagram on the facing page. Now calculate the
median value for the node of a Wagner Neighborhood with traits
4, 1 and 0 for character 7. The results should look like the
second example on the facing page. The node should be
(11000) or "1".

This technique also serves a critical function
in the analysis of coevolutionary relationships among
hosts and parasites. Any cladogram of a parasite group
may be considered a character-state tree, can be converted
into a set of binary characters, and be used to analyze
host phylogenetic relationships. A more complete
discussion of this method for studies in coevolution is
presented in Brooks (1981, Hennig's Parasitological
Method: A Proposed Solution, Systematic Zoology 30:
229-249).

Step 10: Optimizing the tree

The final aspect of quantitative cladistics
to be discussed in this workbook is termed TREE
OPTIMIZATION. This technique, another of the many
developed by J. S. Farris, provides a way to
derive parsimonious inferences about phylogenetic
sequences of character-state changes from a tree.
Consider the following tree (below). Notations at
the ends of the branches refer to presence (1) or
absence (0) of a state. The question in optimization
is this: what is the most parsimonious interpre-
tation of the evolution of those character-states?
The solution involves a 2-step process. First, make
a pass from the top of the tree to the bottom making
generalizations about the nodes. If the two branches
running from above down to the node have the same
character-state (0 or 1) code the node the same way.
If the character-states differ (one 0 and one 1),
give the node a "b" for both. If a "b" and a "1"
come together, give the node a "1"; if a "b" and a
"0" come together, give the node a "0"; for two "b"
branches, give the node a "b". Designate all nodes
as 0, 1, or b.
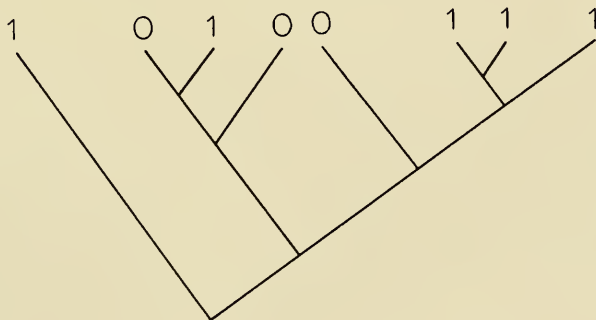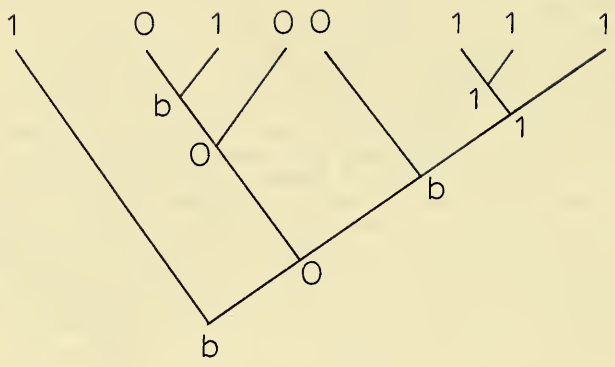
Your diagram should look like the one on the facing page.

The second step in optimization requires designating all "b" nodes as either 1 or 0. The most parsimonious designation of each "b" is the same value as that exhibited by the out-group or immediate lower node. Make a second pass, from the bottom of the cladogram to the top, converting all "b" nodes to the out-group or previous nodal value
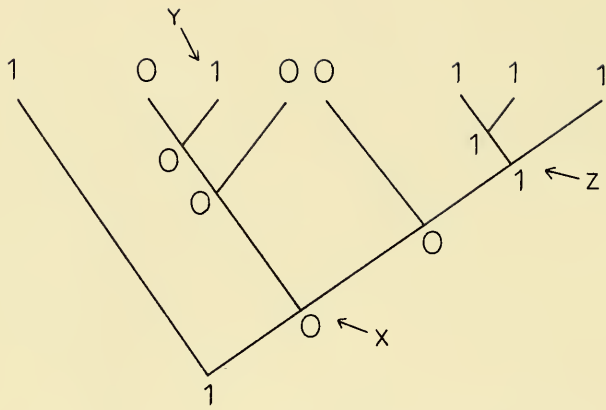
Your diagram should look like the one on the facing page.
The most parsimonious explanation of the sequence of character-
state changes is that state 1 evolved into state 0 at "x"
and then re-appeared twice, once at "y" and at "z."

