

CERITHIOIDEAN PHYLOGENY

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ABSTRACT

Phylogenetic analysis of fifteen families of the superfamily Cerithioidea, using 58 characters derived from shell, radula, soft anatomy, gametes, and spawn was made, using the PHYSYS algorithm. An overview of previous systematic arrangements of the superfamily, its fossil history, and general reproductive biology and ecology are presented. All characters and character states are fully discussed, and a character table of all families and a final cladogram are presented. Within the context of the cladogram, the major clades of cerithioidean evolution are identified and congruence with past phylogenetic schemes, the fossil record, and a UPGMA phenogram are discussed. The Campanilidae is the most primitive group, followed by the Litiopidae. The four remaining major clades include the Melanopsidae and Pleuroceridae; the Cerithiidae, Thiariidae, Planaxidae, and Diastomatidae; the Potamididae, Cerithiidae, Modulidae, and Batillariidae; and the Turritellidae and Vermetidae, which emerge as the most highly derived families.

INTRODUCTION

In terms of familial diversity, numbers of genus-group taxa, and species diversity, the Cerithioidea Férussac, 1819 is one of the largest mesogastropod superfamilies. Only the superfamily Truncatelloidea (=Rissoacea) approaches it in this respect, and both superfamilies are distinctive in having undergone extensive adaptive radiations into freshwater as well as marine habitats. Indeed, much of the freshwater prosobranch fauna throughout the world is composed of members of these two superfamilies. The diversity of cerithioideans, in terms of morphology, size, habitat, feeding methods, and reproductive biology, is notable. The group ranges in morphology from small-shelled families, such as the Dialidae and Litiopidae, to the relatively large-shelled taxa comprising the Potamididae, Cerithiidae, Turritellidae, and the sessile Vermetidae and Siliquariidae. Shell shape may be highly turreted, as in the Turritellidae, Potamididae, and Cerithiidae; moderately turreted as in the Planaxidae and Pleuroceridae; turbinately as in the Modulidae; or uncoiled as in the Vermetidae and Siliquariidae. Our present system of classification relies largely on overall conchological similarity. One looks in vain for detailed anatomical, reproductive, and ontogenetic studies necessary to identify homologies and to supply the characters delineating most families. Often, what is reported about the anatomy and biology of a family is based on the study of a single species which may not be representative of the family. For example, much of what is related about the Turritellidae is based on anatomical and ecological studies of "*Turritella*" *communis* Risso, the common European representative of the group. Aside from an unpublished master's thesis on an Australian species (Carrick, 1980a), the other members of this very large family are unknown. The anatomy, ecology and reproductive biology of many groups remain unknown, incomplete, or anecdotal.

The goals of this study are fourfold: 1, to determine characters derived from shell morphology, anatomy, reproductive biology; 2, to analyze the patterns of morphological diversity in cerithioidean families; 3, to diagnose each family and stabilize its classification; 4, to propose a testable hypothesis of phylogeny for the superfamily. In order to accomplish character selection and analysis, I

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MATERIALS AND METHODS

A cladistic analysis of 15 taxa was made, using the PHYSYS algorithm of Farris and Mickevich (copyright: 1983, 1984, 1985), and employing 58 characters comprising 134 character states. Parsimonious interpretations of multistate characters were derived using the transformation series analysis of Mickevich (1982). In addition, phenograms were produced using unweighted pair-group arithmetic averaging (UPGMA). The families chosen for analysis were those for which there exists sufficient anatomical information to compile a comprehensive data base.

Bishop (1979:77) suggested that the Potamididae are polyphyletic on the basis of anatomical and electrophoretic studies. My own anatomical research on this family convinces me that this is the case; accordingly, for the purpose of cladistic analysis, I have divided the family Potamididae H. and A. Adams, 1854 into three groups (families), Batillariidae, Cerithideidae, and Potamididae, although the *Cerithidea* group may also be considered a subfamily of Potamididae. The diagnostic characters and character states of each of these families are found in Table 5 and in the cladogram (Fig. 2). Transformation series of multistate characters are illustrated in Fig. 1.

Outgroup selection

At first glance, there are a number of superfamilies that would seem to be appropriate for outgroup comparison. Among these are the Cerithiopsodea and the Triphoroidea, until recently traditionally grouped with the cerithiids on the basis of shell morphology and open pallial gonoducts. However, these two groups are now more frequently regarded as good superfamilies in their own rights (Kosuge, 1966; Marshall, 1978, 1983). They were assigned to the suborder Heterogastropoda by Kosuge (1966:297), and more recently to a new suborder Heteroglossa by Haszprunar (1985a,b). Moreover, Healy (1983a:212; 1986:168) has shown that their euspermatozoan morphology separates them from the Cerithioidea. I therefore excluded them as useful outgroups because of their putative systematic distance from the cerithioidean lineage.

The Truncatelloidea (=Rissooidea) and Stromboidea were selected as the most

appropriate outgroups within the Mesogastropoda. Both are large superfamilies and, as microphagous grazers of marine substrates, share the same broad ecological niche. Of these two superfamilies, the Truncatelloidea were considered the closest to the Cerithioidea. Like cerithioideans, this superfamily has a large number of higher-level taxa, some of which have radiated into freshwater environments. The Truncatelloidea and Cerithioidea are sometimes considered as the stem groups from which other prosobranchs and opisthobranchs evolved (Fretter & Graham, 1962:6; Gosliner, 1981: 213). Ponder (1983; 1984: 4; 1988, this volume) postulated that the truncatelloidean families arose from a mesogastropod ancestor that had open male and female pallial gonoducts and lacked a penis, conditions characteristic of the Cerithioidea. Moreover, Ponder (1984) suggested that the earliest rissoids may have evolved from the extinct Pseudomelaniidae, the same family suggested by Bouvier (1887: 153,155) as a possible ancestor of cerithioideans. The rissoid characters used in this analysis were taken from Ponder (1985) and are derived from the genus *Rissoa* Desmarest, 1814, family Rissoidae Gray, 1847.

The Stromboidea were chosen as the other outgroup because they too, comprise a large group of taxa, and share similar habitats with cerithioideans. Several authors have indicated a relationship between cerithioideans and strombids. Risbec (1927: 17) suggested that strombids are close to the Modulidae, and Johansson (1948: 5) indicated that similarities in reproductive organs indicate a relationship between *Aporrhais* da Costa (Strombidae) and Cerithioidea. While I believe there is some affinity between the two groups, I do not think it is a close one and have contested Risbec's assertion elsewhere (Houbrick, 1980a: 137). Strombid anatomical characters were taken from Woodward (1894), Yonge (1932), Little (1965) and Okutani (1965).

Characters

The characters resulted from my own research on the anatomy, reproductive biology, ecology, and systematics of cerithioideans and from published accounts of other authors. Families for which information is lacking or only fragmentary were not used in the cladistic analysis. These are mainly the smaller cerithioidean groups, such as the Finellidae, Dialidae, and Siliquariidae, whose status as families is still uncertain or doubtful. All major families were included in the analysis. The major literature sources for anatomical information about cerithioidean families are presented in Table 1. It should be noted that several large families, such as the Potamididae, Thiaridae, Turritellidae, and Vermetidae, are still very poorly known. On the basis of published anatomical information and my own observations, I suspect some families may be polyphyletic; thus, any comparison among them is beset with difficulties. In addition, analysis and comparison of families is complicated by the wide range of character states and simultaneous presence of binary characters within a given family. There is no easy solution to this problem, but it was thought that by limiting the characters to the taxa for which each family is named, a working cladogram would be produced and used iteratively as a basis for future phylogenetic analyses. For this reason, the characters used in this analysis are derived from the nominal taxa from which the family name was derived, and these taxa are considered as typically representative of the family. A major difficulty with this method is

TABLE 1. Major Sources of Cerithioidean Anatomical Characters

Family	Source
CAMPANILIDAE	Houbrick, 1981c
LITIOPIIDAE	Houbrick, 1987b
MELANOPSIDAE	Belgin, 1973; Starmühlner, 1970
PLEUROCERIDAE	Abbott, 1948; Davis, 1969; Dazo, 1965; Houbrick, (pres. study); Itagaki, 1960; Morrison, 1954; Pace, 1973
PLANAXIDAE	Houbrick, 1987a
DIASTOMATIDAE	Houbrick, 1981b
THIARIDAE	Abbott, 1948, 1952; Binder, 1959; Houbrick, (pres. study); Moore, 1898, 1899; Morrison, 1954; Seshaiya, 1934, 1936; Starmühlner, 1968, 1974, 1976
CERITHIIDAE	Houbrick, 1971, 1974b, 1978, 1985; Marcus & Marcus, 1964
POTAMIDIDAE	Berkeley & Hoffman, 1834; Bishop, 1979; Houbrick (pres. study); Johansson, 1956
CERITHIDEIDAE	Bright, 1958, 1959; Houbrick, 1984
BATILLARIIDAE	Driscoll, 1972; Houbrick (pres. study)
MODULIDAE	Houbrick, 1980a
TURRITELLIDAE	Graham, 1938; Johansson, 1946; Randles, 1900; Carrick, 1980a
VERMETIDAE	Hadfield, 1970; Morton, 1951, 1955
RISSOIDAE	Ponder, 1985
STROMBIDAE	Johansson, 1948; Little, 1965; Okutani, 1965; Woodward, 1894

that the nominal taxon may not really be typical of the family and the apomorphic characters distinguishing it may thus be excluded from the analysis. For binary characters, a character was considered present in a family even if it was absent in some genus-level and species-level taxa. I used homologous characters that would be applicable at the family-taxa level and that appear, from our present knowledge, to be typical of each group. Transformation series of multi-state characters are shown in Fig. 1.

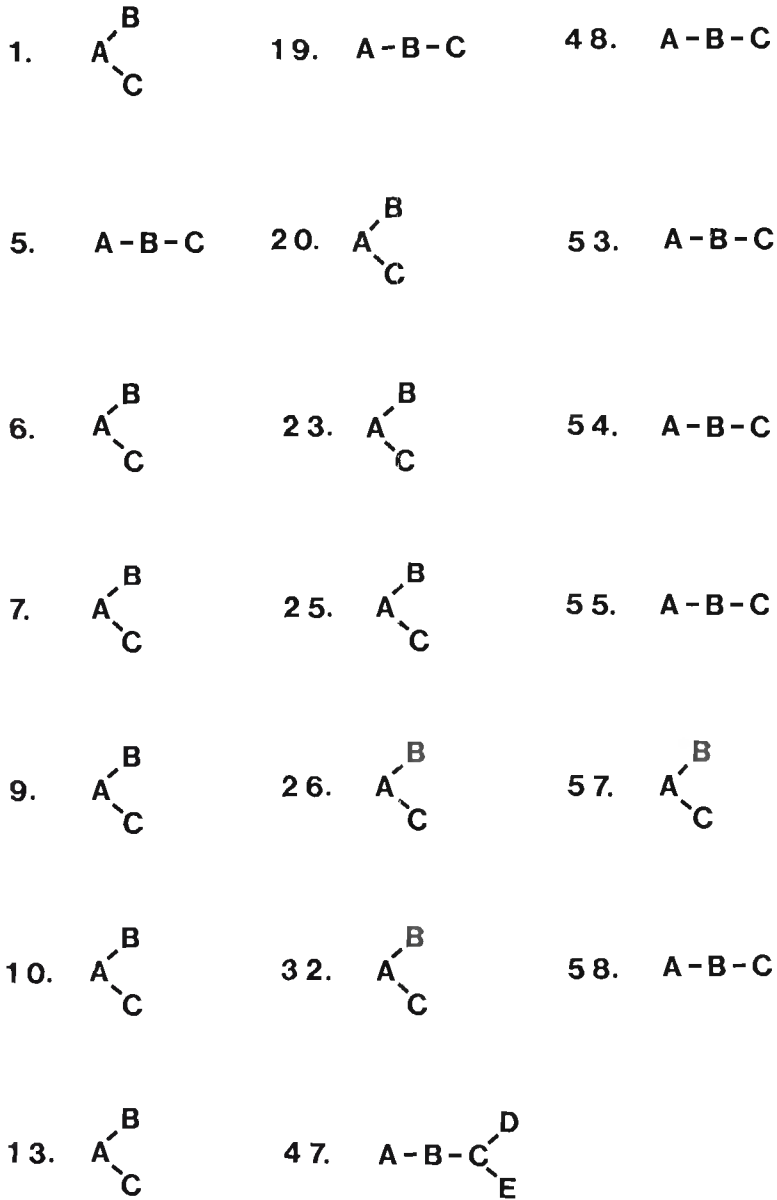


FIG. 1. Character state transformation series for the 20 multistate characters used to construct the cladogram depicted in Fig. 2. Numbers and letters correspond to the characters and character states, respectively, as listed in Table 5.

