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An Analysis of Patterns of Homoplasy
in Freshwater Snails of the Family Planorbidae
(Pulmonata: Basommatophora)

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Donald L. Swiderski

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Robert J. Anstey
Major professor

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AN ANALYSIS OF PATTERNS OF HOMOPLASY IN FRESHWATER SNAILS OF THE FAMILY PLANORBIDAE (PULMONATA: BASOMMATOPHORA)

By

Donald L. Swiderski

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ABSTRACT

AN ANALYSIS OF PATTERNS OF HOMOPLASY
IN FRESHWATER SNAILS OF THE FAMILY PLANORBIDAE
(MOLLUSCA: PULMONATA)

by

Donald L. Swiderski

Homoplasy, the evolution of similar traits in independent lineages can be a serious impediment to phylogenetic analysis. However, phylogenetic inferences can be strengthened if they are based on a consensus derived from contrasting methods. The distributions of traits may also reflect processes of character evolution, independent of any phylogenetic conclusions the data may support.

The Planorbidae diverge from their nearest relatives principally by regression of respiratory structures and elaboration of glandular reproductive organs. Character loss, in all organ systems, produces the derived states most likely to be homoplasic. The most likely homologs are a small number of reproductive states. The phylogenetic relationships are inferred from the homologs in the reproductive tract. These states identify two major divisions within the Planorbidae, and a few smaller monophyletic groups within each division.

ACKNOWLEDGEMENTS

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KEY TO SYMBOLS

a. d.	apertural denticles
a. g.	albumen gland
ac.	acini
an.	anus
ant.	anterior
b. w.	body wall
bu. e.	buccal epithelium
bu. m.	buccal musculature
c. ch.	collecting channels
cen.	central
d. r.	dorsal ridge
e.	eye
eso.	esophagus
f. g. p.	female genital pore
fl.	flagellum
ft.	foot
g. r.	ganglionic ring
gon.	gonad
gz.	gizzard
h. d.	hermaphroditic duct
ic. c.	intercartilage contractor

in.	intestine
j.	jaw
k.	kidney
l. c.	lung cavity
lat.	lateral
lat. c.	lateral cusps
li.	liver
m. g. p.	male genital pore
man.	mantle
mar.	marginal
mo.	mouth
odp.	odontophore
ovd.	oviduct
p.	penis
p. s.	penis sheath
pp.	preputium
pp. g.	preputial gland
pp. g. d.	preputial gland duct
pp. r.	preputial ridge
pp. w.	preputial wall
pr.	prostate
pr. d.	prostate duct
psb.	pseudobranch
pst.	posterior
rad.	radula
rad. s.	radular sheath
rc. r.	rectal ridge

rn. r.	renal ridge
sal. g.	salivary gland
sem. r.	seminal receptacle
sem. v.	seminal vesicles
sh.	shell
si.	siphon
sovd.	spermoviduct
src.	sarcobellum
t.	tentacle
u. vel.	upper velum
ur. p.	urinary pore
v. d.	vas deferens
vel.	velum
ven.	ventricle

INTRODUCTION

As much as we would like to provide definitive answers to systematic questions, conclusive results of phylogenetic research projects are infrequent, pleasant surprises. Several factors create difficulties for the systematist. The ages of taxa, the time since divergence from a common ancestor, contributes to the systematic problem. As the time since divergence increases, the shared traits indicating common ancestry are likely to be obscured by independent morphological changes in all taxa. These independent changes could indicate only that the taxa are different, and may not necessarily reflect genealogical relationships. In the absence of a good fossil record, there would be no record of the accumulation of these differences over time. Extreme rates of morphological evolution also produce systematic problems. Very rapid rates will mimic the effect of great age, obscuring primitive traits; extremely conservative rates do not produce enough new traits for the systematist to discriminate among the taxa. However, the greatest source of difficulty for the systematist is the occurence of homoplasy: the evolution of similar traits in independent lineages.

Wiley (1981) notes that homoplasy arises from two distinct phylogenetic processes: parallelism and convergence. He defines parallelism as the evolution, in independent lineages, of similar derived states from a single primitive state present in the immediate common ancestor of those lineages (Figure 1-b). Wiley defines convergence as the evolution, in independent lineages, of similar derived states from different primitive states (Figure 1-c). This definition of convergence includes evolutionary reversals, in which a derived character state is transformed into a state that resembles an earlier, primitive state (Figure 1-d). These evolutionary patterns can be redefined in terms of character state transformations: parallelism is the repetition of a single character state transformation, convergence is the production of similar derived states by different character state transformations. In both cases, the similarity of independently derived character states can lead to incorrect hypotheses of relationships.

Homoplasy is not the only source of error in phylogenetic reconstruction. Errors may result if the entire study group or the operational taxonomic units are not monophyletic, if the direction of character evolution is misinterpreted, or if variation within the operational taxonomic units is not recognized. These errors are more likely for studies of supraspecific taxa or in analyses based on literature data. Other errors may result from

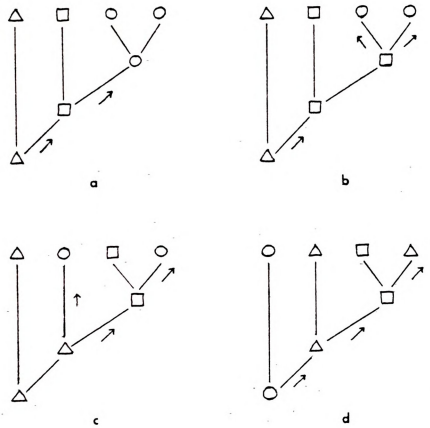

Figure 1. Schematic diagrams of evolutionary events producing homology and homoplasy. a) homology, each derived state produced by a single transformation event. b) homoplasy due to parallelism, a character transformation occurs in independent lineages. c) homoplasy due to convergence, similar derived states are produced by transformations of different primitive states. d) homoplasy due to convergence, reversal of a transformation series.

typing errors, or procedural errors in the algorithms used to analyses the data.

The errors described above are not completely independent of each other or of the problem of recognizing homoplasies. As an extreme, hypothetical example, homoplasic derived states may be interpreted as a shared primitive state that joins two separate taxonomic groups as a single taxon that is actually polyphyletic. While these problems deserve analysis in their own right, my main concern is the recognition of homoplasies, given correct analysis of the taxa and the primitive states.

The recognition of homoplasies entails resolution of the separate evolutionary events that produced them. Homoplasies possibly can be recognized during the initial analysis of the trait's structure and development. However, when these differences are noted and recorded as separate characters prior to the phylogenetic analysis, then there is no systematic problem. Problems arise when homoplasies are discovered in the course of the phylogenetic analysis. The best approach to resolving phylogenetic problems caused by homoplasy involves reexamining the biological properties of the characters in question.

Character reevaluation is not always the most accessible approach. One alternative is to collect more data. Ideally, if more data were available, the systematist would be able to determine which traits are homoplasic. The new data would constitute an independent test, corroborating

or refuting the original hypothesis. However, there is no a priori reason why new data should be less homoplasic than the data already available (Felsenstein 1978). Consequently, homoplasies must be dealt with in their own right.

At this point the systematist can either determine which elements of the data are most likely to be homoplasic, or employ an objective criterion which discriminates among competing phylogenetic hypotheses. Felsenstein (1973) favors a probabilistic approach, but admits that determining the likelihood of evolutionary events is a dubious proposition. Hecht and Edwards (1976) propose a weighting scheme based on generalizations about the information content of particular kinds of characters. These generalizations can be translated into likelihoods of homoplasy. Among the unbiased methods, the systematist can choose the tree with the fewest evolutionary events (Camin and Sokal 1965, Farris 1970), or the tree with the greatest number of homologs (Nelson and Platnick 1981). Whatever approach is taken, the phylogenetic inferences derived from highly homoplasic data will be weakly supported and very general.

Although data sets with several homoplasic states can be refractory to phylogenetic analysis, the pattern of character distributions can still be informative. Some character distributions may indicate phylogenetic patterns which are not contradicted by the distribution of other

characters. These phylogenetic patterns should emerge from any form of analysis. More importantly, the later sections of this paper demonstrate that detailed analyses of character distributions can lead to insights pertaining to general patterns of character evolution.

This study attempts to resolve the relationships of the genera of the family Planorbidae by analyzing patterns of homoplasy in the reproductive tract, the respiratory structures, the radula and the shell. The Planorbidae, with the Chilinidae, the Lymnaeidae and the Physidae are the major groups in the superfamily Lymnaeacea. Because homoplasy is common throughout the family, a preliminary analysis of the relationships of these families is necessary to determine the primitive states of the Planorbidae. All four families have nearly global geographical distributions; they are absent only from Antarctica and some isolated oceanic islands. The geographical ranges of the planorbid genera are listed in Table 1. With the exception of the Chilinidae, the ecological ranges of these families are equally broad. The Chilinidae are restricted to brackish intertidal estuarine habitats, but representatives of the other families may be found in paludal, fluvial or lacustrine environments.

There have been three previous attempts to understand the relationships among the genera of the Planorbidae. These studies have analyzed the Planorbidae alone (Hubendick 1955), or in the context of its relationships to other

Table 1. Genera of the Planorbidae, coiling type and geographic occurrence

Code	Genus	Coiling type	Geographic region
ACR	Acrorbis	helicoid	Neotropical
AME	Amerianna	helicoid	Australian Oriental
ANC	Ancylastrum	limpet	Australian Ethiopian Neotropical
ANS	Ancylus	limpet	Palearctic
ANI	Anisus	discoid	Palearctic
ARM	Armiger	discoid	Holarctic
BIO	Biomphalaria	discoid	Ethiopian Nearctic Neotropical
BUL	Bulinus	helicoid	Australian Ethiopian Palearctic
BUR	Burnupia	limpet	Ethiopian
CAM	Camptoceras	helicoid	Oriental
CHO	Choanomphalus	helicoid	Palearctic
DRE	Drepanotrema	discoid	Neotropical
FER	Ferrissia	limpet	Australian Ethiopian Nearctic Oriental
FOS	Fossulorbis	discoid	Neotropical
GUN	Gundlachia	limpet	Australian Ethiopian Nearctic Neotropical
GYR	Gyraulus	discoid	Ethiopian Holarctic Oriental

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Table 1 (cont'd.).

HLC	Helicorbis	discoid	Oriental
HLS	Helisoma	discoid	Nearctic Neotropical
HIP	Hippeutis	discoid	Palearctic
IND	Indoplanorbis	discoid	Oriental
LAE	Laevapex	limpet	Nearctic
LEN	Lentorbis	discoid	Ethiopian
MEN	Menetus	discoid	Nearctic
MIR	Miratesta	helicoid	Australian
PAT	Patelloplanorbis	limpet	Australian
PHY	Physastra	helicoid	Oceanic Oriental
PAR	Planorbarius	discoid	Palearctic
PBS	Planorbis	discoid	Palearctic
PBU	Planorbula	discoid	Nearctic
PLE	Plesiophysa	helicoid	Neotropical
POL	Polypylis	discoid	Oriental
PME	Promenetus	discoid	Nearctic
PNC	Protancylus	limpet	Australian
RHO	Rhodacmea	limpet	Nearctic
SNA	Segmentina	discoid	Palearctic
SRB	Segmentorbis	discoid	Ethiopian

members of the superfamily Lymnaeacea (Starobogatov 1967, Hubendick 1978). These studies have yielded widely divergent classifications, the results of which are illustrated in Figures 2, 3 and 4, respectively. The inclusion of different genera in each analysis only partially explains the differences among these three studies.

The major sources of conflict are differences in character weighting. Hubendick (1955) argues that the importance of reproduction and the internal carriage of the copulatory organs makes these structures adaptively significant and free from environmental variation. Therefore, Hubendick bases his phylogeny on the copulatory organs. He does distinguish between different arrangements of the prostatic diverticula, but this is only used to confirm the phylogeny based on the copulatory organs. In contrast, Starobogatov (1967) emphasizes the structural importance of invagination and evagination and does not consider diverticular arrangement to be significant. Starobogatov does consider both the prostate and the gonad. Starobogatov and Hubendick both use characters which are not in the reproductive tract to discriminate taxa at lower levels. Starobogatov uses shell characters and Hubendick uses radular and respiratory characters. Hubendick (1978) attempts to synthesize his earlier work and Starobogatov's. Reproductive characters, especially diverticula, are still heavily emphasized, but shell and radular characters are

Figure 2. Taxonomic positions of the genera of the Planorbidae (Hubendick 1955).

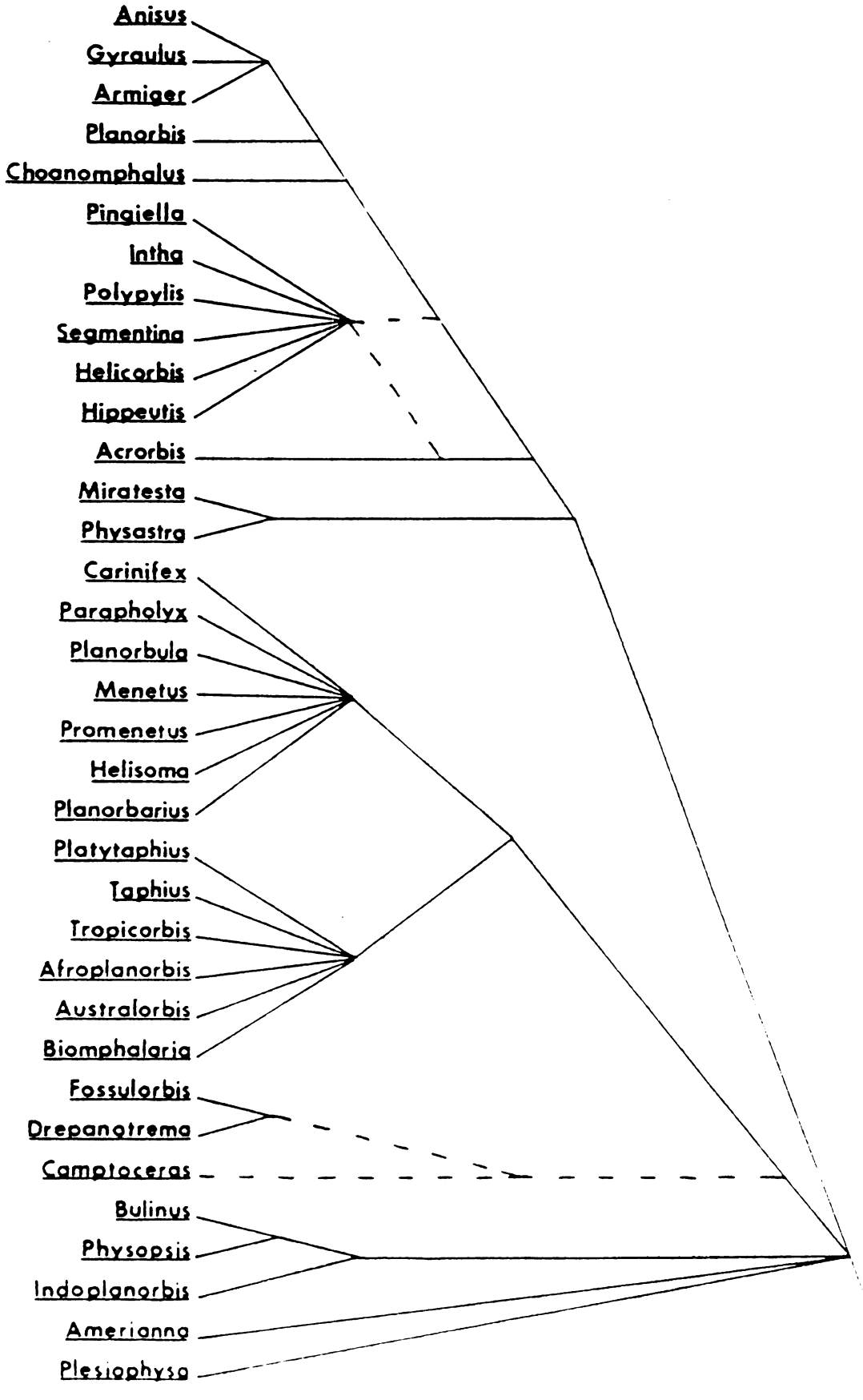

Anisus
Gyraulus
Armiger
Planorbis
Choanomphalus
Pingiella
Intha
Polypylis
Segmentina
Helicorbis
Hippeutis
Acrorbis
Miratesta
Physastra
Carinifex
Parapholyx
Planorbula
Menetus
Promenetus
Helisoma
Planorbarius
Platytaphius
Taphius
Tropicorbis
Afroplanorbis
Australorbis
Biomphalaria
Fossulorbis
Drepanotrema
Camptoceras
Bulinus
Physopsis
Indoplanorbis
Amerianna
Plesiophysa

Figure 2.

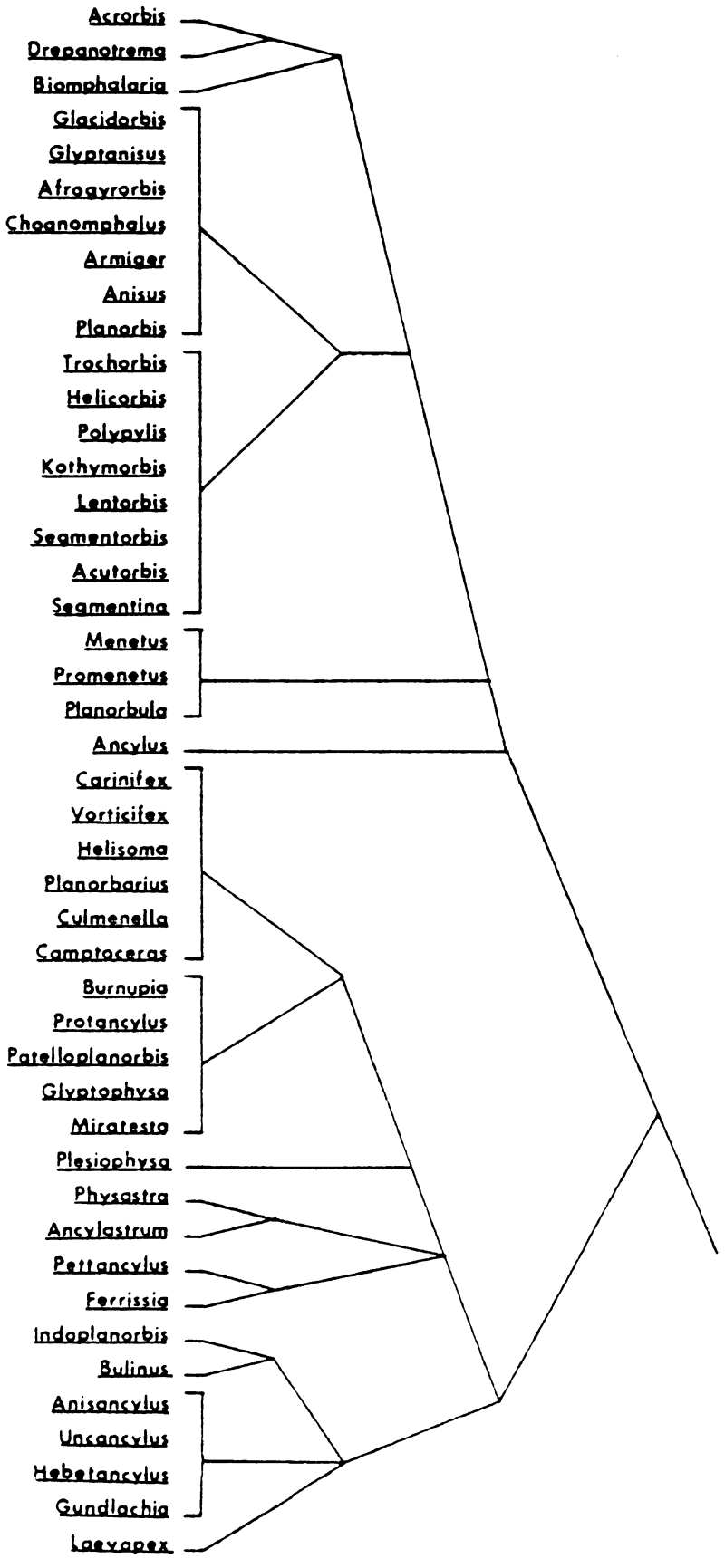


Figure 3. Phylogenetic relationships of the genera of the Planorbidae (Starobogatov 1967) Brackets indicate unresolved subfamilies or tribes.

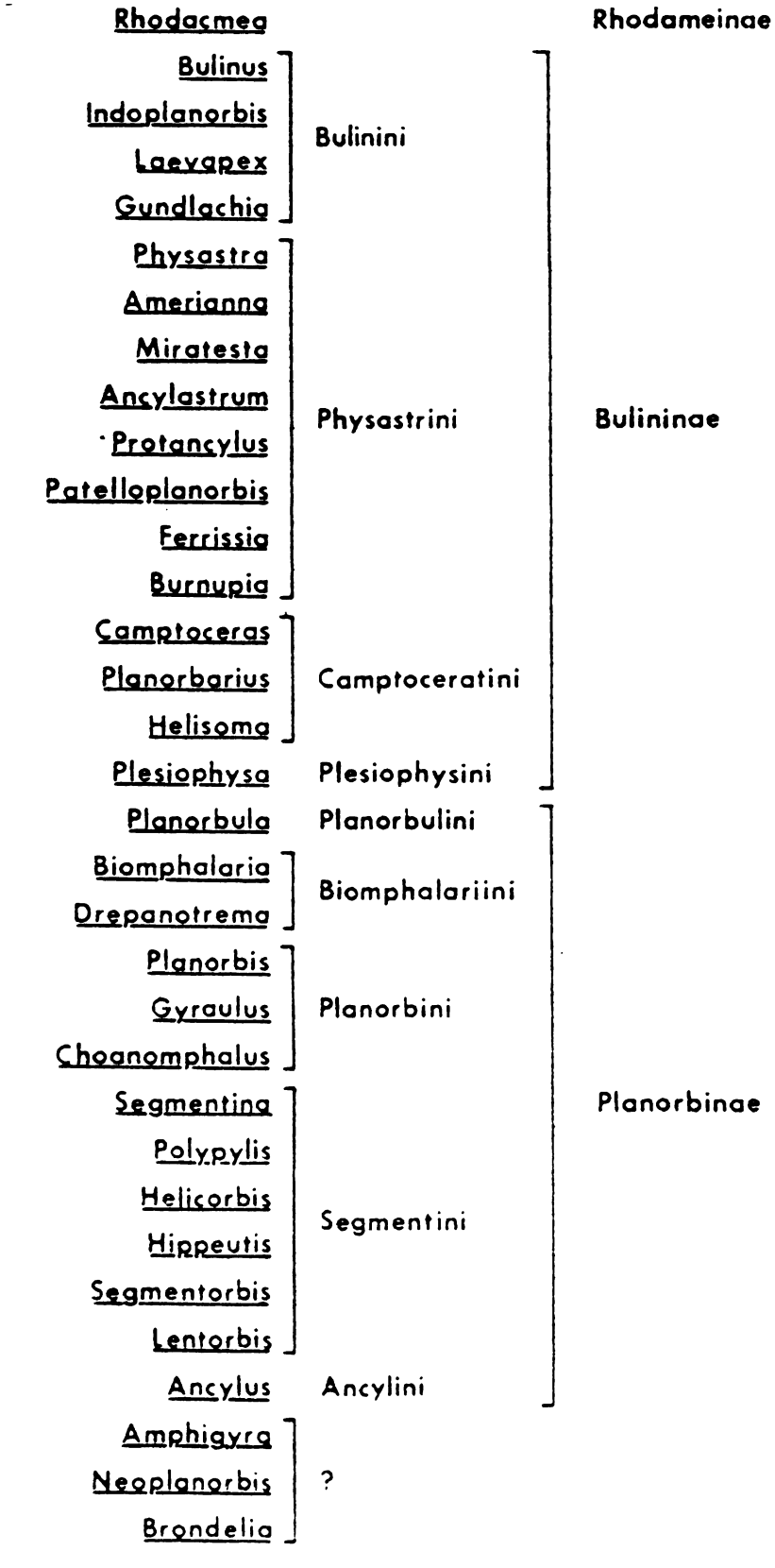


Figure 4. Classification of the genera of the Planorbidae (Hubendick 1978)

considered unimportant. Consequently, three different phylogenies are produced by these studies.

Some of the difficulties in assessing relationships within the Planorbidae and the Lymnaeacea derive from the ages of these groups. The Planorbidae and its closest relatives in the Lymnaeacea date from the Jurassic (Zilch 1960). Figure 5, based on Zilch's classification, illustrates the sparse fossil record of this group. There is no fossil record before the Pliocene for the most primitive lymnaeaceans, the Chilinidae. Both extant genera of Physidae have continuous fossil records extending to the Jurassic. According to Zilch, there are no extinct genera attributed to the Physidae. The Lymnaeidae and the Physidae appear later in the Jurassic than do the Planorbidae. Few planorbid or lymnaeid genera are present in the Jurassic, but the number of genera increases through time. The highest generic diversity of both families occurs in the Recent.

