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Caenogastropoda

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Caenogastropods comprise about 60% of living gastropod species and include a large number of ecologically and commercially important marine families. They have undergone an extraordinary adaptive radiation, resulting in considerable morphological, ecological, physiological, and behavioral diversity. There is a wide array of often convergent shell morphologies (Figure 13.1), with the typically coiled shell being tall-spined to globose or flattened, with some uncoiled or limpet-like and others with the shells reduced or, rarely, lost. There are also considerable modifications to the head-foot and mantle through the group (Figure 13.2) and major dietary specializations. It is our aim in this chapter to review the phylogeny of this group, with emphasis on the areas of expertise of the authors.

The first records of undisputed caenogastropods are from the middle and upper Paleozoic, and there were significant radiations during the Jurassic, Cretaceous, and Paleogene (see subsequent section on the fossil record). They have diversified into a wide range of habitats and have successfully invaded freshwater and terrestrial ecosystems multiple times.

Many caenogastropods are well-known marine snails and include the Littorinidae (periwinkles), Cypraeidae (cowries), Cerithiidae (creepers), Calyptraeidae (slipper limpets), Tonnidae (tuns), Cassidae (helmet shells), Ranellidae (tritons), Strombidae (strombs), Naticidae (moon snails), Muricidae (rock shells, oyster drills, etc.), Volutidae (balers, etc.), Mitridae (miters), Buccinidae (whelks), Terebridae (augers), and Conidae (cones). There are also well-known freshwater families such as the Viviparidae, Thiariidae, and Hydrobiidae and a few terrestrial groups, notably the Cyclophoroidea.

Although there are no reliable estimates of named species, living caenogastropods are one of the most diverse metazoan clades. Most families are marine, and many (e.g., Strombidae, Cypraeidae, Ovulidae, Cerithiopsidae, Triphoriidae, Olividae, Mitridae, Costellariidae, Terebridae, Turridae, Conidae) have large numbers of tropical taxa. A few families have diversified more in cooler waters (e.g., Buccinidae, Eatoniellidae, Struthiolariidae), and many others are diverse in both temperate and tropical seas. Caenogastropod diversity has increased, especially since the Mesozoic (Sepkoski and Hulver

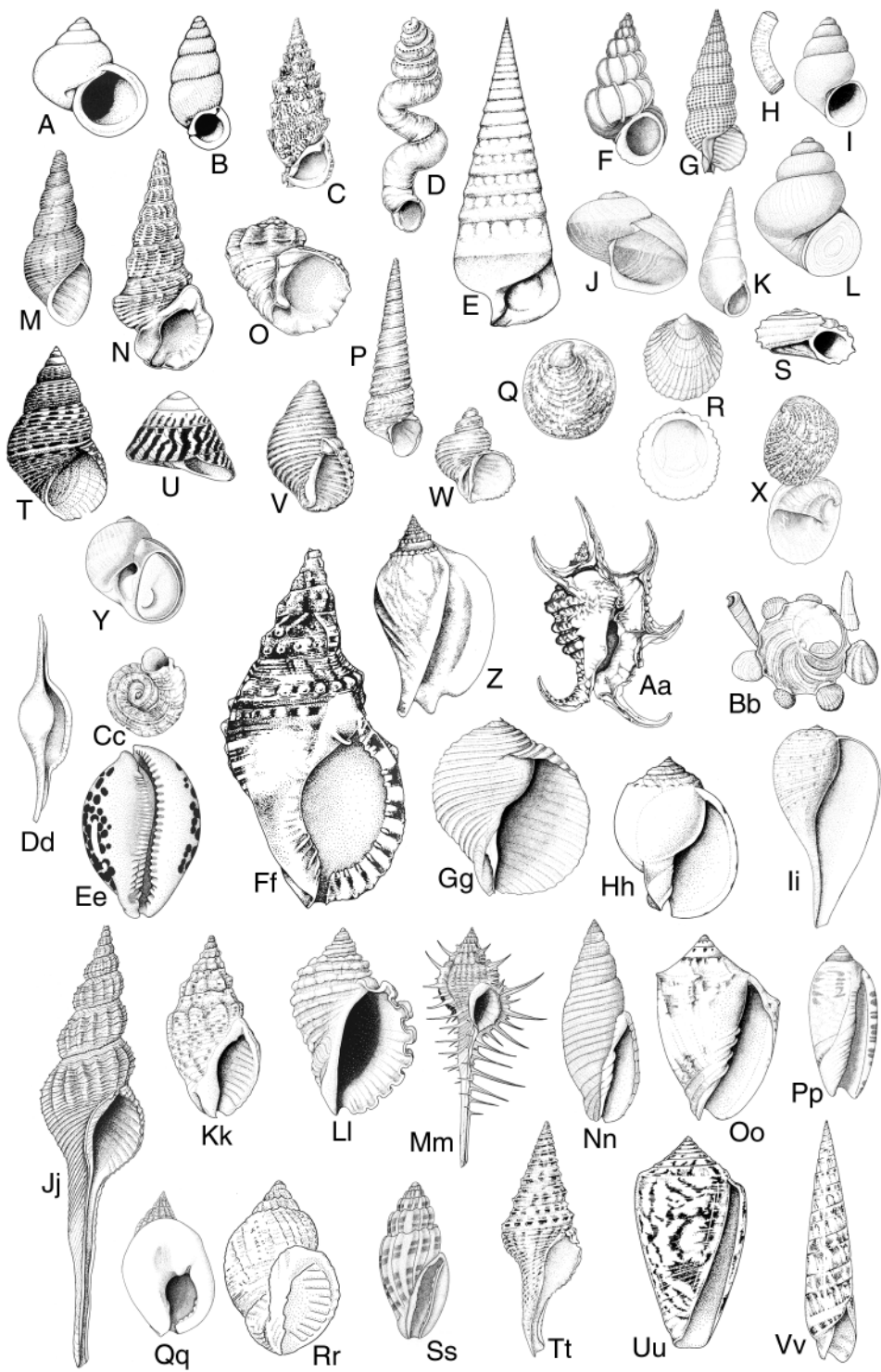


FIGURE 13.1. (Opposite.) Shells of some Recent caenogastropods showing the range of morphology. (A) *Leptopoma* (Cyclophoridae); (B) *Pupinella* (Pupinidae); (C) *Pseudovertagus* (Cerithiidae); (D) *Tenagodus* (Siliquariidae); (E) *Campanile* (Campanilidae); (F) *Epitonium* (Epitoniidae); (G) *Ataxocerithium* (Newtoniellidae); (H) *Caecum* (Caecidae); (I) *Austropyrgus* (Hydrobiidae *sensu lato*); (J) *Janthina* (Janthinidae); (K) *Monogamus* (Eulimidae); (L) *Gabbia* (Bithyniidae); (M) *Melanoides* (Thiaridae); (N) *Pyrazus* (Batillariidae); (O) *Modulus* (Modulidae); (P) *Colpospira* (Turritellidae); (Q) *Capulus* (Capulidae); (R) *Sabia* (Hipponicidae); (S) *Circulus* (Vitrinellidae); (T) *Littoraria* (Littorinidae); (U) *Bembicium* (Littorinidae); (V) *Planaxis* (Planaxidae); (W) *Sirius* (Capulidae); (X) *Crepidula* (Calyptraeidae); (Y) *Notocochlis* (Naticidae); (Z) *Strombus* (Strombidae); (Aa) *Lambis* (Strombidae); (Bb) *Xenophora* (Xenophoridae); (Cc) *Serpulorbis* (Vermetidae); (Dd) *Volva* (Ovulidae); (Ee) *Cypraea* (Cypraeidae); (Ff) *Charonia* (Ranellidae); (Gg) *Tonna* (Tonnidae); (Hh) *Semicassis* (Cassidae); (Ii) *Ficus* (Ficidae); (Jj) *Fusinus* (Fascioliidae); (Kk) *Cominella* (Buccinidae); (Ll) *Dicathais* (Muricidae); (Mm) *Murex* (Muricidae); (Nn) *Cancilla* (Mitridae); (Oo) *Cymbiola* (Volutidae); (Pp) *Oliva* (Olividae); (Qq) *Nassarius* (Nassariidae); (Rr) *Cancellaria* (Cancellariidae); (Ss) *Euclithara* (Turridae *sensu lato*); (Tt) *Lophiotoma* (Turridae); (Uu) *Conus* (Conidae); (Vv) *Terebra* (Terebridae). All figures reproduced with permission from Beesley *et al.* (1998), some slightly modified. Not to scale.

1985; Signor 1985), accelerating during the Cretaceous with the radiation of neogastropods and other predatory gastropods (Sohl 1964; Taylor *et al.* 1980), suggesting that diet and competition (e.g., Vermeij 1978, 1987) played a significant role in their adaptive radiation (discussed later in this chapter). The pattern of steady diversification in caenogastropods differs from that of most other major groups of marine metazoans, which are characterized by marked waxing and waning or even complete extinction (e.g., Ammonoidea).

Since the late Paleozoic, caenogastropods form large portions of the richest known gastropod faunas, both in numbers of species and in abundance of individuals (Table 13.1).

PHYLOGENY AND CLASSIFICATION

SISTER GROUP RELATIONSHIPS

Heterobranchia are usually shown as the sister group to caenogastropods in recent analyses involving extant taxa using morphological (e.g., Ponder and Lindberg 1997) or molecular data (e.g., Tillier *et al.* 1992; McArthur and Harasewych 2003). However, this is not always the case, with neritimorphs being the sister taxon in some molecular analyses such as those of Colgan *et al.* (2000, 2003, 2007) and Aktipis *et al.* (Chapter 9). Whereas modern neritimorphs have highly convolute larval shells with resorbed inner walls, the assumed early members of this clade had planktotrophic larval shells, which are not fundamentally different from those of

caenogastropods (as discussed subsequently). A sister group relationship of Caenogastropoda with Neritimorpha may be just as feasible as one with the heterobranchs, especially as all three groups share aragonitic crossed-lamellar shell structure and lack of nacre. While heterobranchs have a heterostrophic larval shell, in neritimorphs and caenogastropods the larval shell is orthostrophic.

Neritimorphs are sister to the apogastropods (Caenogastropoda + Heterobranchia) in the supertree analysis of published molecular and morphological trees in McArthur and Harasewych (2003, fig. 6.2) and Aktipis *et al.* (Chapter 9), sharing (perhaps convergently) the development of complex genital ducts, the reduction of the pallial organs on the right side, and larval planktotrophy. Some other analyses (Ponder and Lindberg 1997; Colgan *et al.* 2003) show vetigastropods as the sister to the apogastropods.

Heterobranchs have been regarded to be the sister group to caenogastropods by many paleontologists (e.g., Bandel and Geldmacher 1996; Kaim 2004; Figure 13.5A), but some evidence suggests they may not be (Nützel, unpublished data; Figure 13.5B). Putative early heterobranchs have subulitid-like or turreted teleoconchs (Frýda and Bandel 1997), perhaps suggesting a caenogastropod relationship. However, they coexisted with several caenogastropod clades, suggesting that the stem group evolved earlier than indicated by the fossil record. An alternative explanation might be that Heterobranchia

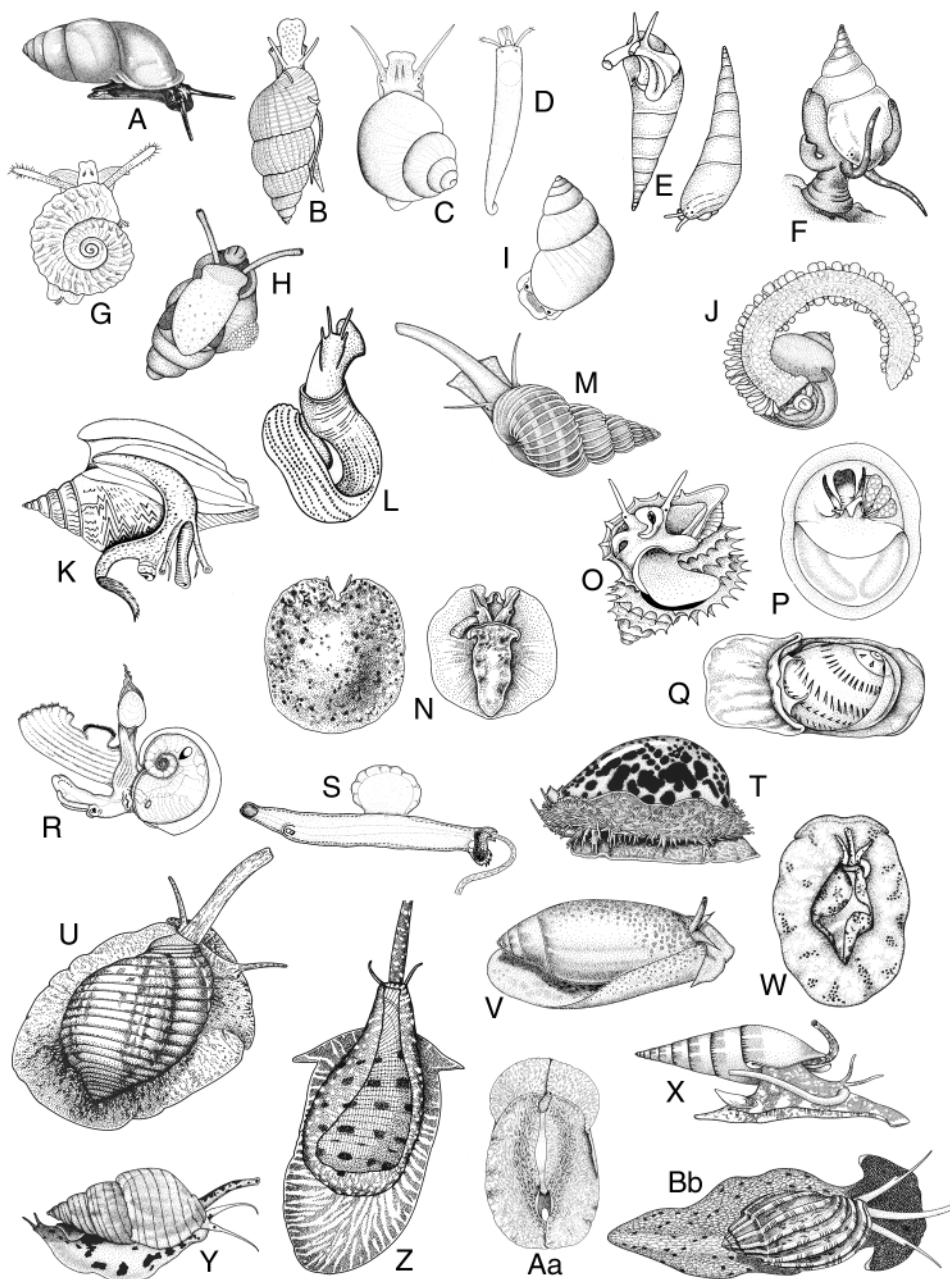


FIGURE 13.2. External morphology of living caenogastropods. (A) *Pupina* (Pupinidae); (B) *Finella* (Scaliolidae); (C) *Gabbia* (Bithyniidae); (D) *Parastrophia* (Caecidae); (E) *Vitreolina* (Eulimidae); (F) *Echineulima* (Eulimidae); (G) *Pseudoliotia* (Vitrinellidae); (H) *Ascorhis* (Hydrobiidae *sensu lato*); (I) *Cryptassimineae* (Assimineidae); (J) *Janthina* (Janthinidae); (K) *Strombus* (Strombidae); (L) *Aletes* (Vermetidae); (M) *Epitonium* (Epitoniidae); (N) *Lamellaria* (Velutinidae); (O) *Trichotropis* (Capulidae); (P) *Sabia* (Hipponicidae); (Q) *Euspira* (Naticidae); (R) *Atlanta* (Atlantidae); (S) *Firoloida* (Pterotracheidae); (T) *Cypraea* (Cypraeidae); (U) *Tonna* (Tonnidae); (V) *Oliva* (Olividae); (W) *Austroginella* (Marginellidae); (X) *Mitrella* (Columbellidae); (Y) *Nassarius* (Nassariidae); (Z) *Ficus* (Ficidae); (Aa) *Ancillista* (Olividae); (Bb) *Harpa* (Harpidae). All figures reproduced with permission from Beesley *et al.* (1998), some slightly modified. Not to scale.

TABLE 13.1
Proportions of *Caenogastropod Species and Individuals*

FORMATION	REFERENCE	MYA	% SPECIES	% INDIVIDUALS
Recent, New Caledonia ^a	Bouchet <i>et al.</i> 2002	0	72	63
Late Triassic, Mission Creek, United States	Nützel and Erwin 2004	205	52	88
Late Triassic, Pucara Formation, Peru	Haas 1953	210	41	29
Late Carboniferous, United States	Kues and Batten 2001	310	56	32

NOTE: Proportions are relative to the total numbers of all gastropods of some rich gastropod collections from the late Paleozoic, early Mesozoic and from a Recent Indo-West Pacific site. Caenogastropods form a major or even dominant part of these faunas.

^aThis site also includes shell-less taxa, so it is not strictly comparable with the fossil faunas; with the shell-less taxa excluded, the proportion of caenogastropods would be higher.

is nested within Caenogastropoda (e.g., Nützel unpublished, fig. 13.5B); although this possibility is concordant with views expressed by some (e.g., Gosliner 1981), we consider it highly unlikely on the basis of current molecular, morphological, and ultrastructural evidence (e.g., Ponder and Lindberg 1997).

In summary, although the sister group of caenogastropods is often the heterobranchs in analyses involving extant taxa, it is also possible that an extinct, non-heterobranch taxon (e.g., a neritimorph) is the actual sister group. Although fossil taxa shed some light on sister taxon relationships, the data are by no means clear (see also Frýda *et al.*, Chapter 10).

OUTLINE OF CLASSIFICATION/PHYLOGENY

RECOGNITION OF THE CLADE CAENOCASTROPODA

Although the name Caenogastropoda was used by Cox (1960a, b) nearly half a century ago to encompass Thiele's (1925–1926) Mesogastropoda and Stenoglossa (= Neogastropoda Wenz, 1938–1944), the general recognition of this group has been relatively recent. Caenogastropods were incorporated in a paraphyletic subclass, Prosobranchia, in synoptic works (e.g., Thiele 1929–1931; Wenz 1938–1944; Cox 1960b) (Figure 13.3A) and the taxonomic overviews of Taylor and Sohl (1962), Ponder and Warén (1988) and Vaught (1989), and they often continue to be treated as such in many textbooks (e.g., Brusca and Brusca 2002) and other literature, keys, indexing systems, and checklists.

Golikov and Starobogatov's (1975) revolutionary classification of gastropods included what we now know as caenogastropods within a subclass Pectinibranchia, which also included neritimorphs and some vetigastropods, notably Trochoidea. Extant caenogastropods, in this scheme, were diphyletic, with two superorders, Cerithiimorpha and Littorinimorpha, both of which included non-caenogastropod taxa, derived independently from "Anisobranchia," a group containing several vetigastropod families. Graham (1985: 174) also found that "the boundary between animals that are clearly archaeogastropod or caenogastropod is extremely blurred," and, in particular, he referred to the architaenioglossan groups and the vent-living neomphaloideans (see Geiger *et al.*, Chapter 12) as being problematic.