OVERVIEW OF CERITHIOIDEA

Systematic position

No modern reviews of the superfamily exist except as smaller parts of major works on prosobranch taxonomy and systematics (Cossmann, 1906; Thiele, 1929; Wenz, 1939; Götting, 1974: 129; Boss, 1982: 992-996). Indeed, most cerithioidean

families have received little systematic revisory attention by recent workers. There have been attempts to differentiate the Cerithioidea within larger molluscan classificatory schemes, but all fall short in that each relies on only one or several characters derived from a single, limited, morphological feature. This is best illustrated in the older, more traditional classifications, which were based on shell characters alone with occasional use of radular characters. Lamentably, even some recent revisions rely only on shell characters (Gründel, 1976a,b; 1981; 1982; Bouniol, 1981: 21). Following the lead of Troschel (1856-1863), who suggested that the radula, and not the shell, is the most important character to understand the natural classification of the Gastropoda, Bandel (1984: 31-62) recently grouped a number of cerithioidean taxa largely by radular configuration. Several recent papers (Haszprunar, 1985a: 458; Maeda, 1986: 32-35) have relied on osphradial morphology as a taxobase. Healy (1982-1983) and Koike (1985: 66-67) have used the ultrastructure of cerithioidean euspermatozoa as a major element defining the superfamily. Several papers review cerithioidean phylogeny on the basis of pallial oviduct morphology: Johansson (1948,1956) was the first to survey and recognize the taxonomic value of the open pallial gonoducts of the Cerithioidea. In a more recent survey of cerithioidean genital ducts, by Houston (1985) the Triphoridae and Cerithiopsidae were wrongly included in the Cerithioidea. Members of the Cerithioidea have been characterized by their fecal pellet morphology (Bandel, 1974: 20), shape of egg masses (Bandel, 1976: 266-267), and by protoconch shape and sculpture (Bandel, 1975: 20-31).

Authors differ as to the exact composition and division of the Recent superfamily, which contains a number of poorly-defined or ill-conceived higher category taxa. A rough, conservative estimate of living cerithioidean taxa, pruned of invalid and suspect higher taxa and their synonyms, reveals a superfamily comprising about 25 families and over 200 genera. This estimate excludes fossil taxa and the cerithiopsids and triphorids. The latter two groups are sometimes still considered as cerithioideans (Houston, 1985) despite substantial evidence to the contrary (Kosuge, 1966; Climo, 1975; Marshall, 1983,1984; Haszprunar, 1985a,b; Healy, 1986c: 195). That the Cerithiopsidae and Triphoridae should be removed from the Cerithioidea has been demonstrated by Healy (1983: 212; 1986c: 168) and, in recent classifications of higher prosobranchs (Haszprunar, 1985a,b: 32), they have been assigned to a separate suborder (Heteroglossa Haszprunar, 1985b).

A number of authors have suggested that the Cerithioidea is the ancestral stem group from which other mesogastropod superfamilies, all other prosobranchs, or, in some cases, opisthobranchs, have evolved (Johansson, 1948; Boettger, 1954; Cox, 1960: 144; Golikov & Starobogatov, 1975: 201; Fretter & Graham, 1962: 638; Fretter, 1980: 226-227; Ponder, 1985). Gosliner (1981: 213) and Haszprunar (1985: 30) have both shown that there is no evidence for a cerithioidean origin of opisthobranchs. Fretter and Graham (1962: 624) have suggested that the cerithioideans are closely related to the truncatelloideans (i.e., rissoaceans) and that both superfamilies were derived from the Pleurotomarioidea through the Loxonematoidea. Gründel (1976b) postulated that the Diastomatidae (cited as Diastomidae) was the primitive group that gave rise in the Jurassic to the Cerithioidea, but his concept of the Diastomatidae is inflated and

based solely on misleading shell characters. I have redefined and set limits to this family based on the anatomy, radula, and reproductive structures of the one living species and have shown that the Diastomatidae originated in the Paleocene and underwent an extensive radiation in the Eocene (Houbrick, 1981b: 614). It is not a primitive group and is an unlikely candidate for progenitor of the Cerithioidea.

Published work on the genetics, tissue proteins, and isoenzymes of cerithioideans is virtually nonexistent. Some electrophoretic work has been done on the Australian Potamididae (Bishop, 1979, unpublished master's thesis). Only six of the Recent cerithioidean families have representatives with known chromosome numbers. These are summarized in Table 2. The average haploid number is 17.1.

TABLE 2. Haploid Chromosome Numbers of Cerithioidean Families

Family	\bar{x} haploid no.	range	no. taxa	source
THIARIDAE	17.7 (31.4)*	16-60	8	Patterson, 1969
PLEUROCERIDAE	15	7-20	14	Patterson, 1969; Davis, 1972
POTAMIDIDAE	18	18	3	Davis, 1972
BATILLARIIDAE	18	18	2	Davis, 1972
CERITHIIDAE	18	18	4	Patterson, 1969; Vitturi and Catalano, 1984
TURRITELLIDAE	16	16	1	Patterson, 1969

*= polyploid number

Despite the numerous data available, one finds few recent higher category classifications that are based on suites of anatomical characters, and reproductive characters, or that attempt to be holistic in their data bases. An exception is the work by Risbec (1955) in which numerous anatomical characters were used in a natural classification for the Cerithioidea within the larger context of the Prosobranchia.

Fossil history

The Cerithioidea is thought to be an ancient group with origins in the Late Devonian when, according to Knight *et al.* (1960: 316), the turritellid lineage began. Fretter and Graham (1962: 624) suggested that the superfamily made its first appearance in the Permian. Although the origin of the Cerithioidea is obscure, the conchologically similar superfamily Loxonematoidea, of Ordovician origin (Knight *et al.*, 1960: 311), has been suggested as being ancestral to it (Houbrick, 1979a: 19). Bouvier (1887: 153,155) believed that the Pseudomela-

niidae (superfamily Subulitoidea), of Jurassic origin (Knight *et al.*, 1960: 125), was the stem group for many Recent cerithioidean families, while Cossmann (1906: 3) thought that the Procerithiidae of Jurassic origin (Cox, 1960: 125), gave rise to the other cerithioideans. Golikov & Starobogatov (1975: 201-202) suggested that the Cerithioidea first appeared in the Triassic and is an independent line of evolution in the subclass Pectinibranchia (=Caenogastropoda). They thought that the Cerithioidea differed sufficiently in morphology from other pectinibranchs to justify placing it into an independent order, Entomostoma. However their concept of this order is based on misconceptions about several cerithioidean groups: they are in error in stating that true pallial oviducts are lacking in the Planaxidae (see Houbrick, 1987a) and that there are closed pallial gonoducts in the Modulidae (see Houbrick, 1980a). Moreover, no significant morphological characters are cited to support the integrity of this new order. According to Cossmann (1906: 9), the superfamily Cerithioidea ("cenacle") had its roots in the Jurassic, with some Recent families (Cerithiidae, Diastomatidae) appearing in the Cretaceous and others (Modulidae, Planaxidae) in the Tertiary. It should be noted, however, that modulids and planaxids may have poor fossil records, because of their habitats. In my opinion, this later origin (Jurassic-Cretaceous) of the superfamily is a more reasonable one to accept.

Opinions about the origin of specific cerithioidean families are likewise varied. The Turritellidae are said to originate in the Devonian (Knight *et al.*, 1960: 316; Sepkoski, 1982: 28), and, if this were true, are thus the oldest cerithioidean family. Other cerithioidean families are alleged to appear in the Triassic or earlier (Bouvier, 1887: 152; Golikov & Starobogatov, 1975: 201; Sepkoski, 1982: 27-28), but given the likelihood of shell convergence in this span of time, it is doubtful that Devonian fossil shells attributed to the Turritellidae are true members of that family; moreover, proper familial allocation for many Paleozoic and Mesozoic fossils cannot always be decided from shell morphology alone. Most Cenozoic fossils, on the other hand, can be correlated with the correct Recent families with much greater confidence. As far as can be judged, most Recent families appear to have arisen in the late Cretaceous-early Tertiary periods.

As seen above, there are many theories about the origins of the superfamily Cerithioidea and the many families comprising it, but as the anatomical morphology of the early fossil taxa postulated as ancestors is unobtainable, their designation as progenitors of Recent groups is largely conjectural. There is no way to ascertain if fossil groups with shell morphologies similar to Recent cerithioideans are truly related or ancestral to them because of the pervasiveness of morphological convergence. It is thus unwise to place too much reliance on purely paleontological interpretations of cerithioidean origins and evolution, because these kinds of hypotheses can never be falsified, and result in a proliferation of scenarios based on mere opinion. At best, the fossil record serves as a good test of more rigorous phylogenetic hypotheses.

Ecology

Most cerithioideans occur in considerable numbers, are tropical in distribution, and many families represent adaptive radiations into specific habitats. The Cerithideidae are specialized for life in mangrove forests, some genera spending

TABLE 3. Ecological distribution of Cerithioidean taxa.

Taxon	substrate	vertical distribution	habitat	geographic zone	feeding type
Cerithiidae	sand, rubble, rock	intertidal-subtidal	marine	tropical-temperate	browser
Batillariidae	sand-mud	high intertidal	estuarine	temperate-subtropical	detritivore
Potamididae	mangroves, mud flats	high intertidal	estuarine	tropical	detritivore
Thiaridae	sand-mud	----	freshwater	tropical	browser
Pleuroceridae	sand-mud	----	freshwater	temperate-tropical	browser
Planaxidae	rock	intertidal	marine	tropical, temperate	browser
Vermetidae	rock	intertidal-subtidal	marine	tropical, temperate	mucous net feeder
Turritellidae	mud-sand	subtidal	marine	tropical	filter feeder
Litiopidae	algae	pelagic, subtidal	marine	tropical	browser
Diastomatidae	sand	subtidal	marine	temperate	browser
Modiolidae	seagrass, rock	subtidal	marine	tropical	browser
Siliquariidae	sponges	subtidal	marine	tropical	filter feeder

most of their lives on tree branches; the Potamididae also occur in mangrove swamps but are mostly confined to the soft mud beneath the trees, and occasionally attaching to the mangrove roots; the Batillariidae occur in estuarine biotopes and have moved into subtropical and temperate zones; the Cerithiidae occur mainly on tropical, marine, soft bottom habitats ranging from the high intertidal to the deep sea, with several groups highly adapted for life in marine angiosperm sea grass beds or intertidal rocky shores; the Modulidae are specialized for subtidal grazing of microalgae on marine grasses or on hard substrates; the Turritellidae appear to be adapted for subtidal filter feeding on soft bottoms; the Vermetidae have uncoiled shells that are permanently attached to hard substrates; the Siliquariidae have uncoiled shells that are embedded in sponges; the Litiopidae are highly adapted for life on algal fronds or filaments, some having a pelagic life history; the large freshwater groups Pleuroceridae and Melanopsidae tend to live in fast flowing streams and rivers while the Thiaridae span environments ranging from rocky, fast moving streams, to broad, slow moving rivers, and quiet lakes. Table 3 summarizes these radiations for several families.

All cerithioideans are herbivores or detritivores and all have a taenioglossate radula, paired salivary glands, a stomach complex with a style sac and gastric shield typically containing a crystalline style, and most have an esophageal gland. Although the majority are grazers, some groups are detritus feeders, mucous net feeders, and filter feeders (see Table 3). These kinds of feeding methods are usually limited to specific families, but feeding guilds of cerithioideans may comprise members of many families.

Reproductive biology

Reproduction in cerithioideans is gonochoristic except in some parthenogenetic thiarids. The aphyllate males produce two kinds of sperm, euspermatozoa and paraspermatozoa, *sensu* Healy (1983: 178), in all known families. Sperm transfer is accomplished by spermatophores in the Cerithiidae (Houbrick, 1974b; 1985), Cerithiidae (Houbrick, 1984: 7), Batillariidae (pers. observ.), Potamididae (pers. observ.), Modulidae (Houbrick, 1980a: 127-129), Planaxidae (Houbrick, 1987a), Vermetidae (Hadfield & Hopper, 1980), and presumably, in all other families. Most cerithioideans lay their eggs in gelatinous masses or strings that are attached to the substrate. Reproduction may involve planktotrophy or lecithotrophy (mixed in most families), brooding in specialized incubatory pouches [Planaxidae (Houbrick, 1987a), Diastomatidae (Houbrick, 1987a: 39), Thiaridae (Abbott, 1948: 286-287; Morrison, 1954), Siliquariidae (Morton, 1951: 35); Fossaridae (Ponder, 1980)]; brooding in the mantle cavity and shell [Turritellidae (Carrick, 1980: 254), Pleuroceridae (Itagaki, 1960: 44; Davis, 1969; 1972), Vermetidae (Morton, 1951, 1965)] and parthenogenesis in many of the Thiaridae (Abbott, 1948: 286-287; Morrison, 1954). Table 4 summarizes brooding among cerithioidean taxa.