There are two problems with interpreting the fossil record as a genealogical record. The most important flaw is that only the shells are preserved and intrinsic traits of the shells provide little or no clue to the nature of the soft internal organs. Therefore, the primitive states of the internal organs are likely to be obscured by independent morphological changes in all taxa. In addition, data gathered by Boycott et al. (1930) and Freeman and Lundelius (1982) indicates a simple genetic basis for gross

Figure 5. Geologic ranges and representative shell morphologies of the genera of the Lymnaeacea. a) Chilina fluctuosa, Recent b) Latia neritoides, Recent c) Acroloxus lacustris, Recent d) Aplexa hypnorum, Recent e) Physa fontinalis, Recent f) Stagnicola kingi, U. Pliocene g) Stagnicola caperata, Recent h) Radix elegans, M. Pliocene i) Radix velutina, L. Pliocene j) Valenciennius annulatus, L. Pliocene k) Lymnaea stagnalis, Recent l) Acella haldemani, Recent m) Acella tenuicosta, L. Paleocene n) Erinna newcombi, Recent o) Lanx patelloides, Recent p) Bulinus newcombi, Recent q) Plesiophysa striata, Recent r) Physastra vestita, Recent s) Anisus krambergi, L. Pliocene t) Gyraulus albus, Recent u) Gyraulus trochiformis, Miocene v) Australorbis glabratus, Recent w) Anisopsis calculus, M. Jurassic x) Helisoma anceps, Recent y) Carinifex newberryi, Recent z) Carinifex binneyi, Miocene aa) Ancylastrum cumingianum, Recent bb) Ferrissia rivularis, Recent

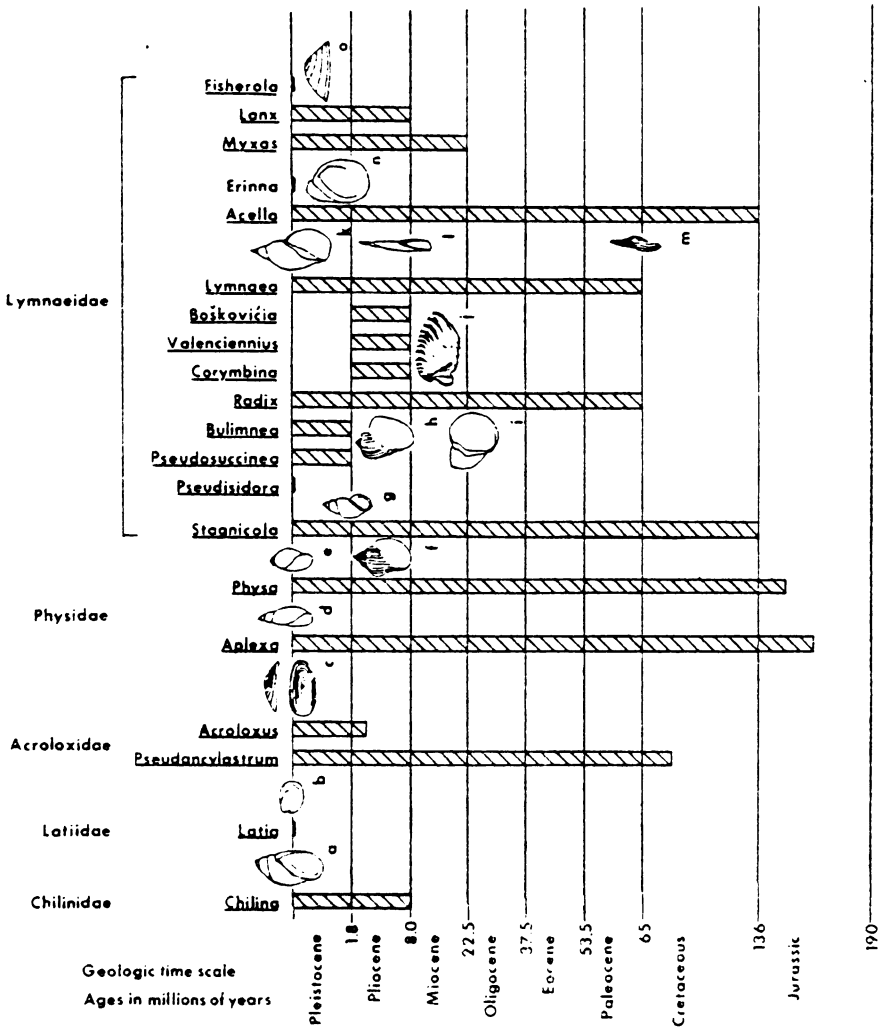

Fisherola
Lanx
Myxas
Erinna
Acella
Lymnaeidae
Lymnaea
Boškovićia
Valenciennius
Corymbina
Radix
Bulimnea
Pseudosuccinea
Pseudisidora
Stagnicola
Physa
Physidae
Aplexa
Acroloxus
Acroloxidae
Pseudancylastrum
Latiidae
Latia
Chilinidae
Chilina
1.8
8.0
22.5
37.5
53.5
65
136
190
Pleistocene
Pliocene
Miocene
Oligocene
Eocene
Paleocene
Cretaceous
Jurassic
Geologic time scale
Ages in millions of years

Figure 5.

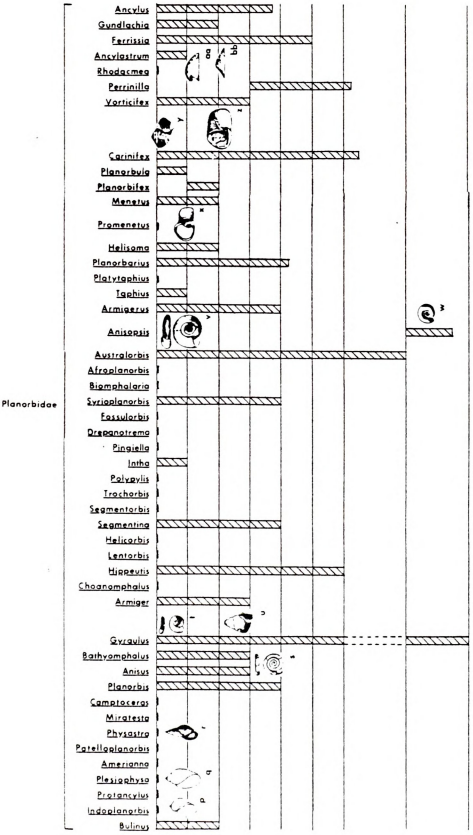


Figure 5 (cont'd.).

differences in shell form within populations of a single species. Their results suggest that shell form does not reliably predict phylogenetic relationships at any taxonomic level. As Figure 5 illustrates, the Planorbidae include forms similar to those in other families. Thus, the fossil record provides a restricted amount of data and the data it does provide are not reliable.

Character state differences among the extant taxa suggest patterns of evolution which are likely to confuse systematists. The number of characters which have evolved new states is relatively small, which implies a conservative rate of morphological evolution. The practical consequence of this slow rate is a small number of traits which permit discrimination among taxa. In addition, many of the new traits which have evolved appear to have arisen independently in more than one lineage. Thus, there is a high frequency of homoplasy, including reversals. This combination of age, conservatism and homoplasy makes it quite difficult to recognize phylogenetic relationships.

Thus, the family Planorbidae provides a data set suitable for an analysis of methods which attempt to resolve homoplasies. The conflicts among previous studies suggest that homoplasies are frequent enough to be serious obstacles to systematic analysis. Furthermore, the distribution of derived states among the genera of this family and its relatives suggests that there are evolutionary tendencies likely to produce many homoplasies. The high probability of

homoplasy is also supported by the small amount of fossil evidence that does exist. Thus, the distribution of derived character states is not only suitable for analysis of homoplasy, the distribution requires analysis of homoplasies if the evolutionary history of the Planorbidae is to be resolved.

METHODS

Two procedures were used to evaluate the distribution of derived character states within the Planorbidae. They include parsimony analysis of Wagner Trees (Farris 1970, Farris et al. 1970), and components analysis (Nelson 1979, Nelson and Platnick 1981). The parsimony analysis was implemented by the PAUP program developed by Swofford (1984). Detailed descriptions of these methods are presented below. Both methods were used to compare their approaches to recognizing and resolving homoplasies. Although these methods represent different styles of phylogenetic inference, both produce generalizations about the distribution of homoplasy in the characters under study.

The Wagner parsimony method is a generalized procedure for estimating evolutionary divergence and branching patterns from a hypothesized primitive groundplan. The parsimony criterion restricts the number of possible solutions to those that require the fewest evolutionary events to explain the distribution of derived character states. Originally, Camin and Sokal justified this application of the parsimony criterion by asserting that evolutionary events are rare. In the analysis of the Planorbidae, I used parsimony as a working principle to

estimate the minimum homoplasy incorporated in the data, as suggested by Nelson and Platnick.

The Wagner method is one of three common approaches to building parsimonious trees. Another method, proposed by Camin and Sokal, is based on the assumption that evolutionary change is irreversible. This method rejects the possibility that a lineage might return to an ancestral state (as in Fig. 1-d). It can only test for the possibility that a transformation from a primitive state to a derived state has occurred more than once (Fig. 1-b). The third method is based on Dollo's assertion that each evolutionary change is unique (Le Quesne 1975, Farris 1977). This method can only evaluate the likelihood of events like that depicted in Fig. 1-d. Thus, the Camin and Sokal method can only evaluate the possibility that a derived state is homoplasic due to parallelism, while the Dollo method can only evaluate possibility that the primitive state is homoplasic due to convergence by reversal. The Wagner method considers parallelism and reversal equally likely and evaluates the relative importance of each.

All three methods are limited to evaluating a single transformation series for each character. They cannot propose alternative transformation series or directly assess competing transformation series. To evaluate alternative models for character evolution it would be necessary to construct separate data matrices compare the competing transformation series across different groups of taxa.

Therefore, parsimony methods cannot directly assess the possibility of convergence due to independent origins (Figure 1-c).

The input format for parsimony programs is a matrix of taxa and character states (Figure 6-a). Characters are coded 0 or 1 to indicate primitive or derived states, respectively. Phylogenetic trees are produced by estimating the hypothetical intermediate ancestor of a pair of taxa (Figure 6-b). The character states attributed to the ancestor are calculated to be those which minimize the deviation of both derived taxa from the ancestor (Farris 1970). When calculated for all taxa and all hypothetical intermediates, this produces the tree with the fewest evolutionary events. For three taxa, there are three possible tree topologies (Figure 6-c). The characters are placed on these trees according to the method of Camin and Sokal, which requires that a transformation occur several times rather than be reversed. Tree III is preferred since it requires the fewest transformation events. In this particular case, the same tree topology would be produced by a Dollo algorithm. Figure 6-d illustrates the interpretation of character evolution required by Dollo, in which the transformation of character B is reversed. According to the Wagner method these two interpretations are equally likely. Figure 6-e illustrates the most parsimonious solutions for all five taxa listed in the data matrix. Tree I is produced by Camin and Sokal; tree II is

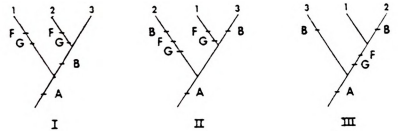
Figure 6. Parsimony analyses of a hypothetic data set. a) Data matrix for 5 taxa and 6 two-state characters. b) Symbolic representation of the occurrence of the derived state of A in taxa 1 and 2. c) Three possible tree topologies for three taxa, character state transformations interpreted according to Camin and Sokal. d) Dollo solution for the same three taxa. e) Camin and Sokal (I) and Dollo (II) solutions for all 5 taxa.

a)

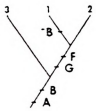
	CHARACTERS						
	A	B	C	D	E	F	G
1	1	0	1	0	0	1	1
2	1	1	0	0	0	1	1
TAXA 3	1	1	0	0	1	0	0
4	1	0	1	1	1	1	0
5	1	0	1	1	1	0	1

b)

c)



d)



e)

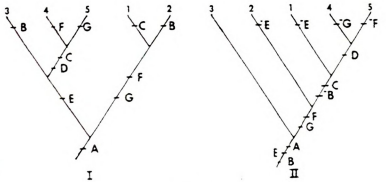


Figure 6.

produced by Dollo. In this instance, the Wagner program would agree with Camin and Sokal since tree I is more parsimonious. There may also be cases in which the Wagner method generates solutions which are more parsimonious than either Camin and Sokal or Dollo.

There are two reasons to prefer the Wagner method for the analysis of planorbid systematics. The first argument for the Wagner method is that it is more general than the other two. The method of Camin and Sokal and that of Dollo can only test for a single type of homoplasy. The Wagner method can assess the possibility of both types of homoplasy for each character since no assumption of irreversibility is made. Therefore, in the absence of any biological information favoring one method, the Wagner method is preferred on the basis of its greater generality. The second argument is the biological information available for the Lymnaeacea. These data, which are presented in the following sections, suggest that there are homoplasies among both primitive and derived characters. Since the Wagner method accomodates both possibilities, this method is also preferable on biological grounds.

Parsimony will be used as a working principle, not an assumption about the nature of evolutionary processes. Therefore, the Wagner Trees produced will be interpreted as estimates of the minimum amount of homoplasy in the data. Those states whose distributions must be explained by multiple evolutionary events are hypothesized to be

homoplasic. An estimate of the minimum number of homoplasic events averaged over all characters can be derived from the consistency index (Table 2). The index is a ratio of the number of derived states over the length of the tree, the number of transformation events proposed by the tree (7/11 for Figure 6-e, I.). For an ideal data set that included no homoplasies, the number of derived states and the number of transformation events would be the same. The inverse of the consistency index is the average number of character state changes per derived state. Thus, the primary results of the parsimony procedure are a hypothesis of relationships, an estimate of overall homoplasy. In addition, the homoplasy of particular character states can be inferred from the proposed phylogeny.

Components analysis uses the same data matrix as Wagner Trees, and like them makes no assumption concerning the most likely direction of evolutionary change. Components analysis differs from Wagner Trees in that it does not directly produce a phylogenetic hypothesis. Instead, components analysis produces nested sets of taxa from which phylogenetic inferences can be made. A component is a set of taxa defined by a derived character state (Figure 7-a). If the character is homologous across all members of the set, then the component is a monophyletic group. The best estimate of phylogeny using this method is the set of nesting components that incorporates the greatest number of monophyletic groups (Figure 7-c, tree I). These components

Table 2. Sample calculations of the consistency index and measures of overall homoplasy

Hypothetical phylogeny	Parameter name				
	S	T	ci	1/ci	D
A	20	22	.91	1.1	10
B	20	24	.825	1.2	20
C	20	25	.8	1.25	25
D	21	28	.75	1.33	33
E	20	30	.667	1.5	50
F	20	40	.5	2.0	100

Definitions of Parameters

S - Number of derived states;

T - Number of transformation events;

ci - Consistency index - S/T

1/ci - Average number of transformation events per state

D - Average percent of derived states homoplasic -

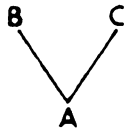
100 x {(T-S)/S}

Figure 7. Components analysis of a hypothetical data set. a) Components, sets of taxa, defined by the derived states of six characters. b) Graphic representation of the relationships of three components. The sets defined by the derived states of B and C are mutally exclusive subsets of the component defined by the derived state of A. c) All possible components relationships for this hypothetical data set. d) Phylogenetic trees implied by each of the components diagrams. e) Character evolution interpreted according to Camin and Sokal for tree I.

a)

CHARACTERS	TAXA
A	1, 2 3, 4, 5
B	2, 3
C	1, 4, 5
D	4, 5
E	3, 4, 5
F	1, 2, 4
G	1, 2, 5

b)



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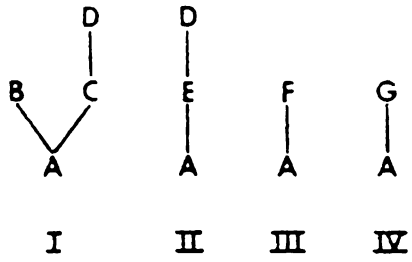

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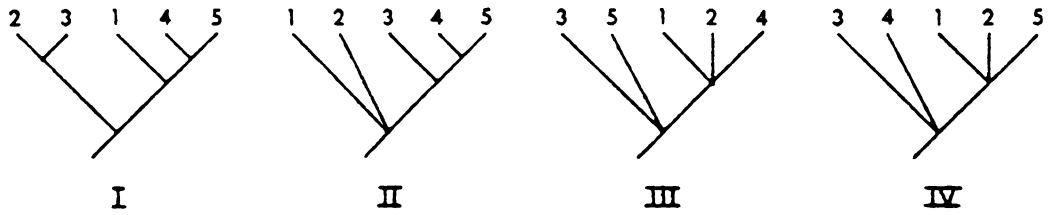


e)

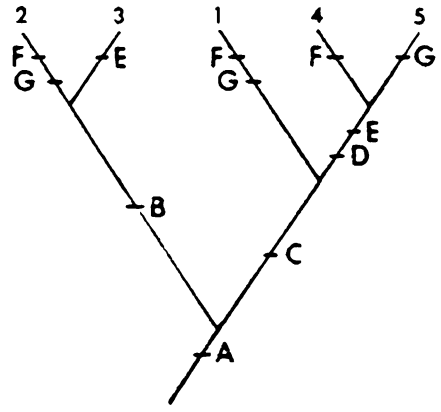


Figure 7.

can be illustrated with a branching cladogram (Figure 7-d). However, the intent of components analysis is to find the largest set of monophyletic groups consistent with the distribution of derived character states, not a fully resolved, bifurcating tree.

Because components analysis does not consider the number of evolutionary events implied by the character distributions, the method does not directly estimate the amount of homoplasy in the data. However, since this method identifies potential monophyletic groups, it can be used to hypothesize which characters are homoplasic. If two characters specify conflicting monophyletic groups, at least one of the characters must be homoplasic (LeQuesne 1969), asuming no other source of error. Thus, the results of components analysis are general hypotheses of relationship and hypotheses of which characters are homoplasic.

Both parsimony analysis and components analysis can be used to explore the possibility of homoplasy in a data set. Parsimony analysis can be used to identify the character states that must be homoplasic even on the shortest trees. Components analysis directly solves for the smallest number of homoplasic characters. Frequently, the components solution may be a subset of the parsimony solutions, but this is not necessarily the case (Figure 6-e vs. Figure 7-e).

Large amounts of homoplasy can be a serious obstacle to both parsimony analysis and components analysis. Parsimony

analysis indicates homoplasic states by identifying those character state transformations which must have occurred more than once. If the number of homoplasic events is greater than the number of homologs, parsimony methods cannot reliably indicate which characters are homoplasic (Felsenstein 1978). Furthermore, Felsenstein reports that under these conditions parsimony solutions are unlikely to improve as more data are included in the analysis. In a components analysis, both states defining a pair of conflicting components are potentially homoplasic. Thus, the number of potentially homoplasic states can be much higher than the number of states that actually are homoplasic. As a result, the principal effect of homoplasies is to reduce the degree of resolution possible in components analysis. Finally, both parsimony analysis and components analysis tend to produce multiple, equally acceptable, solutions. Since no one solution can be preferred, only the general interpretation subsuming all of the alternates is truly acceptable. If homoplasy is especially common, this can leave the systematist with little phylogenetic interpretation of the data.

This frustrating result can be avoided if the probabilities of evolutionary events can be estimated, as proposed by Felsenstein (1973). The critical difficulty with such methods is the derivation of a biologically sound probabilistic model for evolutionary change. An alternative to a strictly probabilistic model is a weighting scheme

derived from generalizations about the relative likelihood of homoplasy. Hecht and Edwards discuss one set of generalizations which can be applied to all taxonomic groups. This weighting scheme is based on the information content of various transformation events. The implication is that the most uninformative transformations are also the most likely to be homoplasic. This broad weighting scheme and evaluations of homoplasy in related taxa were used as hypotheses of homoplasy in the Planorbidae.

For the analysis of phylogenetic relationships and homoplasy in the Planorbidae, all characters were entered in both PAUP and the components analysis. The parsimony analysis was used to confirm hypotheses of homoplasy. Based on Hecht and Edwards, losses and reductions are hypothesized to be the most likely homoplasies. An analysis of interfamilial relationships in Lymnaeacea, which is presented in the next section, suggests that many traits of the shell and radula may also be homoplasic. The likelihoods of homoplasy for losses, reversals, shell and radular traits were tested by comparing the consistency indices of trees generated with and without these characters. A parallel analysis was performed using the components method. In this analysis, the likelihood of homoplasy was tested by scanning the data matrix for consistent patterns of components conflicts. Those character sets which are consistently in conflict with other

characters are likely to be homoplasic. The final results of both methods were then compared.

These two methods constitute independent tests of the phylogenetic interpretations which might be supported by the data. If none of the data were homoplasic, then both methods would produce the same phylogeny. However, since these methods approach phylogeny reconstruction in different ways, the results based on homoplasic data are expected to differ. In fact, the difference between the results may increase as the amount of homoplasy increases. Still, the areas of concordance between the results of different methods should indicate those aspects of the phylogeny that are most reliable (LeQuesne 1982).

PHYLOGENETIC POSITION OF THE PLANORBIDAE

INTRODUCTION

Phylogenetic systematics attempts to reconstruct genealogical relationships on the basis of hypothesized character state transformations. The degree to which the reconstruction approximates evolutionary history is dependent on the accuracy of these transformation series. The accuracy of the transformation series is dependent on recognition of the primitive state of each character, the state inherited from the ancestor of the study group. Hypotheses of primitiveness are commonly derived from four sources of information: the fossil record, ontogeny, the distribution of the character states in the study group, and the phylogenetic context of the study group.

The fossil record of the study group is that portion of its history that has been preserved by geological processes. It presents a chronologically ordered series of forms. The accuracy with which this series reflects the history of transformations depends on the completeness of the fossil record. Stratigraphic completeness can be estimated based on the variability of sedimentation rates in recent environments (Schindel 1980). The completeness of the lithostratigraphic record does set an upper limit for the

potential completeness of the fossil record (Dingus and Sadler 1982, Schindel 1982). Unfortunately, there is no means to determine the actual completeness of any given fossil record. Analyses may be performed to estimate how well a fossil assemblage has been sampled (Sanders 1968), but the assemblage is itself a sample of the contemporaneous biota. Given the unknown quality of the fossil record, it is best used to form hypotheses that can be tested by other sources of information (Eldredge and Cracraft 1980).

The fossil record of the Lymnaeacea imposes further constraints on its utility as a source of information. Typically, only the shells of snails are preserved; and these poorly reflect the morphology of the soft organs they enclosed. The shells of freshwater snails are also quite thin; they are less likely to be preserved than the shells of marine snails. Consequently, the known fossil record of the Lymnaeacea is quite sparse; and therefore, I have restricted my study to extant genera.

The second source for data from which character state transformations may be inferred is the developmental history of the character. The underlying assumption employed in deriving evolutionary history from developmental histories is that those states which occur early in development are evolutionarily primitive. As Eldredge and Cracraft (1980) carefully point out, this assumption is only valid when the evolution of development is peramorphic, adding new states to the end of the developmental process (Gould 1977, Alberch

et al. 1979). Paedomorphic evolution, by deleting later developmental changes, results in the loss of derived character states and is a source of homoplasy (Figure 8). Even if the derived paedomorph differs from the original, primitive state, it still represents unknown evolutionary transformations. As with the fossil record, Eldredge and Cracraft recommend using ontogenies as a source of hypotheses to be tested by other sources of information. Unfortunately, the ontogenetic data available on the Planorbidae is limited to very early development and a small number of later transformations.

Nelson and Platnick support a third method of inference. They analyze the distribution of the characters across the study group. Extinct taxa may be used if the relevant traits have been fossilized; however, it is assumed that the exclusion of taxa has not altered the distributions of the character states. The most widely distributed character states are assumed to be primitive. Character states with more restricted distributions are assumed to be derived. This method of determining the sequence of character state transformations also forms the basis of components analysis of phylogeny. The character state which is most widely distributed defines the largest set of taxa; and therefore, is attributed to an earlier time in the evolutionary history of the group.

A consequence of this argument is that character states whose distributions extend beyond the study group define a

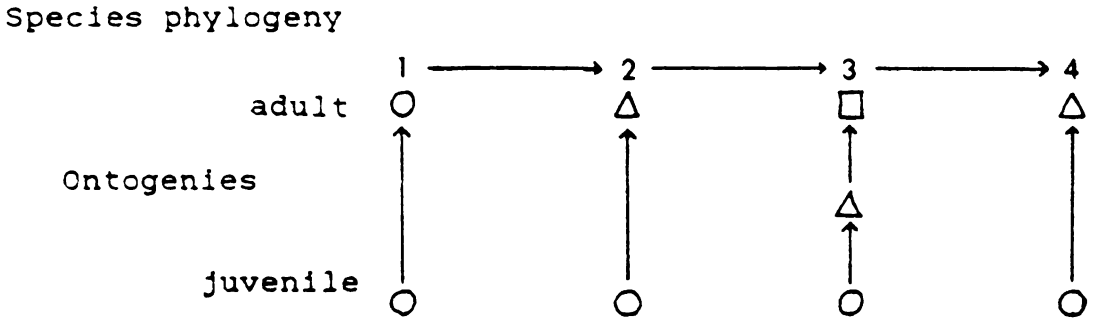


Figure 8. Homoplasy due to paedomorphosis. The adult state, Δ, arises by two different, independent events. In species 2 Δ is an addition to ontogeny, a peramorphic event. In species 4, □ is deleted from ontogeny leaving Δ as the adult state, a paedomorphic event.

component which includes the study group. Therefore, characters present in the study group and its genealogical relatives are the most primitive states in the study group, inherited by the study group and its relatives from their common ancestor. Logically, the best estimate of the primitive states for the taxon of interest is the nearest relative of that taxon (Wiley 1981), whether living or extinct. This nearest relative is the fourth source of information concerning the primitiveness of character states. States determined by previous analyses to be primitive in the nearest relative are assumed to be primitive for the taxon of interest. This is the method of outgroup analysis: primitive states are recognized by comparison of the study group to its nearest relatives. The critical assumption of outgroup analysis is that the phylogeny identifying the nearest relative is correct. If the correct outgroup has not been identified, the phylogenetic analysis of the study group cannot be correct.

Given the theoretical and practical considerations above, outgroup analysis is, operationally, the best method for determining the primitive character states in the family Planorbidae. However, use of this method is critically dependent on a good understanding of the evolutionary relationships of the superfamily Lymnaeacea, which includes the Planorbidae. The following sections examine the currently accepted hypothesis of the position of the

Planorbidae in the Lymnaeacea, and in the subclass Pulmonata.

SYSTEMATICS OF THE PULMONATA

The origin of the subclass Pulmonata and the phylogenetic relationships of its members have been the subjects of continuous debate for nearly one hundred years (Cox 1960). Recent authors do agree that the Pulmonata are a monophyletic group (Hubendick 1978, Tillier 1984, Haszprunar 1985). The defining character cited by all of these studies is the development of a lung from the mantle cavity (Raven 1958, Ghose 1963). In addition, the gills normally found in snails have been lost. Tillier also lists distinguishing traits in the nervous and reproductive systems.

The central problem in understanding the evolutionary history of the Pulmonata is the assessment of relationships among the most primitive members of the subclass. These forms typically inhabit brackish, estuarine intertidal zones. They commonly show reductions of the shell culminating in the evolution of limpets and slugs. Tillier observes that the internal anatomy of these snails undergoes extensive morphological changes, including losses, in conjunction with the reduction and loss of the shell. Similar morphological changes and systematic problems in the gastropod subclass Opisthobranchia have been summarized by Gosliner and Ghiselin (1984). Such convergent tendencies, involving structures throughout the animal's anatomy, make

it quite difficult to discern the evolutionary history of the primitive pulmonates.

Traditionally, the subclass is divided into two orders: the Basommatophora which are generally aquatic in habit, and the terrestrial Stylommatophora. The primitive estuarine pulmonates are classified as basommatophorans. Brace (1983) hypothesizes transitions from these primitive forms to the terrestrial stylommatophorans and to the freshwater, higher basommatophorans of the superfamily Lymnaeacea. This hypothesis is supported by the morphology and behavior of the lymnaeacean genus Chilina, which Brace places at the base of the lymnaeacean lineage. Duncan (1960a), on the basis of just the reproductive systems of the pulmonates, also places Chilina near the point of divergence of the Lymnaeacea and the Stylommatophora. Tillier's more extensive analysis also supports this conclusion.

