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Pergamon

Zoologica Scripta, Vol. 27, No. 4, pp. 361–372, 1998
Elsevier Science Ltd

PII: S0300-3256(98)00017-8 0300-3256/98 $19.00+0.00

Phylogenetic relationships of the lower Caenogastropoda (Mollusca, Gastropoda, Architaenioglossa, Campaniloidea, Cerithioidea) as determined by partial 18S rDNA sequences

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Accepted 9 June 1998

Harasewych, M. G., Adamkewicz, S. L. Plassmeyer, M. & Gillevet, P. M. 1998. Phylogenetic relationships of the lower Caenogastropoda (Mollusca, Gastropoda, Architaenioglossa, Campaniloidea, Cerithioidea) as determined by partial 18S rDNA sequences.—*Zool. Scr. 27:* 361–372.

Phylogenetic analyses of partial sequences spanning approximately 450 nucleotides near the 5′ end of the 18S rDNA strongly support the monophyly of Apogastropoda and its constituent clades, Caenogastropoda and Heterobranchia. Representatives of the architaenioglossan groups Cyclophoroidea, Ampullariidae and Viviparidae invariably emerge within Caenogastropoda in all analyses. While the Cyclophoroidea and Ampullariidae are monophyletic, the varying position of Viviparidae in all outcomes contradicts its hypothesized sister group relationship with Ampullariidae, and thus the monophyly of Ampullarioidea. Because of the position of Viviparidae, Architaenioglossa does not emerge as a clade in any of our analyses. *Campanile* consistently emerges between Cyclophoroidea and Cerithioidea, or in a clade with Cyclophoroidea and Ampullariidae, a position not predicted by previous morphological studies. Maximum parsimony analyses of sequence data show Caenogastropoda to comprise a series of sequentially diverging higher taxa. However, maximum likelihood analyses as well as maximum parsimony analyses using only transversions divide Caenogastropoda into two clades, one containing the architaenioglossan taxa, Campaniloidea and Cerithioidea, the other containing the higher caenogastropod taxa included in Eucaenogastropoda (Haszprunar, 1988) [=Hypsogastropoda (Ponder & Lindberg 1997)]. Denser taxon sampling revealed insertions to be present in the 18S rDNA gene of several caenogastropod taxa. Earlier reports (Harasewych *et al.* 1997*b*) of reduced sequence divergence levels in Caenogastropoda are shown to be restricted to Hypsogastropoda. Based on a broader taxonomic sampling, divergence levels within Caenogastropoda are comparable to those found within Heterobranchia. © 1998 The Norwegian Academy of Science and Letters

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Introduction

The higher classification of the molluscan class Gastropoda has remained static for much of the twentieth century, with most textbooks and reference works currently in use incorporating an arrangement that was proposed by Thiele (1929–1931) and only slightly modified by Wenz (1938–1944). Perhaps catalyzed by a reassessment of prosobranch systematics begun by Golikov & Starobogatov (1975), the past two decades have witnessed a renewed interest in re-evaluating relationships among higher gastropod taxa using large suites of anatomical, ultrastructural and molecular characters, and, more recently, cladistic methodology (*e.g.*, Salvini-Plawen 1980, 1991; Salvini-Plawen & Haszprunar 1987; Haszprunar 1988; Ponder & Lindberg 1996, 1997; Salvini-Plawen & Steiner 1996; Healy 1988, 1996; Tillier *et al.* 1992, 1994; Rosenberg *et al.* 1994, 1997; Harasewych *et al.* 1997*a,b*). These recent studies converge on a broad outline of the evolutionary history of Gastropoda, one significantly different from that formulated by Thiele and Wenz. Nevertheless, the placement and/or composition of a number of key higher taxa remain unresolved or subject to conflicting interpretations. Among these are early radiations of land and fresh-water taxa collectively termed the Architaenioglossa, and the superfamily Campaniloidea, represented in the Recent fauna by a single, relict species. Both groups figure prominently in the early history of the Caenogastropoda, the superorder that contains the majority of living, shelled, marine gastropods.

Architaenioglossa has long been recognized as a tentative assemblage of terrestrial and fresh-water groups that could not be included elsewhere yet "bear little resemblance to one another" (Thiele 1929). The group originally consisted of four families, the terrestrial Cyclophoridae, and the fresh-water Viviparidae, Ampullariidae, and Lavi-

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geriidae (Thiele 1929; Wenz 1943), although the Lavigeriidae were subsequently transferred to the Cerithioidea (Morrison 1954). Most traditional classifications have placed the architaenioglossan families at the base of Caenogastropoda or its paraphyletic component, Mesogastropoda (*e.g.*, Thiele 1929; Wenz 1943; Taylor & Sohl 1962; Boss 1982; Ponder & Warén 1988; Vaught 1989). Architaenioglossa was elevated to ordinal rank (Golikov & Starobogatov 1975; Ponder & Warén 1988) to include the superfamilies Cyclophoroidea and Ampullarioidea (as Viviparioidea), the latter containing the families Ampullariidae (as Pilidae) and Viviparidae. Golikov & Starobogatov (1975) (Fig. 1A) regarded Architaenioglossa to constitute a lineage not closely related to taxa included in Caenogastropoda by most authors. Haszprunar (1988) (Fig. 1C) placed Architaenioglossa outside the Caenogastropoda, as sister group to Apogastropoda [=Caenogastropoda + Heterobranchia, as redefined by Ponder & Lindberg, 1997]. This position was reaffirmed by the phylogenetic analyses of Salvini-Plawen & Steiner (1996) (Fig. 1D). However, the analyses of Ponder & Lindberg (1996, 1997) (Fig. 1E and 1F, respectively) indicate that Architaenioglossa emerge within Caenogastropoda, as sister group to all remaining caenogastropod taxa.

The monophyly of Architaenioglossa has been questioned by many recent authors (*e.g.*, Sitnikova & Starobogatov 1982; Haszprunar 1988; Salvini-Plawen & Steiner 1996; Ponder & Lindberg 1997), who noted the absence of well defined synapomorphies to unite the Cylcophoroidea and Ampullarioidea. Haszprunar (1988: 415) further observed that the monophyly of Ampullarioidea is not well supported, since apart from sharing a specialized osphradium, the Ampullariidae and Viviparidae are "remarkably dissimilar" in their nervous, respiratory and excretory systems. Healy (1996) reported that Cyclophoroidea, Ampullarioidea and Cerithioidea share a series of specialized eusperm and parasperm features, and form a distinct group within Caenogastropoda.