Haszprunar's (1988) ground-breaking analysis of gastropod relationships using morphology, including osphradial ultrastructure, showed an unresolved Caenogastropoda (Figure 13.3B) included with Architaenioglossa in a paraphyletic "Archaeogastropoda." This arrangement was modified by Ponder and Warén (1988) (Figure 13.3C), who, as in the morphological cladistic analyses of Ponder and Lindberg (1996, 1997) (Figure 13.3D), had the architaenioglossans as the sister group to the rest of the caenogastropods (the Sorbeoconcha), with the "mesogastropod" groups Cerithioidea and Campaniloidea as sister taxa to the remaining caenogastropods (Hypsogastropoda). The great majority

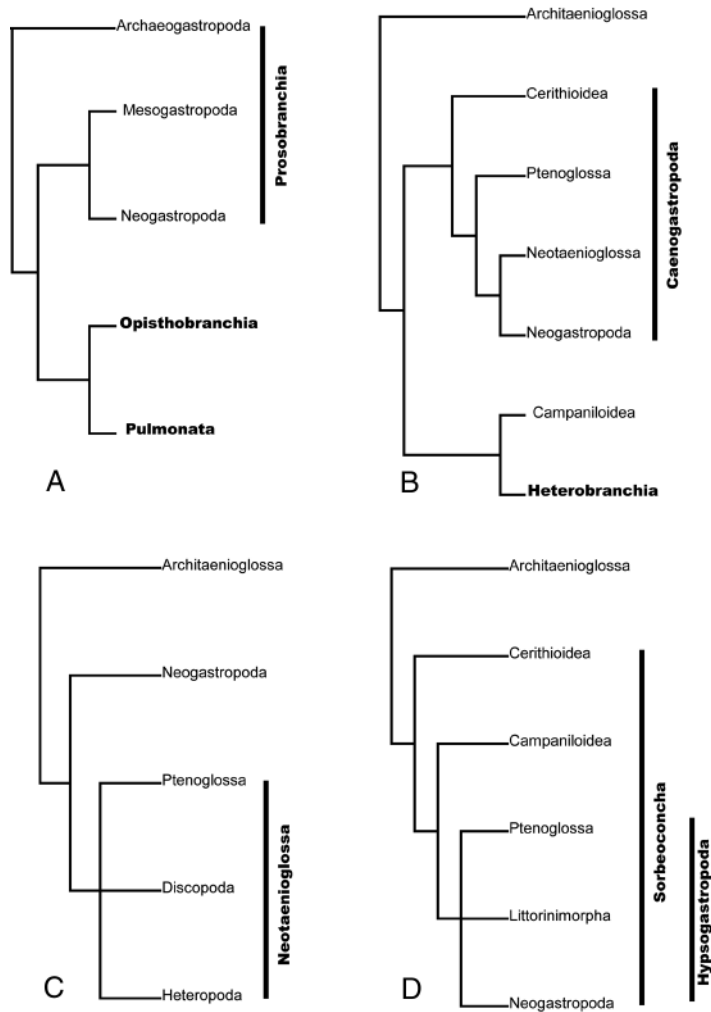


FIGURE 13.3. Some alternative hypotheses from morphology prior to 1999. (A) Thiele (1929–1931). (B) Haszprunar (1988). (C) Ponder and Warén (1988). (D) Ponder and Lindberg (1997).

of caenogastropods are contained within Hypsogastropoda, where there is little resolution to date. Strong's (2003) morphological analysis maintained a monophyletic Architaenioglossa and Neogastropoda, but the sorbeoconchan taxa were contained in two separate clades, one of which also included the only cerithioidean in her analysis (Figure 13.4A).

The major burst of interest in gastropod phylogeny in the last three decades (see Bieler 1992; Ponder and Lindberg 1997; Aklipis *et al.*, Chapter 9) has identified and delineated the major monophyletic groups and most analyses have recognized Caenogastropoda as a clade (Salvini-Plawen and Haszprunar 1987; Ponder

and Warén 1988; Bieler 1992; Tillier *et al.* 1992, 1994; Rosenberg *et al.* 1994; Ponder and Lindberg 1996, 1997; Taylor 1996; McArthur and Koop 1999; Colgan *et al.* 2000, 2003, 2007; Strong 2003; McArthur and Harasewych 2003).

In terms of rank, Cox (1960b) treated Caenogastropoda as an order, but Bandel (1991b, 1993; Bandel and Riedel 1994) used Caenogastropoda as a subclass. It was treated as a superorder by Ponder and Warén (1988; within Prosobranchia) and Beesley *et al.* (1998; within Orthogastropoda), while Ponder and Lindberg (1997), Strong (2003), and Bouchet and Rocroi (2005) treated caenogastropods as an unranked major clade.

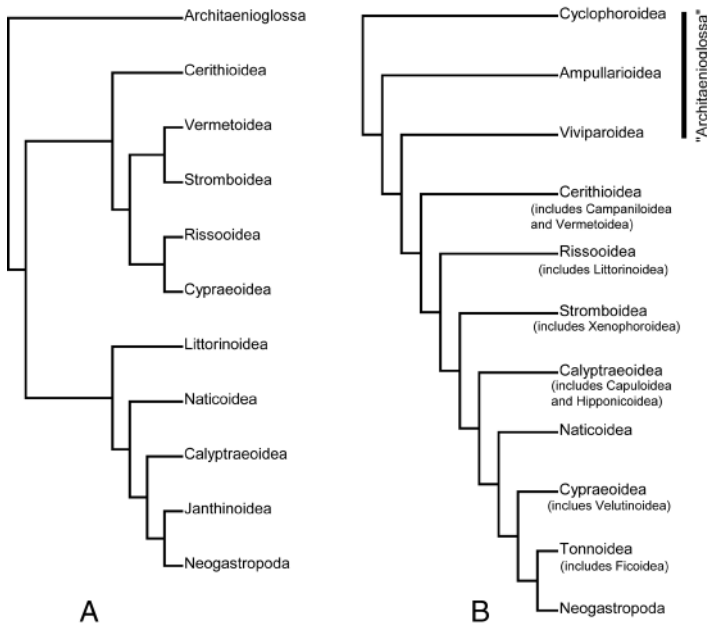


FIGURE 13.4. Phylogenies from the most recent analyses of caenogastropod phylogeny based on morphology. (A) Strong (2003). (B) Simone (2000a).

In summary, caenogastropods are currently thought to comprise the majority of the Mesogastropoda of Thiele (1929–1931) and all of the Neogastropoda. Several groups (Architectonicoidea, Rissoellidae, Omalogyridae, Pyramidellidae, Valvatidae) previously included in Mesogastropoda are now included in Heterobranchia (Haszprunar 1985b, 1988; Ponder and Warén 1988; Healy 1990d, 1993b; Bouchet and Rocroi 2005). Although the monophyly of Caenogastropoda is well supported in recent morphological analyses (Ponder and Lindberg 1997; Strong 2003), it is often not strongly supported in molecular analyses (see discussion below).

MAIN DISTINGUISHING FEATURES

Caenogastropods are defined by a number of significant characters, including a shell that is typically coiled, with a multispiral, orthostrophic protoconch and crossed-lamellar shell structure. The foot is typically simple and usually bears an operculum. The mantle cavity organs are reduced, including a single (left) monopectinate ctenidium with skeletal rods; a single left osphradium, which is typically hypertrophied and has unique histology; and a single (left) hypobranchial gland. The heart has a single auricle, and

the rectum never passes through the ventricle. Only the left kidney remains, although elements of the right kidney are incorporated in the oviduct. There is a single pair of buccal cartilages, and the radula is plesiomorphically taenioglossate. The esophagus lacks conspicuous ventral folds, the intestine is not markedly looped, and fecal pellets are produced. Pallial genital ducts enable internal fertilization and, consequently, the production of encapsulated eggs and non-planktonic early development (i.e., lacking a trochophore stage). Planktonic larvae are often planktotrophic. The nervous system is concentrated with well-defined cerebral and pedal ganglia. Most caenogastropods are epiathroid (the pleural ganglia lie close to, or are fused with, the cerebral ganglia), in contrast to the condition in vetigastropods, where the pleural ganglia are close to the pedal ganglia (the hypoathroid condition).

PHYLOGENY OF CAENOGASTROPODA

Despite the great diversity and extensive fossil record of caenogastropods, detailed relationships within the group have remained largely unresolved, although a few broad groups have usually been recognized (Table 13.2). Release

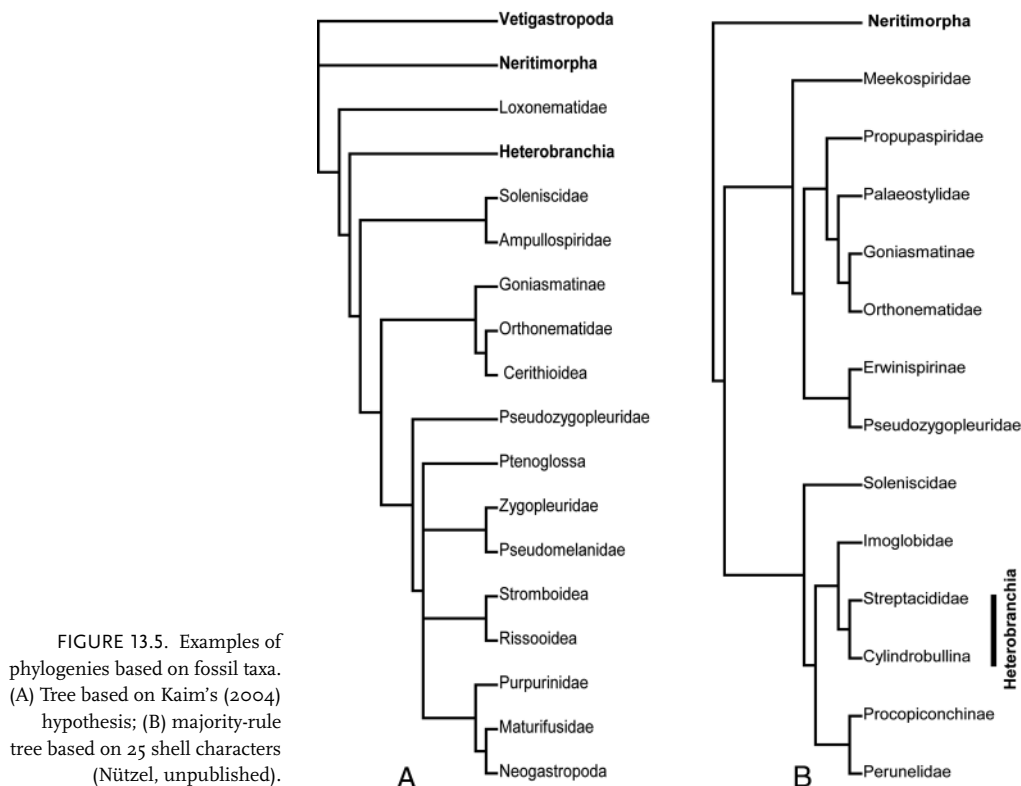


FIGURE 13.5. Examples of phylogenies based on fossil taxa. (A) Tree based on Kaim's (2004) hypothesis; (B) majority-rule tree based on 25 shell characters (Nützel, unpublished).

from the constraints of ancestral adult morphologies (Ponder and Lindberg 1997) appears to have played a major part in the evolution of the group, although the differentiation of innovation and ancestral conditions in various traits has often been difficult or impossible to determine in the absence of a robust phylogeny. Compounding this lack of resolution are the significant and rapid radiations that occurred during caenogastropod history and, in particular, during the latter part of the Mesozoic.

MAIN GROUPS RECOGNIZED WITHIN CAENOGASTROPODS

ARCHITAENIOGLOSSA This exclusively non-marine grouping, which may represent a grade, not a clade, is usually regarded as the sister to all other living caenogastropods. It comprises the terrestrial cyclophoroideans (the major group of operculate land snails) and two freshwater families, previously in Ampullarioidea but now included in separate superfamilies,

Ampullarioidea (Ampullariidae) and Viviparoidae (Viviparidae). While having some shared plesiomorphic characters, including a partially or fully hypoathroid nervous system and subradular organ, the included taxa do not share any obvious synapomorphies. Considerable modification in some features has occurred as a result of the nonmarine habitat of all living architaenioglossans. These include the protoconch, which is typical of many direct-developing caenogastropods; in cyclophorids, modifications due to terrestriality, notably loss of the pallial organs; in ampullariids, development of a separate lung in the mantle cavity as a consequence of their amphibious habits; and, in viviparids, modifications due to filter feeding.

Architaenioglossa was included as part of the Mesogastropoda by Thiele (1929–1931) and Wenz (1938–1944) and included in the caenogastropods by Cox (1960b) and Ponder and Warén (1988) but excluded by Haszprunar (1988, 1993). In Simone's (2004b) analysis the

TABLE 13.2
Some Recent Classifications of Living *Caenogastropoda*

HASZPRUNAR 1985a	PONDER AND WARÉN 1988	HASZPRUNAR 1988 ^a	PONDER AND LINDBERG 1997	BOUCHET AND ROCROI 2005
Caenogastropoda	Caenogastropoda	Archaeogastropoda	Caenogastropoda	Caenogastropoda
Architaenioglossa (including Valvatoidea)	Architaenioglossa	Architaenioglossa	Architaenioglossa	Architaenioglossa (informal)
Neotaenioglossa	Neotaenioglossa	Apogastropoda ^b	Sorbeoconcha (Cerithioidea and Campaniloidea)	Sorbeoconcha (Cerithioidea and Campaniloidea)
Heteroglossa	Discopoda (including Campanilidae)	Caenogastropoda	Hypsogastropoda	Hypsogastropoda
Stenoglossa	Ptenoglossa	Cerithiimorpha	Ptenoglossa	Littorinimorpha
	Heteropoda	Ctenoglossa	Littorinimorpha	Ptenoglossa (informal)
	Neogastropoda	Neotaenioglossa	Neogastropoda	Neogastropoda
		Stenoglossa		
		Campanilimorpha		
		(Campanilidae)		

NOTE: See text for explanation of names.

^aHaszprunar (1988) provided several alternative classifications; the one summarized in the table is based on his figure 5, “the most probable phylogenetic reconstruction.”

^bHaszprunar also included in Apogastropoda Ectobranchia (Valvatidae), Allogastropoda (Architectonicidae, Rissoellidae, Omalogyridae), while the remaining heterobranchs (*sensu* Haszprunar 1985b; Ponder and Warén 1988; Ponder and Lindberg 1997) were included in the “subclass” Euthyneura. Ponder and Lindberg (1997) used Apogastropoda to encompass both Caenogastropoda and Heterobranchia.

architaenioglossan taxa were paraphyletic, forming three branches of basal caenogastropods.

SORBEOCONCHA This term was introduced by Ponder and Lindberg (1997) to include all caenogastropods other than the architaenioglossan clade or grade. Basal members are Cerithioidea and Campaniloidea, the former including numerous freshwater taxa, notably the Thiaridae and several related families (e.g., Lydeard *et al.* 2002). This grouping differs primarily from the architaenioglossan grade in having a primary emphasis on control of the inhalant water flow rather than the exhalant flow (Ponder and Lindberg 1997; Lindberg and Ponder 2001), with corresponding emphasis on the chemosensory role of the osphradium. This is correlated with three synapomorphic osphradial characters (Haszprunar 1985a, 1988; Ponder and Lindberg 1997): an increase in size, the presence of ciliated lateral fields, and Si₄ cells (Haszprunar 1985a). Other synapomorphies identified by Ponder and Lindberg (1997) include an epiathroid nervous system, the formation of a seminal vesicle, a coiled radular sac, and the formation of a polar lobe in early development (Freeman and Lundelius 1992).

HYPGOGASTROPODA This term was introduced by Ponder and Lindberg (1997) to include the great majority of extant caenogastropods (most “mesogastropods” and all neogastropods)—that is, all caenogastropods other than architaenioglossans, Cerithioidea, and Campaniloidea. It equates with the “higher caenogastropods” of Healy (1988a) and is defined by Ponder and Lindberg (1997) by some sperm characters (Healy 1988a); a single statolith in each statocyst, rather than several statoconia; exophallic penis (Simone 2000a); osphradial Si₁ and Si₂ cells (Haszprunar 1985a); and absorptive cells in the larvae (Ruthensteiner and Schaefer 1991). Members are largely marine and include families of medium to large size such as the Littorinidae, Cypraeidae, Calyptraeidae, Tonnidae, Cassidae, Ranellidae, Strombidae, and Naticidae; small-sized families such as the very diverse Rissoidae, Triphoridae, and Eulimidae; and the pelagic heteropods. Freshwater families

include the rissooidean Hydrobiidae and some related families, some of these groups having undergone large radiations. A few terrestrial groups are found in the Littorinoidea (Pomatiidae) and Rissooidea (some Truncatellidae, Pomatiopsidae, and Assimineidae). A major subgroup of Hypogastropoda is the Neogastropoda (= Stenoglossa), members of which are almost exclusively marine and virtually all are carnivorous. It contains well-known, diverse, and ecologically significant families such as Muricidae, Volutidae, Mitridae, Buccinidae, and conoideans (Turridae *sensu lato*, Terebridae and Conidae). Members of this large clade share several apomorphies (Ponder and Lindberg 1997; Strong 2003) related to the digestive system, including unique structures such as a rectal (=anal) gland, tubular accessory salivary glands, and the possession of either a stenoglossan or a toxoglossan radula. Additional significant characters include the salivary gland ducts not passing through the nerve ring, the esophageal gland separated from the esophagus (as the gland of Leiblein or poison gland), and the enlargement of the ventral tensor muscle of the radula (mu of Simone 2003), working to enable the sliding movement of the radula (this muscle does not function in this way in other caenogastropods; Simone 2000a).

OTHER GROUPINGS Neotaenioglossa is a paraphyletic (e.g., Ponder and Lindberg 1997) grouping used by Haszprunar (1988) and Ponder and Warén (1988), but with different concepts. The latter encompassed all the non-architaenioglossan “mesogastropods” (other than those now treated as basal heterobranchs), whereas the former excluded the Campaniloidea, Cerithioidea, and Ptenoglossa.

The higher category names Cerithiimorpha and Littorinimorpha were used by Golikov and Starobogatov (1975), the former being used for the basal group of caenogastropods (from which architaenioglossans were excluded) by Haszprunar (1988). Most recently Bouchet and Rocroi (2005) have used Littorinimorpha to encompass the taenioglossate Hypogastropoda.

Heteropoda comprises only the pelagic Pterotracheoidea (= Carinariidea) and was used as a high-rank taxon until recently. It is included in the Littorinimorpha by Bouchet and Rocroi (2005).

Ptenoglossa (= Ctenoglossa, e.g., Bandel 1993) is a probably polyphyletic grouping (see following paragraphs) of Eulimoidea, Janthinoidea, and Triphoroidea. This assemblage was based on the presence of an acrembolic¹ proboscis and, in some members, a ptenoglossate radula and two pairs of salivary glands. The group, with Eulimoidea excluded, is treated as monophyletic by Nützel (1998) in a study using fossil and Recent taxa. Ponder and Lindberg (1997) argue that the broader concept of Ptenoglossa (including Eulimoidea) is polyphyletic, and this view is supported in molecular analyses (Colgan *et al.* 2000, 2003, 2007).

Suggestions of heterobranch affinities of Epitoniidae have been made by Robertson (1985) and Collin (1997) on the basis of the supposed homology of pigmented mantle organs and shared hydrophobic larval shells, respectively, but other characters and molecular data do not support such a relationship.

Heterogastropoda was erected by Kosuge (1966) to encompass Ptenoglossa and Architectonicoidea,² which he considered to lie between the meso- and neogastropods.

For further discussion of the status and composition of some of these groups, see the later section "Summary of Major Groups."

Present caenogastropod classifications are essentially based on a few key shell and anatomical (including radular) details, although Healy (e.g., 1988a, 1996b; see also below) used sperm ultrastructure to determine the relationships of several groups. Available data suggests that some of the currently recognized higher taxa (orders, suborders) are probably paraphyletic or even polyphyletic, and the

relationships of intermediate groups (superfamilies, families) are unresolved. Only one phylogenetic hypothesis has been previously published for caenogastropods as a whole³ based on morphological data (Strong 2003), but phylogenies of some family group (or higher) taxa within caenogastropods have been proposed, examples being Risssoidea (Ponder 1988; Wilke *et al.* 2001); Cerithioidea (Houbrick 1988; Ponder 1991; Lydeard *et al.* 2002; Simone 2001); Neogastropoda (Taylor and Morris 1988; Kantor 1996); Littorinidae (Reid 1989; Williams *et al.* 2003); Ampullariidae (Berthold 1991; Bieler 1993); Olivioidea (Kantor 1991; Kantor and Pavlinov 1991); Muricidae (Rapaninae) (Kool 1993); toxoglossans (Conoidea) (Taylor *et al.* 1993; Kantor 1996; Rosenberg 1998; Simone 2000b; Kantor and Taylor 2002); "neomesogastropods" (Bandel and Riedel 1994); Tonnoidea (as Cassoidea) (Riedel 1995, 2000); Ptenoglossa (excluding Eulimoidea) (Nützel 1998); Columbellidae (deMaintenon 1999); Nassariidae (Haasl 2000); Calyptraeidea (Simone 2002, 2006; Collin 2003); Muricidae (Oliverio *et al.* 2002); Cypraeidae (Meyer 2003, 2004); Stromboidea (Simone 2005), Cypraeoidea (Simone 2004a); Architaenioglossa (Simone 2004b); and Buccinidae (Hayashi 2005).

THE PALEONTOLOGICAL PERSPECTIVE

Although several higher-level caenogastropod taxa have been proposed in the paleontological literature, there are few attempts to frame explicit hypotheses using cladistic methodology and even fewer involving fossil caenogastropods using maximum-parsimony methods. Frýda (1999) introduced Perunelomorpha, a group with open-coiled protoconchs, initially as a sister taxon to Caenogastropoda, but they were later (Bouchet and Rocroi 2005) incorporated within it. Bandel (1991b, 1993, 2002) proposed higher taxa, some based primarily on the time of their appearance in the fossil record

1. In an acrembolic proboscis, the proboscis retractor muscles are attached to the distal end of the proboscis so that the buccal mass lies behind the retracted proboscis (Fretter and Graham 1962).