Optimization also provides means for determining
which of two or more trees best fits a set of data.
Consider an alternative tree to the one on the facing
page (below):
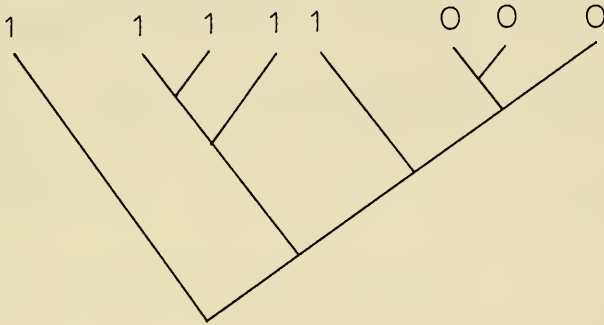
Optimizing this tree produces an interpretation that
state 1 evolved into state 0 once. The total number of
postulated changes for the first tree is 3; for the
second tree it is 1. Thus, the second tree represents
a better, more parsimonious explanation of the character
data. Such comparisons can be made for all characters
in a data set in terms of any possible alternative tree.

It was the realization of the utility of cladistic
analysis in allowing parsimonious choice of alternative
trees which made cladists aware that cladistics represented
more than just another way to group taxa. Every hypothesis
in any aspect of Comparative Biology may be represented
symbolically by a branching diagram. Alternative possi-
bilities may then be tested according to the criterion
of which one best fits all data. A preference for one
may be stated according to empirical constraints.
Systematics has thus become an empirical science as
"hard" as any other and assumes its role of General Reference
System for Comparative Biology.

PART 4: GLOSSARY OF TERMS

Page numbers where terms first appear in this workbook, excluding the essay by Dr. Platt, are given in brackets after each word or phrase.

ADDITIVE BINARY CODING (71): A means of converting characters which occur in more than two states (multistate characters) into a series of two-state characters (binary characters), thus increasing the likelihood of polarizing the states correctly. It allows the formulation of median values for multistate characters.

APOMORPHIC (23): A character derived from its preexisting homologue is termed apomorphic (relatively derived or special traits).

AUTAPOMORPHY (43): An attribute unique to only one group of individuals and thought to originate in that group of individuals (a trait present in only one terminal taxon in a cladogram).

BINARY CHARACTERS (25): Characters which possess only two states.

CHARACTERS (5): General category of comparative units some form of which is present in all taxa.

CHARACTER-STATES (25): Specific expressions of characters exhibited by individual taxa.

CHARACTER-STATE TREE (72): An arrangement of character-states in sequences beginning with the most ancestral.

CLADISTIC ANALYSIS (5) (or Phylogenetic Analysis): A method that attempts to recover geneological relationships among groups of organisms, and attempts to produce trees that reflect these relationships.

CLADOGRAM (23): A branching diagram representing the most informative display of patterns or traits in a data set.

CONGRUENT (41): Two cladograms are said to be congruent when all taxa present on both cladograms demonstrate identical cladistic relationships with respect to one and other. When only some of the taxa present on both cladograms demonstrate identical cladistic relationships with respect to one and other the cladograms are termed partially congruent.

CONVERGENCE (53): Two apparently similar characters which developed from different preexisting characters. It is recognizable on a cladogram as a character occuring in two taxa separated by at least two nodes. Convergence is a type of homoplasy.

DICHOTOMOUS (37): A node splitting into only two branches: Dichotomous sequences are fully resolved.

FULLY-RESOLVED (37): A cladogram in which all nodes split into only two branches.

HOMOLOGOUS (70): Characters having a common origin.

IN-GROUP COMPARISON (21): Determining which state of a character is novel for a group of taxa based on the distribution of the character-states among that same group of taxa. This leads to false estimates of phylogeny.