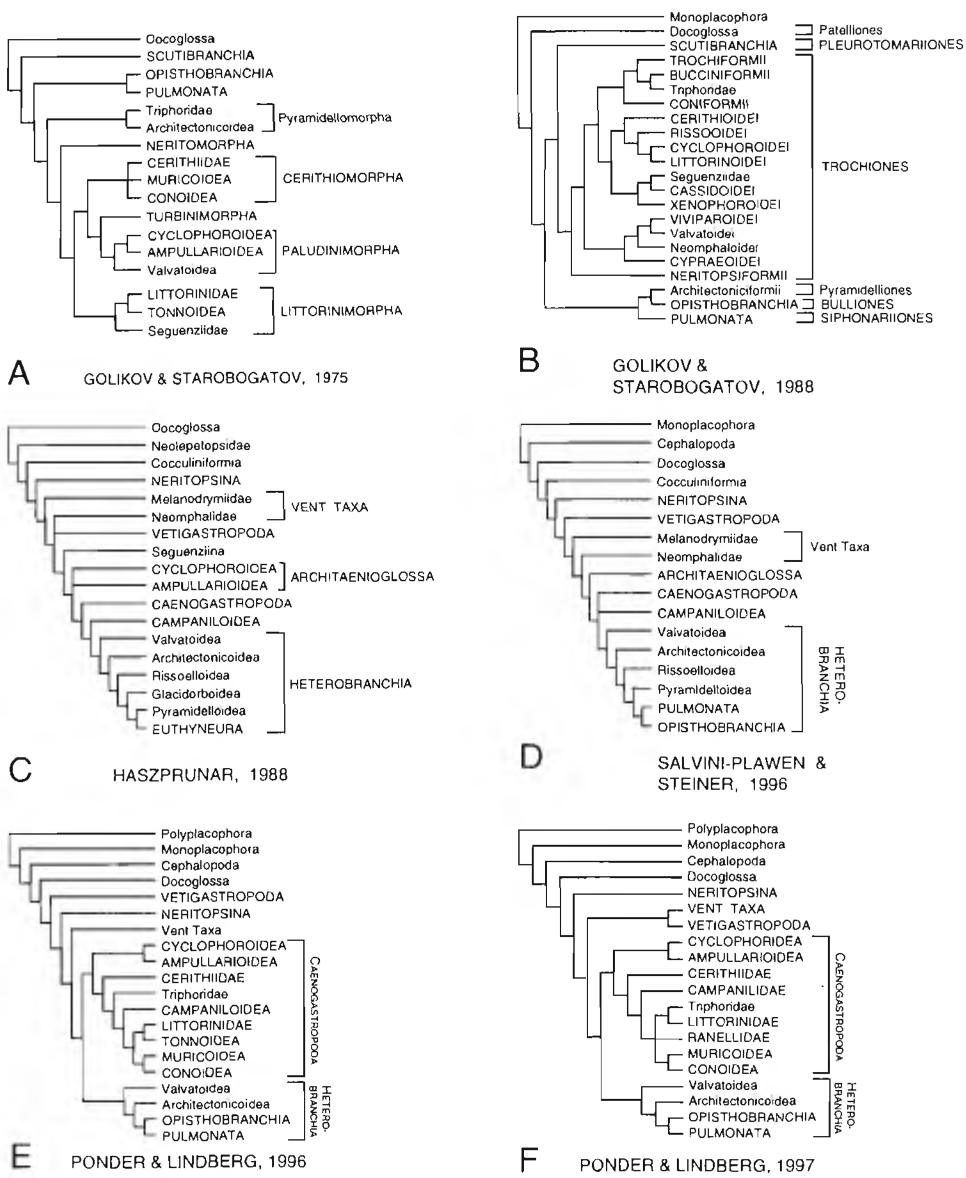

Fig. 1. Recent morphology-based hypotheses of gastropod evolution. Nomenclature and taxon rank have in some instances been modified to facilitate comparisons. Taxa listed in UPPER CASE are represented in the present study.—A. Golikov & Starobogatov (1975: fig. 6).—B. Golikov & Starobogatov (1988: composite of figures 2, 3, 6, 9, 16, 17 and 27).—C. Haszprunar (1988: fig. 5).—D. Salvini-Plawen & Steiner (1996: composite of figures 2.6 and 2.7).—E. Ponder & Lindberg (1996: fig. 11.3 D).—F. Ponder & Lindberg (1997: fig. 5).

In a detailed study of architaenioglossan systematics, Sitnikova & Starobogatov (1982) transferred Cyclophoridae (as Cyclophoroidea) and Ampullariidae (as Pilidae) to Littorinimorpha, while retaining the Neocyclotoidea and Viviparoidea together with the newly added Pomatioidea, Archimedielloidea and Valvatoidea in their order Vivipariformes, which, together with Cypraeiformes, comprises their superorder Vivipariformii. Apart from Golikov & Starobogatov (1988) (Fig. 1B) this arrangement had not gained widespread acceptance.

Until the publication of a detailed anatomical study of *Campanile symbolicum* Iredale, 1917, the only living species of Campanilidae (Houbrick 1981), this family had been included within the superfamily Cerithioidea. The distinctive anatomical organization of this species prompted Salvini-Plawen & Haszprunar (1987) and Haszprunar (1988) to place Campanilidae between the rest of the Caenogastropoda and the Allogastropoda + Euthyneura [= Heterobranchia]. Haszprunar (1988) proposed the new suborder Campanilimorpha to reflect the phylogenetic position of *Campanile*. Houbrick (1989) revised his earlier work and placed this genus in the superfamily Campaniloidea, which he regarded to be an early radiation from the stem-group that gave rise to "modern" Cerithioidea and Caenogastropoda. Healy (1996) noted that, based on sperm morphology, the Campaniloidea, in which he included Campanilidae and Plesiotrochidae (previously also considered to be a cerithioidean), comprise a separate group within Caenogastropoda, one that shares more features with Architaenioglossa and Cerithioidea than with the remaining caenogastropods. In the phylogenetic analyses of Salvini-Plawen & Steiner (1996) (Fig. 1D) the Campanilidae emerged as an unresolved polytomy with the Caenogastropoda and Heterobranchia, indicating that it may be sister taxon either to Caenogastropoda, Heterobranchia, or to Apogastropoda.

Ponder & Lindberg (1996) (Fig. 1E) placed Campanilidae within Caenogastropoda, and hypothesized that it diverged after Triphoridae to become sister taxon to the higher caenogastropods. In a revised version of their phylogeny (Ponder & Lindberg, 1997) (Fig. 1F), the Campanilidae is shown to diverge after the Cerithioidea, as sister group to the "higher caenogastropods" [Hypsogastropoda Ponder & Lindberg, 1997 = Eucaenogastropoda Haszprunar, 1988], which this time include the Triphoridae.

With a single exception, neither *Campanile* nor any architaenioglossan taxon have previously appeared in a molecular phylogeny of the Gastropoda. Partial sequences of the 18S rDNA gene have provided independent support for the monophyly of the Apogastropoda and its component subclades Caenogastropoda and Heterobranchia (Harasewych *et al.* 1997*a*, *b*). While this portion of the 18S rDNA gene was unable to resolve the relationships among families of Neogastropoda, or even between neogastropods and higher caenogastropods (Harasewych *et al.* 1997*b*), it unequivocally placed the single architaenioglossan (*Cipangopaludina*) included in that study within Caenogastropoda, uniting it with the only cerithiid (*Cerithium*) as the basal clade in Caenogastropoda. At the time, it was unclear whether the insertion in helix 10 of *Cipangopaludina* might be a diagnostic synapomorphy of Architaenioglossa, or whether it has a more limited distribution.