PHYLOGENY OF THE LYMNAEACEA

The definition of the superfamily Lymnaeacea is in need of revision. Members of this group are traditionally recognized by the loss of a free-swimming larval stage and the absence, even in embryonic stages, of an operculum to close the shell (Hubendick 1978). Although these losses are not common in other gastropod groups, Hubendick observes that they are not unique, even within the subclass Pulmonata. Consequently, these traits are not necessarily a valid basis for classification. A derived state shared by the lymnaeaceans and unique among pulmonates is the

specialization of regions of the oviduct for different secretory functions (Duncan 1960a). This definition of the superfamily has the additional advantage of being based on a character which is an addition, not a loss.

On the basis of Duncan's observations, the families Chilinidae, Latiidae, Acroloxidae, Lymnaeidae, Lancidae, Physidae and Planorbidae form a monophyletic group, the superfamily Lymnaeacea. Figure 9-a represents the currently accepted phylogeny (Hubendick 1947, 1978, Duncan 1960b, Harry 1964, Starobogatov 1967). Three families, Latiidae, Acroloxidae and Lancidae, are each composed of a single genus of limpets. Because these families are derived offshoots of the Chilinidae and the Lymnaeidae, they cannot provide information about the relationships of the Chilinidae and the Lymnaeidae to the Planorbidae. Therefore, the Latiidae, Acroloxidae and Lancidae will be omitted from further consideration. Figure 9-b illustrates the conventional hypothesis of relationships among the four remaining families.

The conventional taxonomy is based primarily on subjective analyses of similarities in small sets of structures. Rarely are the states of several characters compared, and the primitive family, Chilinidae, is rarely compared to the other lymnaeaceans. The following sections analyze the data presented in earlier studies with the explicit intention of determining derived character states relative to those present in the Chilinidae. These

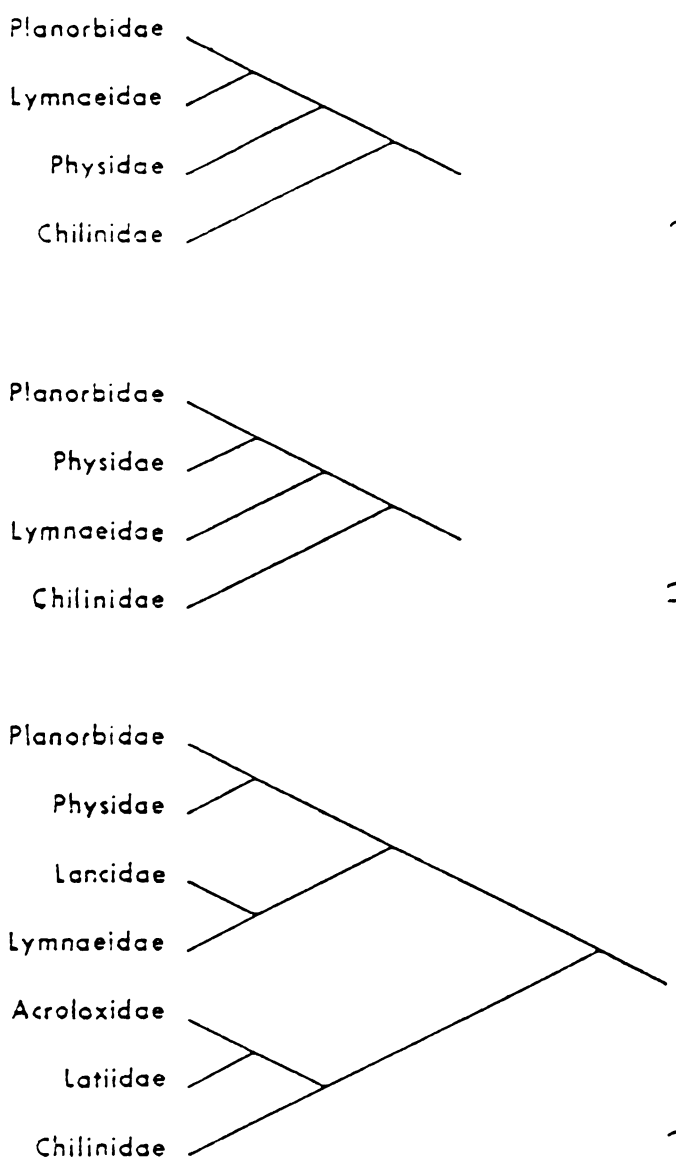


Figure 9. Hypotheses of the relationships among lymnaeacean families a) conventional hypothesis for all families b) relationships of the four principal families, following a) c) alternative hypothesis to b)

transformation series will be used to test the conventional phylogenetic hypothesis against an alternative (Figure 9-c). This discussion does not challenge the primitive position of the Chilinidae, only the relationships among the families Lymnaeidae, Physidae and Planorbidae. These three families will be called collectively, the "higher" lymnaeaceans.

In the following discussion, the families Chilinidae, Physidae and Lymnaeidae are each represented by a single genus as an exemplar. Lymnaeacean taxonomy is currently in a state of considerable flux. Recent genetic and morphological studies cited by Hubendick (1978) suggest that these families are grossly oversplit. Therefore, only the type genera Chilina, Physa and Lymnaea are used to represent these families.

The discussion below reexamines a broad range of data currently available in the literature. Figure 10 illustrates the anatomy of Lymnaea, and may be used as a general outline of the anatomical arrangement of all members of the superfamily Lymnaeacea. This analysis focuses on studies of the reproductive tract (Duncan 1960b, Starobogatov 1967) and the feeding apparatus (Demian 1962). Additional studies, especially the more general analyses by Hubendick (1947, 1948a, 1948b, 1978), are included to provide data on the tentacles, shell and respiratory system. The discussions of general anatomy by Hubendick, and Raven's discussion of development illustrate a lack of variation among the Lymnaeacea in other organ systems.

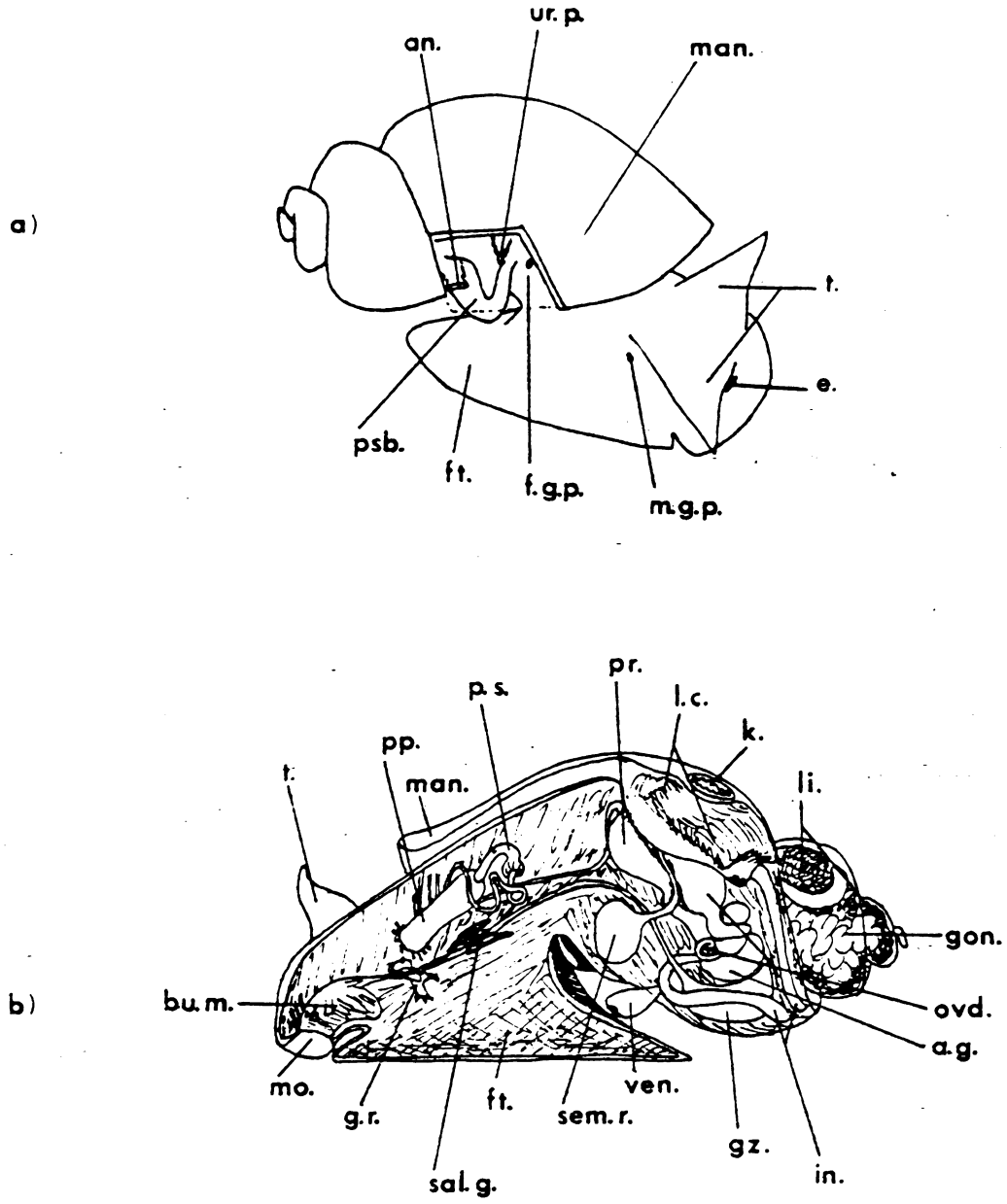


Figure 10. Major anatomical features of a representative lymnaeacean, Lymnaea catascopium. a) external view, with a portion of the mantle cut away to show the external respiratory structures. b) longitudinal section, showing the principle internal organs. (Walter 1969.)

Reproductive System

The reproductive system of the Lymnaeacea includes a large number of characters that differ among the members of the superfamily. These differences include both structural and histological variations. Figure 11 illustrates the morphology of the reproductive organs of representative members of each of the four main families in the Lymnaeacea. Like all pulmonates, lymnaeaceans are hermaphroditic; the single gonad produces both male and female gametes. The gametes pass through a system of ducts producing nutritive and protective secretions, and then pass out of the body through separate apertures. Although cross-fertilization is the norm, self-fertilization can occur (Abdel-Malek 1954). One region of the reproductive duct, the seminal vesicles, will not be considered in this discussion. Their morphology does not vary systematically among the lymnaeaceans, and their precise function is unknown. The organs that will be analyzed are the gonad, the glandular portions of the duct system, and the penial complex.

The lymnaeacean gonad is composed of one or two atria and several acini, diverticula opening into the atria. Gametes are produced in the acini and collect in the atria. The number of atria and the gross morphology of the acini provide significant characters from which phylogenetic relationships within the superfamily could be inferred. The number of atria serves to distinguish the Chilinidae from the other three families; and the morphologies of the acini

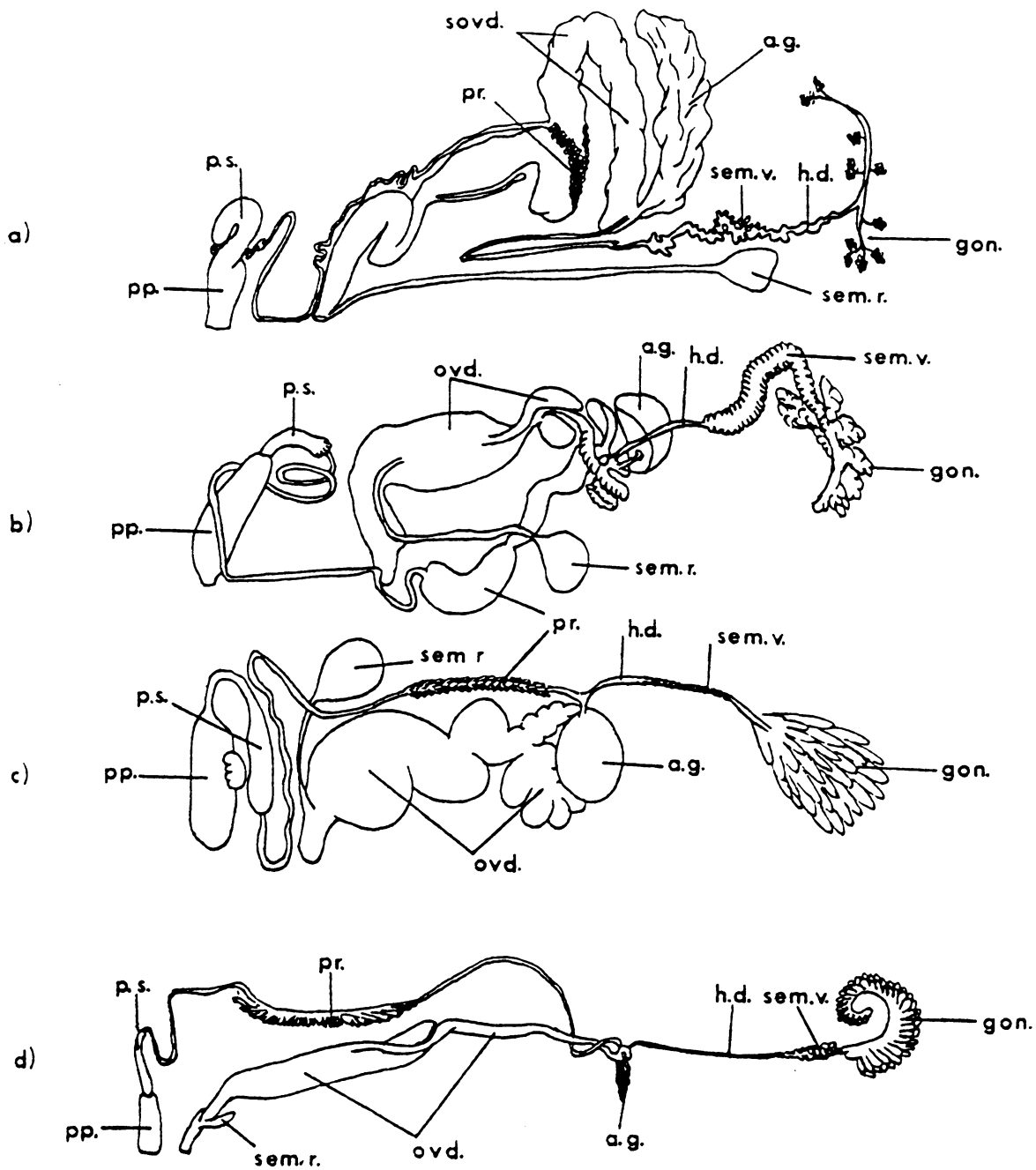


Figure 11. Dissected reproductive tracts of representatives of the four principle lymnaeacean families. a) Chilina b) Lymnaea c) Physa d) Biomphalaria.

permit further differentiation among the higher lymnaeaceans.

The normal number of atria among the Lymnaeacea is one; only the Chilinidae characteristically have two atria (Figure 11). The planorbid genus Bulinus also has this bicornulate condition (Walter 1968). In view of the great genealogical distance between Chilina and Bulinus, it is probable that the bicornulate condition is homoplasic. In turn, the homoplasy of this state casts doubt on its primitiveness, and therefore argues against use of this character in phylogeny reconstruction. If the bicornulate condition is primitive, then the unicornulate condition present in other lymnaeaceans resulted from a loss of one of the atria. Hecht and Edwards argue that loss characters should be given low weight in phylogenetic reconstruction. They base their argument on the inability to determine whether one or more loss events are involved. In any event, the number of gonadal atria does not distinguish between the families Physidae and Lymnaeidae. At best, it suggests that the higher lymnaeaceans are a monophyletic group.

The acini of the gonad show greater variation than do the atria. In Chilina, the acini are small round bodies. The acini of Lymnaea are broad irregular lobes and those of Physa and the Planorbidae are narrow and cylindrical. The acini of the chilinid gonad do not open directly into the atria as they do in other lymnaeaceans. Instead, they

cluster about a common duct, and the gametes pass from the acini through the intermediate duct into an atrium.

The families Physidae and Planorbidae appear to share a common gonad morphology. Unfortunately, the gonadal morphologies of the higher lymnaeaceans are not obviously related to the gonadal morphology of Chilina. Raven reports only that the pulmonate gonad develops by forming a central lumen, from which the acini arise by evagination. On the basis of this developmental information, the gonadal morphology of the higher lymnaeaceans may be close to the primitive state, while that of the Chilinidae is more derived. This developmental information does not indicate whether the similar gonadal morphologies of the Physidae and the Planorbidae are primitive or derived relative to that of the Lymnaeidae. Therefore, similarity between physid and planorbid gonads cannot be used to support a hypothesis of close genealogical relationship between the Physidae and the Planorbidae.

From the gonad, both sperm and ova pass through a common, hermaphrodite duct before following different routes. In the higher lymnaeaceans the different routes are physically separated, but the organs remain in close proximity. Histological divergence of the male and female ducts is slight but definite. In addition, both male and female ducts express distinct trends which differentiate among the four families.

The glandular portion of the reproductive system of Chilina is structurally hermaphroditic, although folds and cilia do segregate sperm and ova (Duncan 1960a). The reproductive system is structurally divided into male and female ducts below the prostate. In the higher lymnaeaceans, the glandular regions of the reproductive system are completely separated as well. Fraser (1946) reports that in Lymnaea the division of the male and female glandular ducts is accomplished by a longitudinal split of the glandular tissues. He states that the lower, non-glandular ducts separate in the same fashion in all pulmonates. Therefore, the separation of the male and female glandular ducts continues a process present in other pulmonates. Raven (1958) cites other research reporting the division, by the same means, of the glandular ducts of the planorbid Bulinus. Thus, a common developmental sequence supports the monophyly of the higher lymnaeaceans and their derivation from a primitive condition retained by the Chilinidae.

The female reproductive tract of all lymnaeaceans is distinguished from that of all other pulmonates by its division into histologically recognizable zones (Duncan 1960a). Although Duncan recognizes some morphological features associated with these zones, descriptions of the female glands are usually omitted from taxonomic reports. Attempts have been made to quantify the morphology of the female glands, but they have been frustrated by the seasonal

variation of these structures (Hubendick 1955, Schutte and van Eeden 1959). Consequently, the histology of these structures are available for phylogenetic reconstruction, but not the morphology. The number of histological zones is correlated with the number of egg case layers, but the precise correlation of oviduct zones to egg case layers is not apparent (Bondeson 1960). Two oviduct zones are recognized in Chilina (Duncan 1960a). Three zones are recognized in Lymnaea and Physa, and four zones in the planorbid genus Planorbarius (Duncan 1960b). Although the planorbid limpet Ancylus has only two zones in the oviduct, it does possess a zone homologous to the fourth zone of Planorbarius (Duncan 1960b). This suggests the the oviduct of Ancylus is reduced relative to that of Planorbarius, and it suggests that the fourth zone is shared by other planorbids. However, since the zonation does not discriminate between Lymnaeidae and Physidae, it cannot support either phylogenetic hypothesis under consideration.

One other structure of the female reproductive system, the albumen gland, has phylogenetic significance. Unlike the oviduct glands discussed above, the albumen gland is not simply a glandular expansion of the oviduct. Rather, it is a compact body which, according to Raven, arises as a distinct cluster of evaginations from the oviduct. Duncan reports that the albumen gland appears in the same position in all lymnaeaceans, just below the point where the male and female tracts can be distinguished. In all lymnaeaceans

except the Physidae, the albumen gland remains as a diverticulum which empties its products into the oviduct. In the Physidae alone, the albumen gland has become an integral part of the reproductive tract, and ova must pass through it to reach the oviduct proper. Since this position of the albumen gland is a unique attribute of the Physidae, this trait confirms the monophyly of the Physidae. However, it does not indicate the relationship of the Physidae to the other lymnaeaceans.

Only one large gland develops from the male reproductive duct, the prostate. Its morphological variations have been a key point in arguments supporting the Physidae as the closest relative of the Planorbidae (Hubendick 1947, Duncan 1960b, Harry 1964, Starobogatov 1967). Both the Physidae and the Planorbidae have prostates composed of diverticula emptying into the sperm duct (Figure 11, c and d). In constrast, the entire prostatic region of the sperm duct of the Lymnaeidae is greatly dilated, forming a large sack (Figure 11-b). Invaginated folds increase the internal surface area of the lymnaeid prostate. Thus, the prostate of the Lymnaeidae is morphologically distinct from the prostates of the Physidae and the Planorbidae. The lymnaeid prostate is also histologically distinct, but it is only composed of unusual proportions of cell types present in the prostates of the other families (Duncan 1960b). The primitive prostate of Chilina is usually a simple glandular patch along the

spermoviduct; however, small alveolar diverticula may develop (Harry 1964) (Figure 11-a). These small diverticula of the chilinid prostate may be precursors of the large cylindrical diverticula which comprise the physid and planorbid prostates. If so, the derived state shared by these families represents a simple size increase. Hecht and Edwards argue that such derived states are likely to be homoplasic, since the genetic changes required can be small. By their argument, the morphological similarity of the physid and planorbid prostates should be given low weight in phylogenetic reconstructions. This low weighting would be consistent with the histological primitiveness of these prostates.

Hubendick (1947, 1948a, 1948b, 1951, 1955, 1964, 1978) has put particular importance on the penial complex for determining phylogenetic relationships. This complex includes the penis, its enveloping tissues, and various associated glandular structures. Hubendick (1955) argues that these characters should be highly weighted because they potentially play a critical role in reproductive isolation during speciation. However, there have been no studies to indicate the likelihood of this possibility.

Because these structures are more accessible for morphological study, their ontogenetic and morphological variations are better known than those of most other organs. According to Raven (1958), the organs of the penial complex are epidermal derivatives, developing from an invagination

which becomes the male aperture. The walls of the pocket formed by this invagination differentiate into an upper penis sheath and a lower preputium. Where the apex of the penis sheath meets the vas deferens, the penis develops as an outgrowth into the lumen (Figure 12). The common developmental origin of the penial complex elements is reflected in their structural similarity. All three elements are composed of a glandular epithelum supported by layers of connective tissue, and longitudinal and circular muscles (Hubendick 1947). The principle difference between the penis sheath and the preputium is size. Variations of the basic plan include the development of accessory glands, loss of the penis, or delamination of the muscular layers to increase the extension of the copulatory organs. Most of these variations only differentiate among genera (Hubendick 1951, 1955, 1964, Te 1975).

Two characters of the penial complex are of some use at the family level. The penis sheath of the Physidae is poorly developed relative to the other lymnaeaceans. In the Chilinidae, Lymnaeidae and Planorbidae the supporting layers of muscle and connective tissue are well developed, but they are almost absent from the physid penis sheath (Hubendick 1947). In contrast, the preputium shows increased development of the longitudinal muscles in the Lymnaeidae and most of the Planorbidae. These enlarged muscles, which may aid in retraction of the penis, form prominent ridges occupying much of the preputial lumen (Hubendick 1948a).

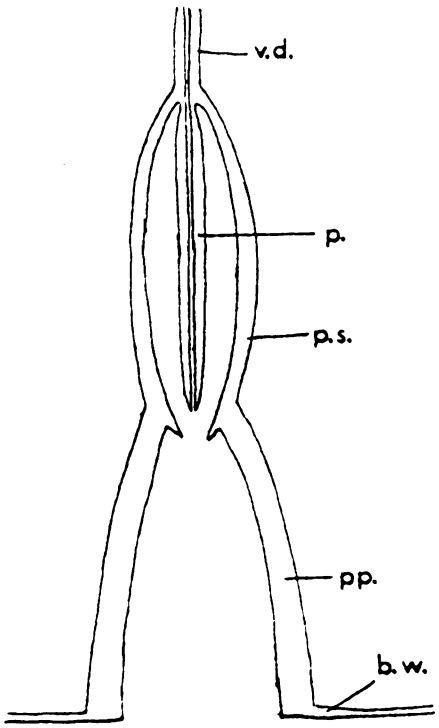


Figure 12. Schematic cross-section of the lymnaeacean penial complex.

The preputial ridges are present in all lymnaeids and a large majority of the planorbids. This majority among the planorbids suggests that the presence of the ridges is a primitive trait for that family. Thus, the distribution of the preputial ridges suggests that the Lymnaeidae and the Planorbidae share a character state which is derived relative to the Chilinidae and the Physidae.

The characters of the reproductive system have been a key support for arguments favoring the Physidae as the closest relative of the Planorbidae. However, this analysis indicates that these characters are ambiguous, at best. Only the diverticula of the gonad, the diverticula of the prostate and the preputial ridges discriminate between the hypotheses represented in Figure 9. The significance of each of these characters is subject to debate. For both sets of diverticula, identification of the primitive state is problematical. With regard to the preputial ridges, while they are clearly derived, there is a significant possibility that they are homoplasic. Therefore, it is not possible on the strength of reproductive characters alone to determine whether the Physidae or the Lymnaeidae is the closest relative of the Planorbidae.

Tentacles

The tentacles are one of the few obvious external characteristics of snails. Among the lymnaeaceans the tentacles take two forms: flat lobes in Chilina and Lymnaea, narrow cylinders in Physa and the Planorbidae.

Both Hubendick (1947) and Harry (1964) have argued that these differences in tentacle shape indicate that the Physidae are the closest genealogical relatives of the Planorbidae. However, Raven (1958) does not report any structural or developmental differences between the two tentacle forms; only the outline of the tentacle varies. Since the differences in outline may be attributed to simple changes in growth rates, this character should not be weighted highly. Furthermore, Hubendick (1947, 1948a) has observed intermediate tentacle forms in Bulinus and some other planorbids. These intermediates are an additional indication that tentacle shape may be homoplasic.

Shell

According to Hubendick (1978), shell characters are no longer accorded high weight when discriminated between genera or higher taxonomic levels. This is certainly true of the ridges, grooves and knobs which may ornament the shell. Prominent shell sculpture is rare and restricted to unusually thick shelled taxa among the lymnaeaceans. Microscopic sculpture is common, but it is highly variable within families. In contrast to ornamentation, overall shell form still does exert a strong subjective influence on phylogenetic studies. For example, there is a strong tendency among systematists to segregate limpets and slugs into distinct families. This tendency persists despite comprehensive studies showing such groups to be phylogenetically heterogeneous (Hubendick 1978, Gosliner and

Ghiselin 1984, Tillier 1984). This particular issue was discussed earlier in this chapter. One distinction, between right-handed and left-handed coiling, is retained in lymnaeacean systematics.