2. Now in Heterobranchia.

3. Simone (2000a) presented a phylogeny (see Figure 13.4B), but as of this writing the full details have not yet been published.

and not on explicit phylogenetic hypotheses. These include the Palaeo-Caenogastropoda for those with Paleozoic origins, the Meta-Mesogastropoda for those first appearing in mid Mesozoic times, and the Neo-Mesogastropoda, which appear in the late Mesozoic and are united by an “expanded ontogeny,” but does not include the Neogastropoda. Bandel (1993) also erected the Scaphoconchoidea for taxa with larvae that have their true larval shell surrounded by a pseudoshell—the echinospira and limacosphaera types of larvae. Riedel (2000) proposed two additional high-level taxa: the Latrogastropoda and Vermivora. Latrogastropoda included the Pleurembolica [encompassing Trochelina (Trochelina Bandel and Riedel, 1994 composed of Laubierinioidea and Calyptraeidea) + Vermivora]. Vermivora included Ficoidea, Tonnoidea, and Neogastropoda.

Although comprehensive analyses of fossil caenogastropods are difficult because there are comparatively few shell characters, there are cladistic hypotheses using parsimony methods for a few groups (Roy 1994 for Aporrhaidae; Nützel *et al.* 2000 for Subulitoidea; Wagner 2002 for early Paleozoic gastropods including caenogastropod ancestors). Other phylogenetic studies involving fossil taxa but not using parsimony methods include studies on “higher” caenogastropods (Latrogastropoda: Neomesogastropoda + Neogastropoda) by Bandel and Riedel (1994) and Riedel (2000). According to Riedel (2000), the origin of Latrogastropoda is obscure, but he suggested a relationship with rissooideans and proposed Ficoidea as the sister taxon of neogastropods. Kowalke (1998: figs. 12, 13) presented phylogenetic hypotheses for Cerithimorpha (*sensu* Golikov and Starobogatov 1975 (= Cerithioidea *sensu lato*)) and vermetoideans that are almost exclusively based on larval shell morphology (especially ornament) of a few Cretaceous, Cenozoic, and Recent representatives of these groups. Nützel (1998) investigated ptenoglossans (excluding Eulimoida) and their possible stem groups. Modern Triphoroidea formed a clade with the extinct Protorculidae as the sister group. Janthinoidea and

the fossil Zygopleuridae were the sister groups to that clade. The Paleozoic Pseudozygopleuridae were identified as the extinct stem group to Triphoroidea + Janthinoidea, while the Paleozoic precursors of the Cerithioidea were shown to be the possible sister group to the combined grouping. Although the monophyly of Recent ptenoglossans is widely seen as unlikely (see subsequent discussion), the long separation of the triphorid/cerithiopsid line from that of the Janthinoidea, as suggested by the fossil record, could explain the marked disparity of their living representatives. Nützel *et al.* (2000) analyzed the Late Paleozoic Subulitoidea, and although several genera could be arranged in family level groups (Soleniscidae, Meekospiridae, Imoglobidae), monophyly of the ingroup could not be established with various outgroups, suggesting probable nonmonophyly of the traditional Subulitoidea. Polyphyly has also been hypothesized for the Early Paleozoic Subulitoidea (Wagner 2001, 2002).

MORPHOLOGICAL DATA

Traditional taxonomic work on caenogastropods has mainly focused on shell and radular characters, and this is one of the reasons there is a paucity of anatomical information for many groups.

SHELL/PROTOCONCH

The shell (Figures 13.1, 13.2, 13.6, 13.13) is typically coiled, very elongate to flattened, loosely coiled to uncoiled, as in Vermetidae (Figure 13.1Cc) and Caecidae (Figure 13.1H), or openly coiled, as in Siliquariidae (Figure 13.1D) and a few members of other families (e.g., Cyclophoridae, Epitoniidae, Hydrobiidae *sensu lato*; Rex and Boss 1976). Others have secondarily become limpet-like (Capulidae, Figure 13.1Q; Calyptraeidae, Figure 13.1X; and Hipponicidae), while a few families produce one or two limpet-like taxa (e.g., *Thyca* in Eulimidae; *Concholepas* in Muricidae; *Quoyula* in Coralliophilidae). Remarkably, only two small groups of caenogastropods have lost their postlarval shell: a few endoparasitic, worm-like Eulimidae and the pelagic Pterotracheidae.

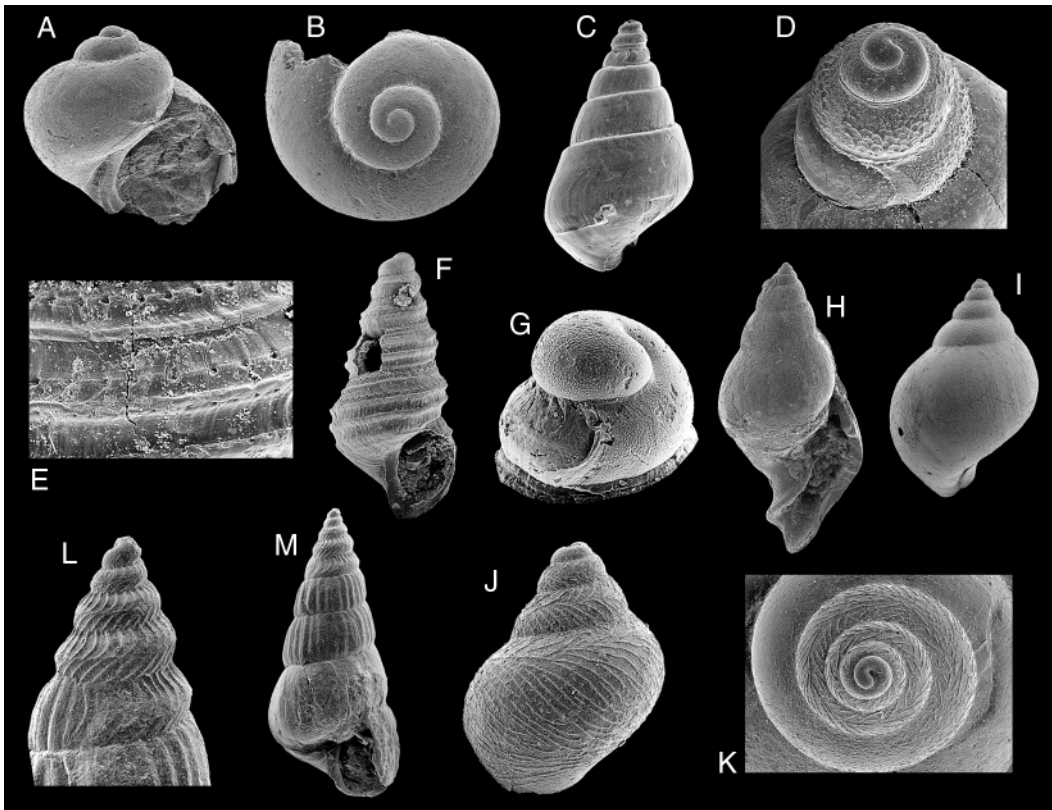


FIGURE 13.6. Selected Paleozoic (Carboniferous/Permian) caenogastropods and putative outgroup taxa. (A, B) Protoconch of a naticopsid (Neritimorpha) from the Mississippian (Lower Carboniferous, ca. 330 Mya; Ruddle Shale, Arkansas, United States). Protoconchs of Recent neritimorphs are highly convolute with resorbed inner whorls; however, protoconchs of Naticopsidae show no major differences from those of caenogastropods, except for a relatively high whorl expansion rate. Width 0.8 mm (from Nützel and Mapes 2001). (C, D) Cerithimorph caenogastropod from the Upper Carboniferous (Late Moscovian, c. 305 Mya; Buckhorn Asphalt deposit, Oklahoma, United States); this small heliciform, planktotrophic larval shell resembles the protoconch of some modern cerithioids. C, height 2.0 mm; D, height 0.4 mm. (E–G) *Stegocoelia* (Goniasmatidae, Palaeostyloidea), a slit-bearing caenogastropod from the Upper Carboniferous (Late Moscovian, c. 305 Mya; Buckhorn Asphalt deposit, Oklahoma, United States), representative of a rich late Paleozoic group of *Murchisonia*-resembling caenogastropods; E, teleoconch detail showing slitlike structure (selenizone) slightly above mid-whorl; width 0.5 mm; F, height 2.0 mm; G, protoconch in side view, a lecithotrophic larval shell with a distinct sinusigera. Protoconchs of planktotrophic species of this group resemble Figure 13.6D; height 0.36 mm (from Bandel *et al.* 2002). (H) *Soleniscus*, a widespread subulitoid (Soleniscidae) from the Upper Carboniferous (Gzhelian, c. 300 Mya; Finis Shale, Texas, United States), showing a distinct, twisted siphonal canal, a columellar fold, and a smooth larval shell; height 3.2 mm (from Nützel *et al.* 2000). (I–K) *Imogloba* (Imoglobidae) from the Mississippian (Lower Carboniferous, c. 330 Mya of Arkansas, United States); these globular, subulitoid gastropods have an open coiled initial whorl followed by early whorls (probably larval shell) with a very characteristic ornament of noncollabral threads; I, height 2.5 mm; J, probably isolated larval shell, height 0.85 mm; K, width 4.4 mm. (L, M) *Pseudozygopleura* (Pseudozygopleuridae) from the Late Carboniferous (ca. 300 Mya, Gzhelian, Ames Shale, West Virginia, United States); pseudozygopleurids were abundant and diverse for about 100 million years (during the late Paleozoic) and became extinct at the end-Permian mass extinction event; they have highly characteristic larval shells with an ornament of curving, collabral ribs that form a spiral thread (from Nützel 1998); L, larval shell; height 0.86 mm; M, height 3.0 mm.

The sluglike Velutinidae (= Lamellariidae) (Fig. 13.2N) have a reduced internal shell. Most caenogastropods have dextral shells, with members of only one family (Triphoridae) being almost entirely sinistral, although sinistral taxa

occur sporadically in some families (Robertson 1993).

Preliminary phylogenetic analyses (Nützel, unpublished) suggest that high-spired shells could be diagnostic for some Paleozoic and early

Mesozoic clades. Although there are many cases of convergent teleoconch morphology with representatives of each of the other major gastropod clades (vetigastropods, neritimorphs, heterobranchs), the protoconch morphology and shell microstructure can be used to determine the group. Specialists are usually able to recognize members of a particular group reliably by the teleoconch morphology alone, suggesting that this is often diagnostic, although differences can be subtle and difficult to quantify, resulting in a low number of scorable characters. It is also frequently difficult to establish homology and consistent coding of shell characters because many are not sufficiently complex to reject convergence convincingly. Nevertheless, Wagner (2002) comprehensively coded teleoconch characters of Early Paleozoic gastropods, and Schander and Sundberg (2001) have shown that shell characters can provide a similar level of resolution to other data sets in some analyses.

Growth lines and the shape of the outer lip can reflect the organization of the mantle cavity (especially inhalant and exhalant flows) and the orientation of the shell. For paleontologists, these not only provide clues about the way the organism functioned but can have phylogenetic significance. Many modern caenogastropods have straight or slightly opisthocline growth lines, with inhalant and exhalant flows restricted to the anterior and posterior corners of the aperture, which are often modified with siphonal notches or canals. This configuration is seen in the Late Paleozoic *Pseudozygopleuridae* and *Subulitoidea*, but many other fossil caenogastropods have strongly parasigmoidal (loxone-matoid) growth lines or possess slits, sinuses, and selenizones. A slit occurs in Late Paleozoic probable caenogastropods⁴ of the family *Goni-asmatidae* (Nützel and Bandel 2000; Bandel *et al.* 2002; Nützel and Pan 2005). Although it has been suggested that the slit or deep sinus in this group may indicate the presence of a pair

of ctenidia (Cox 1960b: 143), slits (e.g., *Siliquariidae*) or deep notches (e.g., some *Turritellidae*) are known in a few modern caenogastropods with a single monopectinate gill.

When shell growth ceases and the lips of the aperture thicken, they are sometimes modified in shape or have special ornament. This determinate growth is found in many caenogastropods but is typically clade specific (Vermeij and Signor 1992). Apertural thickening may also occur intermittently during growth, and the thickened part of the outer lip may be retained as a distinct varix.

The shell microstructure of caenogastropods is aragonitic crossed-lamellar, and although comprehensive comparative studies are lacking, there are some indications of significant variation (e.g., Falniowski 1989), although these differences can sometimes be correlated with environment (e.g., Taylor and Reid 1990). Nacre is absent in all *Caenogastropoda*, and calcite is rare (e.g., *Epitoniidae*) (see Bandel 1990 for a review of caenogastropod shell microstructure).

Protoconchs, as extensively shown by the work of Bandel (1982 and subsequently), are a rich source of characters and reflect life history. The following parameters have proved useful for defining at least species and sometimes genera: size and ornament of embryonic shell; size and shape of entire protoconch; number of larval whorls; transition from protoconch to teleoconch (abrupt, presence or absence of sinusigera, fluent) and whorl shape. Protoconch morphology can be very useful for taxonomy at generic and species levels (e.g., *Triphoridae*, Marshall 1983), but they are also assumed to be diagnostic for caenogastropods because larvae of modern representatives of basal clades (vetigastropods, patellogastropods) are never planktotrophic. Heterobranchia have sinistral protoconchs, and modern neritimorphs have highly characteristic convolute larval shells (e.g., Bandel 1982). Thus, multi-whorled, orthostrophic larval shells characteristic of planktotrophic larvae are present only in *Caenogastropoda*. As indicated previously, the situation appears to

4. They have crossed-lamellar shell structure, have multiwhorled planktotrophic larval shells, and are high spired.

be more complicated in the Paleozoic because presumed early neritimorphs (Naticopsidae and Trachyspiridae) can have planktotrophic larval shells (Figure 13.6A, B) that show no signs of resorbed inner whorls (Nützel and Mapes 2001; Nützel *et al.* 2007) and thus are not fundamentally different from those of caenogastropods. Moreover, some Paleozoic gastropods with typical pleurotomarioid teleoconch morphology (and thus assumed to be vetigastropods) have simple, smooth larval shells of about two whorls (Nützel and Mapes 2001; Kaim 2004).

In caenogastropods, it is especially easy to infer larval feeding strategies (i.e., planktotrophic vs. non-planktotrophic) from the larval shell with well-preserved material (e.g., Bandel 1982). Jablonski (1986) tested possible selectivity of larval strategies at the end-Cretaceous extinction event, and Nützel (1998) separated larval strategies of Late Paleozoic and Triassic zygopleuroid gastropods based on protoconch measurements.

Although the phylogenetic utility of shell characters is considerably increased with protoconch data, the latter have greater value if coded from species with the same or a similar ontogenetic strategy (e.g., only from planktotrophic species). Often the protoconch shows less evolutionary change than the teleoconch (e.g., in the families Pseudozygopleuridae, Epitoniidae, and Cerithiidae) and, in such cases, can provide apomorphies for families or even higher taxa. However, there are other cases in which protoconch morphology is highly variable within families, especially in groups with diverse life history traits. Also, protoconchs, like any other character complex, are subject to convergence and other homoplastic phenomena.

HEAD-FOOT, OPERCULUM, AND MANTLE EDGE

Head-foot characters (Figure 13.2) have not been greatly used in morphological analyses to date. The foot is plesiomorphically elongate-oval but has been extensively modified in many groups. Lateral expansion of the foot has occurred in several groups (e.g., many neogastropods, tonnoideans) or it has become disk-like for clamping in

limpet-like taxa. The foot is laterally compressed in stromboideans and xenophorids, where it can be used as a lever or for leaping, and in the actively swimming heteropods.

In some, lateral flaps emerge from the sides of the neck or foot (e.g., Viviparidae, Vanikoridae), while in others the shell can be covered by lateral or anterior extensions of the foot and/or mantle in Naticidae (Figure 13.2Q), Triviidae, Olividae (Figure 13.2V, Aa), some Volutidae, Marginellidae (Figure 13.2W), and Cypraeoidea (Cypraeidae, Figure 13.2T; Ovulidae), with the shell becoming internal and reduced in Velutiniidae (Figure 13.2N).

Some amphibious or terrestrial rissoidae taxa (e.g., Assimineidae, Pomatiopsidae) have a deep omniphoric groove running down each side of the neck, which carries mucus and waste to the sides of the foot. A few taxa possess tentacles that emerge from the sides of the foot (e.g., some Cerithiidae [Bittinae] and Litiopidae) or posteriorly (e.g., the neogastropod Nassariidae, Figure 13.2Y, and some rissoidae: Stenothyridae, some Rissoidae, and Vitrinellidae, Figure 13.2G). Tentacles emerge laterally from the opercular lobe in some Eatoniellidae (Ponder 1965). The foot is very reduced and lacks a sole in vermetids.

The cephalic tentacles are typically long and narrow, with the eyes on swellings at their outer bases (Figure 13.2A–H, L–P), although there is considerable variation in the length of the tentacles, and they are lost in some Assimineidae (Figure 13.2I). The tentacles, especially of small-sized taxa, can have complex patterns of ciliation, with some developing long compound cilia distally. Although the eyes may be on short stalks or situated along the tentacle (Figure 13.2K, Bb), they are always located on the outer side of the tentacles (plesiomorphic in gastropods), in contrast to most basal Heterobranchia. A cephalic penis arises from the right to center of the head behind the base of the tentacles in many hypogastropods, where it appears to have been derived independently in several groups. In contrast, cerithioideans, cingulopsoideans, vermetoideans, triphoroideans, and janthinoideans

lack a penis, and penial structures are differently derived in the three architaenioglossan clades: two from noncephalic structures (Viviparoidea from right tentacle, Ampullarioidea from mantle) and one cephalic (Cyclophoroidea).

An operculum is usually present but is lost in the adults of a few groups (e.g., Cypraeidae, Triviidae, Ovulidae, Velutiniidae, Carinariidae, Pterotracheidae, Calyptraeidea *sensu stricto*, Mitridae, Marginellidae, and many Volutidae). Checa and Jiménez-Jiménez (1998) distinguished three main types of operculum: (i) flexiclaudent spiral (mostly multispiral) operculum, the shape of which does not fit the aperture, (ii) rigiclaudent spiral, fitting the aperture and usually paucispiral, and (iii) rigiclaudent concentric, also fitting the aperture. Their study showed that the rigiclaudent spiral type predominates in caenogastropods, with flexiclaudent spiral opercula found in some cerithioideans. Concentric opercula are predominant in higher caenogastropods.

A well-developed, narrow snout, typical of basal caenogastropods, is sometimes very extensible (e.g., some rissooideans, stromboideans, and cerithioideans) and is used to assist in locomotion in some Truncatellidae and Pomatiopsidae. The snout has become infolded to form a proboscis (introvert) convergently in several groups (e.g., Ptenoglossa, Neogastropoda, Tonnoidea), and in many such taxa the proboscis is capable of considerable extension (e.g., Figure 13.2M, X). Unique structures can be associated with the snout/proboscis; a pseudoproboscis is formed in the Capuloidea (e.g., Pernet and Kohn 1998) and an epiproboscis in the Mitridae (Ponder 1972; West 1990). Two main types of proboscis are usually recognized in caenogastropods: the acrembolic and pleurembolic (Fretter and Graham 1962), which differ in the way in which they lie in the body in their retracted state. In the acrembolic type of proboscis, the tip of the proboscis is fully inverted by retractor muscles that attach mostly to the anterior buccal region. With the pleurembolic type, the retractor muscles are inserted on the sides of the proboscis, so that the anterior part is not

inverted on retraction. The acrembolic type has appeared independently several times in gastropods, including some heterobranchs, while the pleurembolic proboscis may have appeared only once. This latter type is a synapomorphy of the node that precedes the calyptraeideans in Simone's (2000a) cladogram (Figure 13.4B) and includes all the higher hypsogastropods, while in Strong's (2003) analysis (Figure 13.4A) the proboscitate taxa also form a separate clade, although it comprises both pleurembolic and acrembolic taxa.

The mantle edge can have one or more short to moderately long papillae or one or two ciliated anterior or posterior tentacles, rarely very long, as in *Finella* (Figure 13.2B). The anterior mantle edge is extended as a siphon in many caenogastropods, although this may have arisen independently in Cerithioidea, Stromboidea, and the higher Hypsogastropoda (Simone 2005) and probably also Triphoroidea. A siphonal notch or canal in the shell is found in many cerithioideans and stromboideans, but they do not have any clear modification of the mantle edge (Simone 2001, 2005). On the other hand, a clearly defined siphon at the mantle border (i.e., a long fold in the inhalant canal separated from the mantle edge) occurs in most higher hypsogastropods and is elongated, mobile, and exploratory in many (Figures 2U–Bb). The specialized inhalant siphon is a synapomorphy of the node that precedes the calyptraeideans in Simone's (2000a) cladogram (Figure 13.4B), with a reversal in the naticoideans, while in Strong's (2003) analysis (Figure 13.4A) the siphonate hypsogastropods are found in two separate clades.