Healy (1983a: 71) established two groups of cerithioideans on the basis of euspermatozoan ultrastructure. Healy's "group one" is distinguished by euspermatozoa having the midpieces and axoneme surrounded by two large and two small midpiece elements. This group may be further divided, on the basis of ultrastructural differences, into two subsets: one comprising the Cerithiidae,

TABLE 4. Distribution of brooding and reproductive strategies among the Cerithioidea

Taxon	Location of Brood Pouch	Type of Brooding	Type of Development	Sexes	Source
PLEUROCERIDAE					
<i>Semisulcospira</i>	pallial oviduct	complete	ovoviviparous	gonochoristic	Morrison, 1954
THIARIDAE					
THIARINAE					
<i>Brotia</i>	head-foot	complete	ovoviviparous	gonochoristic	Morrison, 1954
<i>Thiara</i>	head-foot	complete	ovoviviparous	parthenogenetic	Morrison, 1954
<i>Melanoides</i>	head-foot	complete	ovoviviparous	parthenogenetic (males rare)	Morrison, 1954 Houbrick, 1987a
<i>Pachymelania</i>	head-foot	complete	ovoviviparous	gonochoristic	Binder, 1959
<i>Stenomelania</i>	mantle	partial	planktotrophic	gonochoristic	Starmühlner, 1976
<i>Cubaedomus</i>	head-foot	complete	ovoviviparous	parthenogenetic	Morrison, 1954
<i>Aylacostoma</i>	head-foot	complete	ovoviviparous	parthenogenetic	Morrison, 1954
<i>Tarebia</i>	head-foot	complete	ovoviviparous	parthenogenetic	Morrison, 1954
<i>Sermyla</i>	head-foot	complete	ovoviviparous	parthenogenetic	Morrison, 1954
<i>Sulcospira</i>	head-foot	complete	ovoviviparous	parthenogenetic	Morrison, 1954
MELANOPSINAE					
<i>Faunus</i>	head-foot	partial	planktotrophic	gonochoristic	Houbrick, 1987a
PALUDOMINAE					
<i>Lavigera</i>	oviduct	complete	ovoviviparous	gonochoristic	Moore, 1899
<i>Potadomoides</i>	oviduct	complete	ovoviviparous	gonochoristic	Leloup, 1953
PARAMELANIINAE					
<i>Tanganyicia</i>	head-foot	complete	ovoviviparous	parthenogenetic	Moore, 1898
<i>Bathanalia</i>	mantle cavity	complete	ovoviviparous	parthenogenetic	Moore, 1898
<i>Tiphobia</i>	oviduct	complete	ovoviviparous	gonochoristic (penis in males)	Moore, 1898
DIASTOMATIDAE					
<i>Diastoma</i>	head-foot	complete?	lecithotrophic	gonochoristic	Houbrick, 1987a
FOSSARIDAE					
<i>Fossarus</i>	head-foot	partial?	lecithotrophic	gonochoristic	Ponder, 1980
PLANAXIDAE					
<i>Planaxis</i>	head-foot	partial	planktotrophic	gonochoristic	Risbec, 1936, this study
<i>Planaxis</i>	head-foot	complete	ovoviviparous	parthenogenetic?	Thorson, 1940, Barkati & Ahmed, 1982
<i>Fissilabia</i>	head-foot	partial	lecithotrophic	gonochoristic	Houbrick, 1987a
<i>Supplanaxis</i>	head-foot	partial	planktotrophic	gonochoristic	Houbrick, 1987a
<i>Angiola</i>	head-foot	partial	planktotrophic	gonochoristic	Houbrick, 1987a
<i>Hinea</i>	head-foot	partial	planktotrophic	gonochoristic	Houbrick, 1987a
SILQUARIIDAE					
<i>Pyxipoma</i>	head-foot	complete	ovoviviparous	gonochoristic	Morton, 1951

Turritellidae, Litiopidae (Healy, 1983a: 71-73), Dialidae and Siliquariidae (Healy, 1986b: 193); and the second subset including the Planaxidae and Batillariidae (Healy, 1983a: 71-73). Healy's "group two" is distinguished by euspermatozoa with four equal-sized midpiece elements and midpiece flange structures and includes the Potamididae, Modulidae, Cerithideidae (Healy, 1983a: 71-73), and possibly the Pleuroceridae (Koike, 1985; Healy, 1986b: 193) and Thiaridae (Kohnert & Storch, 1984).

DISCUSSION OF CHARACTERS

Characters were derived from conchological, radular, anatomical and reproductive features. Of the many characters utilized for descriptive purposes only 70 could be confidently coded or used for all 15 families, but of these only 58 were used for cladistic analysis, as autapomorphies that appeared at terminal branches were excluded from the data matrix. Characters are grouped into categories, each of which is followed by the number of characters comprising it. These are: shell (6), operculum (3), external anatomy (14), mantle cavity (6), radula(6), alimentary tract (5), nervous system (5), reproductive system (12), and spawn (1). Of these, 38 were binary and 20 multistate characters, comprising a total of 134 character states. Transformation series of multistate characters are shown in Figure 1. The 58 characters and their states are listed in Table 5 and are discussed below, under each category.

Shell characters (1-6)

The six shell characters were based on general morphological shapes and were not derived from trivial sculptural elements, as these are subject to considerable homoplasy at the family level. Among cerithioideans, only the vermetids are sessile and uncoiled; thus, these characters were considered autapomorphies. Most cerithioideans have an elongate, turreted shape. Only the Modulidae are turbinatae, while the Planaxidae, Melanopsidae, and some thiarids and pleurocerids are ovate-conical in shell shape. The presence of an anterior canal in varying degrees of development and length is characteristic of most families but this character is completely lacking in the Vermetidae and Turritellidae. Long siphonal canals are common in many genera of the Cerithiidae and become pronounced in the genus *Rhinoclavis* Swainson and especially so in the subgenus *Longicerithium* Houbriek (Houbriek, 1978: 85). Ovate or round apertures are usually correlated with the presence or absence of an anterior canal, respectively. Most cerithioideans have relatively smooth outer lips but in some families, notably the Potamididae, Batillariidae, Cerithideidae, and Cerithiidae, the outer lip may be considerably flared and crenulate. An umbilical chink is an autapomorphy of the Modulidae. Periostracum is smooth in most cerithioideans but is hispid in the Planaxidae and Diastomatidae (Houbriek, 1981b: 600; 1987a: 21,33). The unique periostracum of the Campanilidae is pitted and calcareous (Houbriek, 1981c: 268).

Opercular characters (7-9)

Opercular shape, placement of the nucleus and the number of spirals are all obviously interrelated characters. The two most common shapes are the round, multispiral kind with a central nucleus, and the ovate, paucispiral type with eccentric or near terminal nucleus. The former kind occur in the Potamididae (Bentham Jutting, 1956: 427, 445), Batillariidae (Bequaert, 1942), Cerithideidae (Houbriek, 1984), Modulidae (Houbriek, 1980a), Turritellidae (Randles, 1900: 57), and Vermetidae (Morton, 1965). A round operculum is not necessarily associated with a round, siphonless aperture, as the potamidids, cerithideids, and batillariids have round opercula as well as well-developed siphonal canals (pers.

observ.). With the exception of the above mentioned families and the Planaxidae, which have a lenticular operculum (Houbrick, 1987a: 5), all other cerithioidean families have ovate, paucispiral opercula.

External anatomy characters (10-23)

Snout length appears to be related to feeding: a short snout occurs among the Turritellidae, most of which are ciliary feeders (Graham, 1938; Yonge, 1946; Andrews, 1974: 1136-1137; Petuch, 1976: 322; Carrick, 1980a: 254; Vaughan, 1983) and among the Vermetidae, many of which are mucous net feeders (Morton, 1950, 1951, 1955, 1965; Hadfield, 1970: 306-307; Hughes & Lewis, 1974: 537-542). The Siliquariidae, known only from a single species, are ciliary feeders, but do not use a mucous net (Morton, 1951: 37). All the other cerithioidean taxa are grazers and have long snouts, except for the aberrant Campanilidae, in which a short snout occurs. The snout is especially well-developed in the Cerithideidae and Potamididae (pers. observ.), in the Diastomatidae (Houbrick, 1981c: 601) and in some cerithiid genera, such as *Rhinoclavis* (Houbrick, 1978: 6). Long, mobile, cephalic tentacles appear to have a tactile, sensory function in all families (pers. observ.) except for the sessile Vermetidae, where they are short (pers. observ., Morton, 1955) and obviously not as important as in exploratory, free-moving taxa. However, the Campanilidae, which are free living forms, also have short, stubby cephalic tentacles (Houbrick, 1981c: 270). The Modulidae are the only cerithioideans that have eyes at the mid-tentacular stalk and have this character in common with the Stromboidea (Houbrick, 1980: 137).

All cerithioideans have a large foot except for vermetids (Morton, 1955; Hadfield, 1970), presumably because of their sessile habit. The anterior pedal mucous gland is present at the front margin of the propodium in all families but is very highly modified for mucus production and sunk deep into the head-foot beneath the buccal cavity in the vermetids (Morton, 1955; Hadfield, 1970: 302). The anterior pedal mucous gland extends halfway around the sole in the planaxids (Houbrick, 1987a: 27) and circles the entire edge of the sole in *Campanile* (Houbrick, 1981a: 271).

A large mesopodial mucous gland that produces mucous attachment threads occurs in the Litiopidae (Houbrick, 1987b: 11). This kind of gland also occurs in the rissoid outgroup (Ponder, 1985: 15) and in the Turritellidae (Randles, 1900: 57), but in the latter family presumably has a different function than in the litiopids and may not be homologous. Its presence in the Turritellidae was therefore not coded in the phylogenetic analysis, and it was considered as autapomorphic in the Litiopidae.

Metapodial tentacles occur in the rissoids (Ponder, 1985: 15), but usually as a single posterior one, which may be secondarily divided into three or five in one genus. Among cerithioideans, they occur in the Litiopidae, where they are highly developed (Houbrick, 1987; Luque *et al.*, 1988, this volume), and in the Vermetidae, in which there is a short pair in all genera except *Vermetus*, in which they are very long (Morton, 1951: 37, 1955; Hadfield, 1970: 302). Although scored in this analysis as homologous, they could be independently derived in each family.

The presence of a ciliated groove leading from the exhalant siphon down the right side of the foot in females is a common, presumably homologous character in

all cerithioideans (pers. observ.) except for the turritellids and vermetids. Feces and other debris expelled from the mantle cavity are removed by this groove, but its primary function appears to be the transport of eggs from the distal end of the pallial oviduct, from which it originates, to the foot. The groove leads to a bulbous, glandular ovipositor that is present in all groups (Houbrick, 1984: 10) except for the Vermetidae, Planaxidae, Siliquariidae, and Diastomatidae, which brood their young. There is a small gland on the right side of the foot of unknown function in *Turritella* (Randles, 1900: 57) that may represent the vestige of an ovipositor, but in the cladistic analysis, the Turritellidae were not scored as having an ovipositor.

Brooding cerithioideans do so in the mantle cavity, within a modified portion of the pallial oviduct, or in specialized brood pouches in the head-foot. Vermetids attach their eggs to the interior wall of the shell adjacent to the mantle, or to the ctenidial wall (Yonge, 1932: 271; Morton, 1955: 6, 1965; Hughes, 1978: 114, 125; Hadfield *et al.*, 1972), while turritellids brood their young in a uterine brood pouch formed from the pallial oviduct (Johansson, 1946; Carrick, 1980b: 254). In the planaxids, thiarids, siliquariids, and diastomatids, the ovipositor has become modified to form a brood pore which opens into a large brood pouch of ectodermal origin located in the head-foot (Thorson, 1940; Morton, 1951: 36; Abbott, 1952: 92-95, 1955: 11; Ponder, 1980; Houbrick, 1981b: 608-609, 1987a: 38-39). Table 4 shows the distribution of various methods of brooding and reproduction throughout the Cerithioidea.

A long, strap-like columellar muscle is a distinctive character of the Campanilidae (Houbrick, 1981c: 284) and the Vermetidae (Morton, 1965: 615; Hughes, 1978: 115). Some animals of both these groups are able to retract very deep within their shells to avoid attacks by predators. Morton (1965: 615) considered a long columellar muscle an advanced evolutionary trait. Although not mentioned specifically by him, the Turritellidae are depicted by Randles (1900: Pl. 10, fig. 2) as having a long columellar muscle, which is not surprising, as they have a very deep mantle cavity and a long turreted shell.

The mantle edge of cerithioidean taxa varies greatly in regard to the absence or presence, size and location of mantle papillae. They are lacking in the Litiopidae (Houbrick, 1987b: 11), Planaxidae (Houbrick, 1987a: 5), and Vermetidae (Morton, 1965), very small and few in the Potamididae (pers. observ.), Cerithiidae (Houbrick, 1984: 3) and Batillariidae (pers. observ.), and can be quite long in the Cerithiidae (Houbrick, 1974b: 41, 1978: 6, 1985: 27), Thiaridae (Abbott, 1948: 286, 1952: 78; Pace, 1973: 54,59), Modulidae (Houbrick, 1980a), and Turritellidae (Randles, 1900: 57; Graham, 1938: 454). Their function is probably a sensory one, but in the Turritellidae (Yonge, 1946: 377) and in some modulids (Houbrick, 1980a: 121) mantle papillae may also serve as a coarse filter to the mantle current. Normally the mantle papillae are located only on the dorsal surface of the mantle edge but in the Campanilidae (Houbrick, 1981c: 283) and Turritellidae (Graham, 1938: 453; Fretter & Graham, 1962: 101) they occur around its entire circumference. As characters, mantle papillae and their disposition are of poor diagnostic value in phylogenetic analysis and have a low consistency value.

Mantle cavity characters (24-29)

One of the synapomorphies of the Turritellidae and Vermetidae is the

TABLE 5. Character table of cerithioidean families and rissoidae outgroup.

Legend: BA= Batillariidae; CA= Campanilidae; CD= Cerithideidae;
 CE= Cerithiidae; DI= Diastomatidae; LI= Litiopidae; MO=Modulidae;
 ML= Melanopsidae; PL= Pleuroceridae; PO= Potamididae; PX= Planax-
 idae; TH= Thiaridae; TU= Turritellidae; VE= Vermetidae; ?= missing
 data or absence of character set; out = outgroup (Rissoidae).

Explanation of character states follows matrix.