The direction of shell coiling is known to be related to the fundamental asymmetry of the body (Crampton 1894). This asymmetry can be traced to the direction of the first spiral cleavage (Meshcheryakov and Beloussov 1975). Thus, sinistral shells have a common developmental origin. This association also allows discoid forms with sinistral cleavage to be grouped with sinistral spired forms. Consequently, the sinistral families Physidae and Planorbidae have been considered closely related. However, studies on populations of Lymnaea peregra (Boycott et al. 1930, Freeman and Lundelius 1982) have shown that the direction of cleavage is controlled by alleles at a single gene locus. The conversion from dextral to sinistral is attributed to a single mutation and there is a high rate of back mutation from sinistral to dextral (Boycott et al. 1930, Freeman and Lundelius 1982). These reports have also illustrated a number of planispiral shells and other shell coiling abnormalities associated with alleles at this locus. Similar analyses of coiling reversal in pulmonates have been reported in populations of Laciniaria biplicata (Degner 1952) and Partula (Murray and Clark 1966). Clearly, shell coiling patterns are especially prone to homoplasy and should not be used as a basis for phylogenetic analysis.

Respiratory System

As was mentioned earlier in this chapter, pulmonates are distinguished from other gastropods by the presence of a lung. Although the lung may have arisen in amphibious intertidal snails, the Lymnaeacea are wholly aquatic. Accordingly, the lymnaeaceans have several accessory respiratory organs that appear to improve or supplement the respiratory capabilities of the lung (Figure 13). The internal surface of the lung may form ciliated, vascularized ridges which divide the lung cavity into two chambers and increase the respiratory surface area. Cilia regulate the flow of water through the lung (Sullivan and Cheng 1974, Pilkington et al. 1984). At the opening of the lung are one or two broad lobes. These lobes are generally considered to be replacements for the lost gill, and are accordingly termed pseudobranchs (Hubendick 1947, Harry 1964). In some cases a lobe may be rolled into a tube, the siphon, which functions as a snorkel. Although these accessory structures also occur in more primitive basommatophorans, and their homology is not certain, they are characteristic traits of the Lymnaeacea. Consequently, the occurrence of these structures and their variations have been considered to reflect phylogenetic relationships within the superfamily.

Harry (1964) reports that Chilina possesses a pair of pulmonary ridges. The pair of ridges is actually a single ridge which runs from the aperture of the lung to its apex, where it is reflected back along the dorsal roof. The

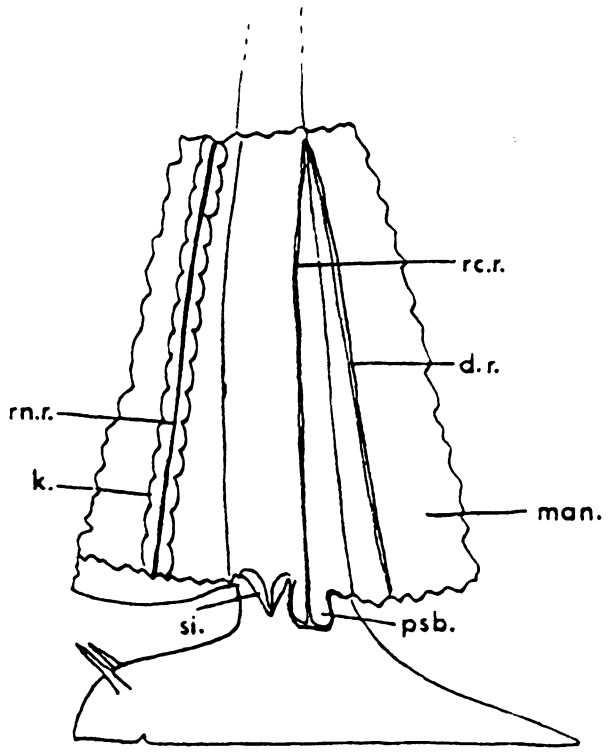


Figure 13. Respiratory structures of Biomphalaria. The shell has been removed and the lateral wall of the lung cut and opened away to expose internal structures.

ventral limb runs just above the rectum and the dorsal ridge is directly opposite the rectal ridge. These ridges are entirely absent from Lymnaea and Physa, according to Harry. In the Planorbidae, the distribution of these ridges is more complex (Hubendick 1955). Both dorsal and rectal ridges are present in some genera, but either ridge may be lost independently of the other. In addition, a few genera lack both ridges. Since Lymnaea and Physa share the same character state, this character does not discriminate between the two phylogenetic hypotheses under consideration.

The systematic distribution of pseudobranch variations is more complex than are the distributions of the pulmonary ridges, although several similarities are evident. Chilina has a single pseudobranch lobe, with anterior and posterior regions demarcated by the rectum (Harry 1964). In the Planorbidae, the two portions are usually completely separated lobes. The anterior lobe forms the siphon and the posterior lobe continues to function as a gill. Either the siphon or the posterior pseudobranch may be absent. In both Lymnaea and Physa only the siphon is present. Consequently, the variations of the pseudobranch also do not support either phylogenetic hypothesis, but suggest that the Planorbidae may have retained a primitive character state.

The character states of the respiratory system could be interpreted as support for a third phylogenetic hypothesis (Figure 14). The pulmonary ridges only weakly support this hypothesis, however. Since the ridges are absent from many

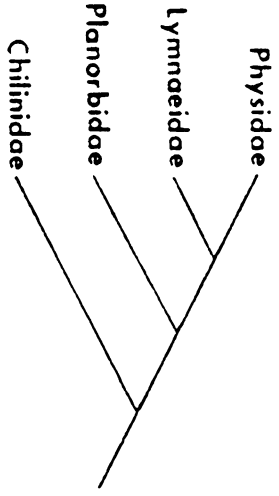


Figure 14. Phylogenetic relationships supported by respiratory character states.

planorbids as well as from the Lymnaeidae and the Physidae, either the ridges or their absence must be homoplasic. As discussed previously, Hecht and Edwards argue that functional and topographic similarities are unlikely to be homoplasic. Thus, the ridges are likely to be homologous and primitive, and the losses do not support any phylogenetic hypothesis.

The pseudobranch and siphon present a more difficult problem (Figure 15). Several planorbid genera have a single pseudobranch similar to the pseudobranch of Chilina. Other planorbids have both a posterior pseudobranch and an anterior siphon. The pseudobranch is commonly reduced to a rudiment. The Lymnaeidae and the Physidae posses only the siphon. This sequence suggests that differentiation of the siphon occurred in the Planorbidae (Figure 15-a) and that Lymnaea and Physa represent the final stage in the replacement of the pseudobranch by the siphon (Figure 15, b - d). Hecht and Edwards consider reductions only slightly more reliable than losses, but less reliable than simple growth shifts. Therefore, the variations in the siphon and pseudobranch should be given little weight.

The problem of the undivided pseudobranch in some planorbids (Figure 15-a) still must be resolved. This form is rare among coiled lymnaeaceans, but occurs in nearly all limpets. Again, functional significance and structural similarity argue in favor of the homology of the anteroposterior differentiation. In addition, the frequency

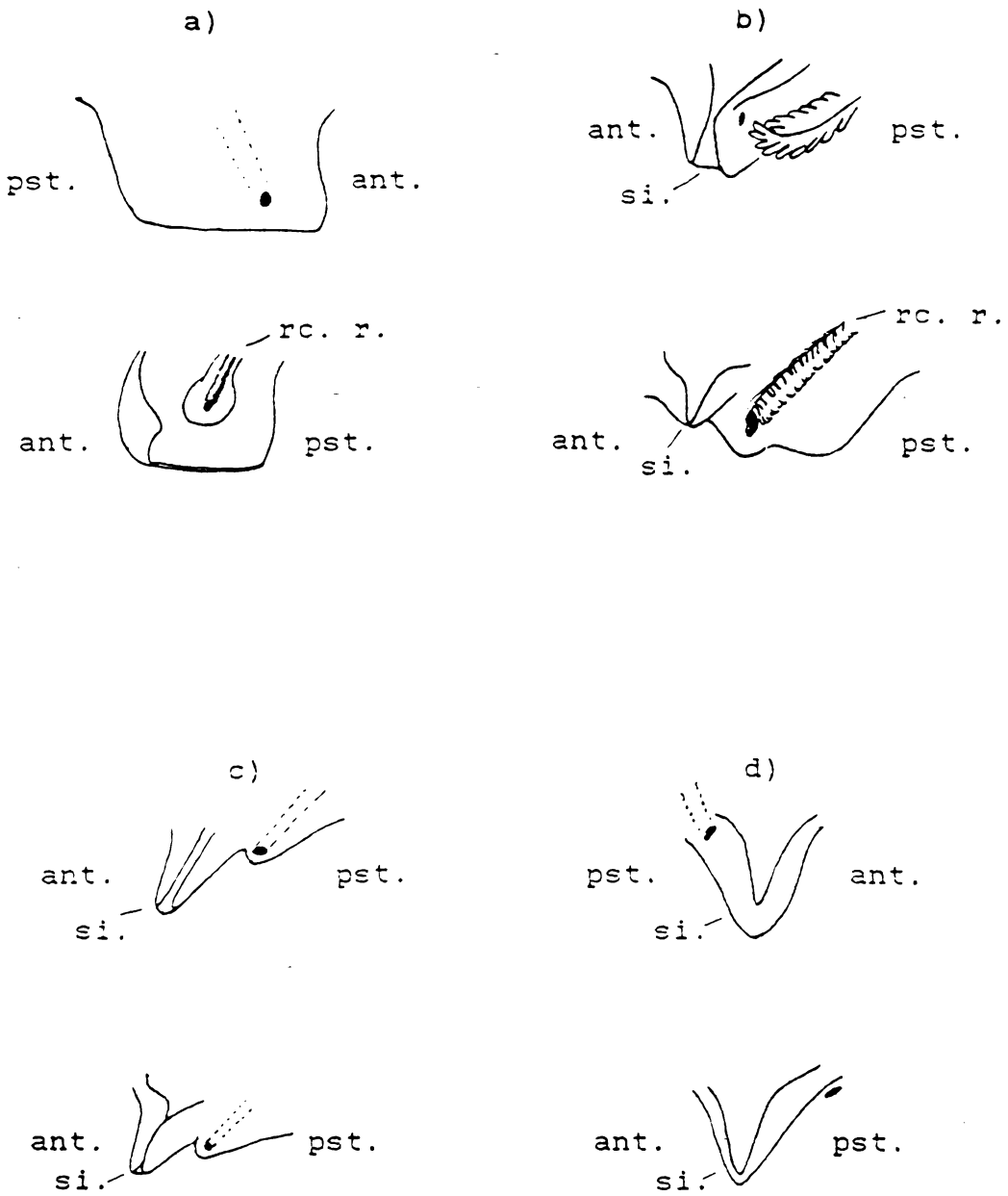


Figure 15. Lymnaeacean mantle lobes. a) pseudobranch, single lobe, Chilina upper, Camptoceras lower, b) siphon and pseudobranch, Bulinus upper, Biomphalaria lower, c) siphon, pseudobranch reduced, Armiger upper, Drepanotrema lower, d) siphon only, Lymnaea upper, Physa lower.

of differentiation and the high propensity for regression, especially among limpets, must be considered. Both suggest that the differentiation of the siphon is a primitive state of the Planorbidae. Since the siphon is also shared by the Lymnaeidae and the Physidae, this must be a primitive state of higher lymnaeaceans, as a group. The loss of the posterior pseudobranch by members of all three families must be homoplasic, therefore. Thus, the distributions of these character states do not support any phylogenetic conclusion concerning relationships among the higher lymnaeaceans.

Alimentary System

The digestive tract of the pulmonates is composed of a simple gut, salivary glands, liver and a large, complex feeding apparatus. Except for the feeding apparatus, the alimentary system is considered by Hubendick (1947, 1978) to have little or no phylogenetic significance. The salivary glands, gizzard and liver do vary across the pulmonates, and some differences are evident among the lymnaeaceans, but the differences are only variations in the degree of development. The feeding apparatus, on the other hand, is considered to be phylogenetically important, especially within the Lymnaeacea.

The central component of the feeding apparatus is the radula; a stiff, flexible ribbon on which are numerous rows of teeth. The radular ribbon is underlain by a cartilaginous odontophore which provides both a solid support for the radula and a site for muscle attachment

(Figure 16) (Demian 1962). Opposite the radula is a chitinous jaw. The shape and structure of the jaw varies too widely within families to support phylogenetic inferences (Hubendick 1978). Also, according to Demian, the buccal musculature varies in response to the shape of the odontophore and the overall shape of the animal, and is therefore likely to be homoplasic. In contrast, the odontophore and the shape and arrangement of the radular teeth all vary independently and do permit differentiation among the lymnaeacean families.

The are two forms of the odontophore found in lymnaeaceans. The more common form is constructed of a unitary mass with a thin trough between two thick ridges (Figure 17-a). The radula rests in the trough and the buccal musculature attaches to the ridges and underside of the odontophore. This unitary odontophore is found in Chilina (Brace 1983) and in Lymnaea and the Planorbidae (Demian 1962). According to Demian, the physid odontophore lacks the trough, the ridges retain only a thin flange on the medial surface of each (Figure 17-b). The ridges are connected by a broad ligament which allows the odontophore to function as a unit. Accompanying this structural change is a significant rearrangement of the musculature. Unfortunately, this indicates that only the Physidae have diverged from the primitive state. The fact that the Lymnaeidae and the Planorbidae both retain the chilinid odontophore does not argue for their common ancestry.

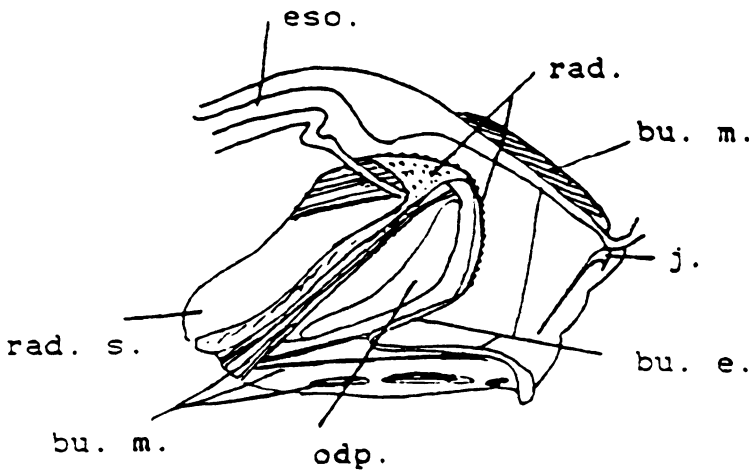


Figure 16. Major features of the feeding apparatus of Lymnaea.

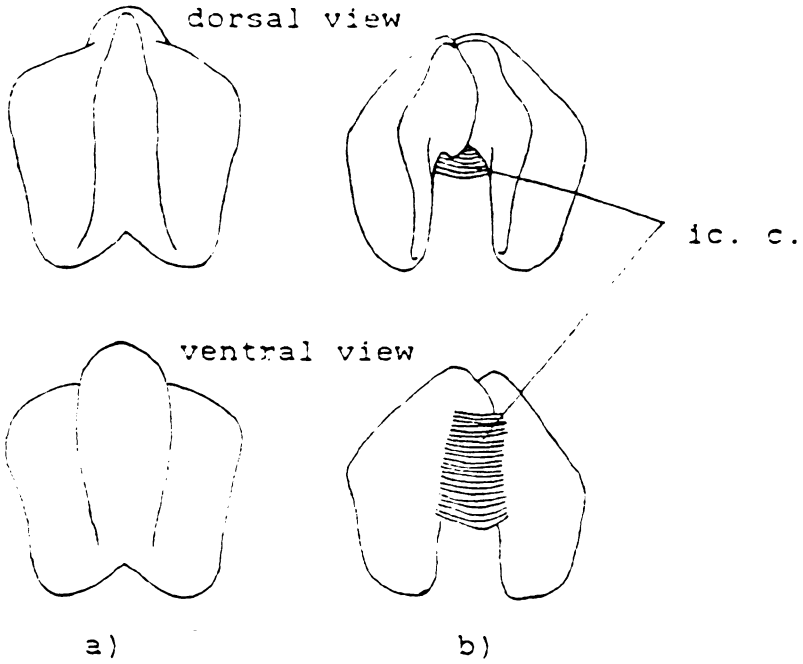


Figure 17. Odontophore morphologies. a) Lymnaea, b) Physa.

There are also two arrangements of the teeth on the radula (Hubendick 1978). In the Chilinidae and the Physidae the rows of teeth form chevrons hinged about the central tooth. Thus, the Physidae retain the primitive state. In the Lymnaeidae and the Planorbidae the teeth form straight, horizontal rows across the radula. Thus, the Lymnaeidae and the Planorbidae share a derived state, which clearly supports the hypothesis that these two families are derived from a common ancestor.

The evolution of the shapes of the radular teeth has evidently been more complex than the evolution of the above characters (Figure 18) (Hubendick 1978). The central tooth is similar in all four families. It varies in cusp number, but this feature is not consistent within the families. The base of the tooth is L-shaped in lateral view. The central tooth does not permit any distinctions between families but it does form the basis for comparing the shapes of the other radular teeth.

In Chilina the remaining teeth can be sorted into two groups: laterals and marginals. These outer groups have a straight profile and are club shaped in frontal view (Figure 18-a). The marginals are distinguished from the laterals by a laterally directed spur. In the physid radula there is no distinction between marginals and laterals. All teeth lateral to the central resemble the chilinid marginals (Figure 18-b). The physid teeth differ from the chilinid marginal due to apparent rotation of the spur and the tooth

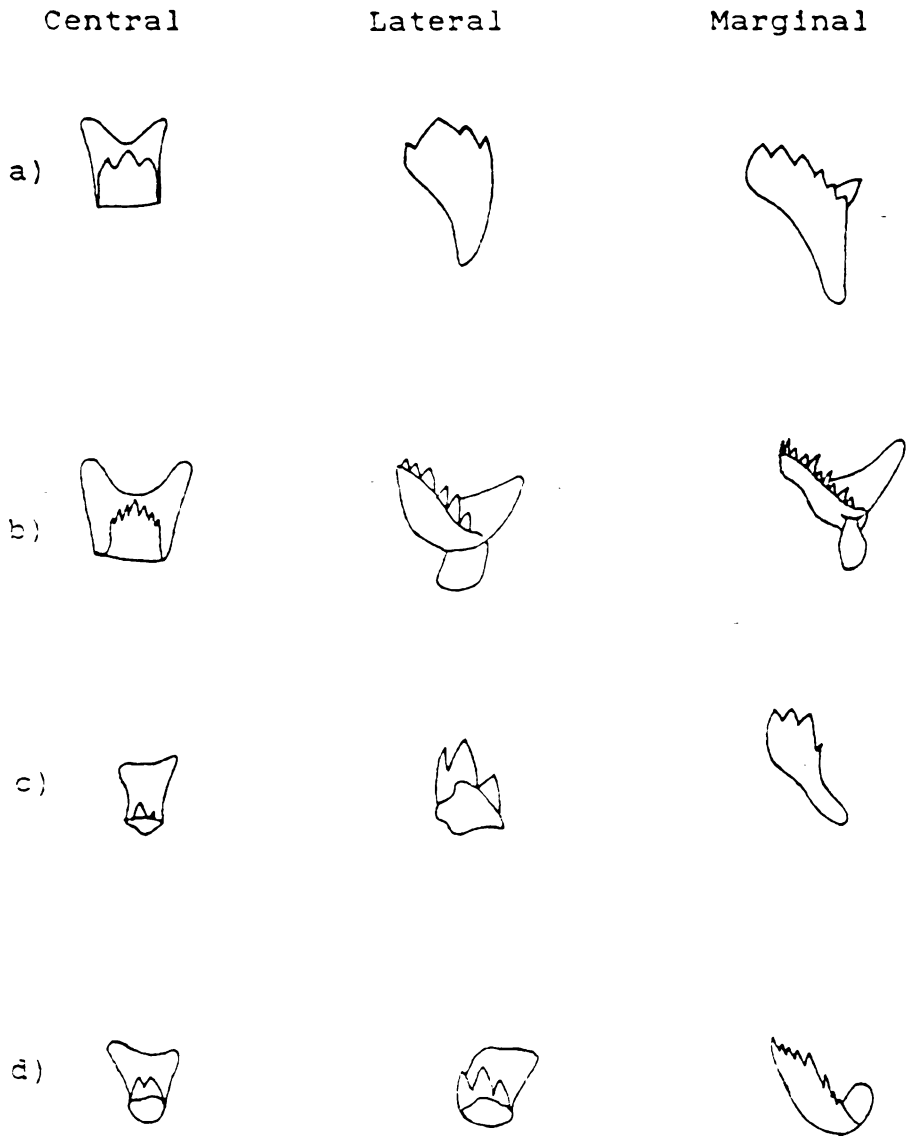


Figure 18. Lymnaeacean radular teeth. a) Chilina, b) Physa, c) Lymnaea, d) Planorbarius.

bearing head relative to the base. Consequently, these outer physid teeth have a Y-shaped profile. The lymnaeid radula shows a third set of tooth shapes (Figure 18-c). In Lymnaea, the lateral teeth resemble the chilinid central with the L-shaped base. The frontal views of the centrals and the lymnaeid laterals differ only slightly. The centrals are straight in this view, while the lymnaeid laterals are bent. The marginals of Lymnaea are more variable than the laterals. They may resemble either the chilinid laterals with the straight profile, or the chilinid centrals with the L-shaped profile. The planorbid radulae express the same set of shapes as the lymnaeid radulae (Figure 18-d).

These tooth shape variations may be developmentally related. Raven (1958) has shown that all of the teeth in the radula develop form a single primordium. If these teeth are developmentally linked, Hecht and Edwards would argue that centrals, laterals and marginals constitute a single character. Even so, these data clearly indicate that the higher lymnaeaceans have diverged from the Chilinidae in different directions: one followed by the Physidae, one followed by the Lymnaeidae and the Planorbidae.

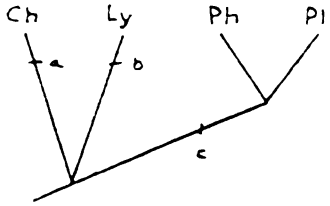
The states of the feeding apparatus support a phylogenetic conclusion more clearly than any of the other characters discussed above. The odontophore of the Physidae and the shape of its teeth indicate that this family has diverged from the primitive lymnaeacean ancestor

independently of the Lymnaeidae and the Planorbidae. Both the shape and the arrangement of the radular teeth suggest that the Lymnaeidae and the Planorbidae shared a common ancestor independent of the Physidae. Thus, this suite of characters conflicts with the conventional hypothesis (Figure 9-b), but is consistent with the alternative (Figure 9-c).

CONCLUSION

Only a few of the characters discussed above support any hypothesis of the relationships of the higher lymnaeaceans. They are: gonad diverticula, prostate morphology, preputial morphology, tentacle shape, radular tooth arrangement and radular tooth shape (Figure 19). Three characters support the conventional hypothesis (Figure 19, a, b and d); three support the alternative (Figure 19, c, e and f). Thus, at first glance there is no conclusion to be gained from this analysis. Closer evaluation of these characters does permit a solution, however.

The first character, the gonad diverticula, should be eliminated from further consideration. Either the lobulate form or the cylindrical form may be primitive. If the lobulate form is primitive, then this character does support the conventional hypothesis. But, if the cylindrical form is primitive, then neither hypothesis is supported. However, there is no means to determine which state is primitive. The little developmental information that exists suggests only that Chilina is highly derived, with respect

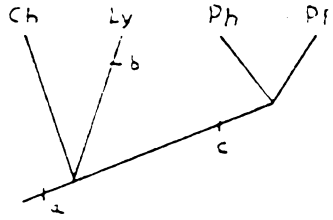


Gonad

a - alveolar diverticula and collecting ducts

b - lobulate diverticula

c - cylindrical diverticula

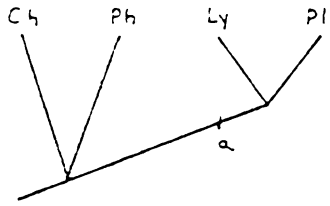


Prostate

a - alveolar diverticula

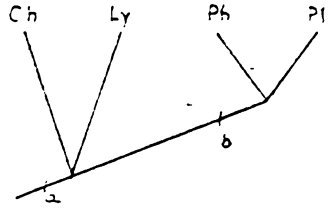
b - diverticula lost

c - cylindrical diverticula



Preputium

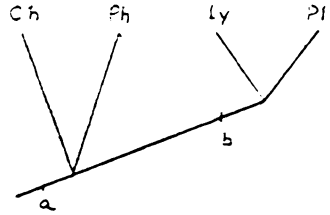
a - longitudinal muscular ridges



Tentacles

a - lobate

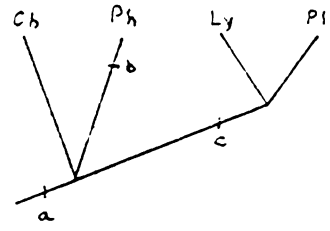
b - cylindrical



Radular rows

a - chevron

b - horizontal



Radular tooth shapes

a - 3 distinct types

b - 2 types, laterals and marginals similar

c - 2 types, laterals and central similar

Figure 19. Summary of the character state distributions that resolve relationships among the principle lymnaeacean families. Ch - Chilinidae, Ph - Physidae, Ly - Lymnaeidae, Pl - Planorbidae.

to this character. Since the origin of the Lymnaeacea is obscure, there is no reference from which the primitive state of this character can be determined. Without such a reference, morphological similarities have no necessary genealogical significance. Therefore, this character is rejected from further consideration.

Of the remaining characters, three represent simple differences in growth rates: the morphologies of the prostate, the preputium and the tentacle. Hecht and Edwards argue that growth shifts should not be weighted highly; although they do consider such characters more reliable than losses or reductions. At the same time, the radular characters should be functionally integrated. In addition, the variations in tooth arrangement and shape might have a developmental basis. For either reason, Hecht and Edwards would regard these traits as a single character. However, their different distributions suggest that these two traits have evolved independently of each other, and independently of other characters of the feeding apparatus. Therefore, the two radular characters should be kept distinct.

A simple count of the five remaining characters would favor the hypothesis that Lymnaeidae and Planorbidae form a monophyletic group. This conclusion is strengthened by the greater reliability of the radular characters. Although this hypothesis is not supported strongly, the above data clearly demonstrate that there is no support for the conventional hypothesis. Thus, the Lymnaeidae seem more

likely than the Physidae to accurately predict the primitive states of characters used to analyze the phylogenetic relationships within the Planorbidae.

CHARACTER EVOLUTION IN THE PLANORBIDAE

INTRODUCTION

42 characters were used to analyze relationships within the Planorbidae. Each character varies within the family, but most do not vary within genera. Those character states also present in the outgroup Lymnaeidae are considered to be the primitive states. For some characters, especially those of the respiratory system, this method would be inappropriate since some planorbids retain states which are more primitive than those in the Lymnaeidae. In these cases, the Chilinidae is the reference outgroup, since it represents the primitive condition of the entire superfamily Lymnaeacea. Unless otherwise cited, the data for this section are derived from the following sources: Harry 1964 (Chilina), Hubendick 1951 (Lymnaea), Hubendick 1955 (coiled planorbids) and Hubendick 1964 (planorbid limpets).