RADULA

The radula has been used as an important character set at both the species level and higher levels within caenogastropods, representing the basis of such names as Stenoglossa, Ptenoglossa, and Taenioglossa. By far the most significant historical review is the work of Troschel and Thiele (1856–1893), synthesized and added to by Thiele (1929–1931). These early workers relied on light microscopy, but the advent

of scanning electron microscopy provided an excellent tool for more detailed examination and illustration of radulae. Most subsequent studies have focused on lower-rank taxa; a notable exception being Bandel's (1984) study of the radulae of Caribbean caenogastropods.

The taenioglossate condition, with seven teeth in each row (two marginals and a lateral on each side and a central tooth) is found in all architaenioglossans and many sorbeoconch caenogastropods. Remarkably, this type of radula is retained by the majority of the group with very little modification to reflect the enormous diversity of feeding strategies (see subsequent section on Adaptive Radiation). Exceptions are the neogastropods and some of the ptenoglossate groups. Within neogastropods the toxoglossan type (5–1 teeth per row) is found in the Conoidea, with the most extreme modification being the toxoglossan “harpoon” tooth (Shimek and Kohn 1981; Kantor 1990). An unusual, very elongate tooth type (nematoglossan) is found in Cancelarioidea, while the remaining neogastropods have a rachiglossan (3–1 teeth per row) radula.

The typical ptenoglossate radula occurs in Epitoniidae and Janthinidae, exhibiting numerous similar simple teeth in each radular row. Multiple similar teeth are also known from a few eulimids (Warén 1984), and tooth multiplication is seen in some cerithiopsids (Marshall 1978) and triphorids (Marshall 1983), although some other triphoroideans have taenioglossate radulae. The spongivorous triphorids possess a modified radula with 5–63 teeth per row (the rhinioglossate condition). Although cerithiopsids are also spongivorous, they usually retain a taenioglossate radula but the tooth morphology is extremely variable, with some genera having very elongated teeth (Marshall 1978; Nützel 1998).

The radula has been lost in some conoidean taxa (e.g., Ponder 1974; Kantor and Sysoev 1989), some other neogastropods (Ponder 1974), and many eulimids (Warén 1984).

ANATOMY

Major synoptic anatomical studies on caenogastropods were undertaken in the late nineteenth

century, including those on the nervous system (Bouvier 1887), kidney (Perrier 1889), pallial cavity (Bernard 1890) and anterior gut (Amaudrut 1898). Many anatomical accounts have been published since. Notably, these include a large body of work by Fretter and Graham and their students on mainly European taxa (summarized in Fretter and Graham 1962, 1994) while the Marcuses provided detailed accounts of mainly Brazilian taxa (e.g., Marcus 1956; Marcus and Marcus 1963, 1965). Many aspects of caenogastropod anatomy and histology were reviewed by Fretter and Graham (1962, 1994), Hyman (1967), and Voltzow (1994). Reviews of the evolution of organ systems for gastropods in general, including the gut (Salvini-Plawen 1988), kidney (Andrews 1988), and mantle cavity (Lindberg and Ponder 2001) are also relevant.

Recent morphological studies include Strong's and Simone's detailed investigations. Strong's (2003) study, based on the examination of 16 caenogastropods (Figure 13.4A), resulted in the reformulation of homologies for several key characters (jaw, subradular organ, buccal pouches) and the identification of characters new to caenogastropod systematics, including those of the kidney (blood circulation patterns), nervous system (tentacular nerve, siphonal ganglion), foregut (esophageal ventral folding) and stomach (= midgut; details of the gastric shield and style sac ciliary tracts). As an illustration of how reinterpretations of some of these structures change our ideas of homology, we detail the following examples from the anterior gut. Based on criteria of position (Figure 13.5A–C) and histological detail (Figure 13.7D–F), Strong (2003) proposed that the glandular structures below the radula in many sorbeoconchan taxa are homologous to the subradular organ (Figure 13.7A–F, sro) of architaenioglossans. Also, in contrast to long-held views (Graham 1939; Salvini-Plawen and Haszprunar 1987; Haszprunar 1988; Ponder and Lindberg 1997), the buccal cavity and anterior esophagus of some basal caenogastropods were shown to possess the ventral folding characteristic of vetigastropods (Figure 13.7G–I), including a mid-ventral fold (Figure 13.7G–I, vf)

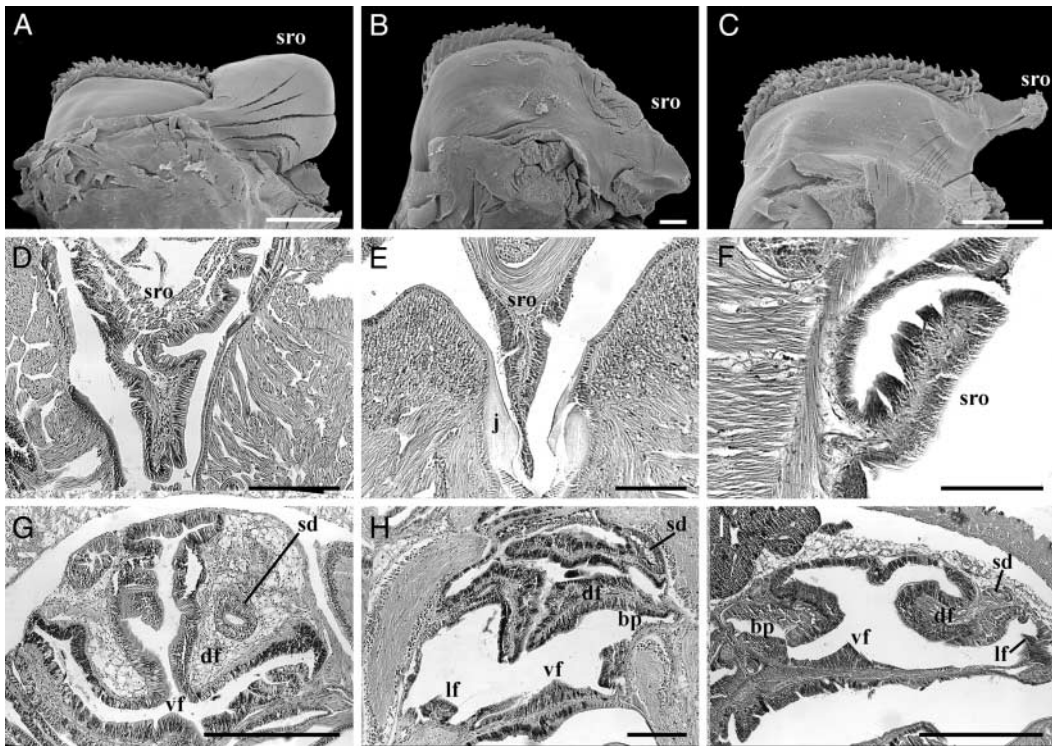


FIGURE 13.7. Foregut characters. (A–C) Scanning electron micrographs of subradular organ. Right lateral view of radular apparatus, ventral is to the right. (D–F) Histology of subradular organ. Transverse section through subradular organ, ventral is below. (G–I) Histology of foregut showing ventral folding. Transverse section through anterior esophagus, ventral is below. A. *Neocyclotus dysoni*. Scale bar, 0.5 mm. B. *Lampanella minima*. Scale bar, 100 µm. C. *Littorina littorea*. Scale bar, 0.5 mm. D. *Neocyclotus dysoni*. Scale bar, 0.25 mm. E. *Lampanella minima*. Scale bar, 1 mm. F. *Littorina littorea*. Scale bar, 1 mm. G. *Neocyclotus dysoni*. Scale bar, 0.5 mm. H. *Lampanella minima*. Scale bar, 1 mm. I. *Littorina littorea*. Scale bar, 0.5 mm. Abbreviations: bp, buccal pouch; df, dorsal fold; j, jaw; lf, ventro-lateral fold; sd, salivary gland duct; sro, subradular organ; vf, mid-ventral fold. Reproduced from Strong (2003).

and two ventro-lateral folds (Figure 13.7H, I, lf). The ventro-lateral folds, commonly associated with the inner margins of the buccal pouches, are retained in many caenogastropods, even in those lacking buccal pouches. In contrast to vetigastropods, the mid-ventral fold is not associated with an underlying gland.

Strong's (2003) analysis also included detailed stomach morphology that built on earlier functional studies, particularly that of Graham (1949). She identified several stomach characters found in a broad spectrum of taxa, regardless of feeding mode, which demonstrated an underlying phylogenetic, rather than functional, signal. This was also shown by Kantor (2003) in buccinoidean neogastropods, and it is likely that this set of characters can be

extended given the diversity of neogastropod stomach morphology (e.g., Smith 1967). Some important caenogastropod stomach characters are shown in Figure 13.8. They include a ventral gastric shield (gs) and a ciliary tract along the major (and sometimes minor) typhlosome of the style sac (ct). Complex typhlosolar folding and the presence of a discrete ciliary rejection current in the proximal stomach are plesiomorphic for caenogastropods (Strong 2003). The simplification of these and other features, such as development of the sorting area (sa) and complexity of the style sac (ss), are not necessarily related to the innovation of carnivory. The two architaenioglossans included in Strong's (2003) analysis were characterized by the presence of mucus-secreting glandular pouches (gap), a

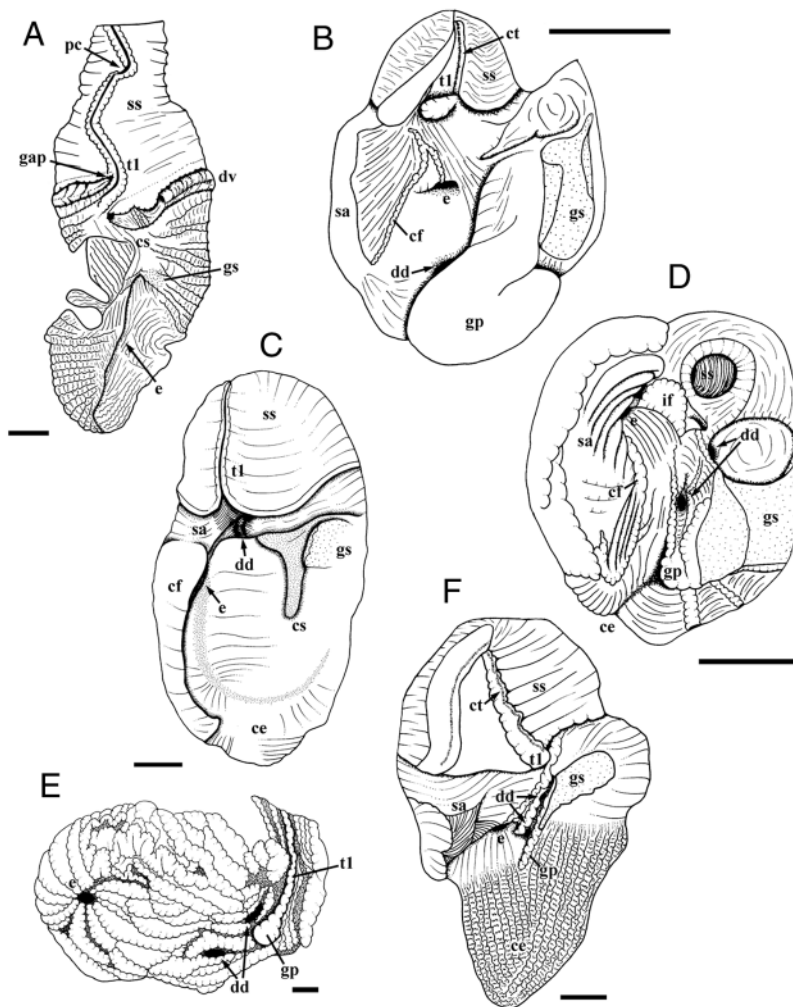


FIGURE 13.8. Stomach characters. (A) *Neocyclotus dysoni* (macrophagous grazer). (B) *Lampanella minima* (microphagous grazer). (C) *Littorina littorea* (microphagous grazer). (D) *Strombus mutabilis* (microphagous grazer). (E) *Conus jaspideus* (carnivorous predator). Scale bar, 100 μ m. (F) *Ilyanassa obsoleta* (opportunistic scavenger). Scale bar, 100 μ m except E, 1 mm. Abbreviations: ce, cecal extension; cf, ciliated fold; cs, ciliated strip; ct, ciliary tract; dd, duct of digestive gland; dv, digestive diverticulum; e, esophagus; gap, gastric pouch; gp, glandular pad; gs, gastric shield; if, intestinal flap; pc, pyloric cecum; sa, sorting area; ss, style sac; tl, major typhlosole. Reproduced from Strong (2003).

digestive gland vestibule bearing the apertures of the digestive gland ducts (dv) and pyloric caecae at the distal end of the style sac (pc). The latter were also found to be present in cypraeids, where they are probably convergent, as are various cecal extensions (ce), which originate from different portions of the stomach.

Simone has studied the anatomy of over 250 species in most extant families and carried out cladistic analyses at the level of superfamily or groups

of closely related superfamilies (1999, 2000b, 2001, 2002, 2004a, b, 2005, 2006). These and ongoing studies of some superfamilies, including representatives for most caenogastropod families, have generated much new comparative anatomical data. The overall intention of this work was to obtain a better definition of each superfamily and their relationships. Some details resulting from his unpublished analyses are outlined later in the Summary of Major Groups section.

Simone's work has paid particular attention to the odontophore and buccal muscles, clarifying their homology and standardizing their terminology. These muscles are reduced in number in comparison with those of vetigastropods and neritimorphs, in part related to the possession of a single pair of odontophoral cartilages. Additionally, the muscles between the odontophoral cartilages and the radula stretch over the odontophoral cartilages (Figure 13.9). The main muscles of the caenogastropod odontophore (Figure 13.10) are the pair of lateral-dorsal tensor muscles of the radula (called "m4" in Simone's papers). These large muscles are located mostly between the cartilages and subradular membrane, an arrangement that prevents the two structures from sliding across each other, except in neogastropods, in which sliding movements between the radula and cartilages occur. In that group, the pair of ventral tensor muscles of the radula, that is responsible for the sliding movement, appears to be derived from median fibers of the m4 muscles, not the ventral tensor muscles as in neritimorphs and vetigastropods.

Ontogenetic data for some apomorphic structures in the anterior gut have proved useful in testing putative homologies. Such studies include the development of the anterior gut (e.g., Page and Pedersen 1998; Page 2000, 2002, 2005), the neogastropod accessory salivary glands (Ball *et al.* 1997b), and the proboscis (Ball *et al.* 1997a; Ball 2002). Similarly, recent detailed studies of the anatomy, histology, and ultrastructure of gut structures, such as those by E. Andrews (e.g., anal gland, Andrews 1992; digestive gland, Andrews 2000; salivary glands, Andrews 1991; Andrews *et al.* 1999) have provided data to test phylogenetic relationships.

ULTRASTRUCTURAL DATA

Ultrastructural information on sperm and sensory organs has contributed significantly to our current understanding of gastropod phylogeny, but other tissues may prove equally useful in the future if investigated in comparable detail. The ultrastructural findings of Haszprunar (1985a)

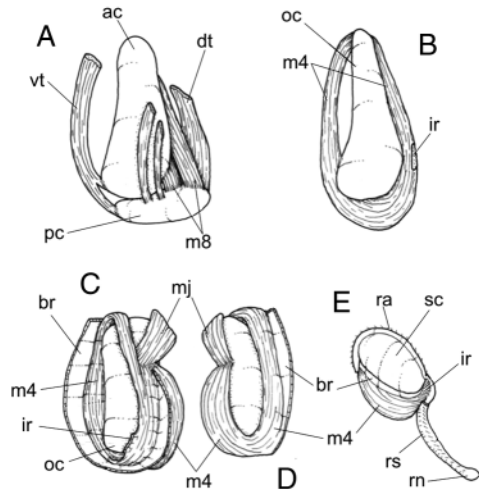
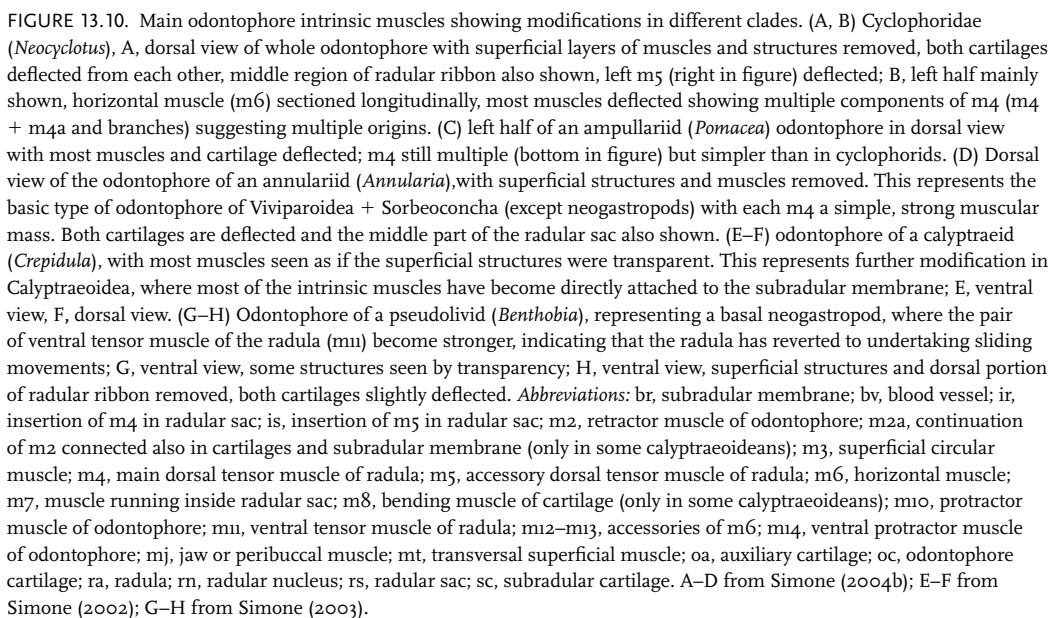


FIGURE 13.9. Modification of the main tensor muscle of the radula (m4) as an example of odontophoral muscle modifications in caenogastropods. Most other muscles and structures are not shown. (A) Typical vetigastropod (e.g., *Haliotis* [Haliotidae], *Calliostoma* [Trochidae]) with two pairs of cartilages and several pairs of muscles; showing left side of odontophore (internal view), with most structures except cartilages and adjacent muscles removed. (B–E) Typical basal caenogastropod (e.g., *Cerithium* [Cerithiidae]; B, corresponding view to A, with a single muscle (m4) present. C, ventral view, right half (left in figure) removed, some adjacent structures also shown; connection between subradular membrane (br) and tensor muscle (m4) suggesting its function as a tensor. D, dorsal view; E, schematic representation of position of left m4 in odontophore, most other muscles not shown. Not to scale. *Abbreviations:* ac, anterior cartilage; br, subradular membrane; dt, dorsal tensor muscle of radula; ir, insertion of m4 in radular sac; m4, main tensor muscle of radula; m8, approximator muscle of cartilages; mj, peribuccal muscles; oc, odontophore cartilage; pc, posterior cartilage; ra, radula; rn, radular nucleus; rs, radular sac; sc, subradular cartilage; vt, ventral tensor muscle of radula. Illustrations from Simone (2000a).

on the osphradium have been valuable in gastropod phylogenetic studies but do not provide resolution within Sorbeoconcha. Scanning electron micrographic (SEM) studies of osphradial surface morphology (Taylor and Miller 1989) showed many features with potential phylogenetic utility (e.g., leaflet structure, ciliary patterns/type) in the families they examined, but most of these results have not yet been sufficiently developed or scored in enough taxa to be incorporated in analyses.