Character	Taxon														out
	CA	LI	ML	PL	PX	DI	TH	CE	PO	CD	BA	MO	TU	VE	
1	a	a	a	a	a	a	a	a	a	a	a	b	a	c	a
2	b	b	b	b	b	b	b	b	b	b	b	b	a	a	b
3	a	a	a	a	a	a	a	b	b	b	a	a	a	a	a
4	b	b	b	b	b	b	b	b	b	b	b	b	a	a	a
5	b	b	b	b	b	b	b	c	b	b	b	b	a	a	a
6	c	a	a	a	b	b	a	a	a	a	a	a	a	a	a
7	a	a	a	a	b	a	a	a	c	c	c	c	c	c	a
8	a	a	a	a	a	a	a	a	b	b	b	b	b	b	a
9	a	a	a	a	b	a	a	a	c	c	c	c	c	c	a
10	a	a	a	a	a	a	a	a	a	a	a	c	a	b	a
11	b	a	a	a	a	a	a	a	a	a	a	a	b	b	a
12	b	a	a	a	a	a	a	a	a	a	a	a	a	b	a
13	c	a	a	a	b	a	a	a	a	a	a	a	a	a	a
14	a	b	a	a	a	a	a	a	a	a	a	a	a	a	b
15	b	b	b	b	b	b	b	b	b	b	b	b	b	a	b
16	a	b	b	b	b	b	b	b	b	b	b	b	a	a	a
17	b	a	a	a	a	a	a	a	a	a	a	a	a	b	a
18	b	a	a	a	a	b	b	b	b	a	b	b	b	a	a
19	c	b	b	b	b	a	a	a	c	b	c	a	a	b	c
20	b	a	a	a	a	c	c	c	c	a	c	c	b	a	c
21	a	a	a	a	b	b	b	a	a	a	a	a	b	a	a
22	a	a	a	a	b	b	b	a	a	a	a	a	a	a	a
23	?	?	?	?	c	c	c	?	?	?	?	?	b	a	?
24	a	a	a	a	a	a	a	a	a	a	a	a	b	b	a
25	c	a	a	a	a	b	a	b	a	a	a	a	a	a	a
26	c	a	b	c	b	a	b	a	a	c	a	b	a	a	a
27	a	a	a	a	a	a	a	a	b	b	a	a	a	a	a
28	b	b	b	a	b	b	a	b	b	a	b	b	b	b	a
29	b	a	a	a	a	a	a	a	a	a	a	a	a	a	a
30	a	a	a	a	a	a	a	a	a	a	a	a	b	b	a
31	b	a	a	b	b	a	b	a	b	a	a	a	a	a	a
32	a	b	a	b	c	a	b	b	b	b	a	a	a	a	a
33	b	b	b	b	a	b	b	b	b	b	a	b	b	b	a

TABLE 5 (cont.)

Character	Taxon														out
	CA	LI	ML	PL	PX	DI	TH	CE	PO	CD	BA	MO	TU	VE	
34	a	a	a	a	b	a	b	a	b	b	a	a	a	a	a
35	a	a	b	b	b	a	b	b	b	b	b	b	a	a	a
36	b	b	b	a	b	a	b	b	a	a	b	b	b	a	a
37	a	b	b	b	b	b	a	b	b	b	b	b	a	a	a
38	b	a	a	a	a	a	b	a	a	b	b	a	a	a	b
39	a	a	a	a	a	a	a	a	b	b	a	a	a	a	a
40	b	a	a	a	a	a	a	a	a	a	a	a	b	b	a
41	b	a	b	a	a	?	a	a	a	b	b	a	b	a	a
42	b	a	a	a	a	a	a	a	a	a	a	b	b	b	a
43	a	a	b	b	b	a	a	a	a	a	a	a	a	a	a
44	a	a	a	a	b	b	b	a	a	a	a	a	a	a	a
45	a	a	b	a	a	b	a	a	b	b	a	b	b	a	a
46	a	a	?	a	a	?	a	a	a	a	a	a	a	b	b
47	b	c	?	e	d	?	?	c	e	e	d	e	c	a	a
48	b	c	?	c	c	?	c	c	c	c	c	c	c	c	a
49	b	b	b	b	b	b	b	b	b	b	b	b	b	b	a
50	b	b	b	b	b	b	a	b	b	b	b	b	b	b	a
51	b	a	b	a	a	a	a	a	a	a	a	b	a	a	a
52	a	a	a	a	a	a	a	b	a	b	a	a	a	a	a
53	?	a	b	b	b	b	?	c	b	c	b	b	b	b	?
54	a	b	b	b	b	b	?	b	b	b	b	c	c	b	?
55	a	b	b	b	b	b	?	b	b	b	c	c	c	a	?
56	?	b	a	a	a	a	?	a	a	a	a	a	a	?	?
57	a	a	a	a	a	a	?	a	a	a	a	b	a	a	?
58	a	a	a	a	b	b	b	c	c	c	c	c	b	b	a

Alternative Character States

SHELL

- 1 Morphology: a = elongate-turreted; b = turbinate; c = uncoiled
- 2 Aperture: a = round; b = ovate
- 3 Outer lip: a = smooth, rounded; b = crenulated, flared
- 4 Anterior canal: a = absent; b = present
- 5 Anterior canal length: a = absent; b = short; c = long
- 6 Periostracum: a = smooth; b = hispid; c = intratacalyx

OPERCULUM

- 7 Shape: a = ovate; b = lenticular; c = round
- 8 Sculpture: a = paucispiral; b = multispiral
- 9 Nucleus placement: a = eccentric; b = terminal; c = central

EXTERNAL ANATOMY

- 10 Body shape: a = intermediate; b = elongate, vermiform; c = compact, tightly coiled

TABLE 5 (cont.)

- 11 Snout: a = long, extensible; b = short, wide
- 12 Cephalic tentacles: a = long, tapering; b = short, stubby
- 13 Anterior pedal gland: a = anterior sole margin; b = front half of sole;
c = entire sole margin
- 14 Epipodial tentacles: a = absent; b = present
- 15 Ciliated groove on right of foot: a = absent; b = present
- 16 Ovipositor: a = absent; b = present
- 17 Columellar muscle: a = short; b = long, strap-like
- 18 Mantle edge: a = smooth; b = fringed
- 19 Mantle edge papillae: a = many, long; b = absent; c = few, short
- 20 Mantle papillae placement: a = absent; b = entire mantle margin;
c = top half of mantle margin
- 21 Brood pouch: a = absent; b = present
- 22 Subhemocoelic brood pouch: a = absent; b = present
- 23 Brood pouch location: a = mantle cavity; b = pallial oviduct;
c = head-foot

MANTLE CAVITY ORGANS

- 24 Food groove on mantle floor: a = absent; b = present
- 25 Osphradium: a = ridge-like, thin; b = bipectinate, thin; c = bipectinate,
oval
- 26 Osphradial length: a = equal to gill length; b = slightly less than gill
length; c = less than one-half gill length
- 27 Ctenidial filaments: a = long, triangular; b = short, shallow
- 28 Hypobranchial gland: a = weak; b = well-developed
- 29 Hypobranchial gland shape: a = distal leaflets absent; b = distal
leaflets present

RADULA

- 30 Rachidian basal plate: a = marginal ridges absent; b = marginal ridges
present
- 31 Rachidian basal plate width: a = wide; b = narrow
- 32 Rachidian lateral basal extensions: a = short; b = absent; c = long
- 33 Rachidian basal cusps: a = present; b = absent
- 34 Outer marginal tooth: a = outer flange absent; b = outer flange present
- 35 Outer marginal shape: a = long, scythe-like; b = long, spoon-like

ALIMENTARY TRACT

- 36 Esophageal gland: a = absent; b = present
- 37 Salivary gland placement: a = above and anterior to nerve ring; b =
through nerve ring
- 38 Salivary gland shape: a = uncoiled or slightly coiled tubes; b = tubes
form coiled masses
- 39 Style sac: a = short; b = long
- 40 Spiral caecum: a = absent; b = present

TABLE 5 (cont.)

NERVOUS SYSTEM

- 41 Zygoneury: a = absent; b = present
 42 Cerebral ganglia: a = short connectives; b = long connectives
 43 Subesophageal ganglion: a = close to pleural; b = separated from pleural
 44 Pedal extensions: a = absent; b = present
 45 Cerebral-pedal connective: a = long; b = short

REPRODUCTION

- 46 Euspermatozoan midpiece ultrastructure: a = with 4 elements; b = without 4 elements
 47 Arrangement of midpiece crystal plates: a = absent; b = midpiece group 3; c = midpiece group 1A; d = midpiece group 1B; e = midpiece group 2
 48 Paraspermatozoa: a = absent; b = 2 kinds; c = 1 kind
 49 Males: a = phallate; b = aphallate
 50 Pallial oviduct condition: a = closed tube; b = open tube
 51 Proximal pallial oviduct: a = closed; b = open
 52 Number of seminal receptacles: a = one; b = two
 53 Seminal receptacle location: a = lateral lamina; b = medial lamina; c = both laminae
 54 Spermatophore bursa location: a = absent; b = medial lamina; c = lateral lamina
 55 Sperm gutter location: a = absent; b = medial lamina; c = medial and lateral laminae
 56 Sperm gutter size: a = long; b = short
 57 Lateral lamina baffle: a = baffle absent; b = baffle present
 58 Egg mass deposition: a = large gelatinous mass; b = internal; c = jelly string

presence of a food groove on the mantle floor (Randles, 1900: 61; Graham, 1938: 455; Morton, 1955). This groove is probably related to filter and mucous net feeding. Similar food grooves occur in calyptraeids (Fretter & Graham, 1962: 107) and struthiolariids (Morton, 1950), which have a similar filter feeding habit.

The structure of the osphradium has recently been shown by Haszprunar (1985a) to be an important character for phylogenetic estimation. Cerithioideans that have been investigated possess osphradia with laterally situated ciliated epithelia and ultrastructural features defined by the Si1/Si2/Si4 cell types, as categorized by Haszprunar (1985a: 487). The osphradium is a simple ridge in most cerithioideans but is bipectinate and well-developed in the Cerithiidae (Houbrick, 1974b: 43; 1985: 27) and Diastomatidae (Houbrick, 1981b: 602). The Campanilidae has an oval, bipectinate osphradium, autapomorphic among cerithioideans, but similar to the those seen in many Neogastropoda. The position of the osphradium in cerithioideans is adjacent to the ctenidium. Osphradial length varies among families: it may equal the ctenidium in length, as in the Litiopidae (Houbrick, 1987b: 13), Cerithiidae (Marcus & Marcus, 1964: 500; Houbrick, 1985: 27), Potamididae, Batillariidae (pers. observ.), Vermetidae (Morton, 1965: 588), and Turritellidae (Randles, 1900: 62); may be a little less

than the ctenidial length, as in the Diastomatidae (Houbrick, 1981b: 603), Melanopsidae (Belgin, 1973: 382), Modulidae (Houbrick, 1980a: 123), Planaxidae (Houbrick, 1987a), and Thiaridae (Abbott, 1952: 92; Starmühlner, 1976); or may be less than half the ctenidial length as in the Campanilidae (Houbrick, 1981c: 270,272), Cerithiidae (Houbrick, 1984: 5) and Pleuroceridae (Itagaki, 1960: pl.4; Dazo, 1965: 33, fig. 7). Osphradial length appears to be a poor comparative character as it has a low consistency index. Its polarity was determined only by outgroup comparison.

In the Cerithiidae, the bipectinate osphradium is highly developed in the genera *Cerithium*, *Rhinoclavis*, and *Pseudovertagus* (Houbrick, 1971, 1974b, 1978, 1985), and may be correlated with the presence of a long siphonal canal. However, a well-developed bipectinate osphradium also occurs in *Diastoma*, in which there is only a shallow anterior canal (Houbrick, 1981b: 602). Although the exact significance of a bipectinate osphradium is not clear, bipectinate morphology increases surface area and may indicate high reliance on osphradial chemoreceptive ability in relation to algal food specialization. A bipectinate osphradium is undoubtedly an apomorphic character among the Cerithioidea.

Nearly all cerithioideans have long, well-developed ctenidia, but ctenidial filaments are absent or very short in some amphibious potamidids, especially in the genus *Cerithidea*, which occurs in mangroves above and at the high tide mark (Houbrick, 1984: 11). The ctenidium is very long and narrow in the turritellids (Randles, 1900: 62) and vermetids (Morton, 1951: 8), which use it in food gathering as well as for respiration.

The hypobranchial gland is thick and well-developed in most cerithioideans, but weak and thin in the Thiaridae, Melanopsidae, and Pleuroceridae (pers. observ.), which have radiated into freshwater environments. The hypobranchial gland may be absent in the latter two taxa as it is not shown in the figures or sections of Starmühlner (1970) or Belgin (1973). *Campanile* is unique in having distal leaflets of unknown function on the hypobranchial gland (Houbrick, 1981c: 274).

Radular characters (30-35)

The characters derived from cerithioidean radulae are diverse, highly homoplastic, and in most instances, extremely difficult to polarize, except by outgroup comparison. Many have low consistency indices. The basal plate of the rachidian tooth has marginal ridges only in the Vermetidae (Morton, 1965: 623). The rachidian basal plate is narrow in the Planaxidae (Houbrick, 1987a: 36), Pleuroceridae (Itagaki, 1960: pl. 6; Dazo, 1965: 31-32), many Thiaridae (Starmühlner, 1976; Brown, 1980: 94), and the Campanilidae (Houbrick, 1981c: 272). There are long lateral basal extensions to the rachidian tooth in the Planaxidae (Troschel, 1856: pl. 12; Houbrick, 1987a: 36) and to a lesser extent in the Diastomatidae (Houbrick, 1981b: 605). Short extensions are found in the Melanopsidae (Belgin, 1973: 380), Batillariidae (Bandel, 1984: 49; pers. observ.), Turritellidae (Troschel, 1856: pl. 12; Randles, 1900: pl. 6), and Vermetidae (Morton, 1965: 623). Basal cusps on the rachidian plate are distinctive characters of the Planaxidae (Bandel, 1984: 34-35; Houbrick, 1987a: 36) and Batillariidae (pers. observ.) and also occur in the rissoid outgroup (Ponder, 1985: 125). A survey of radular types in Troschel (1856-1863) and Bandel (1984) shows nothing like

these basal cusps in any other prosobranch radula. The outer marginal teeth of turrrellids and vermetids are long and scythe-shaped (Randles, 1900: pl. 6; Morton, 1965: 623). This is also true, to a lesser extent, for the rissoids (Ponder, 1985: 125). An unusual feature of some cerithioidean radulae is the presence of a large lateral flange of unknown function on the outer marginal tooth. A lateral flange occurs in the Thiaridae (Abbott, 1952: 82-84), and Planaxidae (Bandel, 1984: 28; Houbrick, 1987a: 36), and is highly developed in some taxa of the Potamididae (Annandale, 1924: 550; Bishop, 1979), Batillariidae (Bishop, 1979) and Cerithideidae (Troschel, 1856: pl. 12, fig. 4; Houbrick, 1984: 6, fig. 3,h).