The family Planorbidae is represented in this paper by 36 genera (Table 2). The character state series described below are summarized in Table 3. Throughout the remainder of this paper the following notation is used to refer to the characters and states as they are listed in Table 3: e. g., 14:0. The first number refers to the character, the second number refers to the state of the character. Thus,

Table 3. Descriptions and codes for characters and states used to infer relationships of the Planorbidae

Character Number	Character Name	Character State	Code
	Reproductive System		
1	Gonad acinar arrangement	Unordered	0
		Rows	1
2	Prostate length	Long	0
		Short	1
3	Prostate duct	Absent	0
		Present	1
4	Sarcobellum	Present	0
		Absent	1
5	Velum	Present	0
		Absent	1
6	Upper "velum"	Absent	0
		Present	1
7	Penis	Solid	0
		Delaminated	1
8	Aphally	Absent	0
		Present	1
9	Penis pore position	Terminal	0
		Lateral	1
10	Stylet solid	Absent	0
		Present	1
11	Stylet epithelial	Absent	0
		Present	1
12	Stylet epithelial blade "rolled leaf"	Absent	0
		Present	1
13	Stylet epithelial cap	Absent	0
		Present	1
14	Penis sheath	Solid	0
		Sinus	1
		Ultrapenis	2

Table 3 (cont'd.).

15	Flagellum number	0	0
		1	1
		2	2
16	Flagellum glandular	Present	0
		Absent	1
17	Flagellum muscular	Absent	0
		Present	1
18	Preputial pillars	Present	0
		Absent	1
19	Pillars enlarged	Absent	0
		Present	1
20	Pillar bilobed	Absent	0
		Present	1
21	Pillar groove branched	Absent	0
		Present	1
22	Pillar groove closed to form a blind duct	Absent	0
		Present	1
23	Duct reenters penis sheath	Absent	0
		Present	1
24	Duct reenters preputium	Absent	0
		Present	1
Respiratory System			
25	Dorsal fold	Present	0
		Absent	1
26	Rectal fold	Present	0
		Absent	1
27	Renal fold	Absent	0
		Present	1
28	Gill lobes	Ant-Posterior	0
		Single lobe	1
		Dorso-ventral	2
29	Siphon	Present	0
		Absent	1
30	Pseudobranch	Present	0
		Reduced	1
		Absent	2

Table 3 (cont'd.).

Radula			
31	Central tooth, cusp #	2	0
		>2	1
32	1st lateral tooth, cusp #	3	0
		4-5	1
		>5	2
33	Marginal tooth type	Oblique	0
		Square	1
34	Lateral cusps on marginals	Absent	0
		Present	1
Shell			
35	Sinistral coiling	High spired	1
		Low spired	2
		Limpet/whorl	3
36	Discoid coiling	Present	1
		Limpet/whorl	2
		Limpet/ none	3
37	Aperture deflected	Absent	0
		Dextral	1
38	Dextral coiling	Present	1
		Limpet/whorl	2
		Limpet/ none	3
39	Aperture inclined	Absent	0
		Present	1
40	Aperture dilated	Absent	0
		Present	1
41	Apertural "teeth"	Absent	0
		Present	1
42	Rate of whorl increase	Slow	0
		Rapid	1

14: refers to the penis sheath; 14:0 refers to the character state penis sheath solid. The numbers 0-8 which refer to the character state also indicate the inferred position of the state in the linear transformation series of that character. 0 is the most primitive state; 8 is the most derived. 9 is reserved for the following special cases: intrageneric variation of the states present, no information on the states present, or non-applicability of the character (e. g. if the penis is lost or does not carry a hardened stylet, then possible variations in the formation of the stylet are irrelevant). 9 is equivalent to a 0 in the construction of trees, but permits an important distinction to be made in the data tables. Use of the 9 distinguishes between cases in which the presence of the primitive state is known, and cases in which the presence of the derived state is uncertain or impossible to determine.

REPRODUCTIVE SYSTEM

Gonad (1:0-1)

The gonad grows principally by increase in the length of the atrium and in the number of acini (Wu 1972, Wu and Burch 1975). In Lymnaea and some planorbids the acini appear to be randomly placed (1:0) (Figure 20-a), but in most planorbids the acini are arranged in discrete rows (1:1) (Figure 20-b) (Starobogatov 1967). Paraense and Deslandes (1956b, 1956c, 1957) have shown that the number of rows may increase anteriorly in a single gonad. For instance, in species of Drepanotrema there may be one row

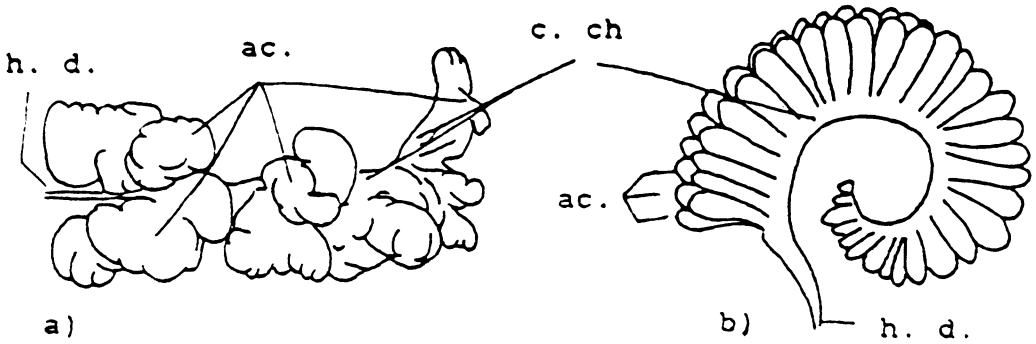


Figure 20. Arrangements of gonad acini. a) Lymnaea, b) Biomphalaria

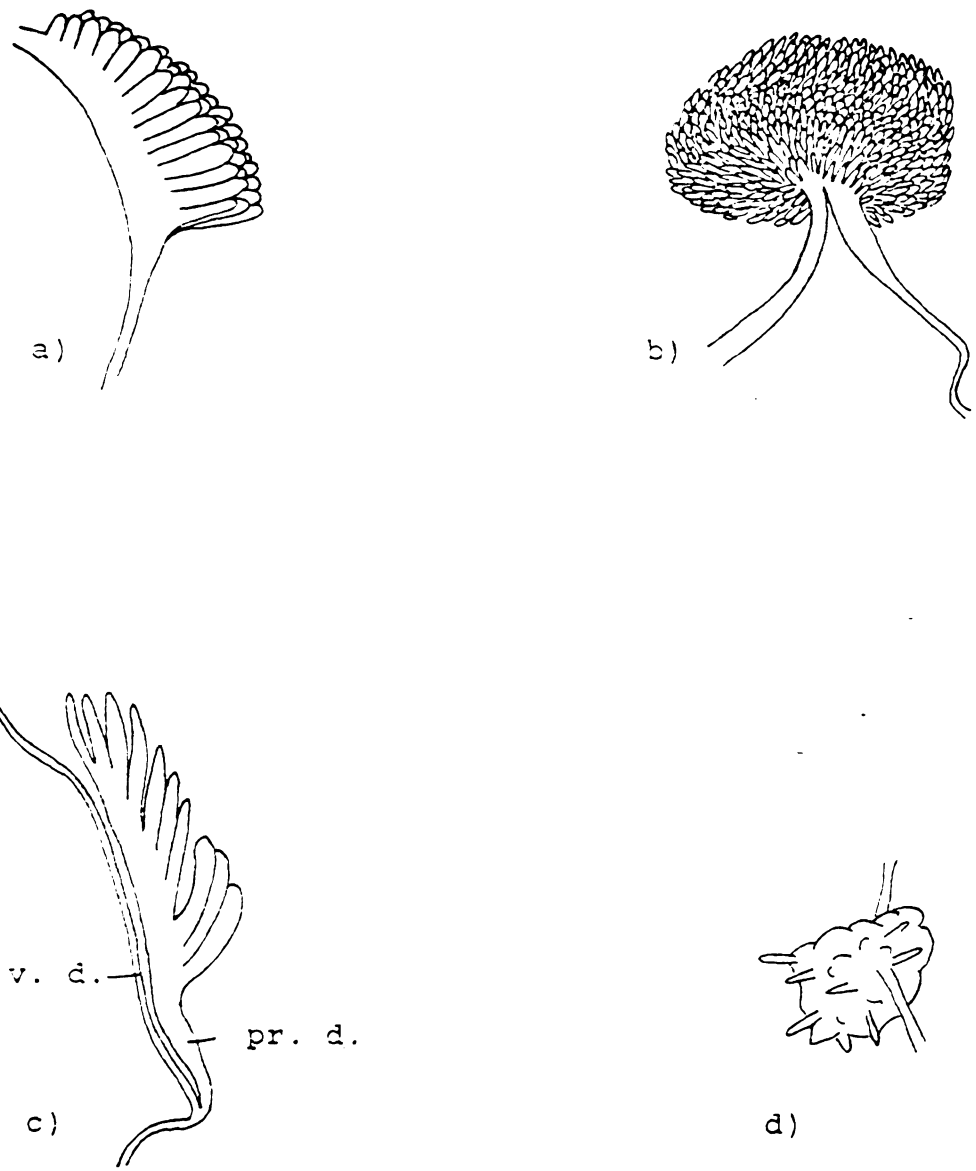


Figure 21. Prostate morphotypes. a) Drepanotrema, b) Bulinus, c) Polypylis, d) Rhodacmea.

apically, increasing to two or three at the base of the gonad. Therefore, further refinement of this state is not practical.

The primitive state occurs in all planorbid limpets. These snails have gonads in which the atrium does not elongate, but remains a short sac. Also, the number of acini is much smaller than in the coiled planorbids. These reductions will not be used to analyze the planorbid phylogeny, since they fit the tendency for convergent reductions in limpets.

Prostate (2:0-1, 9; 3:0-1)

In the Chilinidae and the Physidae the prostatic diverticula occur along a considerable length of the male tract (Duncan 1960a, 1960b). This state is retained by many planorbids (2:0, 3:0) (Figure 21-a). However, two diverticular arrangements have evolved that shorten the length of the prostatic zone of the sperm duct. In several genera the diverticula form a tight cluster, but still empty directly into the sperm duct (2:1) (Figure 21-b). In the other group, the diverticula empty into a collecting duct which leads into the sperm duct (3:1) (Figure 21-c).

The morphology of the prostate in Rhodacmea is unique within the Planorbidae (Basch 1960). It is composed of several short diverticula which empty into the sperm duct, but this region of the duct is shortened and dilated (Figure 21-d). Thus, although the prostate is shorter than the primitive state, the diverticula are not clustered.

Therefore, the prostate of Rhodacmea does not resemble any of the three states described above and has been coded 2:9, 3:0.

Sarcobellum (4:0-1)

The sarcobellum is a ring shaped structure at the distal end of the penis sheath, projecting into the lumen of the preputium (Figure 22-a). This structure is always present in Lymnaea (4:0), but is absent from some planorbids (4:1). The absence of a sarcobellum is interpreted as a loss on the basis of its presence in Lymnaea. The functions of the sarcobellum, vellum (5:) and upper "velum" (6:), which all have similar structures, are unknown.

Velum (5:0-1)

The velum is a ring shaped muscular constriction of the preputium just distal to the boundary of the penis sheath and preputium (Figure 22-a). Like the sarcobellum, the velum is alway present in Lymnaea (5:0), and is frequently lost in planorbids (5:1).

Upper "Velum" (6:0-1)

In the limpet Ancylastrum, an additional constriction of the penis sheath occurs just above the sarcobellum (6:1) (Figure 22-b). This particular ring is unusual since it represents a gain relative to Lymnaea. This structure has not been reported in other planorbids, however.

Penis (7: - 13:)

The lymnaeacean penis has contiguous muscle layers (7:0), a terminal pore (9:0) and lacks any type of chitinous

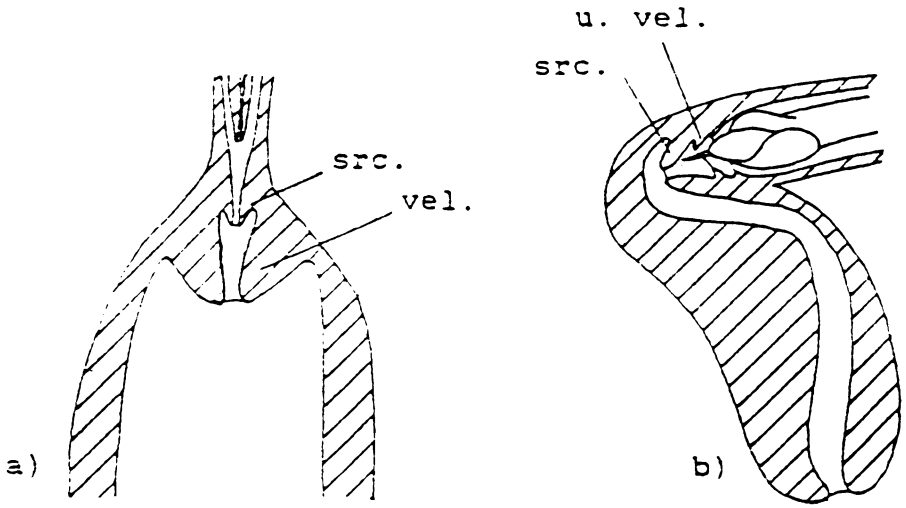


Figure 22. Ring structures of the penial complex. a) Planorbis, b) Ancylastrum.

hardening (10:0, 11:0). Although these are the general conditions for the Lymnaeidae and the Planorbidae, members of these families do deviate from the norm. Two of these deviations are present in both families: delamination of the musculature (7:1) (Figure 23) and loss of the penis (aphally) (8:1). Both conditions are common in the Lymnaeidae, but are rare in the Planorbidae. These two characters are normally variable within planorbid species, but the derived states are fixed in some genera: delamination in Biomphalaria, Burnupia and Fossulorbis; aphally in Bulinus, Gundlachia and Indoplanorbis. Both of these states are likely to be homoplasic since they occur in lymnaeids and planorbids. They are included here to test that possibility.

There are modifications of the penis unique to the Planorbidae: displacement of the pore from terminal to lateral (9:1) and the presence of some type of stylet, a cuticular hardening of the penis tip (10: - 13:). Displacement of the pore always occurs if a stylet develops, but there are some genera in which the pore is displaced and the stylet is absent: Ancylus, Ferrissia, Laevapex, Miratesta and Protancylus (Hubendick 1958a). There is no functional explanation evident for the displacement of the pore in the absence of a stylet. Consequently, Hubendick argues that this condition indicates the loss of a stylet; the lateral pore would be simply a relict. However, since

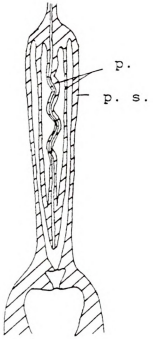


Figure 23. Delaminated penis.

no evidence has been offered in support of this hypothesis, these characters are coded independently.

The stylet is not a unitary character, but encompasses two distinct types. These types are formed by different developmental mechanisns, reflecting different phylogenetic origins. One type of stylet is solid (10:1) formed by condensation and hardening of the cells at the tip of the penis. The second type is formed by an extra-cellular cuticular secretion of the tip cells (11: - 13:). This cuticular layer may form a hollow sheath extending back from the tip (11:1). In Gyraulus, the epithelium is invaginated prior to secretion, and forms a hollow tube parallel to the penial axis. The resulting stylet resembles a rolled leaf blade (12:1) (Figure 24) (Hubendick 1958b). The cuticular stylet may also be limited to a small cap at the tip of the penis (13:1). There are two possible character phylogenies for the cuticular stylets. The rolled leaf form is clearly derived from the sheath; but there is no evidence suggesting the phylogenetic position of the cap. The coding used tests the possibility that the cap is derived, by reduction of the secretory area of the tip.

In this set of penial characters certain character state combinations are logically impossible. The delaminated penis unrolls during eversion; therefore, formation of a stylet would not be possible. Obviously, if there is no penis, there cannot be a stylet. Finally, if

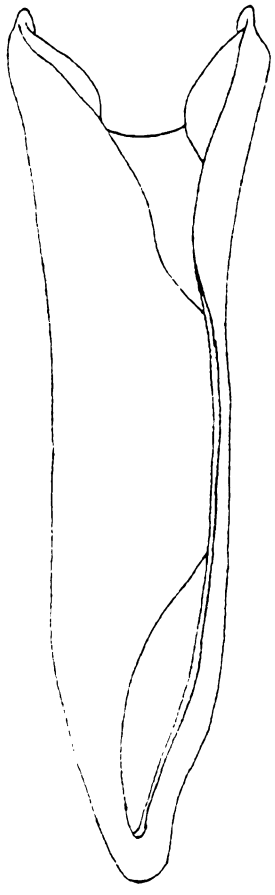


Figure 24. "Rolled leaf" stylet of Gyraulus.

the stylet is solid, the variations of the epithelial stylet cannot be considered.

Penis Sheath (14:0-2)

The penis sheath may become delaminated (14:1) (Figure 25, a and b) by a process similar to delamination of the penis. Raven reports that in the aphallic genera Bulinus and Indoplanorbis, delamination occurs early in development. The inner layer, adjacent to the lumen, then grows at a much higher rate than the outer layer. The resultant structure functions as a penis, and has been named an ultrapenis by Hubendick (1948) (14:2) (Figure 25-c).

Flagella (15: - 17:)

Several planorbids have one or two evaginations from the apical end of the penis sheath (flagella) (Figure 26). In most cases the epithelial histology of the flagella suggests that these structures have a glandular function (Hubendick 1948b). The flagella of several genera also have a muscular basement layer. Three characters were used to describe the variations of the flagella: number (15:0-2), presence or absence of the glandular epithelium (16:0-1) and presence or absence of the muscular basement layer (17:0-1).

Since the other members of the Lymnaeacea do not have flagella, the primitive number is 0 (15:0). However, there is no evidence concerning the relative primitiveness or derivedness of the other states of this character. In the genera which do have two flagella, one is often much smaller than the other. This suggests that changes in number might

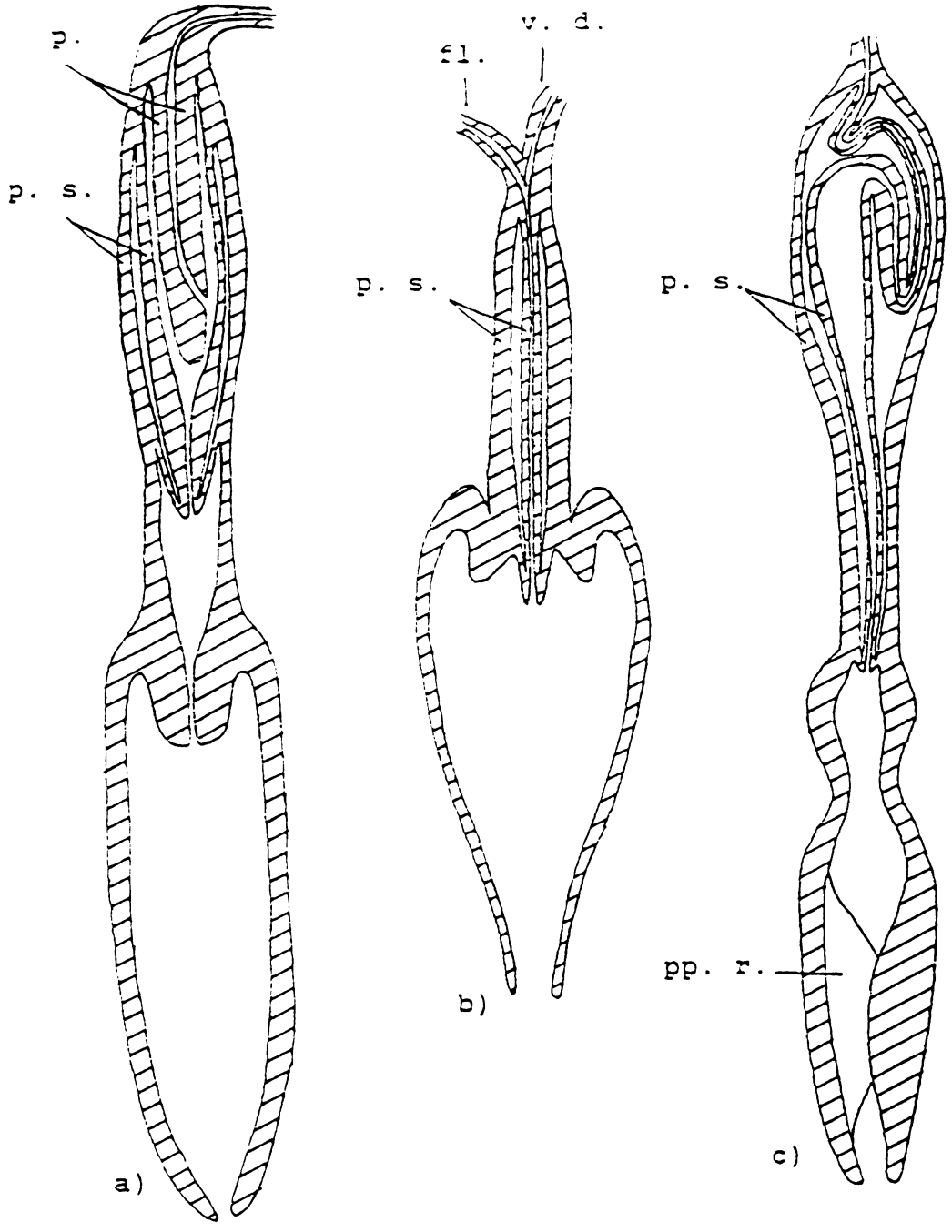


Figure 25. Penis sheath variations. a) penis, penis sheath delaminated, Laevapex, b) aphallic, penis sheath delaminated, Gundlachia, c) inner layer of sheath enlarged to replace penis, Indoplanorbis.

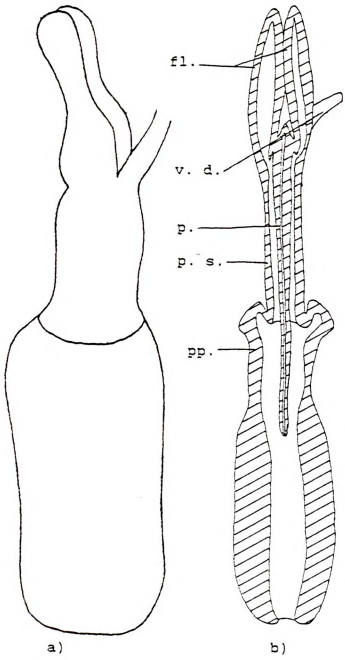


Figure 26. Flagella. a) external view, b) cross-section.

have occurred, but does not indicate the direction of change. Therefore, this character was coded to reflect the different numbers of flagella but was unordered on the Wagner trees. Unordered characters are fit onto the tree produced by the other characters in the most parsimonious fashion possible. This allows the direction of transformation to be determined from the phylogenetic context supplied by the other characters.

The evolution of the other two flagellar characters may be inferred either from their derivation from the penis sheath or from their frequency. Since the flagella develop from the penis sheath, containing both glandular and muscular layers, these layers are expected to be present in the primitive flagella. In most cases the glandular layer is present but the muscle layer is absent. Thus, both sources suggest that the glandular layer is primitive (16:0), but the frequency of occurrence of the muscular layer would suggest that it is derived. Since these sources conflict concerning the direction of change, the muscular layer was unordered on the Wagner trees.

Preputium (18: - 24:)

The preputial lumen of Lymnaea is nearly occluded by a pair of longitudinal muscles enlarged to form prominent ridges (Figure 27-a). These ridges are retained in this form by several planorbids (18:0), but are lost by some genera (18:1). A number of other planorbids possess a variety of glandular preputial organs (19: - 24:)

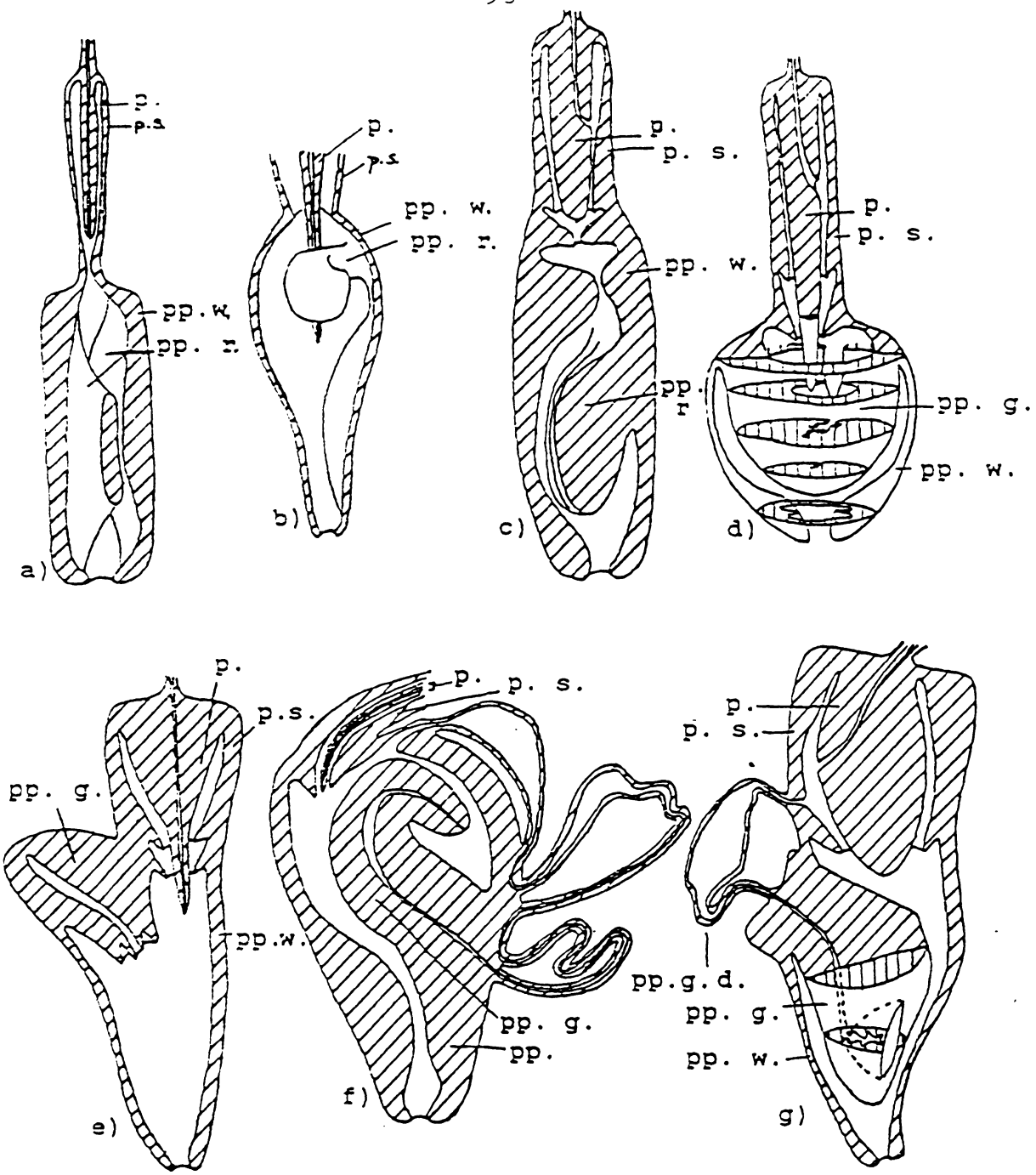


Figure 27. Preputial structures. a) Lymnaea, b) Hippeutis, c) Planorbula, d) Menetus, e) Camptoceras, f) Helicorbis, g) Helisoma.

apparently derived from these ridges. There are no development data to support the derivation of complex glandular structures from the epithelial ridges. However, the positions of these structures, the glandular properties of the preputial epithelium, and a series of intermediate morphologies suggest that the glands and the ridges are homologous.