Spermatozoa of caenogastropods are structurally complex, are usually strongly dimorphic



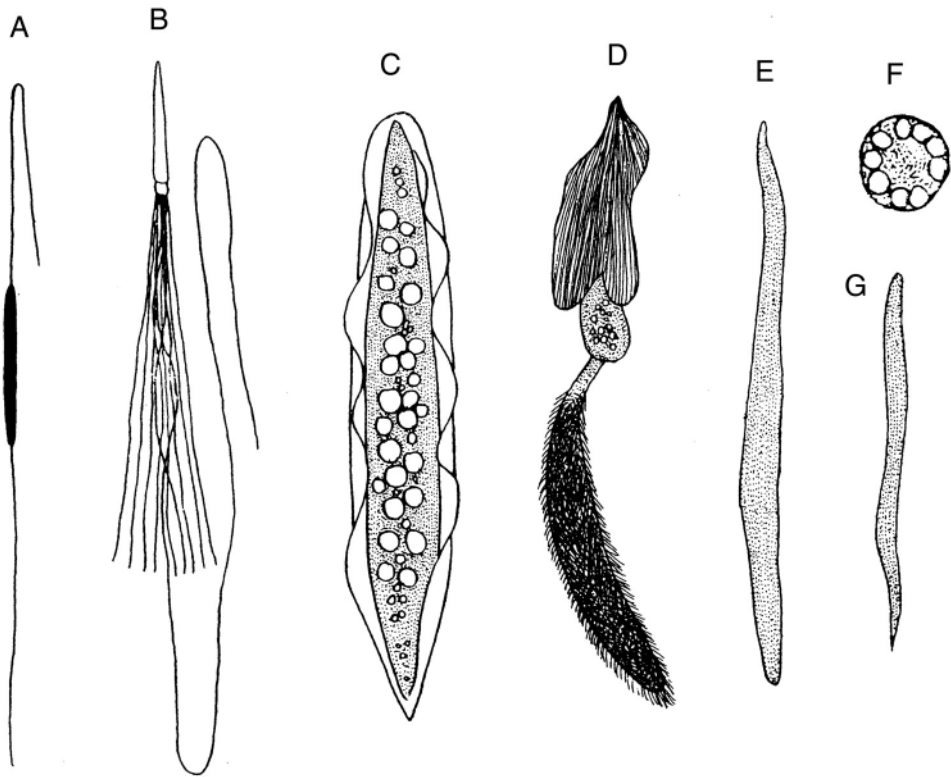


FIGURE 13.11. Types of gastropod paraspermatozoa: (A) with anterior and posterior tail (Neritidae, Neritimorpha); (B) with head and posterior tail tuft (e.g., Cerithiidae, Cerithioidea); (C) with undulating lateral wings (Strombidae, Stromboidea); (D) with numerous attached eusperm (e.g., Epitoniidae, Janthinoidea); (E) vermiform (Cypraeidae, Cypraeoidea); (F) round (*Drupa*, Muricidae, Muricoidea); (G) vermiform (Terebridae, Conoidea). Source of figures: Nishiwaki (1964).

(for reviews see Healy 1988a, 1996a; Buckland-Nicks 1998), and have provided many important characters. For this reason, a detailed summary follows.

Much of the work on sperm morphology has been directed towards the phenomenon of sperm dimorphism (sometimes polymorphism) seen in many caenogastropods⁵ (for reviews or comparative accounts see Melone *et al.* 1980; Healy and Jamieson 1981; Giusti and Selmi 1982; Healy 1988a; Hodgson 1997; Buckland-Nicks 1998; Bulnheim 2000). In such instances, fertile sperm (euspermatozoa) are accompanied by co-occurring nonfertile sperm (paraspermatozoa),

the latter type often showing distinctive shapes that are taxon specific even at the light-microscopic level (see Figure 13.11; Nishiwaki 1964; Tochimoto 1967). For example, the parasperm in Strombidae (Figure 13.11C) have lateral, undulating “wings,” and the ptenoglossan families (except Eulimidae) (Figure 13.11D) have large paraspermatozoa bearing hundreds of attached euspermatozoa—an association known as a “spermatozeugma.” Paraspermatozoa are apparently absent in some taxa (e.g., Eulimoidea, Naticoidea, Risssooidea) (Kohnert and Storch 1984; Koike 1985; Healy 1988a, 1996a).

Transmission electron microscopy (TEM) has revealed taxa-specific features within euspermatozoa that are not visible at the light-microscopic level or with SEM, namely, internal details of the acrosome, nucleus, midpiece, and

5. Paraspermatozoa are also known in Neritimorpha and some Vetigastropoda (see Nishiwaki 1964; Healy 1988a, 1990e).

glycogen deposits (Figure 13.12).⁶ Although not all groups of caenogastropods show wide divergences in eusperm or parasperm ultrastructure (e.g., some families of Neogastropoda), the internal structure of the eusperm midpiece in particular can be very informative, with caenogastropod higher taxa differing in the number of periaxonemal mitochondria, their arrangement relative to the axoneme, and the structure of the mitochondrial cristae (plates) or their derivatives (Figure 13.12H–L; contrast with Figure 13.12D, F showing midpiece of gastropod aquasperm of a vetigastropod). Thus, for example, Campaniloidea are characterized by seven to eight straight mitochondria with unmodified cristae, partly enclosed by a sheath of dense (probably non-mitochondrial), segmented structures (Figure 13.12L); Cerithioidea have four straight mitochondria with complex, parallel cristae and lack any segmented sheath (see Figure 13.12K); and Cyclophoroidea are intermediate between these two, though, like the Cerithioidea, lack the campaniloidean dense sheath (Figure 13.12I). Families such as Campanilidae, Cerithiopsidae, Provannidae, and Vermetidae have been excluded from Cerithioidea largely based on the results of comparative eusperm ultrastructure (Healy 1983a, 1988b, 1990a, b; for discussion and literature see Healy 1996a, 2000). Some families whose affinities were uncertain, even after anatomical study, could be placed within the systematic framework of the Caenogastropoda on examination of their sperm. For example, *Plesiotrochus*, long considered a cerithiid and later separated as a distinct cerithioidean family (Plesiotrochidae, Houbrick 1990), was shown to have *Campanile*-like eusperm and parasperm (Healy 1993a; see Figure 13.12L). Moreover, *Plesiotrochus* and *Campanile* share a simple larval shell morphology (Kiel *et al.* 2000), which is also present in other Recent and fossil basal caenogastropods (Nützel and Pan 2005).

6. For broad, comparative studies see Giusti 1971; Healy 1983a, 1988a, 1996a; Kohnert and Storch 1984; Koike 1985 and literature therein.

While a few vetigastropods (e.g., Healy 1990e) have parasperm, heterobranch euspermatozoa are not accompanied by paraspermatozoa. Heterobranch eusperm are characterized by, among other things, a rounded acrosomal vesicle and a very complex, continuous mitochondrial sheath (Figure 13.12C, E, M, N) (often with paracrystalline layers and an enclosed glycogen helix) (e.g., Thompson 1973; Anderson and Personne 1976; Healy 1983b, 1988a, 1990d, 1993b, 1996a; Healy and Willan 1984, 1991; Giusti *et al.* 1991; Hodgson and Healy 1998; Wilson and Healy 2002; Fahey and Healy 2003).

DEVELOPMENTAL DATA

While there is a great deal of data on caenogastropod larval and intracapsular development (e.g., Thorson 1946; Fretter and Graham 1962, 1994; Fioroni 1966, 1982; Bandel 1975), good data is lacking for some groups.

Detailed studies on early cleavage and embryology have been undertaken on relatively few taxa, these including two viviparids (Johansson 1951; Tanaka *et al.* 1987), an ampullariid (Demian and Yousif 1973a), a turritellid (Kennedy and Keegan 1992), a strombid (D'Asaro 1965), a calyptraeid (Conklin 1897), a naticid (Bondar and Page 2003), a bursid and personid (D'Asaro 1969), two muricids (D'Asaro 1966; Stockmann-Bosbach 1988), two nassariids (Tomlinson 1987), a melongenid (Conklin 1907), and a columbellid (Bondar and Page 2003).

Different modes and timings of D quadrant formation during early embryo development are characteristic of different gastropod clades (Freeman and Lundelius 1992; van den Biggelaar, 1996; van den Biggelaar and Haszprunar 1996; Guralnick and Lindberg 2001; Lindberg and Guralnick 2003). These include the presence of either unequal cell cleavage or polar lobes and the cell stage (i.e., number of cells) at which the 4d cell forms and timing of the formation of the 2a–2d and 3a–3d lineages. Although known only from a relatively small number of taxa, these characters show that caenogastropods have a unique cleavage pattern, with the first cleavages associated with

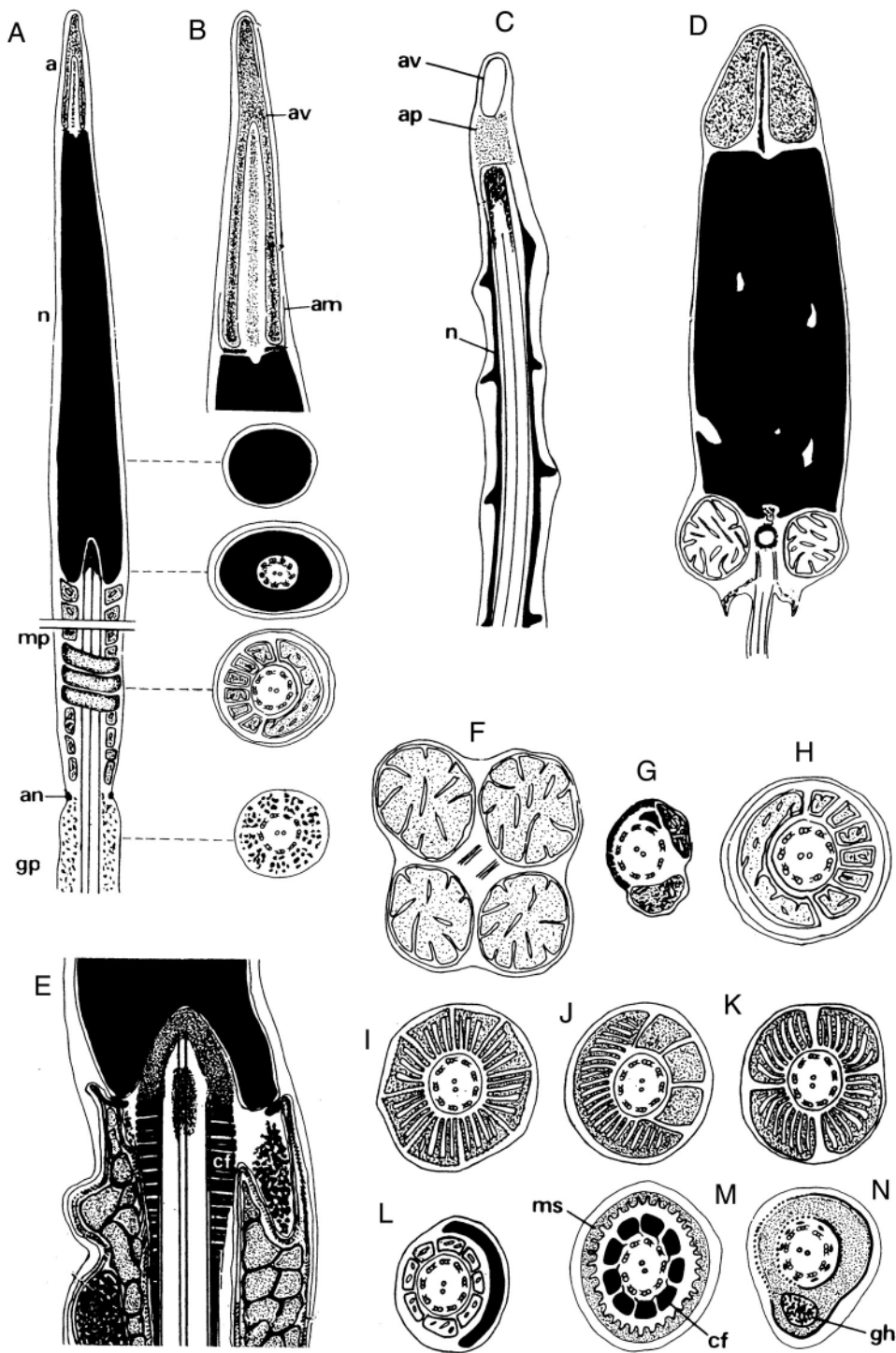


FIGURE 13.12. (Opposite.) Gastropod euspermatozoan features. (A) Basic features of caenogastropod euspermatozoan in littorinid *Bembicium auratum* (a, acrosomal complex, an, annulus, gp, glycogen piece, mp, midpiece, n, nucleus). (B) Acrosomal vesicle (av) (conical) of *Bembicium auratum*: note the accessory membrane (am). (C) Acrosomal vesicle (rounded) associated with acrosomal pedestal (ap) and anterior portion of nucleus and axoneme in the heterobranch *Rissoella micra*. (D) Eusperm of pleurotomariid, *Perotrochus westralis*, showing irregular spaces in nucleus (nuclear lacunae) and short midpiece with relatively unmodified mitochondria. (E) Nucleus-midpiece junction of nudibranch euspermatozoon, showing coarse fibers (cf) and complex mitochondrial sheath (with internal glycogen helix). (F–N) eusperm midpiece in transverse section (F, Pleurotomariidae, 4 round, “unmodified” mitochondrial cristae; G, Neritidae, 2 straight mitochondria; H, Littorinidae, 6–10 helical mitochondria with “unmodified” cristae, the commonest pattern in Caenogastropoda; I–K, with parallel cristal plates, Cyclophoroidea, 7–8 straight mitochondria; J, most Ampullarioidea, 4 helical mitochondria; K, Cerithioidea, 4 straight mitochondria; L, Campaniloidea, 7–8 straight mitochondria, accompanied by a dense segmented sheath; M, Architectonicoidea, Heterobranchia, continuous sheath [ms] with helical grooves, and thick coarse fibers; N, most other Heterobranchia, continuous sheath with paracrystalline layers and glycogen helix [gh]). Sources of figures: A, B, H: Healy (1996b); C, M, N: Healy (1993b); D: Healy (1990c); E: Healy and Willan (1991), F: Healy (1988c), G: Healy (1988a, 1993b); I–L: Healy (1993a).

polar lobe formation (van den Biggelaar and Haszprunar 1996).

Studies on organogenesis are relatively few, with the most comprehensive being those of Demian and Yousif (1973a–d, 1975) on *Marisa* (Ampullariidae). Recent detailed studies by Ball *et al.* (1997a, b), Ball (2002), Page (2000, 2002, 2005), Page and Pederson (1998), Pederson and Page (2000), and Parries and Page (2003) on the ontogenetic development of the anterior gut have substantially added to the available data, although some key taxa (e.g., ptenoglossan groups) have not yet been studied. In some proboscis-bearing gastropods—*Marsenina* (Velutinidae) (Page 2002), the naticid *Euspira* (Page and Pedersen 1998, Pedersen and Page 2000), and the direct-developing neogastropods *Nucella* (Ball *et al.* 1997a) and *Conus* (Ball 2002)—the new anterior gut develops independently to the larval gut and opens at the larval mouth at metamorphosis. However, during the development of the anterior gut in the planktonic larva of *Nassarius* (Fretter 1969; Page 2000, 2005), the larval mouth is sealed off and a new postmetamorphic mouth, develops into which the new anterior gut structures (including the proboscis) open. This separated development has been postulated to facilitate a rapid switch from larval microherbivory to postlarval carnivory. It will be of great interest to see whether this arrangement is common in other carnivorous proboscidate caenogastropods with planktotrophic development, and, if not, how this transition is achieved.

There is considerable morphological variation in caenogastropod spawn, ranging from gelatinous masses to benthic or pelagic capsules. The capsules may be complex, with delicate to tough walls, and their shape and size can vary within families and genera (e.g., Thorson 1946; Fretter and Graham 1962). This variation may be in response to selective pressures, because the encapsulating structures reduce embryo mortality through protection from predation, salinity stress, desiccation, bacterial attack, and, possibly, ultraviolet light (Rawlings 1994; Przeslawski 2004). Some adults actively defend their spawn from predators, whereas others brood capsules in the mantle cavity, oviduct, foot, shell umbilicus, or even a special chamber in the head.

FOSSIL RECORD

The origin and the early evolution of Caenogastropoda are summarized by Frýda *et al.* (Chapter 10). Putative caenogastropods first appeared during the Early Ordovician gastropod radiation (c. 490 Mya) (e.g., Loxonematidae, Subulitidae), although their identity as caenogastropods is not confirmed because information on shell microstructure and protoconchs is not available. It is likely that the last common ancestor of all extant caenogastropods lived in the Paleozoic prior to the Carboniferous and that some stem groups of the various crown group clades were present in the Early Paleozoic.

Recently suggested hypotheses regarding caenogastropod ancestry include Wagner's (2002) analysis of early gastropods based on teleoconch characters. He suggested that in the Early Paleozoic the Murchisoniinae gave rise to four groups, among them the hormotomoids and eotomarioids, the latter being possible precursors of modern vetigastropods. Hormotomoids split into loxonematids, subulitids, and, according to his hypothesis, apogastropods (i.e., Caenogastropoda + Heterobranchia) arose from the hormotomoid-loxonematid lineage (i.e., subulitids are the sister group of loxonematids and apogastropods).

Frýda (1999) assumed that Caenogastropoda and Heterobranchia arose from the Perunelomorpha, a Paleozoic (Ordovician to Devonian) group characterized by an open-coiled initial protoconch whorl and, commonly, fusiform teleoconchs (Frýda 2001; Frýda *et al.*, Chapter 10, Figures 10.4, 10.9) (Figure 13.6I–K). Perunelomorpha was left without assignment to a higher category by Frýda (1999). Bandel (2002) included them in the Procaenogastropoda, a poorly characterized and heterogeneous assemblage of Paleozoic caenogastropods (Nützel and Pan 2005) (discussed subsequently). To date, no explicit phylogenetic hypothesis has been presented clarifying the systematic placement of Perunelomorpha. Late Paleozoic perunelomorphs (Family Imoglobidae) seem to be caenogastropods, as suggested by their teleoconch morphology and dextral planktotrophic larval shell (Nützel *et al.* 2000; Nützel and Pan 2005). Frýda (1999: fig. 7) suggested that Perunelomorpha split into Caenogastropoda and Heterobranchia, but Frýda was not explicit about possible sister group relationships, and no apomorphies were given.

Kaim's (2004: fig. 140) phylogenetic scheme (Figure 13.5A) assumes a sister group relationship of Heterobranchia and Caenogastropoda. As in several previous scenarios, Kaim (2004) placed Loxonematidae as the stem group of apogastropods, while the apogastropod sister group was an unresolved cluster of taxa previously included in "Archaeogastropoda." Kaim (2004: fig. 140) noted loss of nacre, high-spired

shell, and closure of the protoconch umbilicus as apogastropod apomorphies.

Caenogastropods have a rich fossil record from the Devonian, with about one-third of the approximately 190 families extinct (Bouchet and Rocroi 2005). Many superfamilies and orders with living representatives (e.g., Risssooidea, Cerithioidea, Stromboidea, some "Ptenoglossa"⁷) have a fossil record from the early Mesozoic or even late Paleozoic (e.g., Bandel 1993; Nützel 1998; Nützel and Erwin 2004; Kaim 2004). Supposed basal caenogastropods, such as Cerithioidea, Risssooidea, and Littorinoidea, as well as some fossil groups were assigned to a paraphyletic Palaeo-Caenogastropoda (Bandel 1993, 2002). Protoconch morphology and shell microstructure is currently available from the Devonian/Carboniferous onward (ca. 350–400 Mya).

The oldest known gastropod with a preserved caenogastropod-type larval shell, the Devonian *Pragoscutula*, has a limpet-shaped teleoconch (Frýda 2001; see Frýda *et al.*, Chapter 10, Figure 10.10E) and was included in Neritimorpha by Bouchet and Rocroi (2005) because the larval shell of the Devonian *Pragoscutula* is similar to that of some fossil neritimorphs (Figure 13.6A, B; see subsequent discussion). However, this conclusion was reassessed following examination of recently discovered Early Carboniferous pragoscutulid limpets from Australia that have slender, caenogastropod-like larval shells. Pragoscutulids are now interpreted as early (but derived) caenogastropods (Cook *et al.*, in press). It is unlikely that the first caenogastropods were limpets, because if there had been a reversal from limpet to coiled shells in ancestral caenogastropods, there would be significant anatomical implications, of which there is no hint in modern taxa.

Open-coiled protoconchs are present in several Paleozoic gastropod clades (notably the Perunelomorpha), but this character was lost by the Mesozoic (Nützel and Frýda 2003).

7. Triphoroidea, Janthinoidea, and Nystiellidae.

Open-coiled protoconchs may represent the plesiomorphic state in caenogastropods. Based on exceptionally well-preserved material, several Late Paleozoic families have been reported that possess multiwhorled larval shells (indicating planktotrophy) with well-separated, orthostrophic whorls, aragonitic crossed-lamellar shell structure, a high-spined or fusiform shape, and, in some, anterior siphonal structures (e.g., Yoo 1994; Nützel and Cook 2002; Bandel *et al.* 2002; Bandel 2002; Pan and Erwin 2002; Nützel and Pan 2005) (Figures 13.6C–M), characters strongly suggestive of caenogastropod affinities (see also Frýda *et al.*, Chapter 10). However, their relationships to Mesozoic and extant caenogastropod clades are unclear.

Late Paleozoic Orthonematidae and the slit-bearing Goniasmatidae (Figure 13.6E–G) are probably stem group members of the Cerithioidea; they share a simple caenogastropod-type larval shell similar to that seen in extant basal caenogastropods such as Cerithioidea (Nützel 1998; Nützel and Bandel 2000; Bandel *et al.* 2002; Nützel 2002; Nützel and Pan 2005). The same type of larval shell was also reported in Cretaceous Campaniloidea, corroborating the basal position of that group (Kiel *et al.* 2000). The Devonian genus *Murchisonia* (Murchisoniidae) superficially resembles these Late Paleozoic high-spined caenogastropods, but *Murchisonia* is a high-spined vetigastropod (Frýda *et al.*, Chapter 10).