As in the previous papers in this series (Harasewych *et al.* 1997*a*, *b*), the principle objectives of this study are to investigate the major features of gastropod evolution using molecular data, and to provide an independent database to test morphology-based hypotheses of gastropod phylogeny. The present paper reports the results of an investigation into the evolutionary relationships of the Campaniloidea and representative species from the major architaenioglossan groups using sequences derived from a portion of the 18S rDNA gene.

Material and methods

With the exception of *Campanile symbolicum*, all the taxa newly sequenced for this study were freshly collected, frozen while living, transported to the laboratory on dry ice, and maintained at −80 °C until DNA was extracted. Previously published sequences were obtained from GenBank, GSDB, or EMBL. Table I lists the taxa used in this study, together with their collection localities, the tissues extracted, voucher specimen information and sequence accession numbers. Protocols for DNA extraction and PCR amplification, including primers for amplifying and sequencing the 18S rDNA gene region, are identical to those reported in Harasewych *et al.* (1997*a*). Amplification products were purified using Wizard PCR Purification Kits (Promega) and sequenced on an Applied Biosystems 373A fluorescent sequencer using Prism Sequencing Kits according to the manufacturer's protocol. Consensus sequences for each taxon were generated from the assembly of two sequences from each of the four sequencing primers (*i.e.*, 2 in the forward direction, 2 in the reverse direction) using Sequencher 3.0 for the Macintosh (Gene Codes Corp.)

A database consisting of confirmed consensus sequences from each taxon was assembled and viewed using a custom version of Genetic Data Environment (GDE Version 2.0) (Smith *et al.* 1994) on a Sun Sparc10 Computer. The multiple sequences were aligned with CLUSTAL V (Higgins *et al.* 1992) using default settings. Minor adjustments, primarily in the regions of the inserts, were done by hand. Individual sequences were submitted to the public sequence database via GenBank. Aligned sequences are available in nexus format from the corresponding author.

Maximum parsimony analyses were computed using PAUP 4.0.0d63 (Swofford 1997, ppc beta test version) on a Power Macintosh 6100/66. All characters were treated as unordered and weighted equally. Gaps were treated as missing data. Bootstrap (BP) and Jackknife (JK) analyses (1000 replicates) were performed using full heuristic searches with random addition sequences (10 repetitions). Support indices (Bremer 1988) were calculated using TreeRot (Sorenson 1996). The maximum likelihood analysis was run using PAUP 4.0.0d63 for UNIX on a Silicon Graphics Octane Computer. Pairwise comparisons of sequences were calculated using MEGA (Kumar *et al.* 1993), while the effects of alterations in tree topology on tree length were determined using MacClade 3.05 (Maddison & Maddison 1992).

Results

Partial 18S rDNA sequences from near the 5′ end of the gene were determined for *Campanile symbolicum*, four species of Architaenioglossa and six species representing four additional superfamilies of caenogastropods. These were aligned against previously published sequences from eight caenogastropods, including one architaenioglossan, as well as two heterobranchs, two neritopsines and two vetigastropods, which serve as nested outgroups (see Table I for sources). This portion of the gene corresponds to positions 60 to 515 of the 18S rRNA sequence of *Onchidella celtica* (Cuvier 1817) and spans helices 6–17 of the ribosomal RNA (Fig. 2A,a) (see Winnepenninckx *et al.* 1994: 101, fig. 1). The multiple sequence alignment spans 517 positions (Fig. 2, Appendix 1), although length of the gene

Table I. *Locality data, tissues extracted, voucher specimen information, and sequence accession numbers for taxa used in this study*

TAXON	Collection locality	Tissue	Voucher material	Sequence accession number 18 S rDNA
VETIGASTROPODA				
FISSURELLOIDEA				
Diodora cayenensis (Lamarck, 1822)	Sebastian Inlet, FL, USA	Buccal muscle	USNM 888660	† GSDB L78884
TROCHOIDEA				
Astraea caelata (Gmelin, 1791)	Berry Is., Bahamas	Buccal muscle	USNM 888603	† GSDB L78886
NERITOPSINA				
NERITOIDEA				
Nerita versicolor Gmelin, 1791	Big Pine Key, FL, USA	Buccal muscle	USNM 888658	† GSDB L78882
Neritina reclivata (Say, 1822)	Big Pine Key, FL, USA	Buccal muscle	USNM 888659	† GSDB L78883
CAENOGASTROPODA				
"ARCHITAENIOGLOSSA"				
CYCLOPHOROIDEA				
Cyclophorus hirasei Pilsbry, 1901	Amami-O-Shima, Japan	Buccal muscle	USNM 888710	GB AF055644
Neocyclotus seminudus (C. B. Adams, 1852)	Windsor, Jamaica	Buccal muscle	USNM 888718	GB AF055645
"AMPULLARIOIDEA"				
Ampullariidae				
Pomacea bridgesi (Reeve, 1856)	Lake Worth, FL, USA	Buccal muscle	USNM 888715	GB AF055646
Marisa cornuarietis (Linneus, 1758)	Fort Myers, FL, USA	Buccal muscle	USNM 888713	GB AF055647
Viviparidae				
Cipangopaludina japonica (von Martens, 1860)	Yao, Osaka, Japan	Brooded juvenile	USNM 888674	‡ GB U86304
"NEOTAENIOGLOSSA ?= SORBEOCONCHA"				
CAMPANILOIDEA				
Campanile symbolicum Iredale, 1917	Rottnest Is, WA, Australia	Foot muscle	AMS C.203211	GB AF055648
CERITHIOIDEA				
Cerithium atratum (Born, 1778)	Sebastian Inlet, FL, USA	Buccal muscle	USNM 888663	† GSDB L78895
Batillaria minima (Gmelin, 1791)	Sebastian Inlet, FL, USA	Buccal muscle	USNM 888719	GB AF055649
Modulus modulus (Linneus, 1758)	Key Largo, FL, USA	Buccal muscle	USNM 888720	GB AF055650
HYPSOGASTROPODA = EUCAENOGASTROPODA ?= SORBEOCONCHA				
LITTORINOIDEA				
Littorina littorea (Linneus, 1758)	Genbank ex Winnepenninckx *et al.*, 1996			EMBL X91970
Tectarius muricatus (Linneus, 1758)	Missouri Key, FL, USA	Buccal muscle	USNM 888708	GB AF055651
Annularia fimbriatula	(Sowerby, 1825) Windsor, Jamaica	Buccal muscle	USNM 888714	GB AF055652
TRUNCATELLOIDEA				
Truncatella guerinii Villa, 1841	Amami-O-Shima, Japan	Buccal muscle	USNM 888712	GB AF055653
XENOPHOROIDEA				
Xenophora exutum Reeve, 1843	Minabe, Japan	Buccal muscle	USNM 888631	† GSDB L78896
CYPRAEOIDEA				
Cypraea tigris Linneus, 1758	Minabe, Japan	Buccal muscle	USNM 888621	GB AF055664
TONNOIDEA				
Fusitriton oregonense (Redfield, 1848)	Dutch Harbor, AK, USA	Buccal muscle	USNM 888634	† GSDB L78897
NEOGASTROPODA				
BUCCINOIDEA				
Busycon carica (Gmelin, 1791)	Cape Henlopen, DE, USA	Buccal muscle	USNM 888705	‡ GB U86306
"VOLUTOIDEA"				
Oliva sayana Ravenel, 1834	Ft. Pierce, FL, USA	Buccal muscle	USNM 888605	† GSDB L78898
CONOIDEA				
Hastula cinerea (Born, 1778)	Ft. Pierce, FL, USA	Buccal muscle	USNM 888611	† GSDB L78899
HETEROBRANCHIA				
EUTHYNEURA				
OPISTHOBRANCHIA				
Aplysia dactylomela Rang, 1828	Minabe, Japan	Buccal muscle	USNM 888624	† GSDB L78902
PULMONATA				
Siphonaria pectinata (Linneus, 1758)	Sebastian Inlet, FL, USA	Buccal muscle	USNM 888707	‡ GB U86321