The initial stage, expansion of one ridge (19:1), is represented in Hippeutis (Figure 27-b). Further enlargement is accompanied by division of the ridge by a longitudinal cleft (20:1) (Figure 27-c). In Menetus and Promenetus this cleft is complexly branched (21:1) (Figure 27-d). Further development involves closure of the cleft to form an internal duct (22:1), and extension of the duct through the preputial wall into the body cavity (23:1, 24:1). Since the internal duct may be straight (Figure 27, e and f) or branched (Figure 27-g), either the closure or the branching may be homoplasic. The external duct is clearly homoplasic, reentering the penial complex in two places: in the penis sheath (23:1) (Figure 27-g), or in the preputium (24:1) (Figure 27-f).

RESPIRATORY ORGANS

The discussion of the evolution of these characters in the superfamily Lymnaeacea indicated that most of the derived states within the superfamily are losses of structures present in Chilina. Since losses are likely to be homoplasic, the character states present in Lymnaea are

not necessarily the primitive states of the Planorbidae. In fact, many planorbids retain primitive states which are present in the primitive lymnaeacean, Chilina. Therefore, Chilina is more likely to accurately reflect the primitive states of the planorbids.

Pulmonary ridges (25: - 27:)

Only Chilina and some planorbids possess ciliated, vascularized ridges on the inner surface of the lung. Chilina has the dorsal-rectal ridge pair (Figure 13). In the planorbids, generally both ridges are either present or absent. However, there are some planorbids which have lost only one member of the pair. Since these two ridges occasionally do evolve independently, the dorsal and rectal ridges are coded as separate characters (25:0-1, 26:0-1). For both characters, absence of the ridge is the derived state.

A small number of planorbids have a third, renal ridge above the kidney and ureter (27:1). This ridge is not present in Lymnaea or Chilina; and therefore, is derived.

Mantle Lobes (28: - 30:)

Chilina has a single mantle lobe traversed by the rectum (Figure 15). Lymnaea, Physa and most planorbids show evidence of having once had two distinct lobes, a siphon and a pseudobranch. The conclusion reached in the discussion of the Lymnaeacea is that the primitive condition of the higher lymnaeaceans is the presence of both lobes (28:0). Either the siphon or the pseudobranch may be absent, representing a

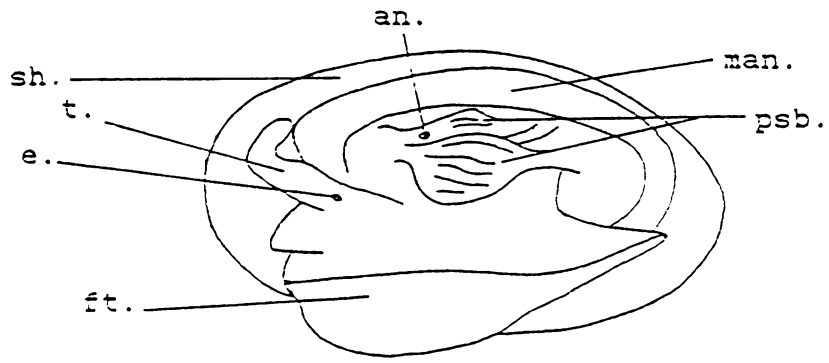
loss (29:1, 30:2). Although several planorbids have a reduced pseudobranch (30:1), only Lentorbis has lost the pseudobranch entirely.

A few planorbids have reverted to the single lobe present in Chilina (28:1). Helisoma represents an intermediate stage in which the lobes are not physically separated, but are differentiated. In those genera no longer having a functional siphon, the position of the rectum still divides the anterior and posterior regions of the mantle lobe. The next step of this series of mantle lobe forms is present in some of the limpets. The single lobe is again divided, but dorso-ventrally rather than antero-posteriorly (28:2) (Figure 28). The two lobes have a common base through which the rectum passes.

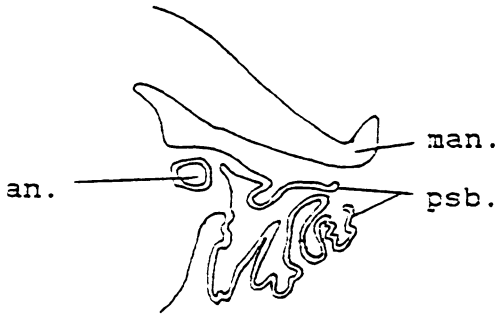
RADULA

The radulae of most lymnaeids and most planorbids are quite similar in shape and generally have the same number of cusps. However, while Lymnaea species may have fewer cusps, planorbid species may have more cusps. The number of cusps only varies on the central tooth and the lateral teeth. The marginal teeth may also vary in shape. The states common to both families were used as the primitive state for the Planorbidae.

Within a single tooth row, cusp number and variability of cusp number generally increase from the central tooth to the outermost marginal tooth. However, the number of cusps on the central tooth and the first few lateral teeth is



a)



b)

Figure 28. Pseudobranch of Gundlachia. a) ventral oblique view, b) schematic diagram of a transverse section.

fixed in most genera. Therefore, only the numbers of cusps on the central tooth (31:0-1) and first lateral tooth (32:0-2) are used. The common cusp numbers are 2 for the central tooth (31:0) and 3 for the first lateral tooth (32:0). Lymnaea may have lower cusp numbers, planorbids may have higher cusp numbers. The number of cusps on the central tooth of planorbids is most often increased to 4. Cusp numbers of 3 or 5 on the central are rare, and numbers higher than 4 are usually variable within a genus. Therefore, the primitive and derived states for the central tooth are coded as 2 cusps (31:0) and >2 cusps (31:1), respectively. On the first lateral, the number of cusps tends to be variable if there are more than 3. Usually the next highest cusp number is 4, but a rudimentary 5th cusp may also be present. Two genera, Polypylis and Segmentina have 6 cusps on the first lateral. The states used for this character are 3 cusps (32:0), 4 - 5 cusps (32:1) and >5 cusps (32:2).

The planorbid marginals are the only teeth which may differ in shape from their lymnaeid counterparts (Figure 29). The form present in both Lymnaea and planorbid species resembles the chilinid lateral teeth and is coded as the primitive state (33:0). In this form, the base of the tooth is oblique to the radular membrane (33:0). In the derived form, the tooth is square to the membrane (33:1).

The marginals of both families may also carry a second set of cusps on the outer edge of the tooth (Figure 29-c)

Figure 29. Radular tooth types. a) oblique, Lymanaea, b) square, Planorbis, c) oblique with lateral cusps, Indoplanorbis.

(34:1). These additional cusps are not common in Lymnaeaidae and may be a derived state of that family rather than a primitive state. Furthermore, if this state was inherited by the planorbids from the lymnaeids, then absence of these additional cusps should be considered a loss. Due to the uncertainty of this character, it is unordered on the Wagner trees.

SHELL

The Planorbidae express a considerable diversity of shell coiling and ornamentation. Most of these features vary within genera and are of questionable value for higher level taxonomy. The likelihood of homoplasic evolution of shell coiling patterns, including derivation of the limpets, was discussed in the previous chapter. However, shells are the only material available to gastropod paleontologists. Therefore, the few characters for which there are consistent reports are included in this analysis: shell coiling patterns and modifications of the aperture. Ornamentation was not used for two reasons. Macroscopic ornamentation is rare; it is present in two genera which each have a unique pattern of ornamentation. Microscopic ornamentation is variable in most genera, is commonly eroded, and is often restricted to the embryonic whorl. The shell characters used will permit an objective evaluation of the utility of overall shell form in phylogenetic reconstruction.

Coiling (35: - 38: , 42:)

The conventional morphological classifications used by conchologists do not convey any sense of transformation between form groups. Therefore, these classifications were not used; but instead, an alternative system was constructed, modeled in part on Raup's (1966) analysis of spiral shapes. Because planorbids exhibit considerable ecological variation, fine divisions based on the Raupian parameters were not used. Instead, this system is based on broad categories encompassing the ranges of variation present in most genera.

Three characters were used to accomodate three directions of coiling: sinistral (35:0-1, 9) (Figure 30, a-c), planispiral (36:0-3, 9) (Figure 30, d-f) and dextral (38:0-3, 9) (Figure 30, g-i). A fourth character (37:0-1) reflects a transition from planispiral to dextral coiling which occurs in some genera (Figure 30-f). Since this transition occurs in the last whorl, all of these genera are considered to be planispiral. No attempt was made to relate the directions of coiling to a phylogenetic pattern. However, within each coiling direction group, there is a series of character states which reflects progress from a coiled form to a limpet. In the sinistral coiling group, this involves transition from a high spire (35:1), to a low spire with a greatly increased body whorl (35:2), to a limpet with a rudimentary apical whorl (35:3). The coding of the other two coiling groups differs slightly. Spire

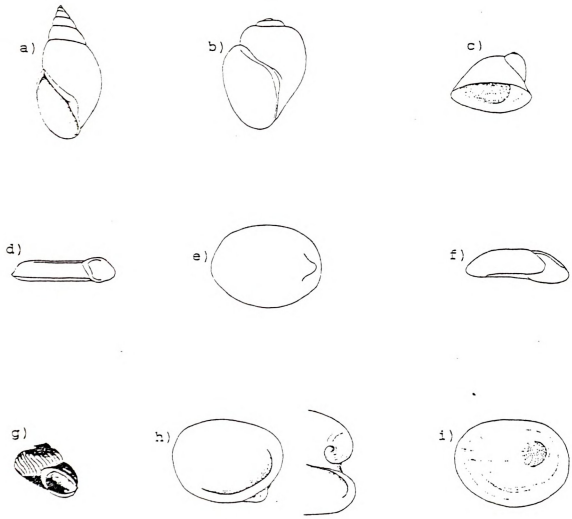


Figure 30. Shell form groups. a) Sinistral - high spire, Physastra sumatrana, b) Sinistral - low spire, Bulinus truncatus, c) Sinistral - limpet, with apical whorl, Patelloplanorbis tigiensis, d) Discoid, Planorbis planorbis, e) Discoid - limpet, Ancylus fluviatilis, f) Discoid - final whorl deflected dextrally, Segmentina nitida, g) Dextral, Acrorbis petricola, h) Dextral - limpet, with apical whorl, Ancylastrum cumingianum, i) Dextral - limpet, without apical whorl, Burnupia stuhlmanni.

height is not as variable in dextral shells, and does not apply to discoid shells; and most of the limpets have lost the apical whorl. Therefore, the series in these groups is from coiled (:1), to a limpet with an apical whorl (:2), to a limpet without an apical whorl (:3).

The characters 35:, 36: and 38: are evaluations principally of the rate of whorl expansion, although they do confound this with the rate of whorl translation (Raup 1966). This is especially true of 35: which considers whorl height. Character 42: is an explicit evaluation of whorl expansion, but it is not applied to the limpets (42:9). This character is based on subjective evaluations published in the literature: slow (42:0) or fast (42:1). Because of the subjectivity involved, it is unordered on the Wagner trees. Inclusion of this character provides a further test of the hypothesized progression from coiled forms to limpets.

Aperture (39: - 41:)

Three characters describe the shape of the shell opening and are independent of the pattern of coiling. The aperture may be square to the axis of the whorl (39:0) or inclined (39:1) (Figure 31-a), it may be abruptly dilated in the final stages of growth (40:1) (Figure 31-b), or it may be partially occluded by tooth shaped projections on the inner surface of the shell (41:1) (Figure 31-c). Each of these derived states occurs only in the Planorbidae.

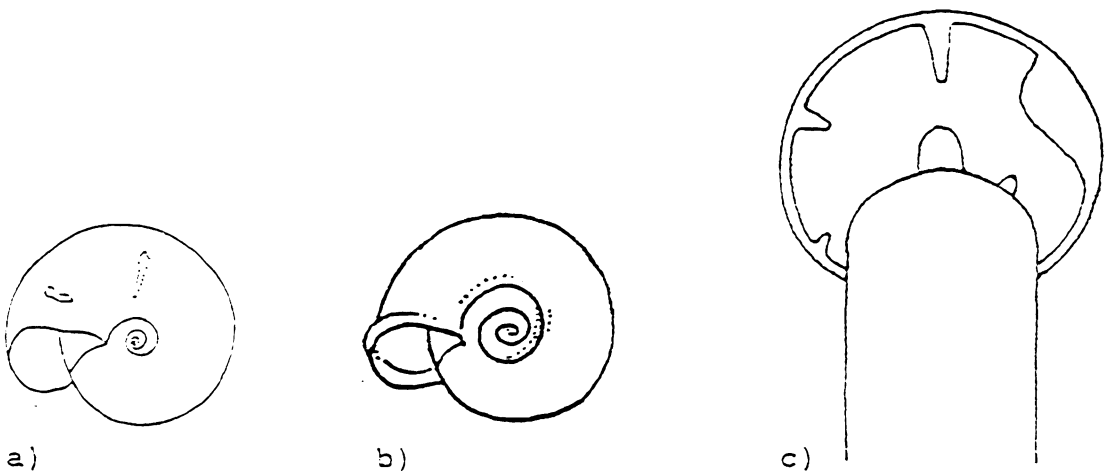


Figure 31. Apertural modifications. a) aperture inclined, Segmentina nitida, b) aperture dilated, Planorbula wheatleyi, c) apertural denticles, Biomphalaria pfeifferi.

DATA ANALYSIS

The parsimony analysis and the components analysis are both based on the same character state distribution matrix (Table 4). Primitive states are coded 0; codes greater than 0 indicate derived states. For linear transformation series with more than one derived state, PAUP permits codes up to 8 to indicate sequential stages in the series. Divergent stages in a branched transformation series must still be coded as separate characters. Missing data and intrageneric variation are indicated by the code 9. This code is also used when the character is not present and differentiation between states is not applicable. States which are coded 9 for a particular taxon are not used in determining the phylogenetic relationships of that taxon. Characters for which the direction of transformation is unknown are unordered. The unordered facility permits a parsimonious interpretation of that character, but the unordered character does not enter into determining phylogenetic relationships. For each method, a series of analyses was performed starting with all 42 states. Several analyses were performed to test hypotheses of homoplasy.

Table 4. Taxon - character state input matrix

Taxa	Characters and states																						
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Root	0	0	0	0	0	0	0	0	0	?	?	?	?	0	0	?	?	0	0	?	?	?	?	?
ACR	1	0	0	0	1	0	0	0	0	?	?	?	?	0	2	0	0	1	0	?	?	?	?	?
AME	0	1	0	0	1	0	0	0	0	?	?	?	?	0	0	?	?	1	0	?	?	?	?	?
ANC	0	1	0	0	1	1	0	0	1	1	0	?	?	0	1	1	1	0	0	?	?	?	?	?
ANS	0	0	0	1	1	0	0	0	1	0	0	?	?	0	1	0	1	0	0	?	?	?	?	?
ANI	1	0	1	0	0	0	0	0	1	0	1	1	0	0	0	?	?	0	0	?	?	?	?	?
ARM	1	0	1	0	0	0	0	0	1	0	1	1	0	0	0	?	?	1	0	?	?	?	?	?
BIO	1	0	0	0	0	0	1	0	0	?	?	?	?	0	0	?	?	0	0	?	?	?	?	?
BUL	0	1	0	0	1	0	0	1	0	?	?	?	?	2	0	?	?	0	0	?	?	?	?	?
BUR	0	1	0	0	1	0	1	0	0	?	?	?	?	0	0	?	?	1	0	?	?	?	?	?
CAM	0	1	0	0	0	0	0	0	0	?	?	?	?	0	0	?	?	0	1	1	0	1	0	0
CHO	1	0	1	0	0	0	0	0	1	0	1	1	0	0	0	?	?	0	0	?	?	?	?	?
DRE	1	0	0	0	1	0	0	0	0	?	?	?	?	0	2	0	0	0	0	?	?	?	?	?
FER	0	0	0	0	1	0	0	0	?	0	0	?	?	?	1	0	1	1	0	?	?	?	?	?
FOS	1	0	0	0	1	0	1	0	0	?	?	?	?	0	2	0	0	0	0	?	?	?	?	?
GUN	0	0	0	0	1	0	0	1	0	?	?	?	?	1	1	0	1	1	0	?	?	?	?	?
GYR	1	0	1	0	0	0	0	0	1	0	1	1	0	0	0	?	?	0	0	?	?	?	?	?
HLC	1	0	1	0	1	0	0	0	1	0	?	0	?	0	2	0	0	0	1	1	0	1	0	1
HLS	1	0	0	0	1	0	0	0	1	0	1	0	0	0	0	?	?	0	1	1	1	1	1	0
HIP	1	0	1	0	1	0	0	0	0	?	?	?	?	0	2	1	0	0	1	0	0	0	0	0
IND	0	1	0	1	1	0	0	1	0	?	?	?	?	2	0	?	?	1	0	?	?	?	?	?
LAE	0	0	0	0	0	0	0	0	1	0	0	?	?	1	0	?	?	1	0	?	?	?	?	?
LEN	1	0	1	?	?	?	0	0	0	?	?	?	?	0	0	?	?	0	1	1	0	0	0	0
MEN	1	0	0	0	0	0	0	0	1	0	1	0	1	0	0	?	?	0	1	1	1	0	0	0
MIR	0	1	0	0	1	0	0	0	1	0	0	?	?	0	0	?	?	1	0	?	?	?	?	?
PAT	0	1	0	0	1	0	0	0	0	?	?	?	?	0	0	?	?	0	0	?	?	?	?	?
PHY	0	1	0	0	0	0	0	0	1	1	0	?	?	0	1	1	1	0	0	?	?	?	?	?
PAR	0	1	0	0	0	0	0	0	0	?	?	?	?	0	0	?	?	0	1	1	0	0	0	0
PBS	1	0	1	0	0	0	0	0	0	?	?	?	?	0	0	?	?	0	0	?	?	?	?	?
PBU	1	0	0	0	0	0	0	0	1	0	1	0	1	0	0	?	?	0	1	1	0	0	0	0
PLE	1	0	0	0	0	0	0	0	?	?	?	?	?	0	0	?	?	0	0	?	?	?	?	?
POL	1	0	1	0	0	0	0	0	1	0	1	0	1	0	2	0	0	0	1	1	0	1	0	1
PME	1	0	0	0	0	0	0	0	1	0	1	0	1	0	0	?	?	0	1	1	1	0	0	0
PNC	0	1	0	0	0	0	0	0	1	0	0	?	?	0	0	?	?	0	0	?	?	?	?	?
RHO	0	?	0	1	1	0	0	0	0	?	?	?	?	0	0	?	?	1	0	?	?	?	?	?
SNA	1	0	1	0	0	0	0	0	0	?	?	?	?	0	2	0	0	0	1	1	0	0	0	0
SRB	1	0	1	?	?	?	0	0	0	?	?	?	?	0	1	0	0	0	1	1	0	0	0	0

Table 4 (cont'd.).

	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
Root	0	0	0	0	0	0	0	0	0	0	9	9	0	9	0	0	0	0
ACR	1	1	0	0	0	0	1	1	1	0	9	9	0	1	1	0	0	1
AME	0	0	1	0	0	0	0	0	0	1	9	9	0	9	9	0	0	1
ANC	9	9	9	1	9	9	0	0	9	9	9	9	0	2	9	0	0	9
ANS	9	9	9	1	9	9	1	0	9	9	9	3	0	9	9	0	0	9
ANI	1	1	0	0	0	0	0	0	1	0	9	1	0	9	1	0	0	0
ARM	1	1	0	0	0	1	0	0	1	0	9	1	1	9	1	0	0	1
BIO	0	0	0	0	0	0	0	0	0	9	9	9	1	9	1	0	9	9
BUL	0	0	0	0	9	9	0	0	0	9	9	9	0	9	9	0	0	9
BUR	9	9	9	2	9	9	1	1	9	9	9	9	0	3	9	0	0	9
CAM	0	0	0	1	9	9	1	1	0	1	1	9	0	9	9	0	0	1
CHO	1	1	0	1	0	1	0	0	1	0	9	9	0	1	9	0	0	9
DRE	1	1	0	0	0	1	1	1	0	0	9	1	0	9	1	0	0	0
FER	9	9	9	1	9	9	1	1	0	0	9	9	0	3	9	0	0	9
FOS	1	1	0	0	0	1	1	1	0	1	9	1	0	9	1	0	0	0
GUN	9	9	9	2	9	9	1	1	9	9	9	9	0	3	9	0	0	9
GYR	1	1	0	0	0	0	0	0	1	0	9	1	9	9	1	0	0	1
HLC	1	1	0	0	0	1	0	0	1	0	9	1	0	9	1	0	0	9
HLS	0	0	1	1	9	9	0	9	0	1	9	9	0	9	1	1	0	1
HIP	0	0	0	0	0	1	0	1	1	0	9	1	0	9	1	0	0	1
IND	0	0	1	0	0	0	0	0	0	1	9	1	0	9	1	0	0	9
LAE	1	1	0	2	9	9	1	1	0	0	9	9	0	3	9	0	0	9
LEN	1	1	0	0	0	2	0	0	1	0	9	1	0	9	1	0	9	1
MEN	0	0	0	0	0	0	0	0	0	1	9	1	0	9	1	0	0	1
MIR	1	1	0	0	9	0	0	0	0	9	1	9	0	9	9	0	0	9
PAT	1	0	0	2	9	9	0	0	0	1	3	9	0	9	9	0	0	9
PHY	0	0	1	0	0	0	0	0	0	1	1	9	0	9	9	0	0	0
PAR	0	0	1	0	0	0	0	0	0	1	9	1	0	9	1	0	0	9
PBS	1	1	0	0	0	0	0	0	1	0	9	1	0	9	1	0	0	0
PBU	0	0	0	0	0	0	0	0	0	1	9	1	1	9	1	1	0	0
PLE	0	1	0	9	9	1	1	0	1	1	9	9	0	9	0	0	0	1
POL	1	0	0	0	0	1	0	2	1	0	9	1	0	9	1	0	1	9
PME	0	0	0	0	1	0	0	0	0	1	9	1	0	9	1	0	0	1
PNC	1	1	0	0	0	0	0	0	0	1	9	3	0	9	9	0	0	9
RHO	1	1	0	1	9	9	0	1	9	9	9	3	0	9	9	0	0	9
SNA	1	1	0	0	1	1	0	2	1	0	9	1	1	9	1	0	1	1
SRB	1	1	0	0	1	0	0	0	1	0	9	1	1	9	1	0	1	1

PARSIMONY TREES

Parsimony analysis constructs phylogenetic trees which account for the distribution of derived states with the fewest number of character state transformations. In these analyses, the character state code 9 is treated as 0. Thus, only those transformation events which are certain are used to determine the phylogenetic pattern. Unordered characters are considered after ordered characters which effectively gives unordered characters a lower weight than ordered characters. Loss states are unordered on all trees, as are characters 15: , 17: , 34: and 42: . This reduces the impact of those characters states whose homology or direction of transformation is most doubtful.

Parsimony analysis seeks to minimize the number of transformation events, and uses this number as a measure of homoplasy (Table 1). If there is no homoplasy, there will be only one transformation event for each derived state. The consistency index, the ratio of the number of derived states to the number of transformation events, measures the level of homoplasy on a scale from 0 to 1, with 1 indicating no homoplasy. The inverse of the consistency index gives the average number of transformation events per character. If there are fewer than 2 events per character, the inverse can be translated to give the percent of derived states which are likely to be homoplasic. Table 5 includes the consistency indices and their inverses for each of the parsimony trees run for this study.

Table 5. Indices of homoplasy for parsimony trees

Data set	Parameter name*			
	S	T	ci	1/ci
All characters Figure 32	53	176	.301	3.3
Shell omitted Figure 33	39	125	.312	3.2
Losses omitted Figure 34	42	118	.360	2.8
Shell and losses omitted Figure 35	27	72	.375	2.7
Reproductive characters only Figure 36	26	65	.400	2.5

Definitions of parameters

S - number of derived states

T - number of transformation events

ci - consistency index - (S/T)

1/ci - average number of transformation events per character

* Parameter D, the average percent of derived states homoplasic, is omitted from this table because in each case the value is greater than 100%

An alternative indication of the level of homoplasy is the number of homologs, states which appear only once on a tree (Table 6). These states define the monophyletic groups which are unambiguously supported by the data.

All characters (Figure 32)

This is the most highly resolved tree, with only 5 multifurcations. According to this tree there is one major branch with some offshoots and a second, minor branch. The consistency index is low, indicating considerable homoplasy. There are 5 derived states which are unique to a particular genus, and only 8 of 53 derived states (15%) define monophyletic groups of genera. Since two states (36:2, 36:3) define identical groups, there are actually only 7 monophyletic groups. 5 of the groups are defined by reproductive characters, the other two are groups of limpets. None of the 7 monophyletic groups nest (Figure 37-a). The lack of nesting and the low number of monophyletic states imply that the high resolution of this tree is potentially misleading, since most branches are defined by homoplasic states.