MONOPHYLETIC LINEAGE (21): A lineage composed of all of the descendents of a common ancestor.

MULTISTATE CHARACTERS (25): Characters found in more than two character-states.

NODE (57): The representation of a speciation event in a cladogram.

OUT-GROUP (5): A group of organisms (species or genus etc.) that is related to but removed from the group of study taxa. One or more out-groups are examined to determine which character-states are evolutionary novelties (apomorphic).

PARALLELISM (53): The development of similar characters independently from the same ancestral character. It is recognizable on a cladogram as a character occuring in two taxa separated by a single node.

PARSIMONY (21): Economy of assumption in reasoning. In a cladistic analysis it requires choosing the cladogram postulating the least number of character-state changes.

PHYLOGENIES (5): Patterns of natural relationships of descent among organisms.

PLESIOMORPHIC (21): The original preexisting character from which its homologous character was derived is termed plesiomorphic (these are generalized or relatively primative traits).

POLARIZATION (21): With a binary character this involves determining the evolutionarily novel (recent) character-state from the preexisting or plesiomorphic character state.

SISTER GROUP (21): The group of organisms most closely related to the study taxa excluding their direct descendents.

SYMPLESIOMORPHIC (43): A character shared among a group of individuals which is found in their common ancestor and thought to have originated in an earlier ancestor is termed symplesiomorphic.

SYNAPOMORPHY (35): A character shared among a group of individuals which is found in their common ancestor and thought to have originated in that ancestor (not an earlier one).

TAXA (21): Groupings of organisms.

THREE TAXON STATEMENT (57): Basic unit of comparison in a cladistic analysis.

TREE OPTIMIZATION (79): A means of deriving parsimonious inferences about phylogenetic sequences of character-state changes from a phylogenetic tree.

WAGNER NEIGHBORHOOD (57): A three taxon statement used in the quantitative phylogenetic approach (Farris Wagner Analysis). It may be any two taxa connected to an out-group.

PART 5:   PERTINENT LITERATURE: Phylogenetic Systematics in
Systematic Zoology.

Anderson, N. M. 1979. Phylogenetic inference as applied to the
    study of evolutionary diversification of semiaquatic bugs
    (Hemiptera: Gerromorpha). Syst. Zool. 28: 554-578.

Avise, J. C., J. C. Patton, and C. F. Aquadro. 1980. Evolutionary
    genetics of birds II. Conservative protein evolution in
    North American sparrows and relatives. Syst. Zool. 29: 323-334.

Baird, R. C. and M. J. Eckardt. 1972. Divergence and relationship
    in deep-sea hatchetfishes (Sternoptychidae). Syst. Zool.
    21: 80-90.

Baker, R. J. and J. W. Bickham. 1980. Karyotypic evolution in
    bats: evidence of extensive and conservative chromosomal
    evolution in closely related taxa. Syst. Zool. 29: 239-253.

Ball, I. R. 1975. Nature and formulation of biogeographic
    hypotheses. Syst. Zool. 24: 407-430.

Baverstock, P. R., S. R. Cole, B. J. Richardson, and C. H. S.
    Watts. 1979. Electrophoresis and cladistics. Syst. Zool.
    28: 214-219.

Bennett, D. K. 1980. Stripes do not a zebra make, part I. a
    cladistic analysis of Equus. Syst. Zool. 29: 309-313.

Bremer, K. and H-E. Wanntorp. 1979. Geographic populations or
    biological species in phylogeny reconstruction? Syst. Zool.
    28: 220-223.

Bremer, K. and H.-E. Wanntorp. 1979. Hierarchy and reticulation
    in systematics. Syst. Zool. 28: 624-626.

Brooks, D. R. 1977. Evolutionary history of some plagiorchioid
    trematodes of anurans. Syst. Zool. 26: 277-289.

Brooks, D. R. 1978. Evolutionary history of the cestode order
    Proteocephalidea. Syst. Zool. 27: 312-323.

Brooks, D. R. 1979. Testing the context and extent of host-
    parasite coevolution. Syst. Zool. 28: 299-307.