Alimentary tract characters (36-40)

Anterior buccal pouches occur in the Littorinoidea but are absent in all cerithioideans except for *Campanile* (Houbrick, 1981c: 275). The buccal pouches appear to share the same histology as the esophageal gland in *Campanile* and are thus probably homologous with those of *Littorina*, as discussed by Ponder (1983: 257-258). Among cerithioideans, however, buccal pouches are autapomorphous characters.

An esophageal gland is present in most members of the Cerithioidea (pers. observ.), but is lacking in the Diastomatidae (Houbrick, 1981b: 607), Pleuroceridae (Dazo, 1965), Vermetidae (Morton, 1965), some potamidids (*Cerithidea* [Houbrick, 1984: 5]), and in the rissoid outgroup. Graham (1939) stated that taxa having a style sac and crystalline style do not have an esophageal gland, but there are numerous exceptions to this among cerithioideans. In many cases, the midesophagus is enlarged by folding of its lateral walls and this has been interpreted as a crop by some workers (Bright, 1958: 134; Houbrick, 1984: 5). However, a series of intergrades between a simple midesophagus and a more elaborately folded, glandular midesophagus, which is undoubtedly an esophageal gland, have been noted. Sections of the enlarged portion of the midesophagus stain darkly in haematoxylin and are lined with glandular epithelium; thus, the line between a crop and an esophageal gland is a thin one and subject to interpretation. This is reflected in a very low consistency index of 20 for this character.

Paired salivary glands originate behind the nerve ring and pass through it prior to emptying into the buccal cavity in all cerithioideans except in the Campanilidae (Houbrick, 1981c), Thiaridae (Abbott, 1952: 81) and Vermetidae (Morton, 1951: 12; Hadfield, 1970: 304), where they lie anterior to the nerve ring. This needs to be confirmed, especially in the Vermetidae, as it is not entirely clear from the literature if portions of the salivary gland pass through the nerve ring, as in some Cerithiidae (Houbrick, 1985: 29). Arrangement of the salivary glands varies; for instance, only a small portion of the left salivary gland lies behind the nerve ring in the Cerithiidae (Houbrick, 1985: 29). Salivary glands comprise a pair of tubes, which vary in layout from simple narrow tubes in most families to tightly coiled masses, as in the Campanilidae (Houbrick, 1981c: 271), Modulidae (Houbrick, 1980a: 124-126), Cerithiidae (Houbrick, 1985: 29-30), and Vermetidae (Morton, 1951: 12). As there are many variations in layout, they are not easily categorized into discrete groups. Salivary glands were classified in this analysis as masses or tubes, and had a low consistency index.

The stomach in cerithioideans is a large, complex structure, comprising a protostyle or a crystalline style, a gastric shield, large folds, major and minor

typhlosoles, one or two openings into the digestive diverticula, and fine sorting areas. Information on the number of digestive gland openings is lacking for many families and was not used in this analysis. The Campanilidae lack the gastric shield and appear to have only a protostyle, as I found no crystalline style present in freshly dissected specimens (Houbrick, 1981c: 275-276). The length of the style sac varies among families and may be extremely long, as in the potamidids where it extends forward into the mantle cavity, or relatively short, comprising only a short anterior bulge, as in planaxids. The style sac and crystalline style are very long (over a third of the animal's length) in the Potamididae (pers. observ.; Seshaiya, 1932; Berkeley & Hoffman, 1834: 437; Graham, 1939; Johansson, 1956: 150,158) and in the Cerithideidae (Seshaiya, 1932; Driscoll, 1972: 379; Houbrick, 1984: 12), and are usually correlated with the ingestion of fine particulate matter. The style sac is much shorter in the Batillariidae (Driscoll, 1972: 379), Turritellidae (Graham, 1938: 458), Melanopsidae (Morton, 1952: 89), and Vermetidae (Morton, 1951;12, pl. 9, fig. 5) and is correlated with detritus feeding, ciliary and mucous net feeding. In other cerithioideans the style sac is short (less than the stomach length) and is associated with microphagous algal feeding. A degenerate spiral caecum occurs in the Turritellidae and Vermetidae and as it is found in many archaeogastropods, is considered a primitive feature by Fretter and Graham (1962: 223). A complex mechanism of spiral leaflets of unknown function occurs in the stomach of *Campanile* (Houbrick, 1981c: 276).

Nervous system characters (41-45)

All cerithioideans thus far examined have epiathroid, dialyneurous nervous systems (Bouvier, 1887: 155-156).

Zygoneury, a new, direct connection between parietal (esophageal) and pleural ganglia, occurs in the marine Campanilidae (Houbrick, 1981c: 277) and Turritellidae (Bouvier, 1887), and also in two freshwater families, the Melanopsidae (Bouvier, 1887: 128-129), and Pleuroceridae (Dazo, 1965: 26). Zygoneury needs to be verified in the latter family, as Dazo is not entirely clear on this matter as regards the North American pleurocerids, and Itagaki (1960: pl. 6, fig. 23) figured only dialyneury in *Semisulcospira* from Asia. Zygoneury occurs in the estuarine families, Potamididae, Cerithideidae, and Batillariidae (Bouvier, 1887: 142-145). It is a very homoplastic character in the cerithioideans, having a consistency index of 20. Its common presence in estuarine and freshwater groups may indicate some kind of selective advantage in this environment although it is apparently absent in the largest freshwater family, the Thiaridae (Bouvier, 1887: 129; Moore, 1899: 159; Seshaiya, 1934: 200; Starmühlner, 1976: 575).

It is thought that a highly concentrated nervous system indicates a more advanced evolutionary state than those less concentrated (Fretter & Graham, 1962: 308-309) and this has been expressed by the RPG Ratio of Davis *et al.* (1976: 263 - length of the pleuro-esophageal connective divided by the sums of the lengths of the supraesophageal ganglion, the pleuro-esophageal connective, and the right pleural ganglion). Because RPG ratios for many families remain unknown, this character was not used in the cladistic analysis. The degree of concentration of the nervous system of various families, as expressed by the RPG ratio, is summarized in Table 6. The lowest value occurs in the Litiopidae and

the highest among the Cerithideidae and Batillariidae. The low value of the Litiopidae may reflect physical restraints imposed upon the nervous system by the small size of members of this taxon.

The absence of statocysts associated with the pedal ganglia in the Vermetidae (Hadfield, 1970: 305) is undoubtedly connected with their sessile life habit, and within the Cerithioidea, is a condition unique to them. Hadfield (1970: 304-305) incorrectly cited zygoneury in the vermetids: what he has depicted is dialyneury.

Elongate extensions of the pedal ganglia enervating complex brood pouches in the head-foot are known to occur only in the Planaxidae (Houbrick, 1987a: 41), Diastomatidae (Houbrick, 1981b: 609, fig. 2,c), and Thiaridae (pers. observ.).

Reproductive tract characters (46-58)

Among the Cerithioidea, many members of the family Thiaridae are said to be parthenogenetic (Morrison, 1954; Jacob, 1959; Brown, 1980: 83), but a spectrum ranging from true parthenogeneticity to bisexual reproduction exists. The genus *Thiara* is truly parthenogenetic with only occasional, nonfunctional males being observed (Chanotis *et al.*, 1980: 96; Stoddart, 1983: 547). Other thiarid genera are parthenogenetic, but not exclusively so, as functional males occasionally are found in some populations (Livshits & Fishelson, 1983). Finally, many genera are dioecious (Davis, 1969, 1971; Brandt, 1974). Since parthenogenesis is an autapomorphy of only some thiarid genera, it was not coded in the cladistic analysis.

Protandry has been suggested in the Campanilidae (Houbrick, 1981c: 277), but among other cerithioideans is known only in one species of turritellid (Carrick, 1980a: 254).

In cerithioidean euspermatozoa, there are four elongate midpiece elements, each with crystal plates, that run parallel to the axoneme. This morphology distinguishes cerithioideans from all other prosobranch groups, except for the Viviparoidea (Healy, 1983a).

Healy (1983a) has shown that it is possible to establish two major groups of cerithioideans (Group 1 and Group 2) based on the arrangement and size of the four elements and the crystal plates. Group 1 species have midpieces composed of the axoneme surrounded by two large and two small midpiece elements while Group 2 species have four equal sized midpiece elements and midpiece flange structures. Furthermore, Group 1 may be subdivided on the shape of the small midpiece elements and by the shape of the acrosome into Group 1(i) and Group 1(ii) (Healy, 1983a: 71-72). Following Healy's (1983a) system, I have placed the families Cerithiidae, Turritellidae, and Litiopidae in Group 1a [=Group 1(i)]; the Batillariidae and Planaxidae in Group 1b [=Group 1(ii)]; the Cerithideidae, Potamididae, Modulidae and Pleuroceridae in Group 2. Healy (1986: 168) found that *Campanile* euspermatozoa have features common to cerithioideans and to other mesogastropods and formed a "connecting link" between the Cerithioidea/Viviparoidea/Cyclophoroidea and other mesogastropod groups. This information was published after the production of the cladogram. Campanilidae sperm type should be assigned to a third group, Group 3, in future analyses.

Paraspermatozoa are common in many mesogastropod groups but have not been observed in the Truncatelloidea (Healy, 1983b: 203). They occur in all cerithioidean families observed and are normally multiflagellate with elongate

midpieces. In the Campanilidae, two kinds of paraspermatozoa have been observed (Healy, 1986: 168), but all other cerithioidean families have only one kind.

Aphallate males and open pallial gonoducts in both sexes are characteristic of the Cerithioidea but also occur among the Eatoniellidae (Ponder, 1965: 51) and members of Haszprunar's (1985a: 488) order Heteroglossa (superfamilies Cerithi-

TABLE 6. RPG Ratios* of Cerithioidean Families (lower values indicate more tightly organized nervous systems).

Family	Mean RPG Ratio	Range	Source
LITIOPIDAE	0.43	----	Houbrick, 1987b
PLANAXIDAE	0.59	0.50-0.67	Houbrick, 1987a
MODULIDAE	0.59	----	Houbrick, 1980a:138
DIASTOMATIDAE	0.69	----	Houbrick, 1981b:609
CERITHIIDAE	0.60	0.59-0.61	Houbrick (1980a:132, 1981a:8, 1985:29)
BATILLARIIDAE	0.73	0.68-0.77	Houbrick, present study
CERITHIDEIDAE	0.79	----	Houbrick, 1984:7

*Length of pleuro-esophageal connective divided by sum of lengths of supraesophageal ganglion, pleuro-esophageal connective, and right pleural ganglion.

opsoidea, Triphoroidea, Epitonioidea, Eulimoidea), formerly known as Heterogastropoda (Kosuge, 1966). Open male pallial gonoducts also occur in the Littorinoidea and Rissoidae (Johansson, 1953; Ponder, 1985; Ponder, 1988, this volume). Although these anatomical features occur in disparate superfamilies, they do not indicate close phylogenetic relationship because during their ontogeny, the gonoducts of all prosobranchs are at first open, and only subsequently are closed (Johansson, 1953: 15-17); consequently, the open condition may be primitive or derived independently a number of times in unrelated lineages. However, open pallial gonoducts and aphallate males appear to be truly homologous among cerithioidean taxa because the presumed homology of the reproductive tract is supported by similar position and developmental pathways and by homologies observed in other organ systems. In addition, the secondary sexual characters of cerithioideans share similar positions in relation to each other as well as to other mantle organs, exhibit nearly identical histology, and have similar functions. Contrary to recent statements of Houston (1985: 187), which, I believe, were based on a polyphyletic conception of the Cerithioidea, almost all known members of this superfamily have open ducts and are all aphallate. The one exception is

some thiarids, such as *Melanoides* Oliver, which have two closed ducts, one an oviduct, and the other a seminal receptacle (Seshaiya, 1936; Pace, 1973: 61).

Male cerithioideans lack a penis, but fertilization is internal and all members of the superfamily probably produce spermatophores. I have observed spermatophores in representatives of numerous families, such as the Modulidae (Houbrick, 1980a: 127-129), Diastomatidae (Houbrick, 1981b: 607), Cerithiidae (Houbrick, 1973: 879; 1974b: 78; 1981a: 7), Potamididae (pers. observ.), Cerithideidae (Houbrick, 1984: 7), Batillariidae (pers. observ.), Planaxidae (Houbrick, 1987a: 29), and Litiopidae (Houbrick, 1987b: 11). Spermatophores occur in the freshwater Pleuroceridae (Dazo, 1965: 38-39) and are probably present in the Campanilidae (Houbrick, 1981c: 278). Pelagic spermatophores have been described in the Vermetidae (Hadfield and Hopper, 1980).

One seminal receptacle appears to be the norm for most cerithioideans, but there are two in the Cerithideidae (Houbrick, 1984: 7), and two in the Cerithiidae. In the last family, there are two seminal receptacles, one in the posterior medial lamina, and the other in the anterior lateral lamina. This condition has been observed in many *Cerithium* and *Bittium* species (pers. observ.), and I have described this layout in detail for *Cerithium nodulosum* (Houbrick, 1971). The question as to the probable identity of the sperm-containing pouch in the anterior lateral lamina of *Cerithium* species with a true seminal receptacle containing oriented sperm, has recently been positively answered by means of histological sections (pers. observ.). It appears to be present only during the reproductive season and is difficult to detect. Thus, I scored the Cerithiidae as having two seminal receptacles in this analysis.