Shell deleted (Figure 33)

As was discussed in preceding sections, the shell character states are expected to be highly homoplasic. If this were true, then removal of the shell characters from the data set would increase the consistency index and increase the number of monophyletic groups defined by the remaining characters. In fact, the consistency index is

Table 6. Character states defining monophyletic groups on Parsimony trees

Data set	Character states
All states	10:1, 12:1, 14:2, 21:1, 24:1, 36:2, 36:3, 38:3
Shell deleted	1:1, 10:1, 12:1, 14:2, 15:2, 21:1, 24:1
Losses deleted	3:1, 10:1, 12:1, 14:2, 21:1, 24:1, 36:2, 36:3, 38:3
Losses and Shell deleted	1:1, 3:1, 10:1, 12:1, 14:2, 21:1, 24:1
Reproductive states only	1:1, 2:1, 10:1, 12:1, 14:2, 21:1, 24:1

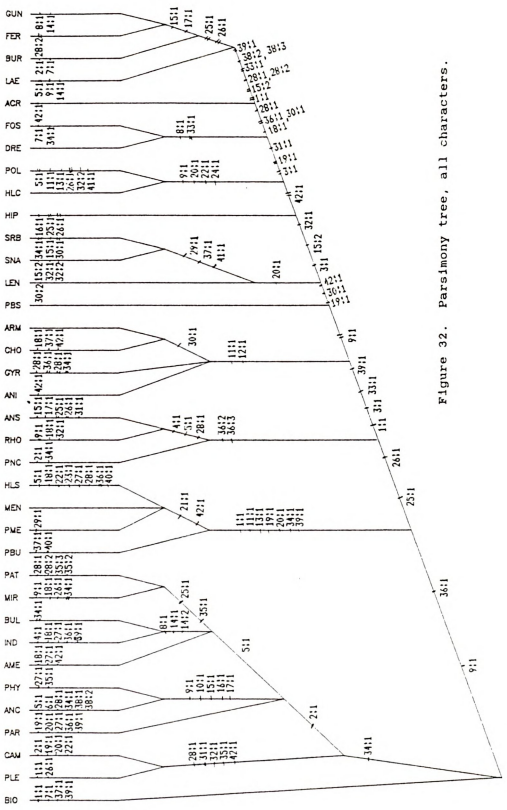


Figure 32. Parsimony tree, all characters.

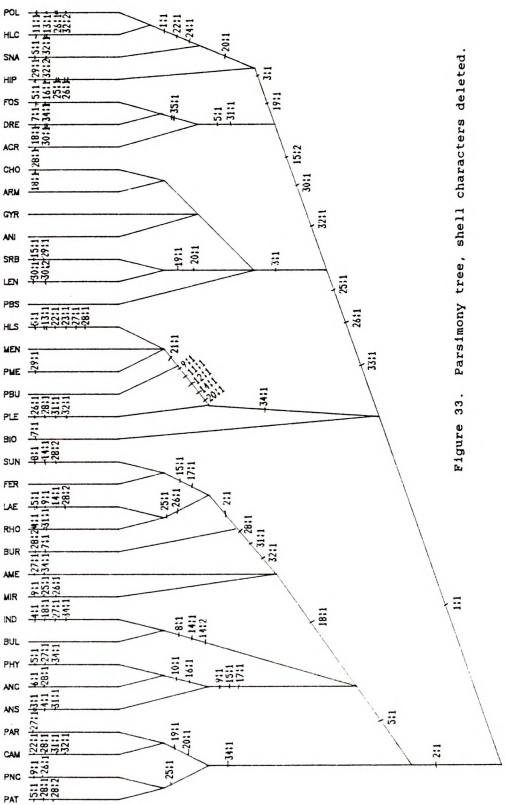


Figure 33. Parsimony tree, shell characters deleted.

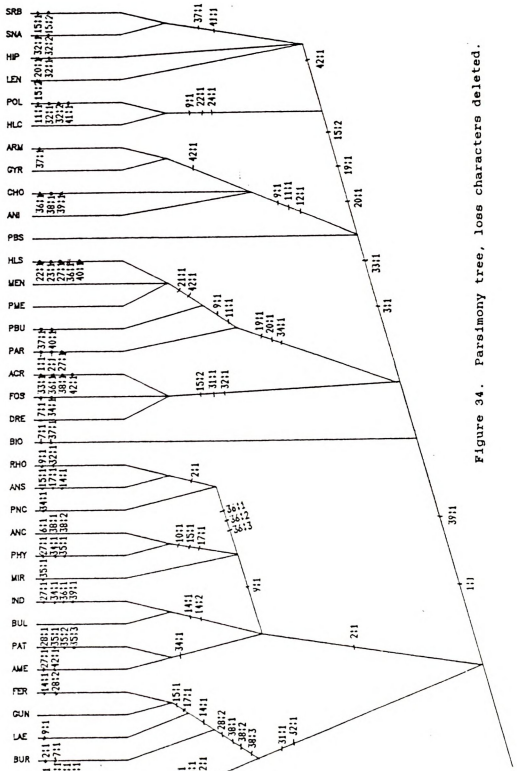


Figure 34. Parsimony tree, loss characters deleted.

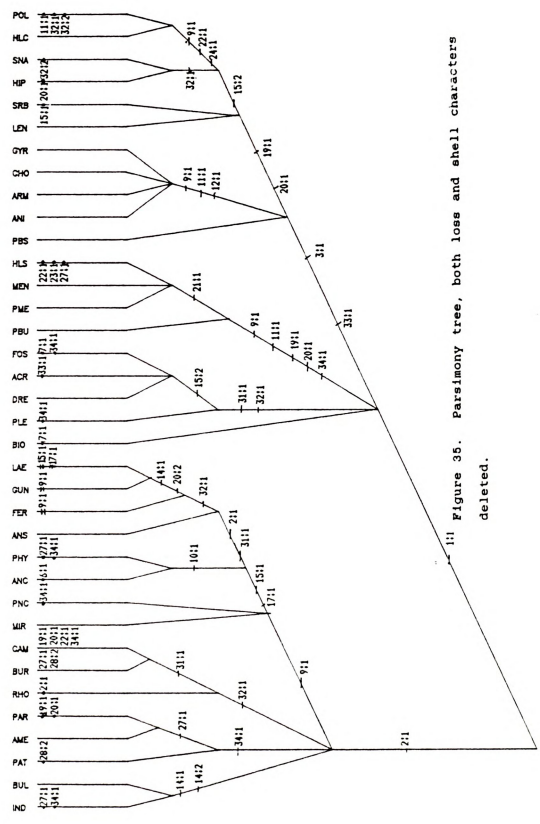


Figure 35. Parsimony tree, both loss and shell characters deleted.

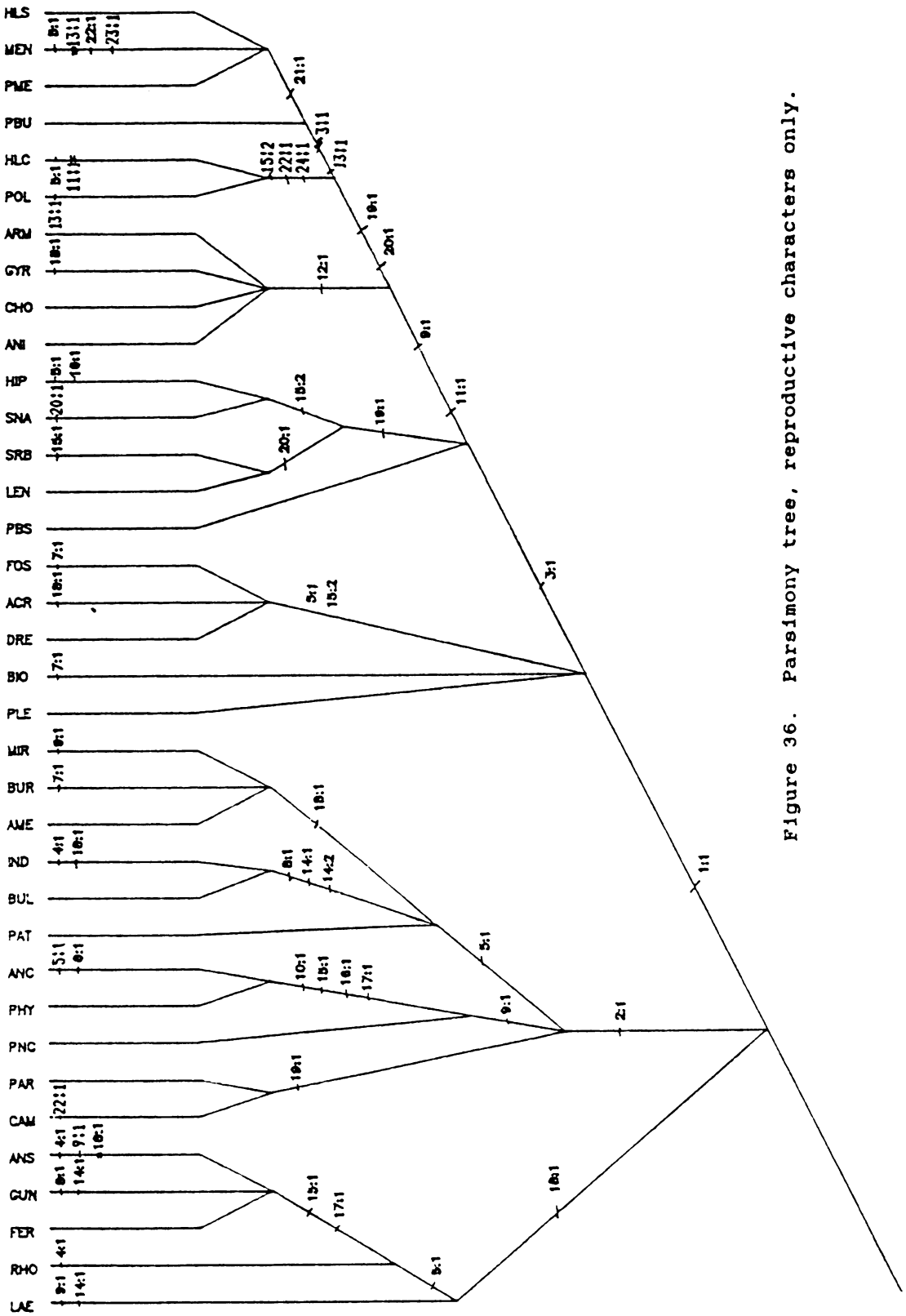


Figure 36. Parsimony tree, reproductive characters only.

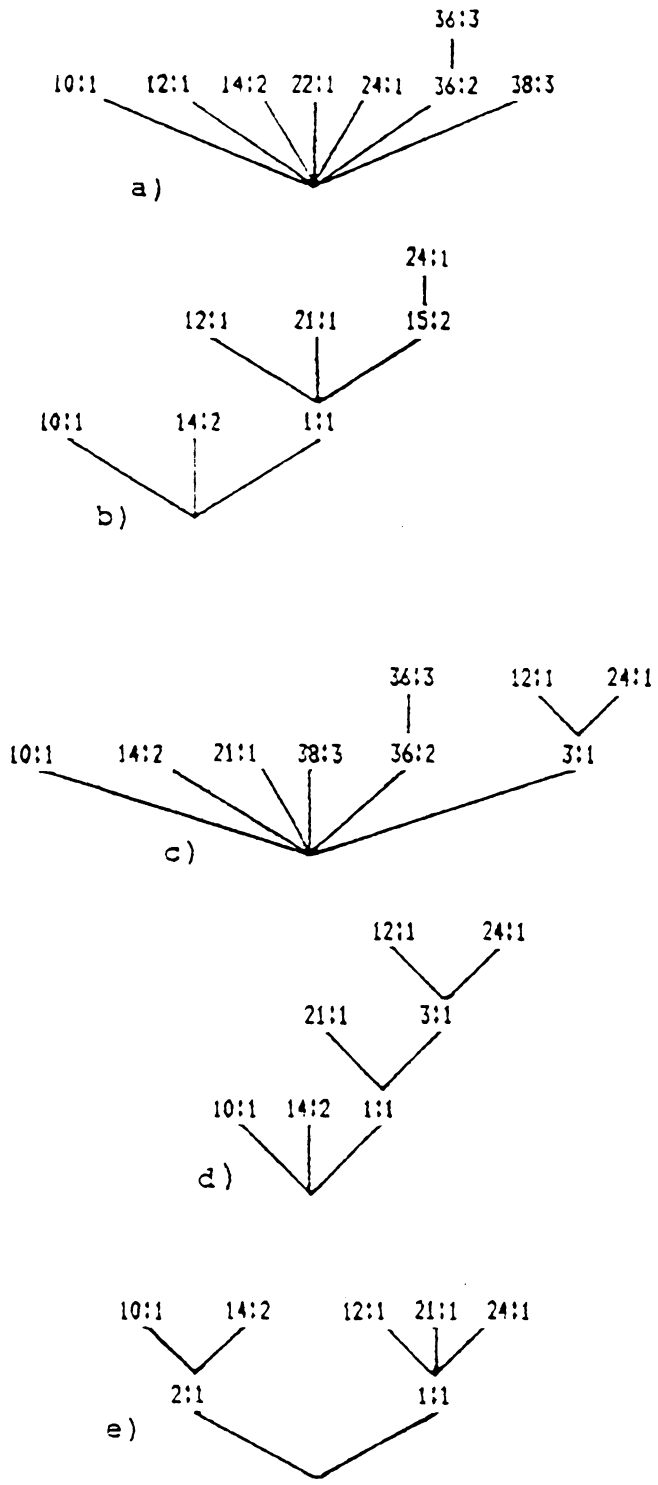


Figure 37. Nesting relationships of monophyletic groups identified on parsimony trees. a) all characters, b) shell characters deleted, c) loss characters deleted, d) both loss and shell characters deleted, e) reproductive characters only.

only slightly improved, from .301 to .312, indicating that the shell characters are probably no more homoplasic than any other sample of characters. On the other hand, 7 of 39 derived states define monophyletic groups comprising a slightly larger proportion of the data set (18%). All of the states which are homologs are reproductive characters. Also significant is the fact that the monophyletic groups recognized by this analysis form nested sets (Figure 37-b), indicating relationships between some groups. The smaller number of states is reflected by the slightly larger number of multifurcations (6).

Losses deleted (Figure 34)

Hecht and Edwards argued that losses and reversals are uninformative and are more likely to be misinterpreted than gains. Therefore, they felt that these characters should be given low weights. Weights were not explicitly applied in these analyses, but the loss characters are unordered where they are used. As unordered characters, they are fit to the structure defined by the ordered states. They are not equivalent to gains in determining the tree structure. Deletion of the losses permits an evaluation of how poorly the losses fit the background determined by the gains. This test is distinct from the Dollo method, which prohibits reversals of the proposed order of transformations. Reversal of the remaining transformations is still possible.

The change in the consistency index resulting from deletion of the losses from the full data set is large (from

.301 to .360). Thus, losses are more likely to be homoplasic than shell characters. However, the differences in the branching patterns of this tree and the one generated from the full data set are slight. All of the monophyletic groups recognized by the full data set are recognized when losses are removed. An additional group defined by the reproductive character state 3:1 is also recognized. Thus, 9 of 42 (21%) derived states define monophyletic groups. There was also a large increase in the number of multifurcations, from 5 to 9.

Shell and Losses deleted (Figure 35)

The data set for the fourth tree excludes both the losses and the shell characters. This leaves most of the reproductive characters, all of the radular characters, and only two respiratory character state transformations.

Since the number of derived states is now less than the number of taxa, the resolution of the analysis should be expected to decrease further. To some degree a reduction in resolution is apparent; however the evidence for it is mixed. There are 8 multifurcations, slightly less than when losses alone are deleted, but there are more branches per multifurcation. Monophyletic groups are defined by 7 of 27 derived states (26%) suggesting improved resolution, and more of the monophyletic groups nest. Therefore, while the general level of resolution is decreasing, resolution of one of the magor branches within the Planorbidae is improving.

The change in the consistency index due to the joint removal of shell and loss characters from the data set is .074. This is nearly equal to the sum of the improvements resulting from the independent removals of shell and loss characters, .011 and .059 respectively. Thus, the changes in the consistency index suggest that shell and loss characters are independent.

The monophyletic groups recognized by this analysis are present on the two previous trees. Except for 15:2 and 3:1, which define conflicting taxonomic groups, the homologs recognized on Figure 35 are present on both preceding trees. Like Figure 33, this tree has two major branches, one of which is defined by the state 1:1. None of the radular states nor the two remaining respiratory states define monophyletic groups.

Reproductive characters (Figure 36)

This data set most nearly approximates the data used in previously published analyses of the Planorbidae. The number of characters is nearly the same as in the preceding set. The radular and repiratory characters are replaced by the losses of the reproductive characters.

The consistency index (.400) is the highest of the five parsimony trees, as is the number of multifurcations (10). The monophyletic groups recognized by this analysis differ slightly from those recognized when the shell characters or the shell characters and losses are deleted. The only difference between the two sets of homologs recognized in

this tree and Figure 35 is the replacement of 3:1 with 2:1. Evidently 3:1 conflicts with the radular characters and 2:1 conflicts with the losses. On this tree, the state 2:1 defines a second major branch. A third group, composed of limpets, is defined by a homoplasic state.

Discussion of Parsimony Results

In all cases the consistency index is quite low. The low number of homologs, and the small difference between the overall consistency index and consistency index of the homoplasic characters indicates homoplasic evolution is not confined to a narrow suite of characters. The increases in the consistency index when loss characters are removed does indicate that these characters are more likely to be homoplasic than others, confirming the opinion of Hecht and Edwards. In contrast, the small improvement in consistency when the shell characters are removed indicates that these characters are only slightly more homoplasic than other gains. The only important difference between Figures 35 and 36 suggests that the radular characters are more likely to be homoplasic than the reproductive character losses.

The monophyletic groups recognized by each analysis provide a more concrete assessment of homology and homoplasy. In each case, derived states of reproductive characters are potential homologs. Only two other states, shell states defining groups of limpets are also possible homologs. All other derived states are homoplasic. Of the reproductive characters, 5 derived states are recognized as

homologs on all trees: 10:1, 12:1, 14:2, 21:1, and 24:1. The states 1:1, 2:1 and 3:1 emerge as homologs when the more obvious homoplasies, shell and loss characters, are eliminated from the analysis. Thus, 1:1, 2:1 and 3:1 are probably also homologs, but the analysis up to this point is equivocal.

Finally, although the limpets tend to be grouped on parsimony trees, the branches on which they occur are usually defined by homoplasic states. In all cases, there are at least two groups of limpets. More importantly, the limpets are not closely tied to coiled forms with the same pattern of coiling.

On the basis of the consistency indices of the five trees, Figures 35 and 36 are nearly equivalent estimates of the phylogeny of the Planorbidae. The tree based only on the reproductive characters does have a higher consistency index; and therefore, is slightly better than any others. In addition the lists of monophyletic groups in Table 6 are dominated by groups defined by reproductive character states. Therefore, the best estimate of the planorbid phylogeny would be based on the derived states of the reproductive tract which are gains. The parsimony analysis suggests that there are two main branches within the Planorbidae and several smaller clusters; however, the relationships of the clusters within each branch are uncertain.

COMPONENTS RESULTS

The distribution of character states (Table 4) was used to produce a list of components (Table 7), monophyletic groups defined by derived character states. Unordered characters were excluded from the components analysis since the alternate interpretations of the direction of transformation would define different components. Components composed of only one genus are excluded since they do not indicate relationships, only the monophyly of that genus. The component defined by 36:2 is also omitted since 36:2 and 36:3 define the same set of taxa.

The character state transformations as currently described do not support any phylogeny unambiguously. Table 8 is a modified version of Le Quesne's (1969) character-pair matrix, indicating both nesting and conflicting pairs of components. Nesting components are consistent with a single phylogenetic interpretation. Components which conflict are inconsistent with a single interpretation, either or both may be homoplasic (Le Quesne 1969). Since every component defined by these derived states conflicts with some other component, all of the states are potentially homoplasic. In addition, most components nest with few others, and therefore, the number of hierarchical levels in any particular cladogram is small. This broad distribution of homoplasy results in a large number of competing cladograms with little or nothing in common (Figure 38).

Table 7. Components defined by derived states of ordered characters

Character state	Genera included in each component
1:1	ACR, ANI, ARM, BIO, CHO, DRE, FOS, GYR, HLC, HLS, HIP, LEN, MEN, PBS, PBU, PLE, POL, PME, SNA, SRB
2:1	AME, ANC, BUL, BUR, CAM, IND, MIR, PAT, PHY, PAR, PNC
3:1	ANI, ARM, CHO, GYR, HLC, HIP, LEN, PBS, POL, SNA, SRB
4:1	ANS, IND, RHO
5:1	ACR, AME, ANC, ANS, BUL, BUR, DRE, FER, FOS, GUN, HLC, HIP, IND, MIR, PAT, RHO
6:1	ANC
7:1	BIO, BUR, FOS
8:1	BUL, GUN, IND
9:1	ANC, ANS, ANI, ARM, CHO, GYR, HLC, HLS, LAE, MEN, MIR, PHY, PBU, POL, PME, PNC
10:1	ANC, PHY
11:1	ANI, ARM, CHO, GYR, HLS, MEN, PBU, POL, PME
12:1	ANI, ARM, CHO, GYR
13:1	MEN, PBU, POL, PME
14:1	BUL, GUN, IND, LAE
14:2	BUL, IND
16:1	ANC, HIP, PHY
18:1	ACR, AME, ARM, BUR, FER, GUN, IND, LAE, MIR, RHO
19:1	CAM, HLC, HLS, HIP, LEN, MEN, PAR, PBU, POL, PME, SNA, SRB
20:1	CAM, HLC, HLS, LEN, MEN, PAR, PBU, POL, PME, SNA, SRB
21:1	HLS, MEN, PME

Table 7 (cont'd.).

22:1	CAM, HLC, HLS, POL
23:1	HLS
24:1	HLC, POL
25:1	ACR, ANI, ARM, CHO, DRE, FOS, GYR, HLC, LAE, LEN, MIR, PAT, PBS, POL, PNC, RHO, SNA, SRB
26:1	ACR, ANI, ARM, CHO, DRE, FOS, GYR, HLC, LAE, LEN, MIR, PBS, PLE, PNC, RHO, SNA, SRB
27:1	AME, HLS, INC, PHY, PAR
28:1	ANC, ANS, BUR, CAM, CHO, FER, BUN, HLS, LAE, PAT, PLE, RHO
28:2	BUR, GUN, LAE, PAT
29:1	PME, SNA, SRB
30:1	ARM, CHO, DRE, FOS, HLC, HIP, LEN, POL, SNA
30:2	LEN
31:1	ACR, ANS, BUR, CAM, DRE, FER, FOS, GUN, LAE, PLE
32:1	ACR, BUR, CAM, DRE, FER, FOS, GUN, HIP, LAE, PLE, POL, RHO, SNA
32:2	POL, SNA
33:1	ACR, ANI, ARM, CHO, GYR, HLC, HIP, LEN, PBS, POL, SNA, SRB
35:1	CAM, MIR, PAT, PHY, PLE
35:3	PAT
36:1	ANS, ANI, ARM, DRE, FOS, GYR, HLC, HIP, IND, LEN, MEN, PAR, PBS, PBU, POL, PME, PNC, RHO, SNA, SRB
36:3	ANS, PNC, RHO
37:1	ARM, BIO, PBU, SNA, SRB
38:1	ACR, ANC, BUR, CHO, FER, GUN, LAE
38:2	ANC, BUR, FER, GUN, LAE
38:3	BUR, FER, GUN, LAE

Table 7 (cont'd.).

39:1	ACR, ANI, ARM, BIO, DRE, FOS, GYR, HLC, HLS, HIP, IND, LEN, MEN, PAR, PBS, PBU, POL, PME, SNA, SRB
40:1	HLS, PBU
41:1	POL, SNA, SRB

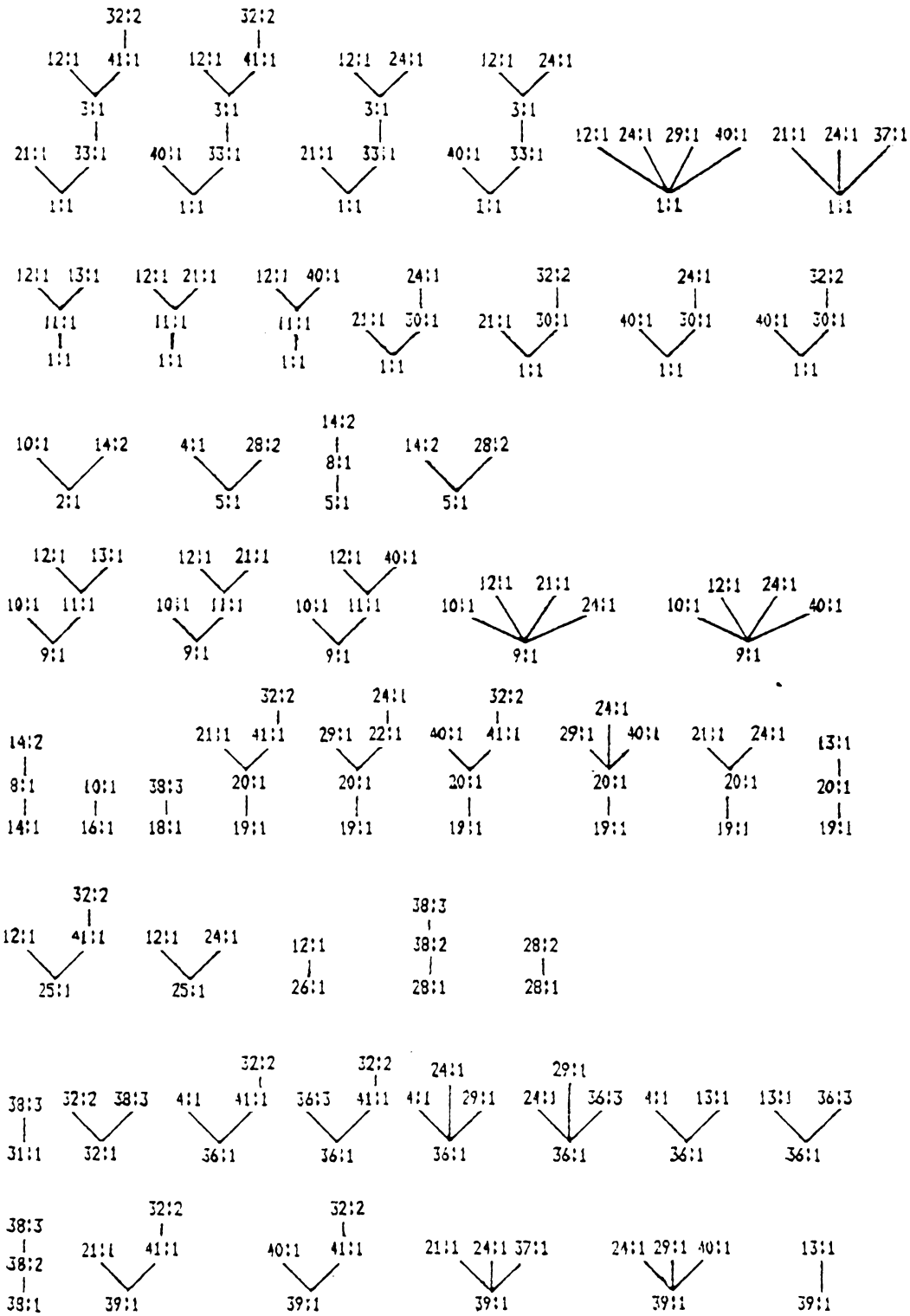


Figure 38. Nesting patterns of all components.