Brooks, D. R. 1980. Allopatric speciation and non-interactive
    parasite community structure. Syst. Zool. 29: 192-202.

Brooks, D. R. 1980. Brooks' response to Holmes and Price. Syst.
    Zool. 29: 214-215.

Brundin, L. 1972. Phylogenetics and biogeography. Syst. Zool.
    21: 69-79.

Byers, G. W. 1969. Review of <u>Phylogenetic</u> <u>Systematics</u> and
    <u>Transantarctic</u> <u>Relationships</u> <u>and</u> <u>their</u> <u>Significance</u>, as
    <u>Evidenced</u> <u>by</u> <u>Chironomid</u> <u>Midges</u>. Syst. Zool. 18: 105-107.

Cracraft, J. 1974. Phylogenetic models and classification. Syst.
    Zool. 23: 71-90.

Cracraft, J. 1975. Paleontology and phylogenetics: a response to
    Bretsky. Syst. Zool. 24: 119-120.

Cracraft, J. 1978. Science, philosophy and systematics. Syst. Zool.
    27: 213-215.

Croizat, L., G. Nelson and D. E. Rosen. 1974. Centers of origin
    and related concepts. Syst. Zool. 23: 265-287.

Cronin, J. E. and W. E. Meikle. 1979. The phyletic position of
    <u>Theropithecus</u>: congruence among molecular, morphological
    and paleontological evidence. Syst. Zool. 28: 259-269.

Engelmann, G. F. and E. O. Wiley. 1977. The place of ancestor-
    descendant relationships in phylogeny reconstruction.
    Syst. Zool. 26: 1-11.

Farris, J. S. 1967. The meaning of relationship and taxonomic
    procedure. Syst. Zool. 16: 44-51.

Farris, J. S. 1967. Comment on psychologism. Syst. Zool. 16: 345-347.

Farris, J. S. 1968. Categorical ranks and evolutionary taxa in
    numerical taxonomy. Syst. Zool. 17: 151-159.

Farris, J. S. 1969. On the cophenetic correlation coefficient.
    Syst. Zool. 18: 279-285.

Farris, J. S. 1969. A successive approximations approach to
    character weighting. Syst. Zool. 18: 374-385.

Farris, J. S. 1970. Methods for computing Wagner trees. Syst.
    Zool. 19: 83-92.

Farris, J. S. 1973. On comparing the shapes of taxonomic trees.
    Syst. Zool. 22: 50-54.

Farris, J. S. 1973. A probability model for inferring evolutionary
    trees. Syst. Zool. 22: 250-256.

Farris, J. S. 1974. Formal definitions of paraphyly and polyphyly.
    Syst. Zool. 23: 548-554.

Farris, J. S. 1976. Expected asymmetry of phylogenetic trees.
    Syst. Zool. 25: 196-197.

Farris, J. S. 1976. Phylogenetic classification of fossils with
    recent species. Syst. Zool. 25: 271-282.

Farris, J. S. 1977. Phylogenetic analysis under Dollo's law.
        Syst. Zool. 26: 77-88.

Farris, J. S. 1977. Some further comments on LeQuesne's methods.
        Syst. Zool. 26: 220-223.

Farris, J. S. 1978. Inferring phylogenetic trees from chromosome
        inversion data. Syst. Zool. 27: 275-284.

Farris, J. S. 1978. An efficient method for finding monothetic
        groups. Syst. Zool. 27: 468-471.

Farris, J. S. 1979. On the naturalness of phylogenetic classification.
        Syst. Zool. 28: 200-213.

Farris, J. S. 1979. The information content of the phylogenetic
        system. Syst. Zool. 28: 483-520.

Farris, J. S. 1980. Naturalness, information, invariance, and
        the consequences of phenetic criteria. Syst. Zool. 29: 360-381.

Farris, J. S. 1980. The efficient diagnoses of the phylogenetic
        system. Syst. Zool. 29: 386-401.