Placement of the seminal receptacle varies greatly among families, but is usually in the posterior medial lamina. In the Litiopidae, it is in the posterior lateral lamina only (Houbrick, 1987). The seminal receptacle may be in both laminae in the Cerithiidae (Houbrick, 1971: 561-562, fig. 1) and in the Cerithideidae (Houbrick, 1984: 7). The location of the seminal receptacle in the pericardium in *Campanile* (Houbrick, 1981c: 277) is a character unique to that family, among the Cerithioidea.

The spermatophore bursa normally occurs in the proximal medial lamina of most cerithioidean families but in the Modulidae (Houbrick, 1980a: 131) and Turritellidae (Johansson, 1946: 2, figs. 1-2) it is found in the lateral lamina, and is absent altogether in parthenogenetic thiarids. The literature about non-parthenogenetic thiarid species does not confirm or deny the presence of a seminal receptacle.

Ciliated gutters that move sperm into the spermatophore bursa and seminal receptacles lie along the free edges of the laminae of the pallial oviduct. Gutters are absent in the parthenogenetic thiarids and in the vermetids. When present, they usually occur on the medial lamina but in the Modulidae (Houbrick, 1980a: 130-131), some potamidids (*Telescopium*, pers. observ.) and Turritellidae (Johansson, 1946: 3, figs. 3-9) they are on both laminae. Gutters are long (a little less than one-half the oviduct length, or more) in most taxa except for the Litiopidae (Houbrick, 1987b: 11). A complex series of baffles, which interact with the ciliated gutters is present in the Modulidae (Houbrick, 1980a: 130, fig. 8). Simple baffles occur in the other families and are lacking in the Planaxidae (Houbrick, 1987a), Diastomatidae (Houbrick, 1981b: 608, fig. 5A), Thiaridae, Melanopsidae

(Starmühlner, 1970: 75; Belgin, 1973: 388-389), and Pleuroceridae (Dazo, 1965: 37-38).

Spawn characters (58)

Spawn masses of cerithioideans may be deposited in the form of tangled or coiled, compact masses, as in the Campanilidae (Houbrick, 1981c: 278), Litiopidae (Houbrick, 1987b: 13-14), and Pleuroceridae (Dazo, 1965: 54,56). In many families such as the Cerithiidae (Houbrick, 1973), Potamididae (pers. observ.), Cerithideidae (Houbrick, 1984: 12), and Modulidae (Houbrick, 1980a: 119, 133) they appear as irregularly coiled or straight strings. In the brooding families, the eggs are kept internally, either in the mantle cavity, pallial oviduct, or in special brooding pouches. Individual eggs are connected by chalazae-like strings in *Campanile* (Houbrick, 1981c: 278), but it is not certain if this is homologous with the chalazae of opisthobranchs. At any rate, the character is an autapomorphy. Individual eggs are surrounded by a thin, hyaline capsule in all cerithioideans except Vermetidae (Hadfield, pers. comm.) and Campanilidae, where the embryos are embedded in a gelatinous matrix (Houbrick, 1981c: 278).

RESULTS

Discussion of cladogram and diagnoses of families

The cladogram shown in Figure 2 is the result of a lengthy iterative process and represents the most parsimonious tree of 400 trials. It is the best interpretation of cerithioidean phylogeny based on the data presented in Table 5. Many other cladograms, using both outgroups, produced results substantially in agreement with the final one herein presented. Initially, only 13 families were analyzed using the Truncatelloidea and the Stromboidea for outgroup comparison. The cladograms produced for each of these analyses were identical, but because the cladograms produced using the Strombidae as an outgroup had lower consistency indices, they were rejected in favor of those generated using the Rissoidae. After these initial analyses, the number of the families was increased to 15 by addition of the Melanopsidae and by separation and elevation to family status of the Cerithideidae from the Potamididae. Transformation series analysis of multistate characters, using the methodology of Mickevich (1982), further improved the consistency index and stabilized the final tree. Transformation series of multistate characters are illustrated in Figure 1.

The cladogram shows much homoplasy, but this is expected at family level analysis. Discounting outgroup characters, there are no reversals. A discussion about the characters of the main stem of the cladogram, branch by branch, follows. Characters defining individual branches and terminal taxa are discussed last. One is hard pressed to find autapomorphies for some families due to the insufficient anatomical data about them. For this reason, families are not formally diagnosed.

Outgroup and tree base. The numerous characters (58) defining the outgroup at the base of the tree (below stem 1) are not shown in the cladogram in Figure 2 because of space limitations, and are listed below: 1a, 2a, 3a, 4a, 5a, 6a, 7a, 8a, 9a, 10a, 11a, 12a, 13a, 14a, 15a, 16a, 17a, 18a, 19a, 20a, 21a, 22a, 23c (coded as a

question mark), 24a, 25a, 26a, 27a, 28a, 29a, 30a, 31a, 32a, 33a, 34a, 35a, 36a, 37a, 38a, 39a, 40a, 41a, 42a, 43a, 44a, 45a, 46a, 47a, 48a, 49a, 50a, 51a, 52a, 53b, 54b, 55b, 56a, 57b, 58a.

Stem 1. These characters help to define the Cerithioidea, but there are few autapomorphic ones. Cerithioideans usually have a single type of paraspermatozoa except for the Campanilidae, which have two [48b]. Members of the superfamily possess a unique euspermatozoan ultrastructure comprising a midpiece of four elements [47b], and most families belong to Group 3 of Healy (1983a: 71-72). Cerithioideans are aphyllate [49b] and nearly all have open pallial gonoducts [50b] with a ciliated groove emerging from it down the right side of the foot [15b]. Their shells are generally tapered and have short anterior canals [4b]. An esophageal gland [36b] and well-developed hypobranchial gland [28b] are also usually present.

Stem 2. Above this stem, all cerithioideans have only one kind of paraspermatozoa [48c]. An ovipositor [16b] is common in many families. The litiopids have smooth mantle edges but most other cerithioideans have papillae on the mantle edge [19b]. The salivary glands pass through the nerve ring [37b] in most taxa.

Stem 3. A single radular character, shape of the tip of the marginal teeth [35b], with a low consistency index of 33.3, separates the lower tree from the melanopsid-pleurocerid branch. If this character were removed, the branch would collapse into a dichotomy with the litiopids.

Stem 5. Most of the families above this stem have mantle edge papillae [18b], usually only on the upper dorsal side of the mantle [20c]. Many of the taxa on this part of the tree internally brood their eggs and larvae [58b].

Stem 9. All families above this stem have a round [7c], multispiral operculum [8b] with a central nucleus [9c].

Stem 10. The taxa above this stem lay their eggs in strings [58c].

Stem 11. The three families above this stem have Group 2 euspermatozoa [47e] (Healy, 1986) and short cerebral-pedal ganglia extensions [45b].

Stem 12. The families Potamididae and Cerithideidae, consistently fell out together in all cladograms and phenograms. These families represent a major cerithioidean adaptive radiation into estuarine habitats and mangrove forests. The stem bearing the two groups is well supported by two unique, unreversed synapomorphies: a well-developed, long style sac [39b], and short, shallow gill filaments [27b]. In addition, the two families on this stem have a large crop instead of an esophageal gland [36a], a change probably associated with the extreme development of the style sac. These two families are characterized by radulae having a lateral flange on the outer marginal teeth [34b], and have lost the lateral basal extensions on the rachidian tooth [32b]. The outer lip of the shell aperture is frequently flared or projected [3b]. Taxa above this stem lack or have vestigial mantle papillae.

Stem 13. This stem supports two terminal families, the Vermetidae and Turritellidae, that are the most highly modified and apomorphic groups among the Cerithioidea. The stem is very well-defined by four unique, unreversed synapomorphies: a round shell aperture [2a]; marginal ridges on the sides of the rachidian tooth [30b]; a food groove on the floor of the mantle cavity [24b] (an adaptation for ciliary-detrital feeding), and a brood pouch for brooding in the

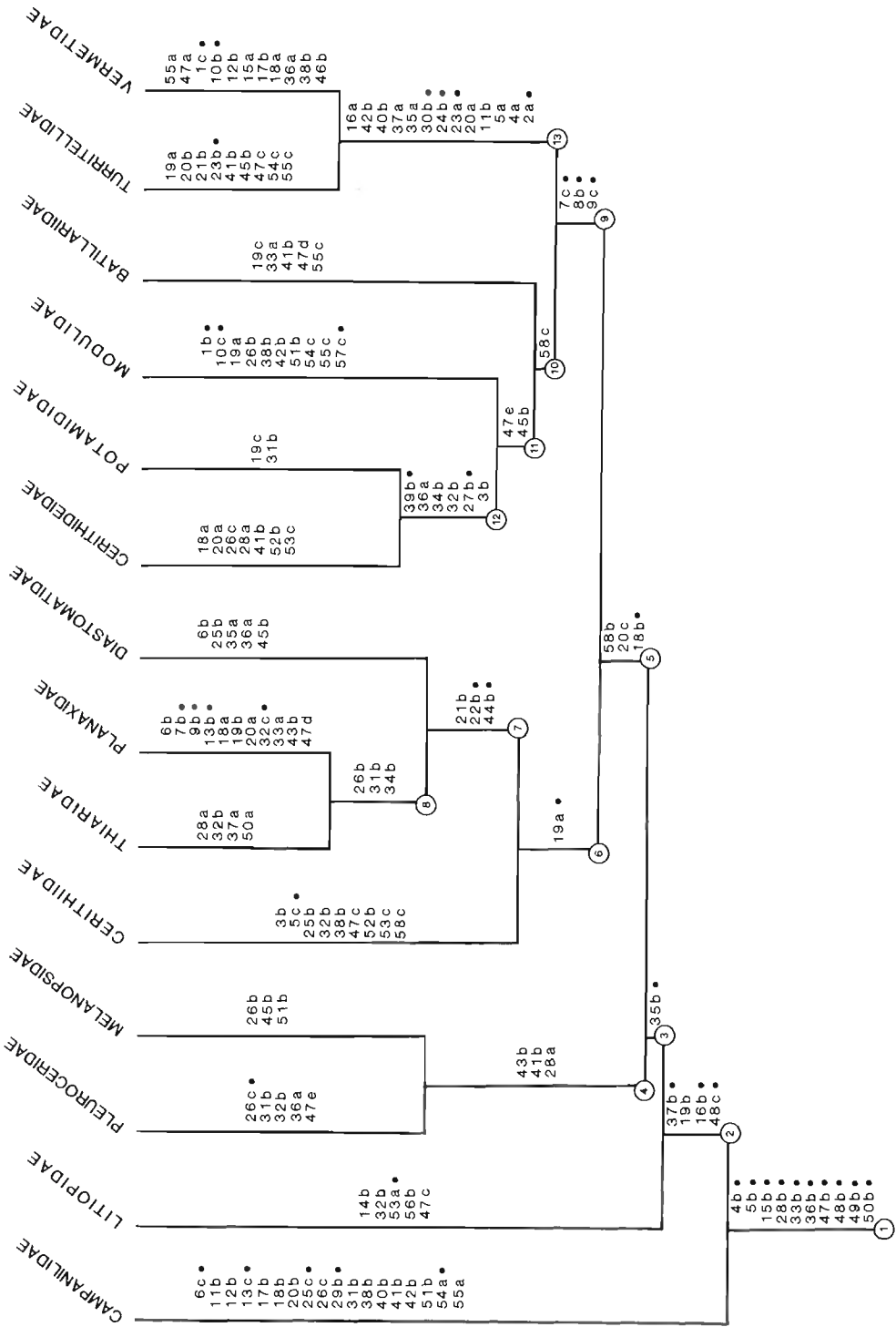


FIG. 2. Cladogram illustrating phylogeny of Cerithioidea (length = 161; CI = 49.69). Numbers refer to characters, and letters to character states, respectively as listed in Table 5. Non-homoplastic characters are indicated by solid circles. Branch numbers are those referred to in the text.

mantle cavity [23a]. Both taxa may incubate their eggs within the mantle cavity or shell, but some turritellids deposit spawn masses externally (Flores & Oliver, 1972). A number of other homoplasious synapomorphies define the stem: loss of the anterior canal [4a]; a wide snout [11b]; loss of the ovipositor [16a]; lack of mantle papillae [19b] (to be regained again by the Turritellidae); scythe-like marginal teeth [35a]; salivary glands anterior to the nerve ring [37a]; a rudimentary spiral caecum [40b] (Carrick, 1980a: 115; Bieler, pers. comm.); and long supraesophageal ganglionic connectives [42b].