A scenario that sees the nonmarine Architaenioglossa as the sister group of all other caenogastropods (Sorbeoconcha) is, not surprisingly, unsupported by the fossil record. Because all extant architaenioglossans are nonmarine and direct developers, they do not build larval shells. Thus, their protoconchs cannot be meaningfully compared with those of marine planktotrophic caenogastropods. Similarly, the recognition of potential ancestral teleoconchs may be complicated by the assumed Paleozoic marine representatives having shell morphologies distinct from those of modern architaenioglossans. The earliest nonmarine gastropods that may be related to architaenioglossans are of Carboniferous age (Wenz 1938–1944; Knight *et al.* 1960)

and were united in the order Procylophorida by Bandel (2002). Others, however (e.g., Solem and Yochelson 1979), interpreted most of these Paleozoic nonmarine snails as pulmonates. Even if the oldest (Carboniferous) nonmarine snails were architaenioglossans, it still remains an open question as to which marine group (or groups) gave rise to them. Caenogastropoda are almost certainly much older than Carboniferous, but the assumption of a basal split between architaenioglossan groups and other caenogastropods (Sorbeoconcha) is neither supported or rejected by the fossil record. Because there are several synapomorphies for the sorbeoconchs that suggest that the architaenioglossan grade/clade lies outside them, it remains a plausible hypothesis that the architaenioglossan lineage (or lineages) is older than the known fossil record suggests.

The Paleozoic/Mesozoic Zygopleuroidea (Figures 13.6L, M, 13.13C–E) contains some groups of the traditional polyphyletic Loxonematoidea (Bandel 1991a; Nützel 1998). The zygopleuroid group represents a grade (Nützel 1998), or, in its present composition, even a polyphyletic assemblage, which encompasses close relatives of extant Janthinoidea and Triphoroidea (Bandel 1991a; Nützel 1998). It is also possible that the zygopleuroid group (grade) contains the ancestors of the Rissooidea and Stromboidea, as indicated by a zygopleuroid teleoconch morphology (high spire with axial ribs) present in several early members of these superfamilies. The oldest certain Rissooidea were reported from the earliest Middle Jurassic (Gründel 1999b; Kaim 2004) (Figure 13.13F). The earliest stromboideans are Aporrhaidae from the Early Jurassic (Figure 13.13K, L). Houbbrick (1979) suggested that the non-planktotrophic Abysochrysidae were modern representatives of the Loxonematoidea (i.e., zygopleuroid group).

The traditional Subulitoidea from the middle and late Paleozoic form a polyphyletic assemblage of caenogastropods (Nützel *et al.* 2000; Frýda 2001) (Figures 13.6H–K). Their relationship to the early Paleozoic subulitids is unclear, as are their links to modern groups. It is very likely

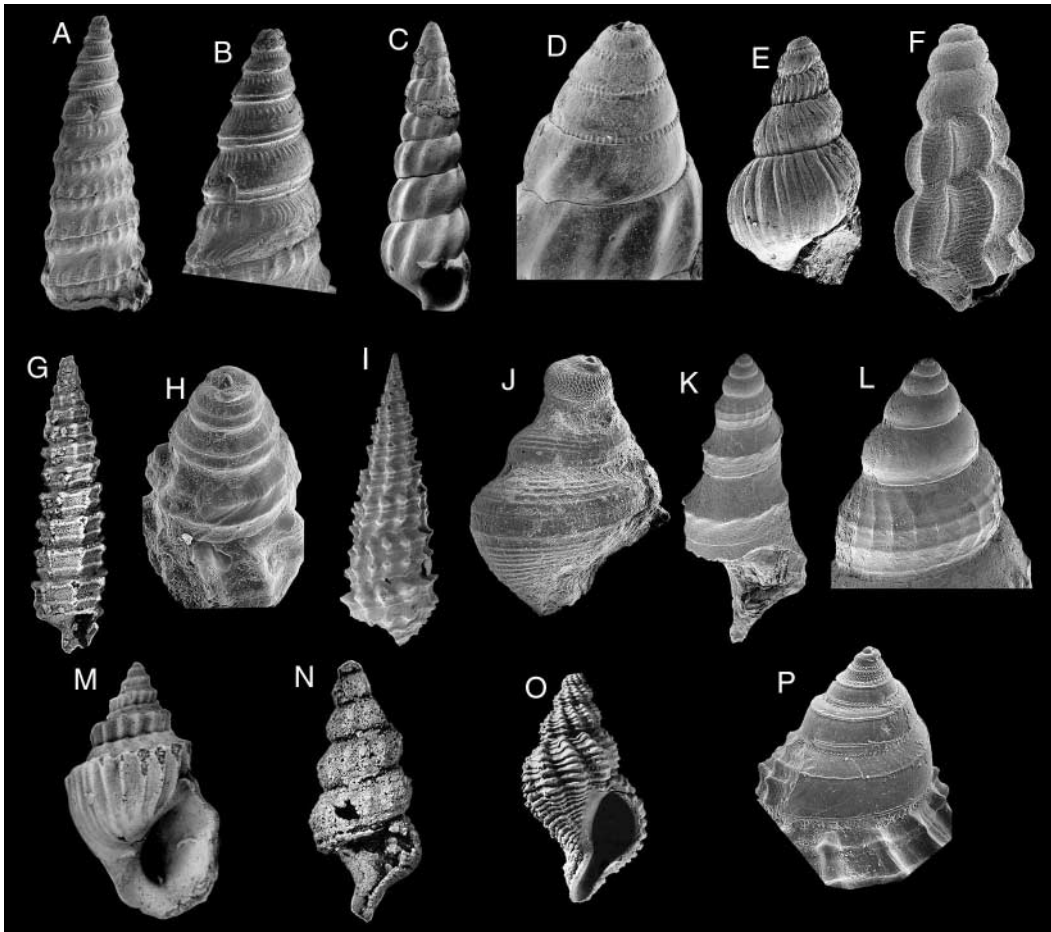


FIGURE 13.13. Selected Mesozoic (Triassic/Jurassic) caenogastropods. (A, B) *Protorcula* (Protorculidae) from the Late Triassic (Carnian, c. 230 Mya; Cassian Formation, northern Italy), a close relative of the modern cerithiopsids (from Nützel 1998); A, height 3.8 mm; B, larval shell, height 2.2 mm. (C, D) *Zygopleura* (Zygopleuridae) from the Late Triassic (Carnian, c. 230 Mya; Cassian Formation, northern Italy); the Zygopleuridae may be related to either modern Janthinoidea or Risssooidea (from Nützel 1998); C, height 5.9 mm; D, larval shell, height 1.0 mm. (E) *Ampezzopleura* (Zygopleuridae) from the Early Triassic Monekopi Formation (c. 247 Mya; Utah, United States); this genus appeared shortly after the end-Permian mass extinction and may be related to the late Paleozoic Pseudozygopleuridae (see Figure 13.6L, M); height 1.4 mm. (F) *Bralitzia* (= *Palaeorissioina*) (Risssoidea) from the Early/Middle Jurassic (Toarcian/Aalenian, ca. 180 Mya; southern Germany); *Bralitzia* is an early rissoid; the teleoconch morphology indicates a possible close relationship with the Zygopleuroidea; height 1.5 mm. (G–I) Jurassic/Triassic species of *Cryptaulax*, a typical, widespread genus of early Mesozoic Cerithioidea (Procerithiidae or Cryptaulacidae); like many modern Cerithioidea, they commonly possess bicarinate larval shells; G, Late Triassic (Norian, c. 210 Mya, western United States), height 10.5 mm; H, Middle Jurassic (southern Germany), showing typical bicarinate larval shell; height 0.8 mm. I, Early/Middle Jurassic (c. 180 Mya, S Germany); height 15.4 mm. (J) Cerithimorph caenogastropod from the Late Triassic (Carnian, c. 230 Mya, Cassian Formation, northern Italy); perhaps an offshoot of the Paleozoic Orthonematidae; height 1.6 mm. (K, L) *Dicroloma* (Aporrhaidae) from the Early/Middle Jurassic (c. 180 Mya; southern Germany); this early member of the Stromboidea has a relatively large, smooth larval shell; the typical apertural spines are broken away; K, height 8.7 mm; L, height 2.5 mm. (M) *Angularia* (Purpurinidae) from the Norian (c. 210 Mya; Idaho, United States); members of this family were sometimes thought to be ancestral or closely related to neogastropods; height 11.8 mm (from Nützel and Erwin 2004). (N) *Astandes* (?) (= *Maturifusus*) (Maturifusidae) from the Norian (ca. 210 Mya; Idaho, United States), one of the earliest distinctly siphonostomatous gastropods with cancellate teleoconch ornament. It could be ancestral or closely related to neogastropods; height 11.8 mm (from Nützel and Erwin 2004). (O, P) *Astandes* (= *Maturifusus*) from the early Late Jurassic (Oxfordian) (c. 154 Mya; Russia) (from Guzhov 2004, by courtesy of A. Guzhov); O, teleoconch showing distinct siphonal canal, height 13.3 mm; P, relatively large planktotrophic larval shell; height 1.2 mm.

that the Early Paleozoic (Ordovician/Silurian) Subulitidae (“true subulitids”) are caenogastropods, as indicated by their fusiform shape and the presence of anterior siphonal canals. However, no data about their protoconch morphology and shell microstructure are available. The same is true for the Permian Ischnoptegmatidae, which are probably closely related to the Soleniscidae. Some subulitoid families (Soleniscidae, Meekospiridae, Imoglobidae, Sphaerodomidae) were placed in a subclass Procaenogastropoda by Bandel (2002), a taxon largely based on a single character: a seemingly fluent protoconch/teleoconch transition. However, the material on which this observation was based was worn, with better-preserved material indicating that members of this group have a normal caenogastropod protoconch (Nützel and Pan 2005). These families are now regarded as early Caenogastropoda (see Bouchet and Rocroi 2005 for current classification).

Subulitoid gastropods, especially Soleniscidae, survived the end-Permian mass extinction event (Nützel 2005) and are possible ancestors of Mesozoic to modern caenogastropod clades. Mesozoic descendants are possibly included in the families Coelostylinidae and Pseudomelaniidae, which represented extremely diverse, largely Mesozoic caenogastropod groups. Generally they possessed high-spined to conical, smooth teleoconchs and probably contained descendants of late Paleozoic subulitoids as well as other caenogastropods of yet unknown affinity. In their present composition, both families are almost certainly polyphyletic.

The Late Triassic to Jurassic/Cretaceous Procerithiidae (Figure 13.13G–I) were globally distributed and diverse (e.g., Gründel 1999a; Nützel and Erwin 2004, Kaim 2004; Guzhov 2004). Many of them have bicarinate larval shells, as in some Recent Cerithioidea (e.g., Kowalke 1998, pl. 2). Procerithiidae were included in a separate superfamily (Procerithioidea) and distinguished from modern cerithioidean families largely on the lack of a pronounced anterior siphonal notch or canal. In all other respects the shells of both groups are very similar, and,

moreover, a number of modern cerithioideans lack an anterior canal whereas some putative procerithiids have a well-developed canal. Thus, the separation of these two superfamilies is not justified. Several families (Ladinulidae, Lanascalidae, Popenellidae, and Prostyliferidae) from the Late Triassic Cassian Formation (Bandel 1992), based on their larval shell morphology, can be included within Cerithioidea.

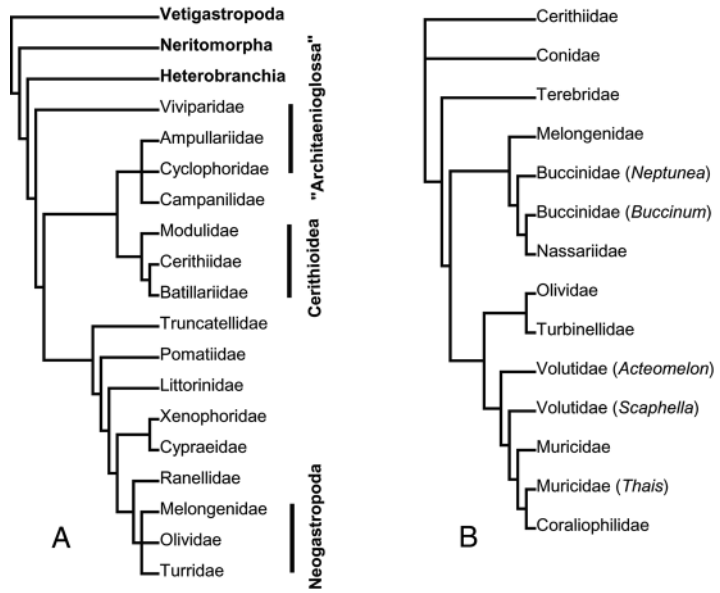
One of the reasons why gastropods (and particularly caenogastropods) are so diverse is their supposed “extinction resistance” (Erwin and Signor 1990). However, it is obvious that the end-Permian mass extinction event about 250 Mya ago had a major impact on the evolution of caenogastropods (Nützel and Erwin 2002; Nützel 2005). Important late Paleozoic families (e.g., the Pseudozygopleuridae; Figure 13.6L, M) became extinct or were marginalized. During the recovery period there was a high degree of turnover, and many new genera and several families appeared (e.g., *Ampezzopleura*, Figure 13.13E; Nützel and Erwin 2002; Nützel 2005). The rise of the modern, strongly ornamented cerithioideans (Figure 13.13G–I) started in the Triassic and could represent a recovery phenomenon. The impact of the end-Triassic mass extinction event on gastropods has not been well studied. Some widespread genera, such as *Protorcula* (Protorculidae; Figure 13.13A, B), seemingly became extinct in the latest Triassic. As far as we know, the end-Cretaceous mass extinction event did not have a major impact on caenogastropod evolution, as no major group became extinct. Highly diverse extant groups (such as neogastropods, tonnoideans, Turritellidae, cerithiopsoids, eulimoidans, and rissoidans) started to radiate in the Cretaceous and continued to undergo major radiations in the Cenozoic. Conversely, a few previously diverse families in the late Mesozoic–early Cenozoic (e.g., Campanilidae; Aporrhaidae) have few living species.

MOLECULAR STUDIES

Some of the more significant molecular analyses, including smaller groups of caenogastropods, are listed above. To date, DNA sequence

FIGURE 13.14. Some previous caenogastropod phylogenies using molecular data.

(A) Strict consensus tree from a maximum-likelihood (ML) analysis using partial 18S rDNA of mainly lower caenogastropod taxa (Harasewych *et al.* 1998).
(B) Single ML tree obtained from partial 18S rDNA of neogastropods using *Cerithium* as the outgroup (Harasewych *et al.* 1997).



data has also been used to address more general questions regarding caenogastropod evolution. These include the monophyly of Caenogastropoda itself, Architaenioglossa, Sorbeoconcha, Hypsogastropoda, Ptenoglossa, Neogastropoda, and several superfamilies for which multiple exemplars are available. The published molecular investigations that included a wide range of caenogastropod taxa are summarized below. Harasewych *et al.* (1997) sequenced parts of the 18S rDNA gene in 21 caenogastropods (17 neogastropods) and part of cytochrome *c* oxidase 1 for 17 of these (16 Neogastropoda) (Figure 13.14B). Harasewych *et al.* (1998) sequenced parts of the 18S rDNA gene in 19 caenogastropods, including five Architaenioglossa (two species of Cyclophoroidea, two Ampullariidae, and one Viviparidae), Campaniloidea, and Cerithioidea (three species) (Figure 13.14A). McArthur and Harasewych (2003) included 18S rDNA data from 23 caenogastropods in their Bayesian analysis of overall gastropod phylogeny but obtained very little resolution within a monophyletic Caenogastropoda with Heterobranchia as the monophyletic sister taxon. Included in Colgan *et al.*'s (2000) study of overall gastropod phylogeny were 17 caenogastropod taxa scored for two segments of 28S rDNA and histone H3. Colgan *et al.* (2003), with 16 caenogastropod taxa, added three extra genes, an

additional segment of 28S ribosomal DNA, small nuclear RNA U2, and part of cytochrome *c* oxidase subunit 1. A larger survey of caenogastropod molecular phylogeny (Colgan *et al.* 2007) added additional data (two segments of 28S ribosomal DNA, histone H3, and cytochrome *c* oxidase subunit 1) and new data from additional genes (part of 12S rDNA domain III, another region of the 28S rDNA) and part of the 18S ribosomal DNA and elongation factor 1 alpha) were also added. The data set comprised more than four thousand aligned bases for 29 caenogastropods (six non-hypsogastropods and 23 Hypsogastropoda) and six outgroup taxa. One of the trees resulting from this analysis is shown in Figure 13.15. Of particular interest is the division into "asiphonate" and "siphonate" clades, support for the Hypsogastropoda, the non-monophyly of the neogastropods, and the long branch length exhibited by the eatoniellid (see Colgan *et al.* 2007, for detailed discussion).

Caenogastropod monophyly has generally been supported in synoptic molecular studies of Gastropoda, although these included limited representation. This was observed for the six caenogastropods included in Tillier *et al.*'s (1992) study of D1 28S rDNA. The five representatives included in McArthur and Koop (1999) were monophyletic in parsimony analyses (but

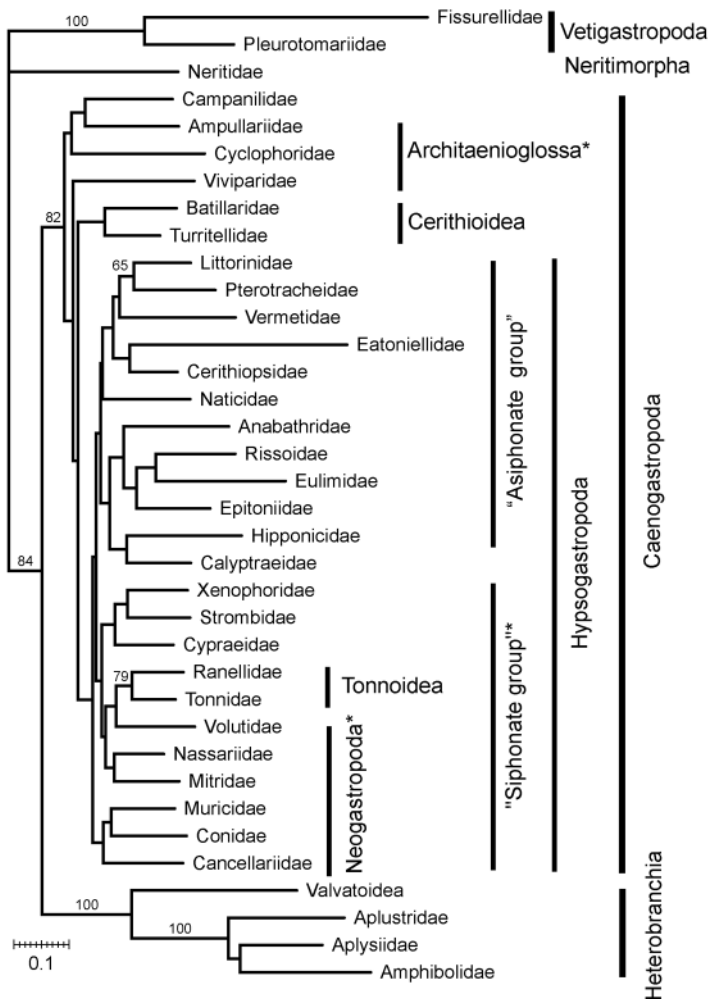


FIGURE 13.15. Maximum likelihood tree obtained by Colgan *et al.* (2007: fig. 2). Numbers on the branches are the maximum-likelihood bootstrap support percentages over 50. Higher-level taxa are indicated by bars to the right of the topology. * indicates a nonmonophyletic group. The scale bar is graduated in units of 0.01 substitutions per site.

not maximum likelihood) when data from both D1 and D6 28S rDNA expansion regions was included. In the larger studies, monophyly was observed in Harasewych *et al.* (1998) and McArthur and Harasewych (2003), in all analyses in Colgan *et al.* (2007), and in some but not all analyses in Colgan *et al.* (2003), with the exceptions mostly due to the inclusion in Caenogastropoda of the sequenced neritimorph or the exclusion of the cyclophorid. Monophyly has never been strongly contradicted.

MORPHOLOGICAL ANALYSIS

Ponder and Lindberg's (1997) data set of 117 morphological characters was used as a starting point to develop characters appropriate to the finer levels of resolution required in this

analysis. In addition to the more traditional characters associated with the shell, radula, head-foot, nervous system, alimentary canal, kidney, and reproductive system, recent studies have targeted the complex musculature of the buccal mass/ proboscis (Simone 2001, 2002, 2004a, b, 2005; Kantor 1988, 1990, 1991; Kantor and Taylor 1991), the stomach (Strong 2003; Kantor 2003) and radular development (Guralnick and Smith 1999). The full character list and data set are available at http://www.ucmp.berkeley.edu/science/archived_data.php.