Farris, J. S., A. G. Kluge, and M. J. Eckardt. 1970. A numerical
        approach to phylogenetic systematics. Syst. Zool. 19: 172-189.

Farris, J. S., A. G. Kluge, and M. J. Eckardt. 1970. On predictivity
        and efficiency. Syst. Zool. 19: 363-372.

Farris, J. S., A. G. Kluge and M. F. Mickevich. 1979. Paraphyly
        of the Rana boylii species group. Syst. Zool. 28: 627-634.

Ferris, V. R. 1980. A science in search of a paradigm?- review
        of the symposium, "Vicariance biogeography: A Critique."
        Syst. Zool. 29: 67-75.

Fink, W. L. 1979. Optimal classifications. Syst. Zool. 28: 371-374.

Goodman, M., J. Czelusniak, G. W. Moore, A. E. Romero-Herrera,
        and G. Matsuda. 1979. Fitting the gene lineage into its
        species lineage, a parsimony strategy illustrated by
        cladograms constructed from globin sequences. Syst. Zool.
        28: 132-163.

Gorman, G. C., D. G. Buth, and J. S. Wyles. 1980. Anolis lizards
        of the eastern Caribbean: A case study in evolution. III.
        A cladistic analysis of albumin immunological data, and the
        definition of species groups. Syst. Zool. 29: 143-158.

Hennig, W. 1975. "Cladistic analysis or cladistic classification?":
        a reply to Ernst Mayr. Syst. Zool. 24: 244-256.

Kluge, A. G. and J. S. Farris. 1969. Quantitative phyletics and
        the evolution of anurans. Syst. Zool. 18: 1-32.

Kiriakoff, S. G. 1959. Phylogenetic systematics versus typology.
        Syst. Zool. 8: 117-118.

Kiriakoff, S. G. 1962. On the neo-Adansonian school. Syst. Zool. 11: 180-185.

Kiriakoff, S. G. 1963. Comment on James' letter. Syst. Zool. 12: 93-94.

Kiriakoff, S. G. 1965. Some remarks on Sokal and Sneath's Principles of Numerical Taxonomy. Syst. Zool. 14: 61-64.

Kiriakoff, S. G. 1966. Cladism and phylogeny. Syst. Zool. 15: 91-93.

Loudenslager, E. J. and G. A. E. Gall. 1980. Geographic patterns of protein variation and subspeciation in cutthroat trout, Salmo clarki. Syst. Zool. 29: 27-42.

Lundberg, J. G. 1972. Wagner networks and ancestors. Syst. Zool. 21: 398-413.

Lundberg, J. G. 1973. More on primitiveness, higher level phylogenies and ontogenetic transformations. Syst. Zool. 22: 327-329.

MacFadden, B. J. 1976. Cladistic analysis of primitive equids, with notes on other perissodactyls. Syst. Zool. 25: 1-14.

Marshall, L. G. 1977. Cladistic analysis of borhyaenoid, dasyuroid, didelphoid, and thylacinid (Marsupalia: Mammalia) affinity. Syst. Zool. 26: 410-425.

Mickevich, M. F. 1978. Taxonomic congruence. Syst. Zool. 27: 143-158.

Mickevich, M. F. 1978. Comments on recognition of convergence and parallelism on Wagner trees. Syst. Zool. 27: 239-241.

Mickevich, M. F. 1980. Taxonomic congruence: Rohlf and Sokal's misunderstanding. Syst. Zool. 29: 162-176.

Mickevich, M. F. and M. S. Johnson. 1976. Congruence between morphological and allozyme data in evolutionary inference and character evolution. Syst. Zool. 25: 260-270.

Morse, J. C. and D. F. White, jr. 1979. A technique for analysis of historical biogeography and other characters in comparative biology. Syst. Zool. 28: 356-365.

Mundinger, P. C. 1979. Call learning in the Carduelinae: ethological and systematic considerations. Syst. Zool. 28: 270-283.

Nelson, G. 1969. The problem of historical biogeography. Syst. Zool. 18: 243-246.

Nelson, G. 1970. Outline of a theory of comparative biology. syst. Zool. 19: 373-384.