Campanilidae. The Campanilidae, which consistently fell out at the base of the cladograms, may also be considered as an outgroup. This group, originally thought to be part of the Cerithiidae, was considered to have full familial status and was retained in the Cerithioidea by Houbrick (1981a: 280). It was included as a member of the superfamily in this analysis, although Houbrick (1981c: 285) and Haszprunar (1985b, 1988, this volume) have suggested it may have opisthobranch affinities. Autapomorphies of the Campanilidae are a periostracum comprising an intratocalyx [6c] (Houbrick, 1981c: 268); a short, oval osphradium [25c] (Houbrick, 1981c: 272); anterior leaflets on the hypobranchial gland [29b] (Houbrick, 1981c: 274); buccal pouches (Houbrick, 1981c: 275); a transverse septum dividing the cephalic hemocoel from the midesophagus (Houbrick, 1981c: 275); a pit with spirally arranged leaflets in the stomach (Houbrick, 1981c: 276); location of the seminal receptacle in the pericardium (Houbrick, 1981c: 277); spawn mass with chalazae connecting individual eggs, and lack of hyaline capsules around the eggs (Houbrick, 1981c: 284). In addition to these characters, *Campanile* differs from all other cerithioideans in having a unique euspermatozoan midpiece and two kinds of paraspermatozoa that show connections within the Cerithioidea to the Cerithiidae, Potamididae, and Turritellidae, and which bridge the gap between the Cerithioidea and the remainder of the Caenogastropoda (Healy, 1986a: 168). Healy (1986b: 216) hypothesized that the Campanilidae probably diverged at an early stage from the primitive cerithioidean stock in which sperm dimorphism was established. These unusual and aberrant characters in *Campanile* and its inclusion in the Cerithioidea and indeed in the Prosobranchia, have been questioned by Haszprunar (1985c: 212), who suggested that it is better referred to the group he calls Heterobranchia Gray, 1840. I concur with Healy (1986b: 216) that *Campanile* should occupy an isolated position within Cerithioidea, at the base of the clade.

Litiopidae. The Litiopidae appears at the base of the cladogram after the Campanilidae. The presence of epipodial tentacles [14b], a mesopodial mucous gland, a short sperm gutter [56b], and location of the seminal receptacle in the lateral lamina [53a] are autapomorphies setting them apart from other cerithioideans. The first two characters are shared with the rissoids.

Stem 4. One of the surprises of this analysis was the sister-group relationship between the Pleuroceridae and Melanopsidae. As little anatomical information is available for either family, the stem bearing them is supported by only three homoplastic characters. Both groups have weak hypobranchial glands [28a] and long supraesophageal connectives [43b]. They both exhibit zygoneury [41b] and have relatively thin, ridge-like, inconspicuous osphradia less than half the tentacular length.

Melanopsidae. The Melanopsidae has been usually considered a subfamily of

the Thiaridae (Thiele, 1939: 690; Starmühlner, 1970: 61; Brown, 1980: 122), but all cladograms generated in this study show a clear, wide separation from the thiarid clade and apomorphies supporting full familial status (Fig. 2). Sister-group relationship between the Melanopsidae and Pleuroceridae, as shown in Figure 2, is contrary to the hypothesis of Morrison (1954: 357), who thought that the Melanopsidae was derived from the marine family Modulidae, on the basis of similar ovipositors. As Brown (1980: 83) pointed out, Morrison's system has not been generally accepted by other workers, and his hypothesis is not supported by my cladogram. The posterior oviduct is open in melanopsids [51b], the cerebral-pedal connectives are short [45b], and the osphradium is less than half the ctenidial length [26b].

Pleuroceridae. The Pleuroceridae is a poorly-defined family. There are few papers on the anatomy of this family. Almost all of our anatomical knowledge of North American pleurocerids relies on the work of Dazo (1965), who studied only two species. Likewise, the anatomy of Asian pleurocerids is little-known: only the anatomy of *Semisulcospira* has been examined (Itagaki, 1960; Pace, 1973), and this genus, unlike the New World pleurocerids, broods its young in the pallial oviduct. Morrison (1954: 367) included *Semisulcospira* and other Asian genera in his concept of the Pleuroceridae, but gave no reasons for doing so. As no hard evidence exists to support the inclusion of the Asian genera with those from North America, I have not included published data about Asian species in this analysis. Pleurocerids have a rachidian tooth with a narrow basal plate [31b] that lacks the basal extensions [32b] common in many cerithioideans. This conclusion is based on examination of the radulae depicted in the literature: no comprehensive survey of pleurocerid radulae has been published. In contrast to the Melanopsidae, pleurocerids apparently lack an esophageal gland [36b]. They have Group 2 euspermatozoa [47e] (Healy, 1986), but lack the flange structures seen in other Group 2 members (Koike, 1985).

Stem 6. A single weak synapomorphy, long papillae on the mantle edge [19a], distinguishes the stem supporting the four branches representing the cerithiids, thiarids, diastomatids, and planaxids. If this character is removed, the stem 6 falls into the basal node of stem 5 to form a trichotomy.

Cerithiidae. The Cerithiidae is a very large, relatively well-known marine family comprising about 25 genera and many hundreds of species. Members of the family frequently have flared outer lips [3b] and long, reflexed siphonal canals [5c]. All possess a well-developed, bipectinate osphradium [25b], and two seminal receptacles [52b], one in each lamina of the pallial oviduct [53c]. As mentioned above, the stem joining the Cerithiidae to the diastomatids, planaxids and thiarids is defined by only one poor character of questionable weight. Moore (1898: 178-179) suggested that the simpler marine dialyneurous cerithiids gave rise to the "cerithio-melaniae" (thiarids) and the potamidids, and his hypothesis is supported somewhat by my cladogram.

Stem 7. The three families above this stem all have brood pouches [21b]. Two unique, unreversed synapomorphies characterize the stem supporting the thiarids, diastomatids, and planaxids: a subhemocoelic brood pouch of ectodermal origin in the head-foot [22b,23c]; long extensions of the pedal ganglia into the foot that innervate the brood pouch [44b]. These three families fall out as a discrete monophyletic group in all of the cladograms generated during the course

of this analysis. The Thiaridae comprises an enormous, freshwater family, while the two marine families, Diastomatidae and Planaxidae, are small ones in terms of numbers of genus and species-group taxa. There is no doubt that these three groups have a close relationship with the Cerithiidae, as they were placed together with it in all cladograms generated. This is in sharp contrast to the hypothesis of Morrison (1954: 357) who thought that the three freshwater families, Pleuroceridae, Melanopsidae, and Thiaridae, were derived from ancestors common to the marine families Cerithiidae, Modulidae, and Planaxidae, respectively.

Diastomatidae. The Diastomatidae is a relict group, which was prolific in the Eocene, but is now represented by only one living species that is distinguished by a long, turreted shell, hispid periostracum [6b] (shared with the Planaxidae), bipectinate osphradium [25b] (shared with the Cerithiidae), short pedal ganglionic extensions [45b], and has lost the esophageal gland [36a] (Houbrick, 1981b). The shells of this group look very much like those of many thiarids, and the position of the Thiaridae relative to the Diastomatidae on the final cladogram (Fig. 2), indicates that the latter marine family is ancestral to the thiarids.

Stem 8. This stem is weakly defined by two homoplastic radular characters and one homoplastic osphradial character, which if removed, would collapse into a trichotomy. The Thiaridae and Planaxidae appear to be sister groups that share a similar subhemocoelic brood pouch and an osphradium shorter than the ctenidium [26b]. Both families have a rachidian tooth with a narrow basal plate [31b] and an outer marginal tooth with a marginal flange [34b].

Planaxidae. The Planaxidae is a well-defined family. The littorinid-like shell is squat and solid. Autapomorphic characters include a lenticular operculum [7b] with a terminal nucleus [9b], an anterior pedal gland extending half-way around the sole of the foot [13b], and radula having a rachidian tooth with a narrow basal plate that has basal cusps [33a] and extremely long lateral extensions [32c]. There are no mantle papillae [19b]. Embryos are released from the brood pouch at the veliger stage and become planktotrophic. One genus, *Angiola*, is bioluminescent (Houbrick, 1987a: 18, 23).

Thiaridae. The Thiaridae comprises a large heterogeneous group of freshwater taxa that needs much systematic attention. Authors do not agree to its composition or subdivisions. As now constituted, the Thiaridae is probably a polyphyletic group (Moore, 1899: 178-179). It has been divided into six subfamilies by Brown (1980), who along with many other authors, included the Melanopsidae as a subfamily. Moore (1899: 178-179) believed that the Thiaridae (cited as Melaniidae) was a polyphyletic group and split it into three divisions: 1) a littorino-melanoid group of freshwater stock; 2) a planaxo-melanid group; 3) a cerithio-planaxoid group of cerithiid marine origin. In this analysis, only characters derived from the Thiarinae, many of which are parthenogenetic, were used. The oviduct is closed in this group [50a] (a situation unique in cerithioideans and undoubtedly a derived condition), salivary glands are anterior to the nerve ring [37a], the hypobranchial gland is weak [28a], and the basal plate of the rachidian has lost its basal extensions [28a].

Batillariidae. Although the Potamididae has previously been divided into the subfamilies Batillariinae and Potamidinae (Wenz, 1940), there are good morphological reasons to accord full familial status to the former subfamily. The

Batillariidae have a mainly subtropical distribution, a nearly smooth mantle edge [19c], are zygoneurous [41b], have euspermatozoa with a midpiece falling into Healy's (1986) Group 1B [47d], and have characteristic paired cusps on the basal plate of the rachidian tooth [33a], a character which they share with the planaxids. Sperm gutters are on both laminae of the pallial oviduct [55c]. In all cladograms, the Batillariidae, although always grouped near the other two potamidid families, was consistently separate from them. On the basis of sperm structure Healy (1983a: 73) suggested familial status for the batillariids.

Modulidae. The Modulidae is a small group comprising two genera. Apomorphic characters are a turbinate shell [1b] with an umbilical chink, a similar turbinate-shaped body [10c], and eyes on the mid-tentacular stalk. Modulids have a complex pallial oviduct with a series of baffles on the laminae [57c] and the spermatophore bursa is in the lateral lamina [54c]. They have two gutters on both laminae of the pallial oviduct [55c], as do the potamidids. The Modulidae appears to be closer to the Potamididae and Cerithiidae than previously thought. In other, less parsimonious cladograms, the Modulidae was separated from the branch supporting the Batillariidae, Potamididae, and Cerithiidae.

Cerithiidae. The Cerithiidae usually live on mangrove roots or trunks and have a siphonal pallial eye on the smooth mantle edge [18a]. The hypobranchial gland is weak [28a] and the osphradium short [26c]. There are two seminal receptacles [52b], one in each lamina of the pallial oviduct [53c]. The nervous system is zygoneurous. Shells are sculptured with axial ribs and have round, expanded or flared apertures. The anterior siphonal canal is short and shallow, and the anal canal may be well-defined.

Potamididae. The Potamididae, which live on mud flats, usually associated with mangroves, comprises mostly large snails with heavy, weakly spirally sculptured shells that frequently have apertures with more tubular, centrally located, anterior siphons. They are characterized by having diminutive mantle papillae [19c], and a tiny radula having a very narrow basal plate on the rachidian tooth [31b]. The laminae of the median pallial oviduct are partially closed, a unique feature among cerithioideans. The anatomy of the Potamididae is poorly known. Bouvier (1887: 145) said that the nervous system of *Telescopium* is purely zygoneurous, but this condition is not found in other potamidids, and was not coded for the family. *Telescopium* differs greatly from other potamidids in shell morphology and may represent the remnant of another monophyletic group.

Turritellidae. The Turritellidae is a large, perhaps ancient family, that is poorly known, anatomically and biologically. Turritellids have many whorled, tall shells. Present information shows that protandry exists in one species (Carrick, 1980b: 254) and zygoneury is known in one species [41b] (Bouvier, 1887). In brooding species [21b] embryos are kept in the pallial oviduct [23b] (Carrick, 1980b: 254). Sperm gutters are on both laminae of the pallial oviduct [55c] and the spermatophore bursa is in the lateral lamina [54c] (Johansson, 1946: 2-3). The mantle edge is fringed with long papillae around its entire circumference [20b].

Vermetidae. The Vermetidae is a large, diverse group and perhaps the most highly apomorphic family among cerithioideans. It is defined by 19 characters on the final cladogram. The attached, long, uncoiled shells [1c] are unusual among prosobranchs, except for the Siliquariidae Anton and in *Vermicularia* Lamarck (Turritellidae). The foot is vestigial and there are no statocysts present

in the nerve ring, presumably due to their sessile mode of life. A long, strap-like columellar muscle [17b] allows most genera to withdraw deeply within the shell. One pair of epipodial tentacles is present on the anterior foot, and the mantle edge is smooth [18a]. Vermetids have wide snouts and short cephalic tentacles. The mucous net feeding habit is reflected in the alimentary tract: the esophageal gland is lost [36a], and the anterior pedal mucous gland is enormously enlarged to secrete the mucous net. Vermetids, unlike any other cerithioidean, produce pelagic spermatophores. Embryos are brooded on the inner shell wall, adjacent to the mantle, or free in the mantle cavity. The vermetids do not have the unique euspermatozoan morphology observed in other cerithioideans, but have features more in common with the Cerithiopsidae and Triphoridae, and are similar to those observed in the Neogastropoda [46b] (Healy, 1986: 168). The terminal placement of the Vermetidae on the cladogram is supported by numerous autapomorphies and indicates that they, and the turritellids, are very different from other cerithioideans. The vermetids are regarded as a separate superfamily by Healy (1988, this volume) and Ponder & Warén (1988, this volume).

CONCLUSIONS

1. Superfamily Cerithioidea. It is difficult to find autapomorphic characters separating cerithioideans from other caenogastropod superfamilies, although Healy (1986: 168) has shown that the Cerithioidea distinctively stand apart from other mesogastropods by the presence of unusual euspermatozoa having a midpiece composed of four elements each with parallel crystal plates - a synapomorphy shared with the Viviparoidea (4 elements), and close to the condition observed in the Cyclophoroidea (7-8 elements). The paraspermatozoa of these three groups are also similar and, as a group, unique. Thus, using sperm morphology, the superfamily is well-defined, and close to the Viviparoidea. Together with the Cyclophoroidea, the three superfamilies appear to form a distinct, primitive clade within the Mesogastropoda.