There are 50 different nesting patterns in Figure 38. Only the first two include as many as seven components. The consensus of these two excludes the components defined by 21:1 and 40:1 and is the best estimate of the planorbid phylogeny supported by the complete data set. This is a disappointing result since it accounts for only a small portion of the taxonomic and morphological diversification.

The results of the analysis of the full data set are relatively uninformative. Therefore, the conflicts in Table 8 were analyzed to discern the presence of any patterns which would indicate the relative probabilities of particular groups of characters. Since conflicts between components indicate that both states may be homoplasic, the relative frequencies of conflicts and nesting can be used as a rough estimate of the probability of homoplasy (Le Quesne 1969). Generalizations addressing the likelihood of homoplasy in particular groups of characters were also tested.

Nearly every character state has a high probability of being homoplasic. Only three components, defined by the states 7:1, 27:1 and 35:1, do not nest with any others. Since these three states are not consistent with any phylogenetic interpretation which includes any other states, they are omitted as the most likely to be homoplasic. In addition, the components defined by the states 22:1, 36:3 and 38:1 only nest with components defined by other states of the same transformation series. Nesting within

transformation series is expected; steps in the series that do not nest with characters outside the series are likely to be homoplasic. Therefore, 22:1, 36:3 and 38:1 are also omitted from further analysis. Unfortunately, elimination of these six components does not improve the analysis of the remainder, since none of the remaining components conflict only with these.

Losses normally nest less frequently than gains. The components defined by the losses 4:1, 5:1, 8:1, 16:1, 18:1, 25:1, 26:1, 28:1 and 30:1 nest with fewer than five other components. Most of these components conflict with others three times more often than they nest with them. However, many gains nest as infrequently as the above losses and the components defined by the losses 13:1 and 29:1 nest as frequently as most gains. Finally, since no gains conflict only with losses, it is clear that losses alone do not account for the high level of homoplasy.

Hecht and Edwards suggest that characters which are functionally related are less likely to conflict with each other than with other components. Therefore, incongruence between components defined by the derived states of functionally related characters is a strong indication that these states are homoplasic. The components matrix was inspected for characters which consistently conflict with others in the same functional group. These characters, or the whole group, were then omitted from further analysis.

Functional catagories roughly correspond to the character sets used previously.

Several subcategories of reproductive tract characters were identified and examined. Penis stylet characters (9: - 13:) fall within a single transformation series. None of them conflict with characters 7: and 8: which describe other aspects of penis evolution. Characters 18: - 24: describe preputial evolution. The one conflict in this group is between the components defined by 21:1 and 22:1. Thus, not only does the component 22:1 not nest with components defined by states in other transformation series, it conflicts with components defined by the same series.

When all of the reproductive characters are considered together, the components defined by 7:1 and 22:1 are omitted by the foregoing analyses. The component defined by 18:1 may also be deleted since it does not nest with any others defined by the reproductive tract. After these three are removed from consideration, only the component defined by 12:1 has no conflicts with the remainder. Therefore, this is the only derived state in the reproductive tract which is not likely to be homoplasic; and the only derived state which is likely to define a monophyletic group.

The derived states of the respiratory system (25: - 30:) are all likely to be homoplasic. Only the components defined by the transformation series of character 28: nested with each other. No other combination of components nest. The potential homoplasy of these

characters is also supported by the rarity of their congruence with any other characters.

Most of the derived states of the radula (31: - 33:) are also likely to be homoplasic. The component defined by 31:1 does not nest with any other components in this set. The component defined by 32:1 only nests with the component defined by 32:2. The only other pair of components in this group that nest are defined by 32:2 and 33:1. In this group the states 31:1 and 32:1 can be rejected as homoplasic.

The analysis of the shell characters (35: - 41:) is not very informative. The three characters describing coiling patterns (35: , 36: and 38:) are mutually exclusive; and the aperture characters (39: - 41:) do not apply to the limpets. Thus, only the independence of the modifications of the aperture and final whorl from the general coiling pattern can be tested. The conflicts do indicate that the terminal modifications are independent of the coiling pattern, and suggests that one of these two groups is likely to be homoplasic.

This analysis of functionally related groups of characters supports the hypotheses that the derived states of the radular, respiratory and shell characters are homoplasic. Virtually all of the respiratory states are potentially homoplasic; most of them are also losses. The only two respiratory states which are not rejected are 32:2 and 33:1. The shell states are not particulary informative, but do appear to be homoplasic as well. In contrast,

comparatively few reproductive character states are rejected as potential homoplasies. Most of the rejected reproductive states are losses. Therefore, this series of restricted group analyses of homoplasy justifies limitting the phylogenetic analysis to those components defined by reproductive character states.

There are 15 cladograms supported by reproductive character states (Figure 39). The components defined by 7:1 and 18:1 do not nest with any others and were excluded. The components defined by losses were not excluded since some nest more frequently than do many gains. Three cladograms (Figure 39 a, h and i) are composed of five components, accounting for more characters than any other interpretation. One cladogram (Figure 39-o) has fewer components; but, with four hierarchical levels, accounts for more evolutionary events within a single lineage. Thus, the reproductive character states support several competing phylogenetic interpretations. Unfortunately, there is no consensus among the four cladograms. No single component is present in all four; only the component defined by 12:1 is present on Figure 39 a, h and i. Because there is no single phylogenetic interpretation based on the reproductive characters, and because none of the cladograms in Figure 39 account for as many evolutionary events as the two cladograms selected from Figure 38, the complete data set provides a better basis for inferring the phylogeny of the Planorbidae.

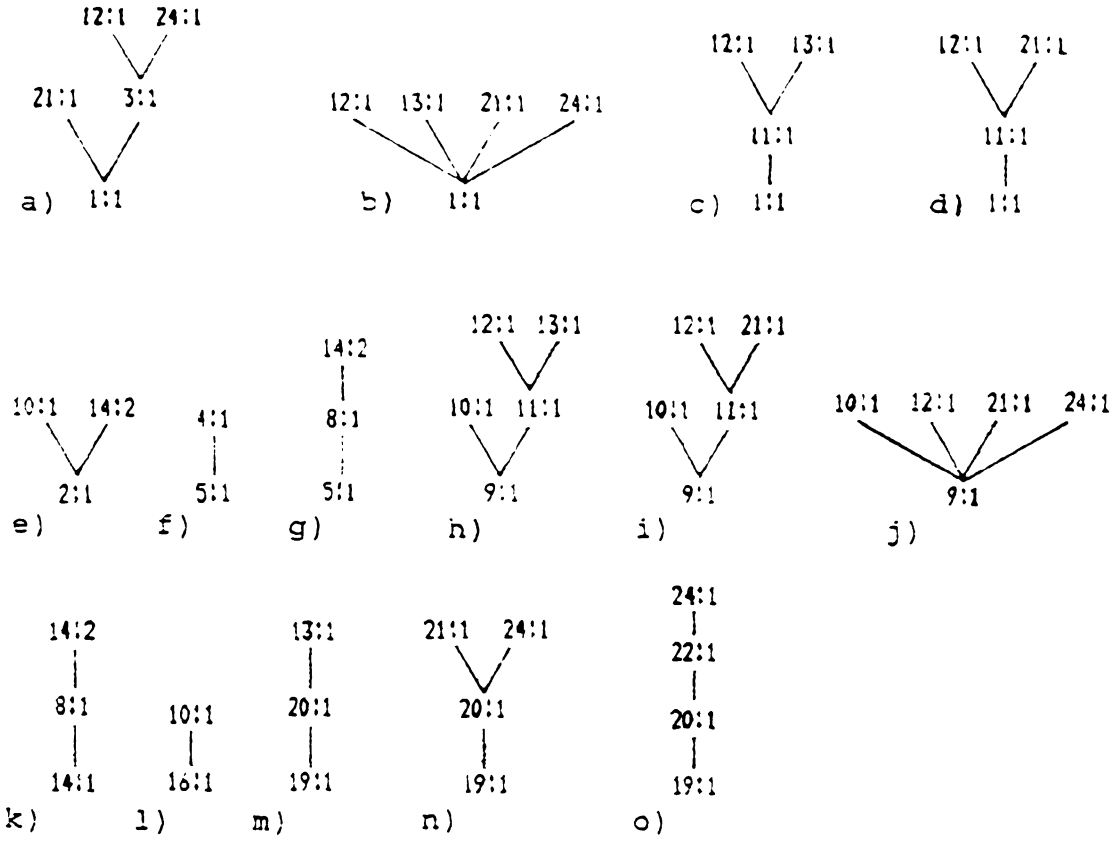


Figure 39. Nesting patterns of all components defined by reproductive character states.

Discussion

The high frequency of conflicts reflects the general level of homoplasy of these characters. The amount of homoplasy severly limits the level of resolution of the components analysis of these characters. However, the broad distribution of homoplasy throughout the data set is more significant. The analyses of particular groups of characters does indicate different levels of homoplasy in different groups, but also highlights exceptions to these generalizations.

The phylogenetic pattern supported by the components analysis incorporates a small number of states and only accounts for 20 of the 37 genera. This leaves nearly half of the genera in a basal multifurcation and leaves several multifurcations within the group that is partially resolved. Although a single solution is supported by these data, it only emphasizes the inability of these characters to elucidate the evolutionary events which produced the taxonomic diversity of the Planorbidae.

CONCLUSION

Although parsimony and components analyses represent different approaches to recognizing homologs and homoplasies, the results are quite similar. In both cases the shell characters are homoplasic, although their level of homoplasy is no greater than the average of the other characters. Losses are recognized as highly homoplasic by both analyses. The components analysis also indicates that

some states do not fit the generalizations. There is also concordance between these two sets of results in the recognition of homologs. The component defined by 1:1 forms the basis of the largest component diagram and is recognized as a monophyletic group on most of the parsimony solutions. The smaller components defined by 10:1, 12:1, 14:2, 21:1 and 24:1 have few conflicts and are consistent with all of the parsimony solutions.

DISCUSSION

CONSENSUS

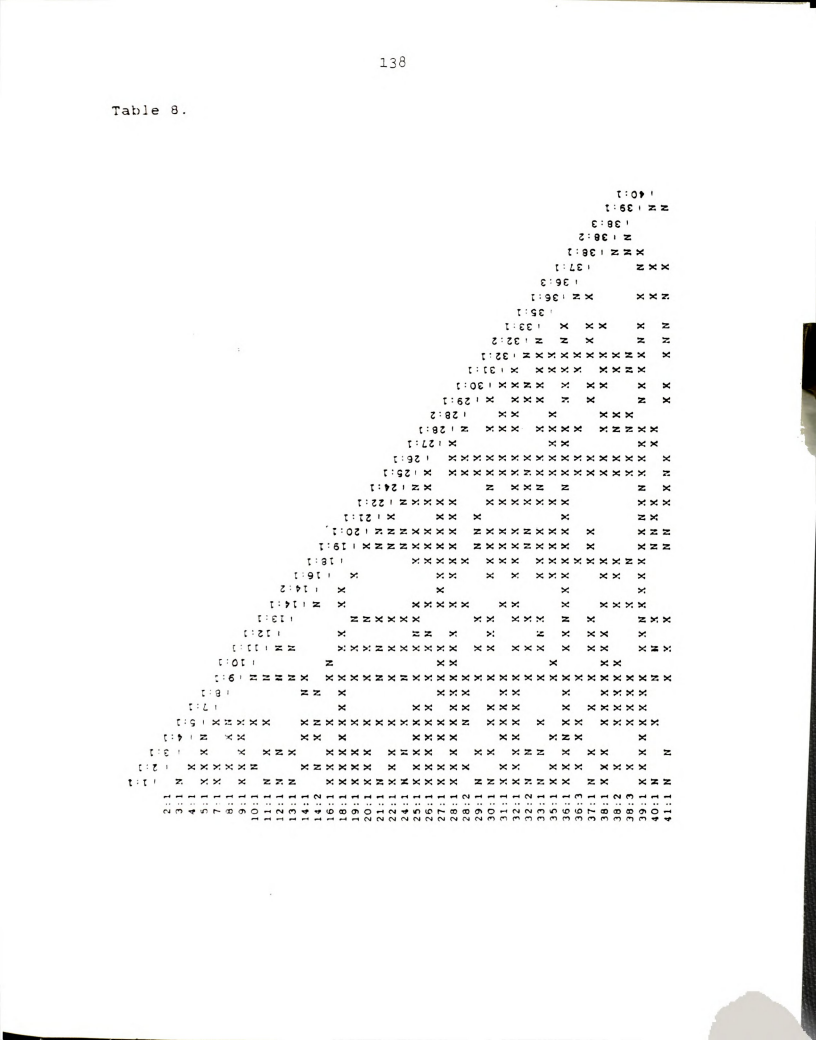
Parsimony analysis and components analysis do not necessarily lead to compatible results, as was illustrated in Figures 6-d and 7-e. Parsimony analysis considers the number of evolutionary events required to explain the distribution of derived states across taxa. The algorithms that use this method cluster taxa based on the number of derived states they share. Components analysis does not attempt to fit taxa together, but finds the set of character states that are all consistent with a single interpretation. This method entails a search for components defining nested sets of taxa. Because parsimony analysis groups taxa and components analysis groups character states, these two techniques can be regarded as independent tests. The shared conclusions are more likely to be consistent with the data than are the unique results of either single analysis.

CHARACTER EVOLUTION

The results common to both analyses confirm several of the hypotheses of homoplasy that were tested. The consistency indices (Table 5) and the components conflicts (Table 8) both indicate that all characters are likely to be homoplasic. However, the largest drop in the consistency

Table 8. Set relationships between components defined by derived states of ordered characters

Table 8.



index occurs when losses are removed from the parsimony analyses. In the components analysis, the losses frequently conflict with other components much more often than they nest. The losses also conflict with each other. Both these patterns are clearly evident in the respiratory characters. For example, the loss 25:1 nests with 4 states and conflicts with 32. Together, the large change in the consistency index and the frequency of conflicts indicate that losses, including respiratory characters, are more likely to be homoplasic than any other derived states.

There are three exceptions to the general pattern described above, the states 13:1, 27:1 and 28:1. The state 13:1 represents a reduction of the penis stylet. This state is less homoplasic than other losses, judging by the pattern of conflicts and nestings in Table 8. It conflicts primarily with characters not in the reproductive tract; however, it does conflict with reproductive characters describing glandular organs, such as 21: - 24: in the prepreputial series. The other exceptions, 27:1 and 28:2, are the only respiratory states which are not losses. This exception is important because these characters have as many conficts as the other respiratory characters. In fact, these two respiratory gains reinforce the generalization that respiratory characters are extremely likely to be homoplasic, both in the family Planorbidae and in the superfamily Lymnaeacea.

The radular characters of the planorbids show a trend of increasing numbers of cusps on the teeth, while lymnaeids tend to decrease the number of cusps. However, the pattern of conflicts in Table 8 indicates that increasing the number of cusps is generally not consistent with the evolutionary patterns of other characters. The state 32:2 is an exception (Figure 38). This state, representing extreme increases in cusp number, is part of the two best components solutions. The radular state 33:1 is also an exception. This state describes a change in marginal cusp shape and is not one of the cusp number characters. This state also appears on both of the two best components solutions in Figure 38. However, none of the parsimony trees list 32:2 or 33:1 as potential homologs (Figure 37).

The results for the shell characters are also equivocal. According to the parsimony analysis only the limpet shell form states are homologs (Figure 37). However, the consistency index is lowest when shell characters are eliminated from the data set (Table 5). In contrast, the two best components diagrams include not the limpet states but two aperture states, 40:1 and 41:1 (Figure 38). Although there is no consensus as to which shell states are homologs, shell characters are much less likely to be homoplasic than losses. One possible interpretation is that the shell states are all homoplasic, but evolve at a slower rate than losses, resulting in a lower perceived level of homoplasy.

Seven reproductive states are identified as potential homologs by the parsimony analysis: 1:1, 2:1, 10:1, 12:1, 14:2, 21:1 and 24:1 (Figure 37). The components analysis confirms that the states 1:1, 12:1 and possibly 21:1 are homologs (Figure 38). The state 3:1 is also included in the components solutions.

The compatibility of 2:1 and 3:1 with 1:1, in different analyses, indicate similar tendencies in the organization of the diverticula in the gonad and the prostate. Especially, the nesting of 1:1 and 3:1 implies that both organs tend to have the diverticula in linear arrangements. Clustering of the prostatic diverticula into a hemispherical mass, 2:2, only occurs when the gonadal diverticular are not linearly arranged. Hubendick's (1955) assertion that penial complex characters reflect phylogenetic relationships is not supported by these data. The only reproductive characters indicated as potential homologs are those few that do not conflict with 1:1, 2:1 and 3:1. Thus, the more proximal glandular organs are better predictors of genealogy than are the penial complex characters.

The high level of homoplasy results in conclusions by both parsimony analysis and components analysis that include small numbers of derived states. In both cases, the reproductive states are most likely to be homologs. Although the two analyses support different sets of homologs, both support states that are consistent with 1:1.

TAXONOMIC EVOLUTION

Two monophyletic groups are clearly suppported by the consensus of the parsimony analysis and the components analysis. Twenty genera are included in the group defined by 1:1. The state 12:1 defines a subset consisting of four genera. These are the most strongly supported monophyletic groups, defined by the two states that are least likely to be homoplasic.

The two states 1:1 and 12:1 form a basis for reexamining the other derived states in the data set. If these two are accepted as homologs, then the states conflicting with them must be homoplasic. The remaining, compatible states, are at least potentially homologs. These remaining states can be divided into two groups: those nesting with 1:1 and those which do not nest.

Because components analysis only considers nesting components, the group of compatible components which do not nest is automatically excluded from the consensus. Table 8 shows 10 derived states that neither conflict nor nest with 1:1. These are: 2:1, 4:1, 8:1, 10:1, 14:1, 14:2, 28:2, 36:3, 36:2 and 38:3. Only these 10 states potentially define monophyletic groups among the 16 genera not included in the subset defined by 1:1. The only nesting patterns among the 10 states that includes more than two states contains 2:1, 10:1 and 14:2 (Figure 38). These three states are also homologs according to the parsimony analysis (Figure 37). Therefore, these three components do comprise

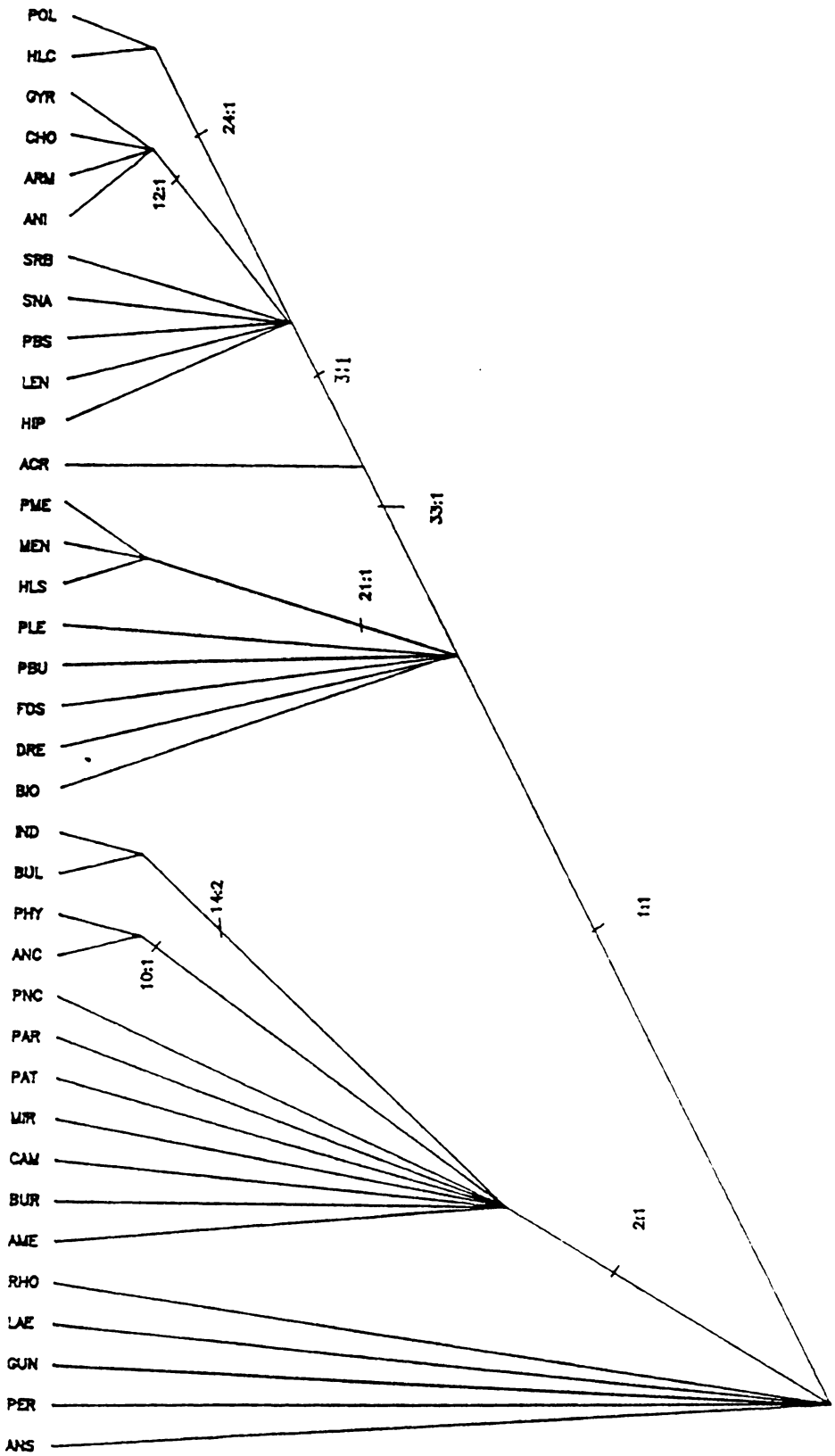


Figure 40. Consensus of parsimony and components analyses.

the most reliable phylogenetic interpretation of the 16 genera not sharing the state 1:1.

The components that nest with 1:1 and do not conflict with 12:1 also comprises a short list of ten states: 3:1, 11:1, 13:1, 21:1, 24:1, 29:1, 32:2, 33:1, 40:1 and 41:1 (Table 8). Two of these states, 13:1 and 29:1 are losses. The above discussion of character evolution points out that these are the states most likely to be homoplasic. Neither 13:1 nor 29:1 is can be considered homologs based on the independent results of the parsimony analysis or the components analysis. One other state, 11:1, is also not supported by either independent result. Therefore, 11:1, 13:1 and 29:1 are removed from further consideration as potential homologs.

Among the remaining states that nest with 1:1 and do not conflict with 12:1, there are three conflicts, between the following pairs: 24:1 and 32:2, 24:1 and 41:1, and 21:1 and 40:1. The states 3:1 and 33:1 conflict with none of the others. In fact, 1:1, 33:1, 3:1 and 12:1 represent a series of nested sets of taxa. These suggest four evolutionary events along one lineage, leading to the four genera characterized by 12:1 : Anisus, Armiger, Choanomphalus and Gyraulus.

The inclusion of 3:1 and 33:1 among the possible homologs is consistent with the patterns of character evolution described in the preceding section. The derived prostate structure represented by 3:1, with the other

prostate trait 2:1 and the gonadal state 1:1, is cited as a reliable indicator of character evolution in the Planorbidae. The state 33:1 differs from the other radular states because it refers to changes in tooth shape rather than changes in numbers of tooth cusps.

Two of the remaining five characters states are shell states: 40:1 and 41:1. Both of these states refer to modifications of the aperture that are potentially independent of shell shape. However, both occur only in planispiral shells. Since these apertural traits are potentially linked to shell shape, which is demonstrably homoplasic, the possibility that the apertural traits are also homoplasic cannot be excluded. Similarly, since radular tooth cusp numbers are clearly homoplasic in other cases, the state 32:2 is considered also quite likely to be homoplasic. Therefore, the states 21:1 and 24:1 are chosen as potential homologs.

Figure 40 has a much lower level of resolution than previously published taxonomies of the Planorbidae. The difference between these results and the previous taxonomies is not the data which were analyzed but the method of analysis. Although Hubendick (1955, 1978) and Starobogatov (1967) recognized a high level of homoplasy, they constructed phenetic groupings on the basis of unique combinations of states rather than the homology of specific states.

Only three of the smaller groups recognized by this analysis are also recognized in the previous studies: Ancylastrum and Physastra (10:1); Anisus, Armiger, Choanomphalus and Gyraulus (12:1); Bulinus and Indoplanorbis (14:2). The group Helicorbis and Polypylis (24:1) is not found, but the tribe to which these genera are assigned is not resolved in any of the earlier studies. The one small group which most differs from the earlier studies is composed of Helisoma, Menetus and Promenetus (21:1). Hubendick (1978) synonymized all three genera; Starobogatov placed them in different families and Hubendick (1955) combined them with several other genera. These differences are exclusively a function of the methods used. The above authors constructed subfamilies and tribes on the basis of broad similarities but did not recognize groups on the basis of single characters.

The two larger components recognized by this analysis (1:1 and 3:1) more closely approximated the groups constructed in the earlier studies. The component defined by 3:1 is divided into two tribes in the earlier taxonomies. Only Starobogatov unequivocally recognized that they form a single group. This analysis does not support the recognition of either tribe as a monophyletic group. The component defined by 1:1 was also closely approximated by Hubendick and Starobogatov. Hubendick (1955) recognized it as a subfamily but was unsure of its monophyly. He also added several taxa to the group and so departed most from

the group defined by the component. Starobogatov and Hubendick (1978) both recognized two major groups as families or subfamilies respectively. One of the groups closely approximated the component defined by 1:1. The principal difference is that the group recognized by Starobogatov and Hubendick excluded Helisoma and Plesiophysa, and included Ancylus. These differences are slight; this study does confirm the recognition of one branch of planorbids as a monophyletic group.

The taxonomic results of the current study support the monophyly of only one subgroup of planorbids. Further resolution of this branch is highly restricted. These data do not support the monophyly of the remaining genera. Only two pairs of these genera can be recognized as monophyletic groups. The only conclusion clearly supported by these data is that these morphological characters do not reflect the phylogenetic relationships of the Planorbidae and the Lymnaeacea.

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