AMS = Mollusk Collection, Australian Museum, Sydney; EMBL = European Molecular Biology Laboratory Data Library; GB = GenBank; GSDB = Genome Sequence Data Bank; USNM = Mollusk collection, National Museum of Natural History, Smithsonian Institution. † = data from Harasewych *et al.*, 1997*a*; ‡ = data from Harasewych *et al.*, 1997*b*. Higher taxa in quotes (" ") are paraphyletic.

ranges between 426 base pairs (bp) (*Xenophora*) and 489 bp (*Truncatella*) among the 25 taxa in this study. Most of the length variation occurs in two regions of insertions, one within the terminal loop of helix 10 (aligned positions 136–165, Fig. 2A,b i1), the other at the terminal stem and loop of helix E-10-1 (aligned positions 208–242, Fig. 2A, b i2). *Truncatella* contains a 30 bp insert that spans the first insert region. *Pomacea* and *Marisa* contain identical 9 bp inserts in this region, while *Campanile* contains a 9 bp insert that differs in only one position from those of the two ampullariids. The 13 bp insert present in *Cipangopaludina* overlaps with only a small portion of the ampullariid and *Campanile* inserts. The remaining taxa in this study contain 0–5 bp in this region, which provisionally align with portions of the *Truncatella* and *Cipangopaludina* sequences, but not with the ampullariid nor the *Campanile* inserts. The second, slightly larger region contains inserts that vary in length from 3 bp (*Cerithium*, *Fusitriton*, neogastropods) to 23 bp (*Truncatella*) and are more difficult to align.

Eight unique, single-nucleotide insertions (aligned positions 7, 25, 190, 339, 358, 388, 443, 508) were excluded from all phylogenetic analyses. Of the remaining 509 aligned positions, 361 were constant, and 62 were parsimony

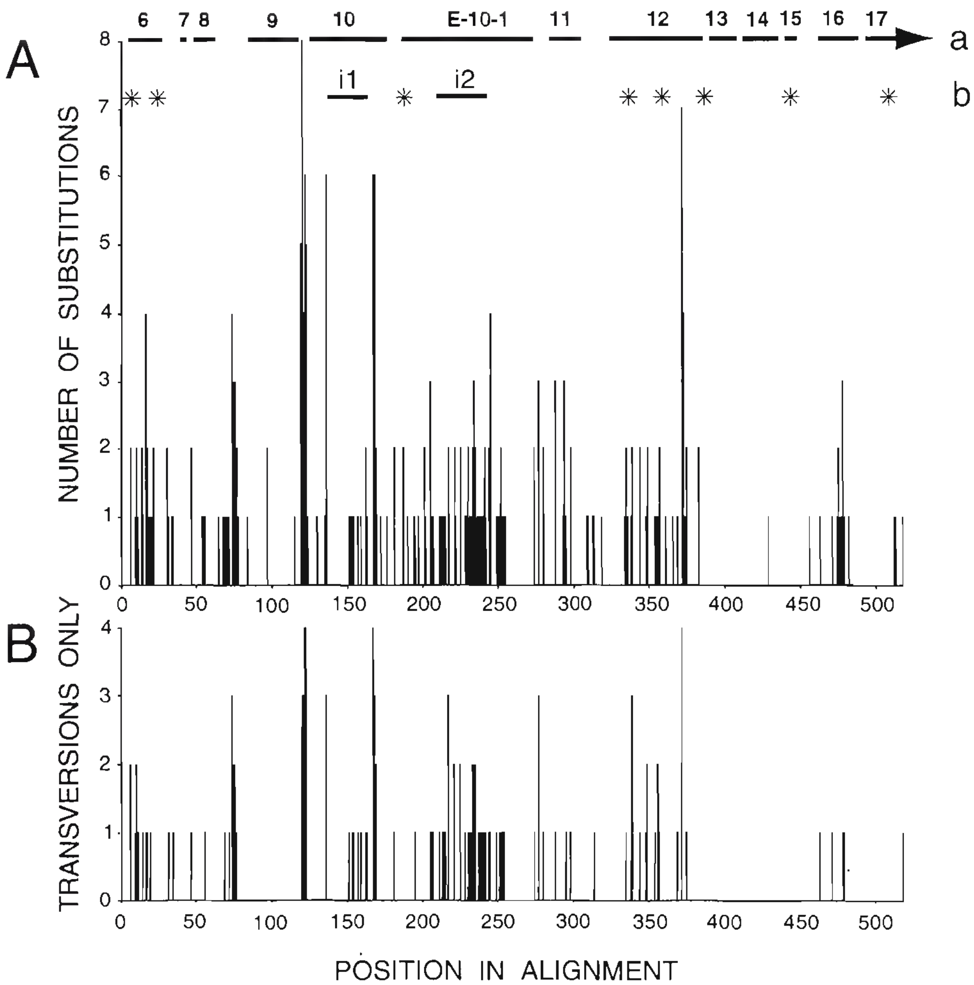

Fig. 2. Variation in sites along the portion of the 18S rDNA gene among the 25 taxa in this study (Table 1).—A. Distribution of variable sites (transitions + transversions).—a. Positions of helices (based on Winnepenninckx *et al.* 1992: fig. 1).—b. Positions of bases excluded from phylogenetic analyses (*) because they were unique, single-nucleotide insertions. i1 = first insert region, i2 = second insert region.—B. Distribution of variable sites (transversions only).

uninformative. Maximum parsimony analyses (branch-and-bound searches using ACCTRAN as well as DELTRAN character optimizations, with multiple states treated as uncertainties, and addition sequence = furthest) each produced two equally parsimonious trees of length 254 (CI = 0.752, RI = 0.772, RC = 0.580) that differed only in whether or not *Fusitriton* was resolved from the neogastropods (*Busycon*+*Oliva*+*Hastula*). Figure 3A illustrates the tree in which *Fusitriton* was resolved. Results of bootstrap/jackknife analyses (1000 replicates) appear above/below those nodes supported at levels above 50%. Hillis & Bull (1993) have shown that, under optimal conditions, bootstrap proportions $\geqslant$70% correspond to a probability of $\geqslant$95% that the corresponding clade is real. Support indices (Bremer 1988) are shown in bold italic. Specifying the Neritopsina to be the outgroup did not alter the results other than to move the root from position A to position B in figure 3A. An identical series of analyses was performed after the two insert regions (Fig. 2A,b, i1+i2) were excluded, resulting in a data set of 444 characters, of which 328 were constant and 38 parsimony uninformative. The 78 informative characters produced six equally parsimonious trees of length 212 (CI = 0.726, RI = 0.781, RC = 0.567). These trees varied in the position of *Campanile* relative to Cyclophoroidea (immediately above, immediately below, or as sister taxon to) as well as in the resolution of *Fusitriton* from Neogastropoda. Figure 3B shows the strict consensus of these six trees, together with bootstrap/jackknife support for nodes supported at levels above 50% and support indices.