In addition to sperm morphology, the Cerithioidea are defined by a combination of characters separating them from other prosobranchs: (1) alimentary tract characters include a taenioglossate radula, complex stomach with style sac and gastric shield; (2) reproductive tract characters are open pallial gonoducts, aphallate males that produce spermatophores and dimorphic sperm, and ovipositors and brooding in females of many groups; (3) the nervous system of all groups is epiathroid, dialyneurous, and occasionally zygoneurous in some families. The Cerithioidea are separated from the architaenioglossan families by the presence of long cerebro-pleural connectives in the latter.

2. Major clades in the Cerithioidea. Five major groups, exclusive of the Campanilidae, may be distinguished on the final cladogram (Fig. 2): (1) The Litiopidae emerge as a well-defined group and are separated from the nearest other families by several good characters; (2) Stems 3 and 4, supporting the Pleuroceridae and Melanopsidae, are weakly defined; (3) A large clade, comprising the Diastomatidae, Planaxidae, Thiaridae, and Cerithiidae, is weakly supported by stem 6 and would collapse into a trichotomy if the character separating it, mantle edge papillae length, were removed; (4) Stem 7, supporting the thiarid, planaxid, and diastomatid clade is well-defined. This grouping differs

from a previous hypothesis that the Planaxidae were closely related to the thiarids and batillariids (Houbrick, 1987a: 41, 51); (5) A large group comprising the Batillariidae, Potamididae, Cerithideidae, and Modulidae is well-defined by stems 9 and 10. Stem 12, terminating in the cerithideids and potamidids, is strongly supported, and represents an estuarine radiation. The Modulidae are united to the Cerithideidae and Potamididae and distinguished from the Batillariidae by two homoplasious characters on stem 11: length of the cerebral connectives, and Group 2 euspermatozoa; (6) The Turritellidae and Vermetidae, both highly apomorphic and each well-defined by numerous characters, comprise a very distinct clade, quite different from other cerithioideans.

3. **Congruence with other phylogenetic schemes.** Bouvier's (1887) ideas of prosobranch phylogeny, resulting from an extensive and detailed review of the nervous system, are interesting to compare with my results. His phylogeny is summarized in his "Table on the Affinities and Classification of the Prosobranchia" in which he groups various families into "series naturelles". His inclusion of the Planaxidae with the Littorinoidea is incorrect, as I have shown the planaxids to have a true cerithioidean morphology (Houbrick, 1987a). Bouvier derived the Cerithiidae and Thiaridae (cited as Melaniidae) from a common ancestor, which is entirely consistent with my conclusions. He included *Melanopsis* with the Thiaridae, but noted that *Melanopsis* is zygoneurous, in contrast to the thiarids. The Melanopsidae is in a separate branch in my analysis, although it is relatively close to the branch supporting the thiarids. Under the cerithiids, Bouvier separated the dialyneurous groups (Cerithiidae, Potamididae) from the zygoneurous ones (Campanilidae, Cerithideidae, Batillariidae, and *Telescopium*, a member of the Potamididae). This is somewhat congruent with my analysis, but splits the family Potamididae between two groups. The zygoneurous Turritellidae are far removed from the other families, as in my cladogram. The results of Bouvier's (1887) study of the nervous system and the more holistic analysis herein are therefore mutually supportive. Zygoneury occurs independently in numerous stems and appears to be a highly homoplastic character.

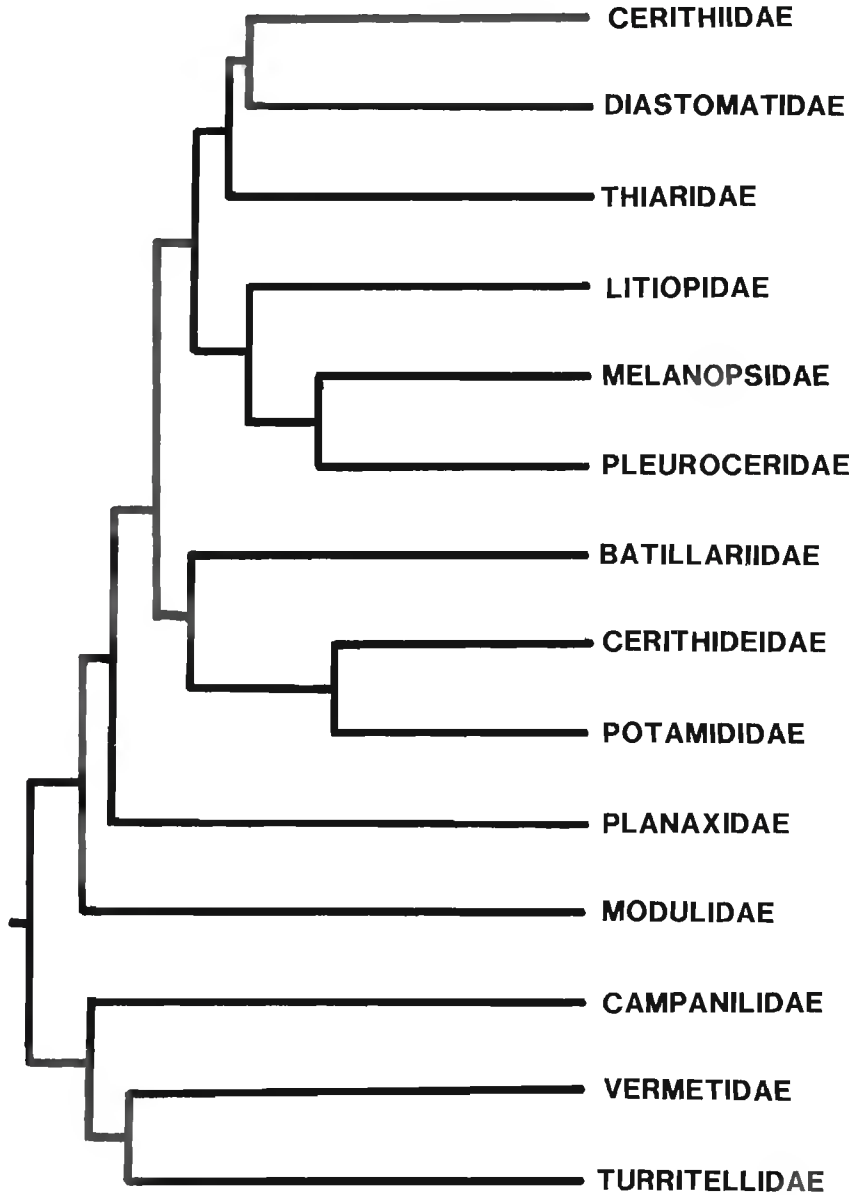
The results of this cladistic analysis are partially incongruent and not entirely supportive of the cerithioidean groups identified by Healy (1983a: 71) on the basis of euspermatozoan ultrastructure. Group 1 (subgroup a), comprising the Cerithiidae, Turritellidae, and Litiopidae, does not fit the cladogram. All three families are widely separated from one another by many branches and numerous, unique, unreversed characters. Group 1 (subgroup b), the Planaxidae and Batillariidae, is somewhat inconsistent with the cladogram; part of Group 2, the Potamididae, Cerithideidae, and Modulidae, is fully congruent with the cladogram, but the Thiaridae and Pleuroceridae, tentatively assigned to Group 2 on the basis of light microscope investigations, do not fit the cladogram. Detailed ultrastructural studies of these taxa may resolve the problem. A recent paper by Healy (1986b) on the euspermatozoa and paraspermatozoa of *Campanile* has added new data, suggesting a third group for the Campanilidae, and emphasizes the isolated position of this family in relation to other cerithioideans. The old data set for *Campanile* spermatozoa used in generating the cladogram (Fig. 2), will have to be modified and scored differently in any new analysis, but will probably not radically change the overall topology. Sperm morphology is very useful in

assessing existing classifications and phylogenies of prosobranch groups such as the Cerithioidea where the method of sperm transfer (spermatophores) and probably the environment of fertilization are reasonably uniform. I agree with Healy (1983a) that euspermatozoan ultrastructure supplies an important character set for analysis, but the data derived from such studies should not be isolated from all other morphological data sets. The construction of a phylogeny using only one character or a very narrow character set is ill-advised. When the ultrastructure of euspermatozoa of these and other families is better known, new data may alter the cladogram and become more supportive and congruent.

The final cladogram (Fig. 2) is somewhat compatible with immunoelectrophoretic experiments (Davis & Suzuki, 1971: 224) on members of the Pleuroceridae (Asian), Thiaridae, Batillariidae (as Potamididae), and Cerithiidae, which suggest that the Batillariidae is more closely related to the Pleuroceridae than to the Cerithiidae and that the Thiaridae and Batillariidae are more closely allied to the Pleuroceridae than to the Cerithiidae. Davis & Suzuki's (1971) work is in agreement with the groups based on sperm ultrastructure suggested by Healy (1983a). Pleurocerids, although poorly known, are separated from the potamidids and thiarids on the cladogram by several stems and a number of unique, unreversed characters. Moreover, the pleurocerid representative used by Davis & Suzuki (1971) in this experiment was *Semisulcospira*, an Asian species whose affinity to the North American Pleuroceridae is not clear. More immunoelectrophoretic work on American pleurocerids and on other cerithioidean families plus further and more detailed anatomical studies may better resolve this incongruence.

If the cladogram (Fig. 2) is compared with the phenogram (Fig. 3) generated with the same data set, using unweighted pair-group arithmetic averaging (UPGMA), there is surprising congruence in the topology of the trees and in the grouping of most families. However, the Planaxidae are placed closer to the potamidid groups, and the Campanilidae are grouped with the Turritellidae and Vermetidae. This kind of analysis is based merely on overall similarity and does not presuppose descent with modification. Therefore, the cladogram presents a better working hypothesis of Cerithioidean evolution.

4. Congruence with the fossil record. As anatomy of extinct taxa is unknown, evolutionary scenarios based on fossil interpretations cannot be falsified, and were not seriously regarded. However, comparison of the fossil record with the cladogram in Fig. 2 should provide an independent test of the results of this study. Unfortunately, data cited in the literature about origins of fossil taxa are incongruent, for the most part, with the cladogram. This is not surprising because the fossil record is incomplete, and many times has been inaccurately interpreted (see my remarks under "Fossil History"). Different times of origins are frequently cited for the same taxon by different authors. Also, concepts of the scope of a given family vary widely in the literature, resulting in splitting or lumping of data. In some cases, suggested origins of cerithioidean families (Turritellidae in the Devonian: Knight *et al.*, 1960: 1317) are earlier than that given for the superfamily itself (Jurassic: Cossmann, 1906: 9; Permian: Fretter & Graham, 1962: 624; Triassic: Golikov & Starobogatov, 1975: 201-202). As many family origins are inferred from shell morphology of fossils, the older the fossil, the more likely classification error has been introduced by morphological convergence.



10 9 8 7 6 5 4 3 2 1 0 UPGMA

FIG. 3. Phenogram based on UPGMA and employing the same data used to construct the cladogram in Fig 2.

Thus the data assembled about mesogastropod family origins by Sepkoski (1982: 27-28) is, in my opinion, highly inaccurate. Given the high probability of shell convergence, I believe the times of origins cited by him for most cerithioidean

families are far too early: most Recent families can only be traced back to the late Cretaceous, with reasonable confidence.

Not all incongruence may be explained away by incomplete data and misinterpretation of fossils: The Turritellidae is probably an old group, and it is troublesome that it appears as one of the terminal taxa in the cladogram. The highly modified, autapomorphous characters found in this family and in the Vermetidae, its sister group, may have masked the symplesiomorphic characters. The cladogram would be intuitively more acceptable if these two families appeared near the base of the stem.

The phylogeny suggested by this analysis is only preliminary in scope and is put forward as a working, testable hypothesis. Its weaknesses reflect the inadequate anatomical information available about many families. Moreover, each family is characterized in this analysis only by the characters known about its respective "type-genus", which in some cases may be atypical, and certainly not always the most "primitive" taxon of the family. In addition, there are the inherent problems of identifying homologies, establishing character polarity, and performing transformation series analyses. These difficulties are freely admitted, but the alternatives are to do nothing, or to invent evolutionary scenarios and "just so stories" incapable of falsification.

ACKNOWLEDGEMENTS

The data collected for this research are the results of many years' work. They have been obtained with the assistance and support of numerous institutions and individuals. Nearly everyone cited in the acknowledgements of my previous publications on cerithioideans should be thanked again. I gratefully acknowledge the financial support of the Smithsonian Secretary's Fluid Research Funds, and Research Opportunities Funds, and the Smithsonian Caribbean Coral Reef Ecosystems Program. This paper is contribution no. 200, Reef and Mangrove Study, Smithsonian Institution, Belize, partly supported by the Exxon Corporation. Much of this work was accomplished at the Smithsonian Marine Station, Ft. Pierce, Florida and this paper is Smithsonian Marine Station Contribution no. 174. I also acknowledge the support of an Australian Museum Fellowship. For use of facilities and field assistance, I thank the University of Guam Marine Laboratory, and the Kewalo Marine Laboratory, Pacific Biomedical Research Center, University of Hawaii, and the Los Angeles County Museum of Natural History. Within the National Museum of Natural History, Smithsonian Institution, I thank Dr. Mary Mickevich for her guidance and assistance in the use of the PHYSYS program, Mr. Victor Krantz for photographic assistance, and the staff of the Smithsonian Scanning Electron Microscope Laboratory. I thank Dr. John Healy, University of Sydney, for useful discussion and correspondence about cerithioidean sperm morphology. Ms. Molly Ryan, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, kindly drew the cladogram.

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PROSOBRANCH PHYLOGENY

W. F. Ponder, Editor

Malacological Review, Supplement 4, 1988

Proceedings of a Symposium held at the 9th International Malacological Congress, Edinburgh, Scotland, 31 August-6 September, 1986

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