The morphological terminals coded in the analysis that generated the tree in Figure 13.16 are composite family-level terminals in order to minimize ambiguity and decrease the amount of missing data. Although not ideal, this approach

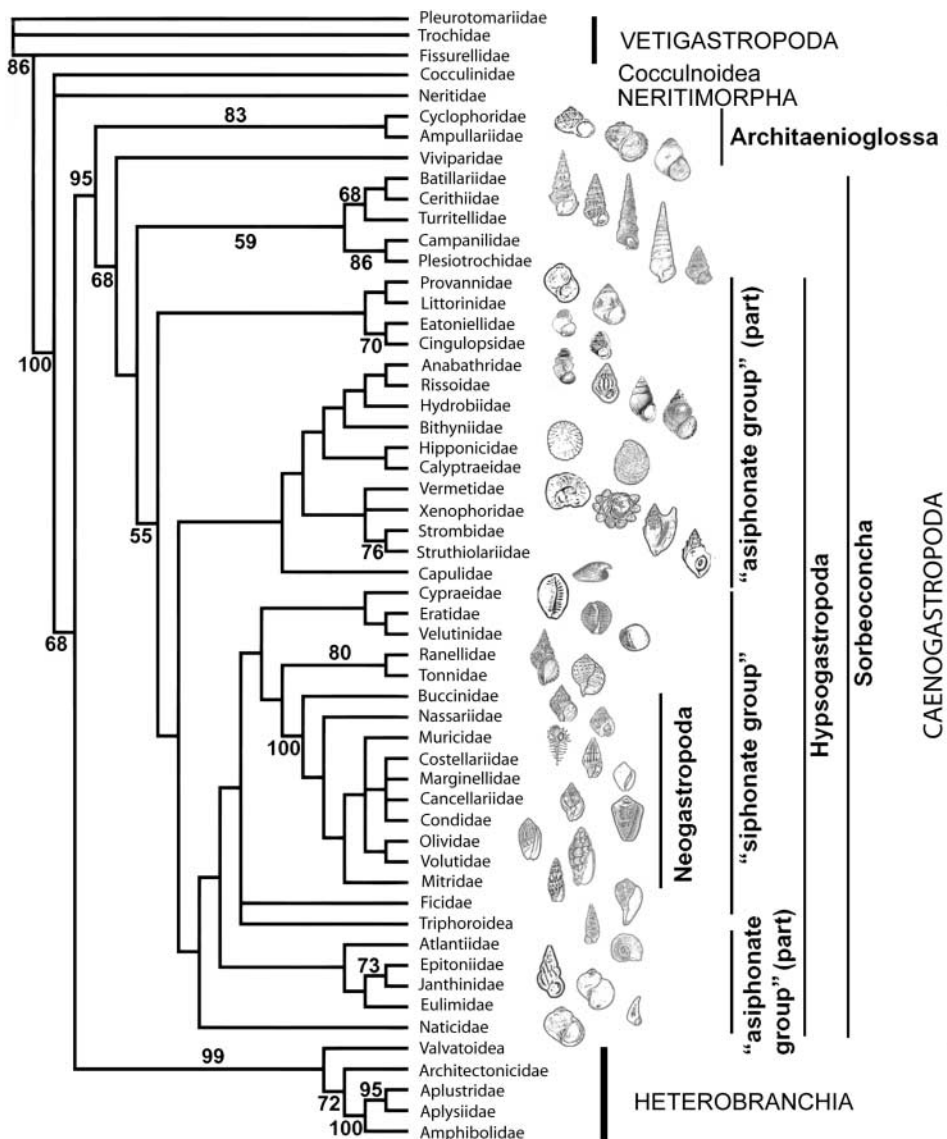


FIGURE 13.16. Strict-consensus tree generated from the morphological data by a heuristic search using PAUP* with 1,000 replications using random addition sequence, tree bisection-recombination (TBR) and with steepest descent not invoked, resulted in 72 trees (length 668, CI 0.436, RI 0.713, RC 0.311, HI 0.564). Bootstrap values > 50 resulting from 100 replications are shown.

has been necessary as a consequence of the often-fragmented anatomical data, with studies focusing on a single organ system or on a subset of characters. Thus, there are few caenogastropod species for which large data sources are available, including (but not universally) comprehensive anatomy for each major organ system, ultrastructure, histochemistry, as well as developmental, ecological, karyological, and cytological

information. These few “model” species include *Marisa cornuarietis*, *Crepidula fornicata*, *Littorina littorea*, *Nucella lapillus*, *Ilyanassa obsoleta*, and *Viviparus viviparus*. Some large families have remained virtually untouched by comparative approaches, with only incomplete information available in a few scattered publications (e.g., cerithiopsids, triphorids), while with others only anatomical information may be available.

Characters and character states in the Ponder and Lindberg (1997) data set that are rendered inapplicable by the restricted taxonomic scope of this analysis have been omitted (for details see data set). Additional characters comprise features of external anatomy and shell morphology that are informative within caenogastropods. The most significant additions are in the areas of buccal musculature, stomach, and nervous system. In the last decade, as discussed previously, the morphological data set for caenogastropods has benefited from broad comparative surveys that have significantly added to our knowledge of caenogastropod anatomy for poorly understood groups (e.g., epitoniids, cyclophorids, and hipponicids) and provided characters new to caenogastropod systematics (Simone 1999, 2000a, 2001, 2002, 2004a, b, 2005; Strong 2003).

The eusperm characters included in the present study are those we consider the most robust and for which substantial amounts of data are available (and for which comparable data is available for the out groups). The paraspERM are divided into different types, which are treated as separate characters, as they are likely not homologous.

The dataset of 55 taxa and 164 characters was used for a maximum-parsimony analysis using PAUP* ver. 4.0b10 (Swofford 2001); for details see caption of Figure 13.16. The strict consensus tree is shown in Figure 13.16. Caenogastropoda is strongly supported, with a bootstrap value of 95. The architaenioglossan taxa are basal but paraphyletic, and Cerithioidea and Neogastropoda are monophyletic. Sorbeoconcha is weakly supported, and, while Hypsogastropoda is not supported by bootstrap values greater than 50%, the Campaniloidea + Cerithioidea are well supported as a clade separate from the rest of the sorbeoconchs. The “asiphonate” clade seen in the molecular analysis, is paraphyletic, but the siphonate clade is supported, with Naticidae being the sister of that group.

COMBINED ANALYSIS

A combined analysis, the first carried out for caenogastropods, was conducted using the

molecular data set of Colgan *et al.* (2007)⁸ with areas of uncertain alignment removed and a pruned (taxa only) version of the morphological data set referred to above. As the molecular dataset is based on species, these were aligned with the taxa in the morphological data set at the family level. The full data set is available at http://www.ucmp.berkeley.edu/science/archived_data.php. A Bayesian analysis was performed using MrBayes version 3.1.2 (Huelsenbeck and Ronquist 2001) with two million iterations and the following parameters: DNA data nst = 6 rates = invgamma; unlink shape = (all); pinvar = (all); statefreq = (all); revmat = (all); prset ratepr = variable; out group Fissurellidae; mcmc ngen = 2,000,000; nruns = 4; printfreq = 100; samplefreq = 100 nchains = 4 savebrlens = yes startingtree = random. 5,000 trees were discarded to allow for convergence.

A strict consensus of the sampled trees is shown in Figure 13.17. The resulting tree contains a monophyletic Caenogastropoda, with Heterobranchia the sister taxon. Within Caenogastropoda, Architaenioglossa is paraphyletic, the Sorbeoconcha is well supported, with Campanilidae sister to the remaining sorbeoconchs and the Cerithioidea are sister to the rest (Hypsogastropoda). The Hypsogastropoda is composed of asiphonate and siphonate clades, similar to those found in the molecular analysis (only the position of Calyptraeidae has changed), although neither is strongly supported.

The neogastropods are monophyletic, with the tonnoideans as their sister group, but Latrogastropoda is not recovered because of the inclusion of Cypraeidae as the sister to the tonnoideans, even though this has poor support. The ptenoglossans are polyphyletic, with the eulimids sister to the rissoids; the triphoroidean is in a poorly supported clade including the littorinid and the heteropod; and the position of the epitoniid is unresolved within the “asiphonate group.”

8. The data set used included the architectonicid *Philippia lutea*, which was not in the Colgan *et al.* (2007) dataset and 18S data for the pleurotomariid was not included. This latter data did not influence the topology.

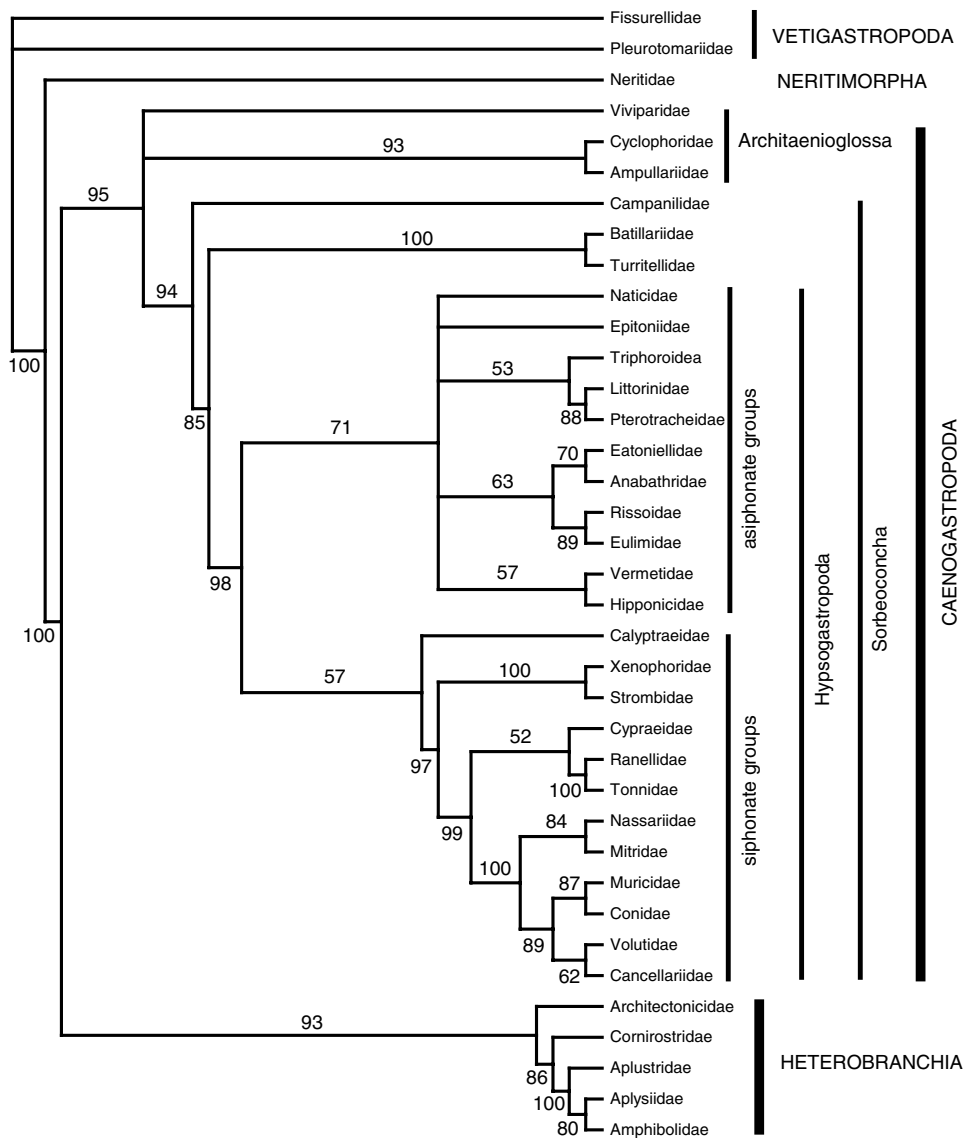


FIGURE 13.17. Strict-consensus tree obtained from a Bayesian analysis using the combined morphological dataset and the molecular data from Colgan *et al.* (2007), with the regions of questionable alignment excluded and an architectonicid (*Philippea lutea*) included. Named higher-level taxa are indicated by bars to the right of the topology. Clade credibility values (>50) are indicated.

SUMMARY OF MAJOR GROUPS

The following discussion summarizes the major groups of caenogastropods as determined by our analyses and other recent work.

ARCHITAENIOGLOSSA

Ponder and Lindberg's (1996, 1997) morphological analyses placed Architaenioglossa as the sister to the rest of the caenogastropods

(Sorbeoconcha). Haszprunar (1988) could not find support for the monophyly of Architaenioglossa, but this grouping, using morphological characters, is weakly supported in Ponder and Lindberg's (1997), Strong's (2003),⁹ and in our morphological analyses (Figure 13.16).

9. Only two (Cyclophoroidea, Ampullarioidea) of the three architaenioglossan superfamilies were represented in this analysis.

However, the contained superfamilies are paraphyletic in Simone's (2000a, 2004b) analyses (Figure 13.4B) and in our molecular and combined analyses (Figures 13.15, 13.17). Similarly, in most molecular analyses to date, the architaenioglossan groups are basal caenogastropods but are not monophyletic (e.g., Figure 13.14A). Harasewych *et al.* (1998), the first molecular study to include a substantial number of non-hypsogastropod caenogastropods, found that non-hypsogastropod taxa comprised a monophyletic group in maximum-likelihood analyses and in parsimony analyses considering only transversions. Monophyly was not found in other analyses by Harasewych *et al.* (1998) or in later analyses of 18S data (McArthur and Harasewych 2003) or other genes (Colgan *et al.* 2007), but it remains an hypothesis worthy of consideration.

Although monophyly of Architaenioglossa is rare in analysis of DNA sequences, Colgan *et al.* (2000) showed monophyly of the two included Architaenioglossa, but as sister to Caenogastropoda plus Heterobranchia and *Nerita* and *Nautilus*. In Colgan *et al.* (2003), the same two Architaenioglossa formed a monophyletic group only in maximum-likelihood analysis of a reduced data set and in Bayesian analyses. In Harasewych *et al.* (1998), Cerithioidea, Ampullariidae, and Cyclophorioidea were monophyletic. However, Ampullarioidea and "Architaenioglossa" were never monophyletic in these analyses because of the (variable) position of Viviparidae.

While molecular studies have consistently included Campaniloidea in Caenogastropoda (Harasewych *et al.* 1998; McArthur and Koop 1999; McArthur and Harasewych 2003; Colgan *et al.* 2000, 2003, 2007), this taxon is grouped with Cyclophoridae (Colgan *et al.* 2003, some analyses; McArthur and Harasewych 2003) or Ampullariidae (McArthur and Koop 1999; Colgan *et al.* 2007, maximum likelihood and some maximum parsimony analyses) rather than as a basal sorbeoconchan as suggested by morphology (Ponder and Lindberg 1997; Simone 2001) and our morphological and combined analyses (Figures 13.16, 13.17).

With the three superfamilies (Cyclophorioidea, Ampullarioidea, and Viviparioidea) comprising the architaenioglossans forming two or three branches of basal caenogastropods, there remains the puzzling question as to why nonmarine taxa are the likely sisters to the largely marine caenogastropods, with the most likely assumption being that their marine ancestors are extinct. However, some molecular analyses (as discussed previously) suggest that the marine Campaniloidea may be associated with one of these branches. Such a relationship is intriguing given the report of a hypoathroid nervous system in the possible campaniloidean *Cernina* (discussed later).

SORBEOCONCHA

This group contains caenogastropods other than the architaenioglossan clade or grade. Within this grouping, the relative position/relationships of the Cerithioidea and Campaniloidea (see also previous discussions), which probably represent the most primitive extant marine caenogastropods, are unclear because morphological (Ponder and Lindberg 1996, 1997; Simone 2000a, Figure 13.4B; Strong 2003, Figure 13.4A) and molecular data (Harasewych *et al.* 1998, Colgan *et al.* 2000, McArthur and Harasewych 2003), give different results (see previous discussion). The enigmatic Campanilidae is represented by a single extant species endemic to southwestern Australia. Plesiotrochidae (Houbrick 1990) is included in Campaniloidea based on sperm morphology (Healy 1993a). *Cernina fluctuata* (previously included in Naticidae) has a hypoathroid nervous system (Kase 1990), suggesting architaenioglossan affinities, but its sperm morphology is like that of campaniloideans (Healy and Kase, unpublished data; J. M. H., personal observation), other members of which are epiathroid. Simone's (2001) morphological analysis of Cerithioidea (which lacks sperm data) has *Campanile* closely related to turritellids and vermetids, with the distinctive characters seen in *Campanile* and Vermetidae interpreted as autapomorphies.

Despite some seemingly good morphological support for Sorbeoconcha (see earlier discussion of main groups recognized within

caenogastropods), this grouping is only weakly supported in the strict-consensus tree in our new morphological analysis (Figure 13.16). Although the Sorbeoconcha has not been supported by any large molecular data set, generally because of the inclusion of a cerithioidean or campaniloidean in the group containing the architaenioglossans (discussed earlier), it is recovered in our combined analysis (Figure 13.17).

CERITHIOIDEA

In the morphological analysis of Simone (2001) the Cerithioidea also included the Campaniloidea and Vermetoidea. Molecular (Lydeard *et al.* 2002) and ultrastructural sperm data (Healy 1983a, 1988a, 1996a), however, support the restricted interpretation of Cerithioidea. In our new morphological analysis the strict-consensus tree (Figure 13.16) has the Cerithioidea and Campaniloidea as sister taxa and the Viviparidae as sister to this clade + Hypsogastropoda. In the majority-rule tree of the combined analysis the Campaniloidea are sister to Cerithioidea + Hypsogastropoda, with Vermetidae included among the partially resolved “lower” hypsogastropods (Figure 13.17), forming an “asiphonate” group.

HYPGASTROPODA

Hypsogastropoda (Ponder and Lindberg 1997) includes all the extant caenogastropods other than architaenioglossans, Cerithioidea, and Campaniloidea. According to the latest classification (Bouchet and Rocroi 2005), this group contains two orders, three suborders, and 30 superfamilies. It is not known whether the “mesogastropod” component of the hypsogastropods (the “higher mesogastropods” *sensu* Healy 1988a) is monophyletic, but the late appearance of clearly identifiable neogastropods relative to “higher mesogastropods” (discussed subsequently) strongly suggests that the latter group is paraphyletic.

Hypsogastropoda is often observed in molecular analyses (all analyses in Harasewych *et al.* 1998; McArthur and Harasewych 2003; most analyses in Colgan *et al.* 2007, Figure 13.15) but is weakly contradicted in Colgan *et al.* (2003). In the analyses in Colgan *et al.* (2003, 2007) that

do contradict monophyly, a clade containing all studied hypsogastropods is still seen, but it also includes cerithioideans (either Turritellidae or Batillariidae, but not both) and, often, Viviparidae. The hypsogastropods are recovered in both our new morphological (Figure 13.16) and combined (Figure 13.17) analyses.

Relationships within Hypsogastropoda are poorly resolved in all molecular and morphological analyses to date. Within Hypsogastropoda, the molecular analysis of Colgan *et al.* (2007) (Figure 13.15) and our combined analysis (Figure 13.17) revealed two main clades: a siphonate paraphyletic clade and one in which the anterior siphon is lacking, apart from Cerithiopsidae, suggesting that the siphon in that group (Triphoroidea) may not be homologous with those in other caenogastropods. The only exception was that the Calyptraeidae changed from the asiphonate clade in the molecular analysis to the siphonate clade in the combined analysis. The siphonate clade was also recovered in the morphological analysis, but the asiphonate clade was paraphyletic.

Apart from the asiphonate and siphonate clades, little consistent structure above the superfamily level has been observed within Hypsogastropoda in published molecular analyses. In Harasewych *et al.* (1998), two of the three Littorinoidea were monophyletic in most analyses. In Colgan *et al.* (2003), Vermetidae plus Epitoniidae was supported in all analyses, with the Cerithiopsidae being the sister group to this pair in a number of analyses, notably when third base positions are excluded.

In Simone’s (2000a) analysis, a sister group relationship between Tonnoidea (including Ficidae) + Neogastropoda (= Latrogastropoda) is supported by several characters including a pleurembolic proboscis.¹⁰ Latrogastropoda is

10. If Tonnoidea + Neogastropoda is a monophyletic group, there remains the question as to whether their proboscis is homologous. Kantor (2002) argued that a short proboscis is plesiomorphic for neogastropods, and the probably basal tonnoidean families Pisanianuridae and Laubierinidae also have a short proboscis, but detailed comparative studies are lacking.

also recovered in part in our morphological analysis (Figure 13.16), with the Ficidae (not included in the molecular analyses), considered to be the sister to the Neogastropoda by Riedel (2000), well outside Tonnoidea + Neogastropoda. In the combined analysis, a similar grouping is achieved, although the cypraeid is in the same monophyletic group as the Tonnoidea (Figure 13.17).