An additional pair (ACCTRAN and DELTRAN optimizations) of maximum parsimony analyses were conducted on the data set from which the two inserts were deleted, this time utilizing only transversions as characters (Fig. 3C). The branch and bound search using 44 parsimony informative characters yielded 63 equally parsimonious trees (L = 98, CI = 0.643, RI = 0.767, RC = 0.493). This reduced data set supports the same relationships among the Vetigastropoda, Neritopsina, Caenogastropoda and Heterobranchia as the previous analyses, but differs in dividing Caenogastropoda into two clades, one grouping *Campanile* with the architaenioglossan and cerithioidean taxa, the other clade containing the higher Caenogastropoda and corresponding to the Eucaenogastropoda of Haszprunar (1988) and the Hypsogastropoda of Ponder & Lindberg (1997). Figure 3C shows the strict consensus of these 63 trees together with bootstrap/jackknife and Bremer support indices for the nodes.

A maximum likelihood analysis of the data set from

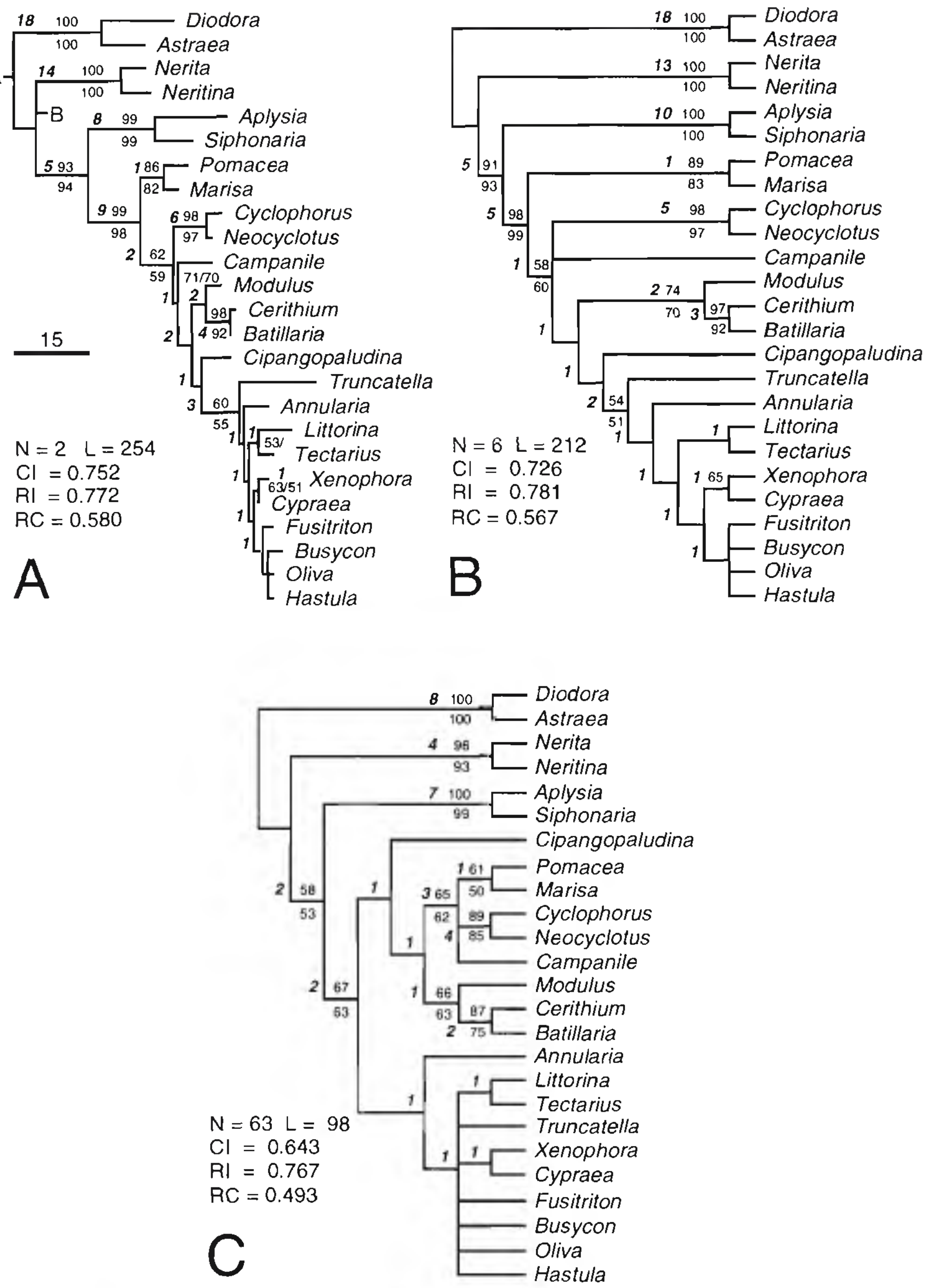

Fig. 3. Maximum parsimony analyses of phylogenetic relationships among the Apogastropoda [sensu Ponder & Lindberg 1997 = Caenogastropoda + Heterobranchia] based on 517 aligned positions (426–489 bp) of 18S rDNA sequence.—A. One of two maximum parsimony trees produced when only the eight unique, single-nucleotide insertions were excluded from data. Tree rooted at A when *Diodora* + *Astraea* selected as outgroup, rooted at B when *Nerita* + *Neritina* selected as outgroup.—B. Strict consensus of six most parsimonious trees produced when the eight unique single-nucleotide insertions as well as the two insert regions (fig. 2Ab, i1 + i2) were excluded from data.—C. Strict consensus of 63 most parsimonious trees produced when eight unique single-nucleotide insertions as well as the two insert regions were excluded, and only transversions used as characters. Bootstrap proportions given in % above, and jackknife proportions given in % below nodes supported at levels above 50%. Bremer support indices are shown in bold italics.

which the two insert regions were deleted was performed using a heuristic search. Nucleotide frequencies, proportion of invariable sites, and transition/transversion ratios were all estimated via maximum likelihood. Rates for variable sites were assumed to follow a gamma distribution with the shape parameter estimated using maximum likelihood. The number of rate categories = 4, with the average rate for each category represented by the mean. The Hasegawa-Kishino-Yano (1985) model with rate heterogeneity was used. Starting trees were obtained via neighbor-joining. The strict consensus of the three resulting trees, shown in fig. 4, divides the Caenogastropoda into the same two clades as the transversion parsimony analysis, one containing *Campanile*, Cerithioidea and the paraphyletic Architaenioglossa, the other the Hypsogastropoda.