Nelson, G. 1971. "Cladism" as a philosophy of classification. Syst. Zool. 20: 373-376.

Nelson, G. 1971. Paraphyly and polyphyly: redefinitions. Syst. Zool. 20: 471-472.

Nelson, G. 1972. Phylogenetic relationship and classification. Syst. Zool. 21: 227-230.

Nelson, G. 1972. "Science or politics?": a reply to H. F. Howden. Syst. Zool. 21: 341-342.

Nelson, G. 1972. Review of Die Rekonstruktion der Phylogenese mit Hennig's Prinzip. Syst. Zool. 21: 350-352.

Nelson, G. 1972. Comments on Hennig's "Phylogenetic Systematics" and its influence on Ichthyology. Syst. Zool. 21: 364-374.

Nelson, G. 1973. The higher-level phylogeny of vertebrates. Syst. Zool. 22: 87-91.

Nelson, G. 1973. "Monophyly again?"- a reply to P. D. Ashlock. Syst. Zool. 22: 310-311.

Nelson, G. 1973. Comments on Leon Croizat's biogeography. Syst. Zool. 22: 312-319.

Nelson, G. 1973. Negative gains and positive losses: a reply to J. G. Lundberg. Syst. Zool. 22: 330.

Nelson, G. 1973. Classification as an expression of phylogenetic relationships. Syst. Zool. 22: 344-359.

Nelson, G. 1974. Darwin-Hennig classification: a reply to Ernst Mayr. Syst. Zool. 23: 452-485.

Nelson, G. 1977. A reply. Syst. Zool. 26: 91.

Nelson, G. 1978. Professor Michener on phenetics- old and new. Syst. Zool. 27: 104-111.

Nelson, G. 1978. Classification and prediction: a reply to Kitts. Syst. Zool. 27: 216-217.

Nelson, G. 1978. Ontogeny, phylogeny and the biogenetic law. Syst. Zool. 27: 324-345.

Nelson, 1978. The perils of perfection: a reply to D. H. Colless. Syst. Zool. 27: 124.

Nelson, G. 1979. Cladistic analysis and synthesis: principles and definitions, with a historical note on Adanson's Familles des Plantes (1763-1764). Syst. Zool. 28: 1-21.

Nelson, G. and N. I. Platnick. 1978. The perils of plesiomorphy: widespread taxa, dispersal and phenetic biogeography. Syst. Zool. 27: 474-477.

Nelson, G. and N. I. Platnick. 1980. Multiple branching in cladograms: two interpretations. Syst. Zool. 29: 86-90.

Platnick, N. I. 1976. Drifting spiders or continents?: vicariance biogeography of the spider family Laroniinae (Araneae: Gnaphosidae). Syst. Zool. 25: 101-109.

Platnick, N. I. 1976. Are monotypic genera possible? Syst. Zool. 25: 198-199.

Platnick, N. I. 1976. Concepts of dispersal in historical biogeography. Syst. Zool. 25: 294-295.

Platnick, N. I. 1977. Parallelism in phylogeny reconstruction. Syst. Zool. 26: 93-95.

Platnick, N. I. 1977. Paraphyletic and polyphyletic groups. Syst. Zool. 26: 195-200.

Platnick, N. I. 1977. Monotypy and the origin of higher taxa: a reply to E. O. Wiley. Syst. Zool. 26: 355-357.

Platnick, N. I. 1977. Cladograms, phylogenetic trees, and hypothesis testing. Syst. Zool. 26: 438-441.

Platnick, N. I. 1978. Adaptation, selection and falsifiability. Syst. Zool. 27: 347.

Platnick, N. I. 1978. Classifications, historical narratives and hypotheses. Syst. Zool. 27: 365-369.

Platnick, N. I. 1978. Gaps and prediction in classification. Syst. Zool. 27: 472-473.

Platnick, N. I. 1979. Philosophy and the transformation of cladistics. Syst. Zool. 28: 537-546.

Platnick, N. I. and H. D. Cameron. 1977. Cladistic methods in textual, linguistic and phylogenetic analysis. Syst. Zool. 26: 380-385.