Kosuge (1966) suggested that his Heterogastropoda lay between the meso- and neogastropods, but Graham (1985: 177) argued that “this suggestion is not acceptable.” Interestingly, Strong’s (2003) analysis has an epitoniid (the only ptenoglossan in her analysis) as the sister to the neogastropods. However, in other analyses involving ptenoglossans and neogastropods (Ponder and Lindberg 1997; Colgan *et al.* 2000, 2003, 2007) there is little or no support for this relationship. This is also the case in our morphological analysis, where the triphorids and Ficidae are unresolved sisters to the “higher” hypsogastropods while the remaining ptenoglossans + Atlantidae are sister to that clade (Figure 13.16). In the combined analysis the ptenoglossan taxa are scattered among the other “lower” hypsogastropod taxa (Figure 13.17).

The placement of the heteropod Pterotrachoidea in our morphological analysis (Figure 13.16) as sister to the eulimids, epitoniids, and janthinids is at variance to a littorinoidean relationship suggested by morphological similarities, primarily in reproductive anatomy (Gabe 1965; Martoja and Thiriot-Quiévreux 1975) and supported with molecular data (Strong and Harasewych 2004; Colgan *et al.* 2007; Harasewych and Strong, unpublished data; our combined analysis, Figure 13.17). Bandel and Hemleben (1987) and Bandel (1993) suggested that the sister taxon to the heteropods was Vanikoridae or Pickworthiidae based on the similarity of their larval shells with those of atlantids; these relationships remain untested, because no molecular or morphological analyses have included representatives of these suggested sister taxa to date. Vanikoridae and Hipponicidae are usually included in

separate superfamilies but are both regarded as Calyptraeidea in Simone’s (2002) morphological analysis. In contrast, Collin’s (2003) molecular analysis involving three genes indicated that vanikorids are well removed from both hipponicids and calyptraeids and that both the latter groups are separate clades. In that analysis vanikorids were sister to the two tonnoideans, although with a very long branch, while *Littorina* and naticids were sisters (Collin 2003: fig. 6).

NEOGASTROPODA

The Neogastropoda are usually considered to be monophyletic, this view being supported by several morphological synapomorphies (Ponder 1974; Taylor and Morris 1988; Kantor 1996; Ponder and Lindberg 1996, 1997; Strong 2003). They tend to have higher chromosome numbers and larger cellular DNA content than other gastropods have (see Thiriot-Quiévreux 2003 and Gregory 2005 for references). In our morphological analysis the neogastropods are recovered as a group, with the Buccinidae as the sister to the remainder, in the consensus tree (Figure 13.16). They were also strongly supported in the combined analysis (Figure 13.17). However, results from molecular data are ambivalent (discussed subsequently).

The origin and subsequent radiation of the Neogastropoda represent a major event in caenogastropod evolutionary history, but the identity of the sister taxon to this group remains unresolved. Different hypotheses have been presented by neontologists: that the neogastropods arose from an “archaeogastropod” or primitive “mesogastropod” (Ponder 1974) or that they arose from a “higher mesogastropod,” usually considered to be a tonnoidean (Graham 1941; Ponder 1974 [gives summary of early literature]; Taylor and Morris 1988; Kantor 2002), or Ficoidea (Riedel 2000), or noncommittal (e.g., Kantor 1996). The “higher mesogastropod” hypothesis has support from morphological (Ponder and Lindberg 1996, 1997; Strong 2003), molecular (Tillier *et al.* 1992, 1994; but not Rosenberg *et al.* 1994, in

which the neogastropods form a clade with the only vetigastropod in their analysis) and ultrastructural data (sperm and osphradium) (e.g., Haszprunar 1985a; Healy 1988a, 1996a). Buckland-Nicks and Tompkins (2005) have recently suggested the Ranellidae (and presumably therefore the Tonnoidea) are the sister taxon to the Neogastropoda, based on shared occurrence of a particular type of vermiform parasperm ('lancet parasperm'), and this is also consistent with eusperm morphology (see Kohnert and Storch 1984; Koike 1985; and Healy 1996a for comparative figures of eusperm and literature). In Colgan *et al.* (2007), Tonnoidea are the sister group to Volutidae in all likelihood-based analyses, sometimes with substantial support. This set of three taxa was generally included in a monophyletic clade including two other neogastropods (Nassariidae and Mitridae).

The identity of fossil sister taxa has been equally contentious. Suggestions that Paleozoic siphonate subulitoid gastropods (Figure 13.6H) or other basal caenogastropods are precursors or close relatives of neogastropods (Cox 1960a; Ponder 1974) have not attracted recent support (e.g., Riedel 2000). The Triassic/Jurassic Purpurinidae (Figure 13.13M) have been hypothesized as close relatives, or even members of, Neogastropoda (Taylor *et al.* 1980; Kaim 2004). These assumptions are based on the more or less fusiform shell shape, teleoconch ornament, and presence of an anterior siphonal notch/canal. Kaim (2004) placed the Purpurinidae in the Neogastropoda, implying that this lineage was present as early as Middle to late Triassic. However, Bandel (1993) and Riedel (2000) doubted that Purpurinoidea are neogastropods, because they have a small larval shell as exemplified in a Triassic member (*Angularia*) (Figure 13.13M; Bandel 1993: pl. 14 fig. 4). The Early Jurassic to Cretaceous genus *Astandes* (= *Maturifusus*, family Maturifusidae) has been repeatedly suggested as a possible early member or close relative of the Neogastropoda (Szabó 1983; Schröder 1995; Bandel 1993; Riedel 2000; Kaim 2004) (Figure 13.13N–P). The cancellate teleoconch ornament, distinctly siphonostomatous

aperture, and the relatively large larval shell suggest that *Astandes* is a neogastropod or closely related. A possible Late Triassic maturifusid was reported by Nützel and Erwin (2004) as the earliest member of this group (Figure 13.13N). However, even if the fossil ancestor is convincingly identified, the identity of the living sister taxon remains necessary for the interpretation of the homology of anatomical characters.

Neogastropoda has usually been contradicted, albeit weakly, in molecular analyses, with monophyly supported by Tillier *et al.* (1992) and questionably by Rosenberg *et al.* (1994) or weakly contradicted by Tiller *et al.* (1994) and Colgan *et al.* (2000, 2003, 2007). Harasewych *et al.* (1997) failed to resolve neogastropod monophyly in their 18S rDNA analyses. Monophyly of Neogastropoda could not be tested with the CO1 data of Harasewych *et al.* (1997), but three of the four superfamilies (Conoidea, Buccinoidea, and Muricoidea) within the group were supported in all analyses. Harasewych *et al.* (1998) recovered Neogastropoda (three taxa) in a few of their analyses (MP ML), but not all. Riedel (2000) was also unable to retrieve a monophyletic Neogastropoda using 16S and 18S sequence data. In Colgan *et al.* (2003), at most two of the five studied neogastropods were included in a monophyletic clade exclusive of other taxa. In one analysis, three Neogastropoda (Conidae, Mitridae, and Cancellariidae) were included in a monophyletic clade with Cerithiopsidae. At most, five of the six studied Neogastropoda were in the same monophyletic clade in parsimony analyses conducted by Colgan *et al.* (2007). Given that the position of any recognizable neogastropod group was predominantly basal within Hypsogastropoda, Colgan *et al.* (2007) argued that the group has a deep phylogenetic history in Hypsogastropoda, implying that the stem group is not yet recognized or extinct.

This large and important group is still in a state of flux, with even some supposedly well-known taxa recently reinterpreted. For example, *Morum* was considered to be a cassid (Tonnoidea) until shown to be a harpid (Neogastropoda) (Hughes 1986b), and the commercially important genus

Babylonia, the subject of many studies and long considered to be a buccinid, was recently included in a separate family related to Olividae and Volutidae (Harasewych and Kantor 2002).

SUMMARY OF WHAT WE KNOW ABOUT THE MAJOR CAENOGASTROPOD LINEAGES

It is apparent that the Caenogastropoda is a monophyletic group and, as far as living taxa are concerned, is sister to the heterobranchs. The basal taxa within the caenogastropods are the architaenioglossan groups, with some molecular results suggesting also the possible inclusion of the Campaniloidea and thus violating the monophyly of the original concept of Sorbeoconcha (all caenogastropods other than architaenioglossans). Cerithioidea is sister to the remaining caenogastropods (Hypsogastropoda) in most molecular and morphological analyses. Hypsogastropods are poorly resolved in morphological analyses. In the latest molecular analysis (Colgan *et al.* 2007) (Figure 13.15) and in our combined analysis (Figure 13.17), two groups of hypsogastropods are identified: asiphonate and siphonate clades. The asiphonate clade is not retrieved in the morphological analysis (Figure 13.16), but the siphonate clade is. In morphological analyses and our combined analysis the neogastropods are monophyletic, but rarely so in molecular analyses. The general lack of resolution in the hypsogastropods may be due to their very rapid radiation, particularly in the early Cenozoic.

ADAPTIVE RADIATIONS

Given our reassessed phylogeny, we now discuss how this assists in interpreting the extraordinary adaptive radiations undergone by caenogastropods and expressed in the great morphological, ecological, physiological, and behavioral diversity in the group.

While most are marine, benthic, and epifaunal, including many of the minute cerithioidean and hypsogastropod taxa that live on algae beneath stones and rocks, some burrow in sediment or even live interstitially. A few

hypsogastropods are pelagic (Janthinidae), or active swimmers (Pterotracheoidea, the heteropods). From our phylogeny, it is clear that these invasions of the water column have occurred independently from different benthic lineages. Other habits, such as burrowing (e.g., Naticidae, Terebridae, Olividae, Struthiolariidae) have also occurred independently. Vermetids are one of only two caenogastropod lineages that can directly cement their shells to hard substrates, sometimes even forming conspicuous intertidal zones, while hipponicids secrete a shelly plate with their foot, which is fused to the substrate independently of the shell. The other direct-cementing caenogastropod is an enigmatic freshwater taxon, *Helicostoa* (Lamy 1926), of probable rissooidean affinities. Some other taxa have independently adopted stationary lifestyles, embedded in corals or sponges (e.g., some Coralliophilidae, Siliquariidae), or their echinoderm host (some parasitic Eulimidae).

Several caenogastropod lineages have members that have independently undergone extensive freshwater radiations (Strong *et al.*, in press). It is uncertain as to whether the architaenioglossan Viviparidae and Ampullariidae shared a marine or a freshwater ancestor. The five families of cerithioideans that live in freshwater entered that habitat independently at least twice (Lydeard *et al.* 2002). The hypsogastropod rissooidean families Hydrobiidae *sensu lato*, Pomatiopsidae, and Bithyniidae probably entered freshwater independently, but there is insufficient evidence to demonstrate this in published analyses. However, some members of the predominantly brackish-water rissooidean families Assimineidae and Stenothyridae have also entered freshwater, as has one genus of Littorinidae. Interestingly, the movement into freshwater habitats is rare in higher hypsogastropods, with only a couple of Recent genera of neogastropods (Buccinidae and Marginellidae) having managed this transition, presumably via estuaries (Strong *et al.*, in press). Similarly, terrestriality has evolved several times. All members of the architaenioglossan Cyclophoroidea and

the hypsogastropod littorinoidean Pomatiidae are terrestrial, as are many species in the rissoidean Assimineidae and Truncatellidae, with members of the latter family having been shown to independently become fully terrestrial a number of times (Rosenberg 1996). No higher hypsogastropods occupy this habitat.

Most caenogastropods are small (< 10 mm in maximum dimension). For example, Bouchet *et al.* (2002) found that small taxa are among the most abundant and diverse caenogastropods in a tropical reef environment. The members of some families are mostly smaller than 5 mm, for example the hypsogastropod rissooideans, cingulopsoideans, most Triphoroidea, Eulimoidea, and Marginellidae, many Columbelloidea and Turridae *sensu lato*, with some a little less than a millimeter in maximum shell dimension. At the other end of the scale, members of some of the higher hypsogastropod carnivorous groups achieve a size of 30 cm or more (e.g., Ranellidae, Bursidae, Cassidae, Volutidae, Fasciariidae, Turbinellidae, and Melongenidae), while members of other hypsogastropod families attain more than 20 cm (e.g., Strombidae, Tonnidae, Buccinidae, and Muricidae). Large size is also attained by some non-hypsogastropods, including Ampullariidae, Campanilidae, Potamididae, and Cerithiidae.

One of the hallmarks of caenogastropod evolution is modification of the mantle cavity organs, with only the left (monopectinate) gill, osphradium, and hypobranchial gland being retained. The move from exhalant to inhalant control of the water currents through the mantle cavity was seen by Ponder and Lindberg (1997) as a critical innovation of the Sorbeoconcha that enabled better utilization of the chemosensory function of the osphradium and is correlated with its enlargement and the development (probably independently in several lineages) of an anterior siphon. Adoption of a semiterrestrial or terrestrial lifestyle resulted in the atrophy or loss of the ctenidium in those lineages and with the development of a lung in the amphibious Ampullariidae.

Feeding strategies range from the supposedly ancestral deposit feeding and surface grazing in most architaenioglossans, cerithioideans, and lower hypsogastropods to herbivory, grazing carnivory, or active predation and, in Eulimidae and a few neogastropods, parasitism. Some hypsogastropod families show a range of feeding habits, with cypraeids grazing on algae or sponges and triviids on algae, sponges, and tunicates. By way of contrast, the related ovulids feed exclusively on soft corals and the velutiniids on tunicates. Such specialization in carnivorous feeding appears to be the norm in many groups; for example, within the ptenoglossan taxa the Triphoroidea (Cerithiopsidae and Triphoridae) feed exclusively on sponges, the epitonoideans on cnidarians, and the eulimoideans on echinoderms. In the neogastropods mitrids feed exclusively on sipunculids, coralliophillines on soft and hard corals, and turrids (*sensu lato*) on polychaetes. Some neogastropod families appear to be more generalist; in marginellids (*sensu lato*), for example, some species graze on bryozoans or tunicates, a few are mollusc shell drillers, and some are suctorial fish feeders (discussed later). Some columbellids are carnivores, and others have become herbivores (deMaintenon 1999). Nassariidae are primarily scavengers (e.g., Morton 2003), but at least one has reverted to selective deposit feeding (Connor and Edgar 1998). Tonnoideans feed on a range of prey including echinoderms, molluscs, and tunicates, although some are more specialized at the family level.

Most carnivorous hypsogastropods feed by biting or rasping at their prey, but the ability to swallow large prey intact has evolved in at least two lineages: the tonnids (Tonnoidea), which engulf entire holothurians, and the fish-eating conids (Conoidea). Other conids and other conoideans (Turridae *sensu lato* and Terebridae) engulf polychaete worms. A few groups feed suctorially, with some cancellariids (O'Sullivan *et al.* 1987) feeding on resting rays (Elasmobranchia), while some colubariids and marginellids suctorially feed

on sleeping parrot fishes (Bouchet and Perrine 1996). Eulimidae feed suctorially on their echinoderm hosts. The hypsogastropod families Naticidae and Muricidae have long been known to drill holes in the shells of their prey and have independently evolved accessory boring organs (Carriker and Gruber 1999). A few other groups also drill their prey (marginellids, Ponder and Taylor 1992; buccinids, Morton 2006; cassids, Hughes and Hughes 1971; Hughes 1986a), but the mechanisms involved have not yet been investigated in detail. Other ways of entering shelled prey have been evolved, including forced entry to bivalves using a spine on the aperture of the predator, a mechanism that has independently evolved in several neogastropod families (Vermeij and Kool 1994).

Macroherbivory is uncommon, with the Strombidae and Ampullariidae being the main groups engaging in this type of feeding, and it is seen in some cypraeids and columbellids (Neogastropoda). This feeding mode is derived within the columbellids (deMainetenon 1999) and Stromboidea because, in the latter case, the ancestral (and paraphyletic; Roy 1994) Aporrhaidae are deposit feeders (as are the stromboideans' sister group, Xenophoroidea). Another stromboidean family, Struthiolariidae, filter feeds (Morton 1951). Other filter (suspension)-feeding taxa have also evolved independently: architaenioglossan Vivipariidae (Viviparoidea), the cerithioidean Turritellidae and Siliquariidae, and, within the hypsogastropods, the Vermetidae (Vermetoidea),¹¹ Bithyniidae (Rissooidea), Calyptraeidae (Calyptraeidea), and Capulidae (*Trichotropis*) (Capuloidea) as well as the Struthiolariidae previously noted. Similar structures (elongated gill filaments, endostyle, food groove) associated with this feeding mode have convergently

developed in these taxa. Many vermetids use a mucus net secreted by pedal glands to ensnare floating food.

Apart from overall shell thickening and the adoption of cryptic habits, some other adaptive changes to caenogastropod shells appear to be responses to predation. These include the development of terminal growth, allowing thickening of the aperture, including the formation of varices and/or spines, as a defense against crab predation in particular (e.g., Vermeij and Signor 1992). Some velutinids employ chemical defense (e.g., Andersen *et al.* 1985), and dramatic escape responses have also evolved in some taxa, as has the convergent autotomy of the posterior end of the foot (e.g., some cypraeids, Burgess 1970; *Harpa*, e.g., Liu and Wang 2002) or mantle (e.g., *Ficus*, Liu and Wang 2002), a mechanism that has also independently evolved in some other groups of gastropods (notably stomatelline trochids).

One of the major innovations in caenogastropod ancestors was internal fertilization. The advent of planktotrophy was also a significant hallmark of the group and may have been associated with internal fertilization, enabling the production of encapsulated eggs and thus allowing larvae to undergo their early development in a protected environment to be released as veligers. A consequence of this was the ability to forgo a planktonic larval stage—so-called direct development, either within an external capsule or in capsules or eggs retained in a brood pouch within the animal. Various mechanisms have been evolved within caenogastropods to provide nutrients to such embryos. These include yolk, albumen, infertile eggs ("nurse eggs"), and cannibalism (adelphophagy). Although there appears to be considerable variation in some groups, particularly the neogastropods, mapping the distribution of these strategies phylogenetically within families and superfamilies will undoubtedly be informative. Egg encapsulation and intracapsular development also facilitated invasion of marginal marine and nonmarine habitats.

11. For an alternative view see Simone (2001), who treats vermetids and turritellids as closely related taxa within Cerithioidea, as was the case in earlier literature (e.g., Thiele 1929).

GAPS IN KNOWLEDGE AND FUTURE STUDIES

Following are some of the significant phylogenetic questions relating to caenogastropods that remain to be resolved using a variety of approaches:

Which extinct lineage is the sister taxon of caenogastropods?

What are the monophyletic groups in the “architaenioglossan” grade?

Is Sorbeoconcha a monophyletic group?

What are relationships within the Hypsogastropoda?

What are the main monophyletic groupings?

What are the relationships of “ptenoglossan” groups?

Establish the composition of the smallest monophyletic group including neogastropods and, if Neogastropoda are monophyletic, identify their sister taxon.

Are some of the large, diverse groups currently recognized as families or superfamilies (e.g., Rissooidea) monophyletic?

To achieve answers to these questions, the numerous gaps in our knowledge need to be addressed. Many characters and character complexes need to be reexamined in a phylogenetic context, and more taxa need to be examined in detail, using histology and ultrastructure as well as examining physiological and functional aspects.

With morphological data, there are still few published studies on the anatomy of many family-level taxa, and in some cases we are still relying on accounts over 100 years old. While there are good data sets available for some families, for others typically only one or a few species have been anatomically described, and often these are known somewhat superficially. Histological data is often not provided, and details are sometimes superficial or lacking for organ systems such as the renopericardial and nervous systems. A good sampling of ultrastructural data is lacking for all systems other than sperm and osphradia. Given that these two systems have contributed so much to our

understanding of gastropod phylogenetics, the potential for substantial new contributions via ultrastructure is considerable.

DEVELOPMENTAL AND GENOMIC DATA

Although the few available items of developmental data appear to be informative with very promising potential, many additional studies are required. Even basic information on spawn and egg capsules has phylogenetic potential but has been little utilized because of many gaps in the available data. Similarly, organogenesis is a key to understanding many of the homology issues, but, again, very few studies have been undertaken.

DNA SEQUENCE DATA

DNA sequence data has only recently begun to add significant insights into caenogastropod phylogeny, but interesting hypotheses are now emerging. These include the close relationships of Littorinidae with heteropods and the association of Campaniloidea with Ampullariidae and Cyclophoridae. A stable understanding of the main lineages within Caenogastropoda will, however, likely require at least double or triple the numbers of aligned base positions and three times the taxa that have already been sequenced. Mitochondrial gene order has hardly been looked at despite its significance in some other gastropods, with changes recently demonstrated even within single families (Vermetidae, Rawlings *et al.* 2001; Ampullariidae, Rawlings *et al.* 2003).

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