Discussion

While the majority of morphological studies (*e.g.*, Haszprunar 1988; Salvini-Plawen & Steiner 1996; Ponder & Lindberg 1997) indicate that Vetigastropoda are more closely related to Apogastropoda than are Neritopsina, others (*e.g.*, Ponder & Lindberg 1996) indicate a closer relationship between Neritopsina and Apogastropoda. Molecular studies (*e.g.*, Rosenberg *et al.* 1994; Harasewych *et al.* 1997*a*) also favor Vetigastropoda as a more proximal outgroup to Apogastropoda. However, Harasewych *et al.* (1997*a*: 14) reported that the position of Neritopsina was strongly influenced by the choice of outgroup. In their study, Neritopsina emerged basal to Vetigastropoda when polyplacophorans served as outgroup. However, when *Nautilus* was specified as outgroup, Neritopsina emerged between Vetigastropoda and Apogastropoda. Representatives of both Vetigastropoda and Neritopsina have therefore been included in the present study. Designation of one or the other as outgroup did not alter tree topology, only the position of the root (Fig. 3A, root A for Vetigastropoda as outgroup, root B for Neritopsina as outgroup).

As in prior studies based on partial (Harasewych *et al.* 1997*a,b*) and entire (Winnepenninckx *et al.* 1998) 18S rDNA sequences, all of the maximum parsimony (Fig. 3) and maximum likelihood analyses (Fig. 4) strongly support the monophyly of Apogastropoda and its constituent clades, Caenogastropoda and Heterobranchia. Each of the analyses is also unequivocal in placing all of the architaenioglossan taxa within Caenogastropoda, as indicated by Ponder & Lindberg (1996, 1997). Maximum parsimony analyses (Figs 3A,B) indicate that Caenogastropoda constitutes a clade in which traditionally recognized higher taxa diverge sequentially from the stem in an order and pattern that is, with few exceptions, concordant both with recent, morphology-based phylogenies (*e.g.*, Ponder & Lindberg 1997), and traditional classifications (*e.g.*, Ponder & Warén 1988). The short branch lengths between nodes as well as the low bootstrap, jackknife, and Bremer support for these nodes suggest rapid differentiation of these higher taxa and/or significant subsequent homoplasy, yielding few synapomorphies with which to reconstruct evolutionary relationships. A maximum parsimony analysis of the sequence data using only transversions (Fig. 3C), which are rarer and therefore less likely to be homoplasous, produced a different tree topology, in which caenogastropods were divided into two clades, one containing the architaenioglossan taxa, *Campanile* and Cerithioidea, the other corresponding to the 'higher' Caenogastropoda [Hypsogastropoda/Eucaenogastropoda]. Maximum likelihood analyses using both transitions and transversions (Fig. 4) also recovered these two clades. While the 'higher' caenogastropods have long been recognized as a clade, most previous authors have considered the 'lower' caenogastropods to comprise a grade rather than a clade. However, Healy (1996) suggested that, based on sperm morphology, architaenioglossans and cerithioideans formed a group distinct from the 'higher' caenogastropods, and that Campaniloidea comprised a third group, one with close affinities to architaenioglossans and cerithioideans.

When proposing the taxon Sorbeoconcha, Ponder & Lindberg (1997: 225) intended it to contain all non-architaenioglossan caenogastropods, explicitly including Cerithioidea and Campaniloidea. However, because the authors defined this taxon phylogenetically, to include "all those taxa sharing a more recent common ancestor with *Conus* (and *Triphora* and *Tonna*) than with *Cyclophorus* and *Ampullaria*," the extent of Sorbeoconcha is dependent on the phylogenetic hypothesis to which it is applied. When used in conjunction with the trees in Figs 3A and 3B, Sorbeoconcha encompasses the taxa originally intended by the authors. When applied to the trees in Figs 3C and 4, however, Sorbeoconcha becomes identical in composition with, and a synonym of, Hypsogastropoda.

Both Ampullariidae and Cyclophoroidea emerge as clades with high bootstrap and jackknife support, although Bremer support is much greater for Cyclophoroidea than for Ampullariidae. The close relationship between the ampullariids *Pomacea* and *Marisa* was predicted by morphological studies of Berthold (1991) as well as by the reanalysis of his data by Bieler (1993). The clade consisting of the two cyclophoroideans (*Cyclophorus* and *Neocyclotus*) is highly robust, contradicting the phylogenetic

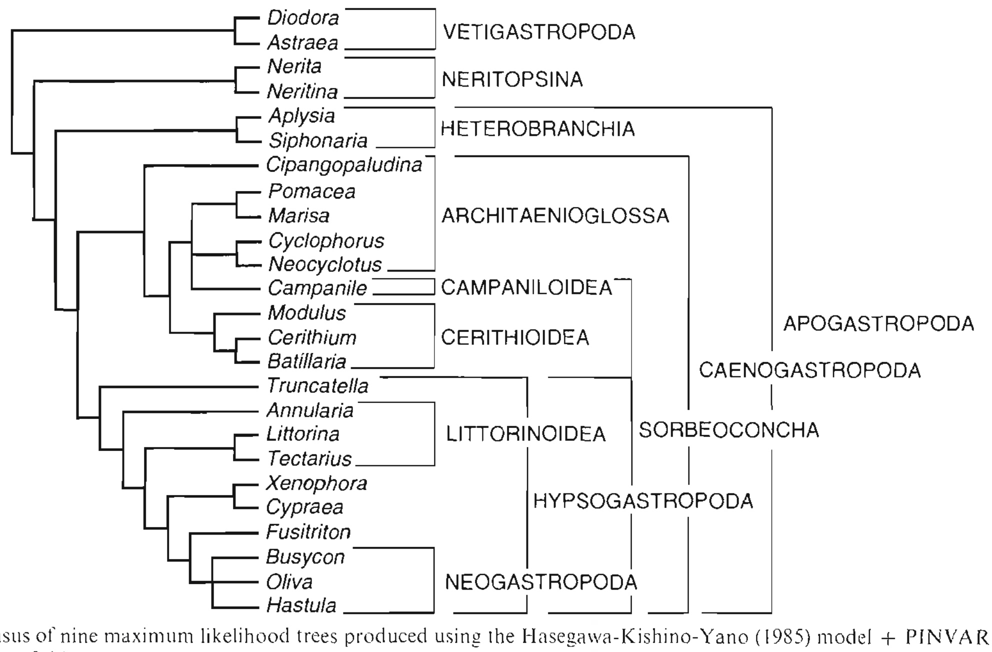

Fig. 4. Strict consensus of nine maximum likelihood trees produced using the Hasegawa-Kishino-Yano (1985) model + PINVAR + GAMMA. See results for derivation of this tree.