Platnick, N. I. and G. Nelson. 1978. A method of analysis for historical biogeography. Syst. Zool. 27: 1-16.

Patterson, C. 1978. Verifiability in systematics. Syst. Zool. 27: 218-221.

Patton, J. C. and R. J. Baker. 1978. Chromosomal homology and evolution of phyllostomatoid bats. Syst. Zool. 27: 449-462.

Presch, W. 1979. Phenetic analysis of a single data set: phylogenetic implications. Syst. Zool. 28: 366-370.

Rosen, D. E. 1974. Cladism or gradism?: a reply to Ernst Mayr. Syst. Zool. 23: 446-451.

Rosen, D. E. 1975. A vicariance meodel of Caribbean biogeography. Syst. Zool. 24: 431-464.

Rosen, D. E. 1978. Vicariant patterns and historical explanation in biogeography. Syst. Zool. 27: 159-188.

Rosen, D. E. and D. G. Buth. 1980. Empirical evolutionary research versus neo-Darwinian speculation. Syst. Zool. 29: 300-308.

Sattler, R. 1963. Phenetic contra phyletic systems. Syst. Zool. 12: 94-95.

Savage, R. J. G. 1976. Review of early Sirenia. Syst. Zool. 25: 344-351.

Schlee, D. 1969. Hennig's principle of phylogenetic systematics, an "intuitive, statistico-phenetic taxonomy"? Syst. Zool. 18: 127-134.

Schuh, R. T. and J. T. Polhemus. 1980. Analysis of taxonomic congruence among morphological, ecological and biogeographic data sets for the Leptopodomorpha (Hemiptera). Syst. Zool. 29: 1-26.

Settle, T. W. 1979. Popper on "When is a science not a science?" Syst. Zool. 28: 521-529.

Settle, T. W. 1981. Kitts on Popper: A Reply. Syst. Zool. 30: 200-202.

Simon, C. M. 1979. Evolution of periodical cicadas: phylogenetic inferences based on allozymic data. Syst. Zool. 28: 22-39.

Smith, G. R. and R. K. Koehn. 1971. Phenetic and cladistic studies of biochemical and morphological characteristics of Catostomus. Syst. Zool. 20: 282-297.

Watrous, L. E. and Q. D. Wheeler. 1981. The out-group comparison method of character analysis. Syst. Zool. 30: 1-11.

Wiley, E. O. 1975. Karl R. Popper, systematics and classification: a reply to Walter Bock and other evolutionary taxonomists. Syst. Zool. 24: 233-242.

Wiley, E. O. 1977. Are monotypic genera paraphyletic?- a response to Norman Platnick. Syst. Zool. 26: 352-354.

Wiley, E. O. 1978. The evolutionary species concept reconsidered. Syst. Zool. 27: 17-26.

Wiley, E. O. 1979. Cladograms and phylogenetic trees. Syst. Zool. 28: 88-91.

Wiley, E. O. 1979. An annotated Linnean hierarchy, with comments on natural taxa and competing systems. Syst. Zool. 28: 308-337.

Wiley, E. O. 1980. Is the evolutionary species fiction?- a
        consideration of classes, individuals and historical
        entities. Syst. Zool. 29: 76-79.

Wiley, E. O. 1980. Must phylogenetic classifications be so
        complicated? Syst. Zool. 29: 309-313.

Yates, T. L., R. J. Baker, and R. K. Barnett. 1979. Phylogenetic
        analysis of karyological variation in three genera of
        peromyscine rodents. Syst. Zool. 28: 40-62.

Additional Suggested Readings:

Camin, J. H. and R. R. Sokal. 1965. A method for deducing
        branching sequences in phylogeny. Evolution 19: 311-326.

Farris, J. S. 1971. The hypothesis of non-specificity and
        taxonomic congruence. Ann. Rev. Ecol. Syst. 2: 277-302.

Farris, J. S. 1972. Estimating phylogenetic trees from distance
        matrices. Amer. Nat. 106: 645-668.