scheme of Sitnikova & Starobogatov (1982), who placed these two taxa in different superorders. *Cipangopaludina*, the only viviparid in our study, does not emerge as a close relative of either group, its position contradicting the monophyly of Ampullarioidea [Ampullariidae + Viviparidae] and of Architaenioglossa. However, the insert in the terminal loop of helix 10 (Appendix I, positions 136–165) in *Cipangopaludina* partially overlaps with an insert shared by *Pomacea*, *Marisa* and *Campanile*. Data on additional viviparid taxa are presently being sought to better resolve the relationships of this family. Manipulation of the topology of the tree in Fig. 3A to unite Cyclophoroidea and Ampullariidae in a clade increased tree length by 6 steps. Joining *Cipangopaludina* and Ampullariidae to produce the traditional Ampullarioidea increased tree length by 9 steps, while producing a monophyletic Architaenioglossa required 11 additional steps. Cyclophoroideans, ampullariids, and viviparids are all present in Jurassic deposits (Tracey *et al.* 1993), although there have been questionable reports of viviparids and cyclophoroideans in strata dating from the Carboniferous (Solem & Yochelson 1979; Bandel 1993).

The three cerithioidean taxa currently represented in our database were united into a well supported clade in all analyses, with *Cerithium* and *Batillaria* appearing more closely related to each other than either is to *Modulus*. This arrangement is concordant with Houbrick's (1988: fig. 3) UPGMA phenogram of Cerithioidean relationships. Manipulating the tree to make *Batillaria* more closely related to *Modulus* (both Paleogene) than to *Cerithium* (Lower Cretaceous), as predicted by Houbrick's (1988: fig. 2) cladogram, increased tree length by 4 steps.

According to sequence data, Campanilidae emerges either in a clade with architaenioglossans (most often as sister taxon to Cyclophoroidea), or intermediate between architaenioglossans and cerithioideans, positions not predicted by previous researchers. Additionally, *Campanile* shares a nine base insert in the terminal loop of helix 10 with *Pomacea* and *Marisa* that differs in sequence from that of these ampullariids at only a single position. Moving *Campanile* to a position between Cerithioidea and the Hypsogastropoda, as predicted by Ponder & Lindberg (1996, 1997) requires only two additional steps, while placing it at the base of Heterobranchia, as in the phylogeny proposed by Haszprunar (1988) increases tree length by 17 steps.

The Hypsogastropoda emerge as a clade in all analyses, although with weak bootstrap, jackknife and Bremer support. Levels of sequence divergence (total differences and transversions only) among hypsogastropod taxa are low, being comparable to those found within Cerithioidea or Ampullariidae (Table II). Harasewych *et al.* (1997*b*: 331, Table II) mistakenly reported that divergence levels among Caenogastropoda were approximately half those found in Heterobranchia due to the high proportion of hypsogastropods in their data set. This observation holds for Hypsogastropoda, which has origins in the latest Jurassic and represents a series of radiations during the Cretaceous and Cenozoic (Tracey *et al.* 1993; Kay 1996; Taylor *et al.* 1980). However, divergence rates among Caenogastropoda as a whole, are, in fact, comparable to those found within Heterobranchia (Table II), reflecting the Devonian divergence between these lineages (Tracey *et al.* 1993).

Within Hypsogastropoda, the two littorinids *Littorina* and *Tectarius* emerged as a weakly supported clade in all analyses. *Annularia*, the only other littorinoidean in our study, consistently emerged below the littorinids rather than as sister taxon to them.

Manipulating the tree to produce the monophyletic Littorinoidea of traditional classifications increased tree length by only a single step. Similarly, it required only one fewer step to unite *Xenophora* and *Cypraea* into a clade than for these taxa to emerge as a grade. As in a previous study (Harasewych *et al.* 1997*b*) this portion of the 18S rDNA gene was incapable of resolving neogastropod taxa, while *Fusitriton*, a tonnoidean, was weakly and inconsistently resolved from Neogastropoda.

Truncatella, which has the largest inserts among the taxa in this study and consequently the longest branch length within Hypsogastropoda, emerged as the sister taxon to the remaining "higher" caenogastropods in all analyses that included transitions as characters. When only transversions were used, *Truncatella* collapsed into a polytomy containing all hypsogastropods except *Annularia*. It is of interest that all species of *Truncatella* studied by Rosenberg *et al.* (1992: Fig. 1) also had inserts in the D6 loop of the 28S rRNA.

A broader taxonomic sampling of Caenogastropoda has revealed inserts to be present in several caenogastropod lineages. With the exception of *Campanile*, all caenogastropod taxa discovered to contain inserts thus far are from fresh-water or terrestrial habitats. Harasewych *et al.* (1997*a*, *b*) observed that the 18S gene provided better phylogenetic resolution of higher taxa that contained inserts than of taxa that did not, even when the inserts were excluded from analyses. A corollary of this observation is that sequence divergences among taxa containing inserts tend to be greater than among taxa lacking inserts. As an example, the closely related Ampullariid genera, which share a small insert, are more divergent in their 18S sequences than are the two cyclophoroidean families, which lack inserts. The presence of inserts in both the limited 18S and 28S sequences of *Truncatella* prompt us to speculate that the occurrence of inserts in one ribosomal subunit might be predictive of their presence in other ribosomal subunits.

Neither this 450 bp portion of the 18S rDNA gene (Harasewych *et al.* 1997*b*), nor the entire 18S rDNA gene (Winnepenninckx *et al.* 1998) diverge at a rate sufficient to resolve the phylogeny of the Neogastropoda, which radiated rapidly during the Upper Cretaceous. Both partial and entire 18S rDNA sequences, however, begin to resolve relationships within Hypsogastropoda, which differentiated during the Lower Cretaceous, and of the more basal branches within Caenogastropoda, which date to the early Mesozoic or late Paleozoic. In a study of evolutionary rates of the 18S rDNA gene in metazoan phyla, Philippe *et al.* (1994) calculated that rapid adaptive radiations spanning less than 40 million years generally cannot be resolved using data from the entire 18S gene. More recently, Harasewych *et al.* (1997*a*,*b*, this study) have found the 18S gene to be capable of a broad range of resolutions within the class Gastropoda. In clades that lack inserts in the 18S

TABLE II. *Number of base differences in the portion of 18S gene used to construct parsimony trees summarized in figure 3B* (443 *aligned positions, inserts and unique single base insertions excluded). Gaps and uncertain base calls removed from pairwise comparisons. Total number of nucleotide differences above the diagonal, transversions only below the diagonal*