Farris, J. S. 1977. On the phenetic approach to vertebrate
        classification. in Hecht, Moody and Hecht eds. Major
        Patterns in Vertebrate Evolution. Plenum Press,
        Inc., New York.

Fitch, W. M. and E. Margoliash. 1967. Construction of phylogenetic
        trees. Science 155: 279-284.

Hennig, W. 1977. Phylogenetic systematics. Ann. Rev. Entomol.
        10: 97-116.

Hull, D. L. 1970. Contemporary systematic philosophies. Ann.
        Rev. Ecol. Syst. 1: 19-54.

McAllister, D. E. and B. W. Coad. 1978. A test between relationships
        based on phenetic and cladistic taxonomic methods. Can.
        J. Zool. 56: 2198-2210.

Wagner, W. H. Jr. 1961. Problems in the classification of ferns.
        in Advances in Botany. University of Toronto Press, Toronto.

Major Texts:

Brundin, L. 1966. Transantarctic relationships and their
        significance, as evidenced by chironomid midges. Kungl.
        Svenska Vetenskapsakademiens Handlingar 11: 1-472.

Cracraft, J. and N. Eldredge (eds.). 1979. Phylogenetic Analysis
        and Paleontology. Columbia Univ. Press, New York.

Eldredge, N. and J. Cracraft. 1980. Phylogenetic Analysis and
        the Evolutionary Process. Columbia Univ. Press, New York.

Funk, V. A. and D. R. Brooks (eds.). 1981. Advances in Cladistics: Proceedings of the First Meetings of the Willi Hennig Society. New York Botanical Garden, New York.

Hennig, W. 1966. Phylogenetic Systematics. Univ. Illinois Press, Urbana.

Nelson, G. and N. Platnick. 1981. Systematics and Biogeography: A Critique. Columbia Univ. Press, New York.

Wiley, E. O. 1981. Phylogenetics- The Theory and Practice of Phylogenetic Systematics. Wiley-Interscience, New York.

Pertinent Literature Addenda

Brooks, D.R. 1981. Hennig's parasitological method: a proposed solution. Syst. Zool. 30: 229-249.

Cracraft, J. 1982. Phylogenetic relationships and monophyly of loons, grebes and Hesperornithiform birds, with comments on the early history of birds. Syst. Zool. 31: 35-56.

Farris, J.S. 1982. Simplicity and informativeness in systematics and phylogeny. Syst. Zool. 31: 413-444.

Funk, V.A. and D.R. Brooks (eds.). 1981. Advances in Cladistics. Vol. 1. New York Botanical Garden, New York. 250 pp.

Haiduk, M.W. and R.J. Baker. 1982. Cladistical analysis of G-banded chromosomes of nectar feeding bats (Glossophaginae: Phyllostomidae). Syst. Zool. 31: 252-265.

Hood, C.S. and J.D. Smith. 1982. Cladistical analysis of female reproductive histomorphology in phyllostomatoid bats. Syst. Zool. 31: 241-251.

Lynch, J.D. 1982. Relationships of the frogs of the genus Ceratophrys (Leptodactylidae) and their bearing on hypotheses of Pleistocene forest refugia in South America and punctuated equilibria. Syst. Zool. 31: 166-179.

Mickevich, M.F. 1982. Transformation series analysis. Syst. Zool. 31: 461-478.

Platnick, N.I. and V.A. Funk (eds.). 1983. Advances in Cladistics. Vol. 2. Columbia Univ. Press, New York. 000 pp.

Watrous, L.E. and Q.D. Wheeler. 1981. The out-group comparison method of character analysis. Syst. Zool. 30: 1-11.

EVALUATION SHEET

1. What aspects of this workbook would you like to see presented
    in a different manner? Do you have any specific suggestions
    for a different approach?

2. Would you like to see anything deleted?

3. Would you like to see anything added?

4. General comments

Return this sheet to: Daniel R. Brooks
                        Department of Zoology
                        University of British Columbia
                        2075 Wesbrook Mall
                        Vancouver, B. C. V6T 2A9
                        Canada

5123 003