OTUs	Dio	Ast	Nta	Ntn	Cyc	Neo	Pom	Mar	Cip	Cam	Mod	Cer	Bat	Ann	Lit	Tec	Tru	Xen	Cyp	Fus	Bus	Olv	Has	Apl	Sip
Dio	-	22	57	56	60	59	60	59	61	61	60	60	59	56	56	57	60	58	60	59	59	59	58	61	59
Ast	7	-	50	52	55	53	53	51	53	54	53	53	53	51	52	54	52	50	53	53	54	54	53	53	55
Nta	25	22	-	7	43	41	46	42	44	44	43	43	42	39	41	39	41	40	40	40	41	40	40	41	41
Ntn	23	20	3	-	42	40	45	41	43	43	43	43	42	38	40	38	40	39	39	40	41	40	40	42	42
Cyc	26	27	17	17	-	3	23	17	20	12	18	18	17	19	16	18	20	19	20	20	20	19	19	37	37
Neo	24	25	16	16	3	-	23	17	19	12	16	16	15	18	16	17	19	18	19	19	19	18	18	36	36
Pom	28	26	21	21	12	13	-	8	24	17	23	23	22	21	18	19	20	22	20	21	23	21	20	38	37
Mar	26	24	19	19	8	9	6	-	20	13	19	19	18	21	18	19	20	21	20	21	23	21	20	34	33
Cip	26	21	18	18	15	14	15	13	-	12	14	16	15	11	15	13	10	12	12	14	17	15	13	38	38
Cam	27	25	18	18	7	8	7	5	10	-	13	13	14	16	14	15	13	16	16	14	17	15	14	37	37
Mod	25	24	18	19	14	13	14	12	7	9	-	9	8	13	13	14	11	13	13	13	13	11	11	32	36
Cer	25	24	18	19	12	9	14	12	9	9	4	-	1	14	15	14	15	16	15	14	17	17	16	37	39
Bat	25	24	18	19	12	9	14	12	9	9	4	0	-	13	14	13	14	15	14	15	16	16	15	36	38
Ann	22	19	16	16	17	14	13	15	6	12	9	9	9	-	8	6	5	6	5	4	7	5	5	33	35
Lit	25	25	18	18	11	12	9	11	10	8	9	9	9	6	-	6	7	8	7	7	9	8	6	33	34
Tec	22	23	16	16	13	12	11	13	8	10	7	9	9	4	2	-	7	7	5	5	8	6	6	34	34
Tru	23	21	16	16	15	14	11	13	6	10	7	9	9	2	4	2	-	7	6	6	9	7	5	33	34
Xen	24	21	17	17	15	14	13	14	6	11	8	10	10	5	6	4	3	-	2	5	7	5	5	34	36
Cyp	24	21	16	16	15	14	11	13	6	10	7	9	9	4	4	2	2	2	-	4	6	4	4	34	36
Fus	22	21	16	17	16	15	12	14	7	11	8	10	10	2	4	2	1	4	3	-	5	3	3	33	35
Bus	23	22	15	16	15	14	11	13	8	10	7	9	9	3	3	1	2	4	2	1	-	4	4	34	36
Olv	23	22	15	16	15	14	11	13	8	10	7	9	9	3	3	1	2	4	2	1	0	-	2	33	35
Has	23	22	15	16	15	14	11	13	8	10	7	9	9	3	3	1	2	4	2	1	0	0	-	34	36
Apl	28	23	19	19	22	22	23	21	17	21	19	20	20	15	18	17	17	17	17	16	17	17	17	-	12
Sip	29	27	21	21	22	22	23	19	20	22	20	21	21	18	18	18	16	18	18	17	18	18	18	3	-

Ann = *Annularia*, Apl = *Aplysia*, Ast = *Astraea*, Bat = *Batillaria*, Bus = *Busycon*, Cam = *Campanile*, Cer = *Cerithium*, Cip = *Cipangopaludina*, Cyc = *Cyclophorus*, Cyp = *Cypraea*, Dio = *Diodora*, Fus = *Fusitriton*, Has = *Hastula*, Lit = *Littorina*, Mar = *Marisa*, Mod = *Modulus*, Neo = *Neocyclotus*, Nta = *Nerita*, Ntn = *Neritina*, Olv = *Oliva*, Pom = *Pomacea*, Sip = *Siphonaria*, Tec = *Tectarius*, Tru = *Truncatella*, Xen = *Xenophora*.

gene, the resolving ability of this gene appears to be roughly comparable to that predicted by Philippe *et al.* (1994). However, for clades containing inserts, the 18S gene is capable of much finer levels of resolution, in some cases to species level, even when the inserts themselves are excluded from analysis. Preliminary results suggest that the level of resolution increases with the size of the inserts. Thus, use of more proximal outgroups, the addition of taxa, as well as the use of complete 18S sequences will likely improve resolution and provide increased bootstrap, jackknife and Bremer support for at least the more basal branches within Caenogastropoda. Data from one or more genes that evolve more rapidly than 18S rDNA (possibly cytochrome *c* oxidase I and/or 16S rDNA), either separately or in combination with the 18S rDNA, seems more likely to be informative about post-Jurassic divergences within Caenogastropoda.

Acknowledgements

Thanks are due to Drs Edward J. Petuch, John B. Wise and Ms. Sherry Reed for help with field work in Florida, and to Mr. Yoshihiro Goto, Paul Callomon, Hiroshi Fukuda, Dr Rei Ueshima and Mrs. Thora Whitehead for assistance with field work in Japan. We are grateful to Dr José H. Leal and Mr. Ernesto Lasso de la Vega for supplying living *Marisa*, and to Dr Glenn Goodfriend for providing *Neocyclotus* and *Annularia*. Dr Winston F. Ponder generously sent extracted DNA of *Campanile symbolicum*. We are indebted to Dr David L. Swofford for providing beta test versions of PAUP 4.0, and to Dr Andrew A. McArthur for assistance with the maximum likelihood analyses. We thank Drs John Healy, Andrew McArthur, and David Swofford for their comments on various versions of this manuscript. This is Smithsonian Marine Station at Link Port Contribution Number 444.

References

Bandel, K. (1993). Caenogastropoda during Mesozoic times. In A. W. Janssen & R. Janssen (Eds), *Molluscan Paleontology*, Proceedings of a Symposium held at the 11th International Malacological Congress. *Scripta Geologica, Special Issue 2*, 251–266.

Berthold, T. (1991). Vergleichende Anatomie, Phylogenie und Historisches Biogeographie der Ampullariidae (Mollusca, Gastropoda). *Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg (NF) 29*, 1–256.

Bieler, R. (1993). Ampullariid Phylogeny — Book Review and Cladistic Re-analysis. *The Veliger 36(3)*, 291–299.

Boss, K. J. (1982). Mollusca. In S. P. Parker (Ed), *Synopsis and Classification of Living Organisms, 1* (pp. 945–1166). New York: McGraw-Hill Book Company.

Bremer, K. (1988). The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution 42*, 795–803.

Golikov, A. & Starobogatov, Y. I. (1975). Systematics of prosobranch gastropods. *Malacologia 15 (1)*, 185–232.

Golikov, A. & Starobogatov, Y. I. (1988). Problems of Phylogeny and Systematics of Prosobranchiate Gastropod Mollusks. pp. 1–77. In Y. I. Starobogatov (Ed), *Systematics and Fauna of Gastropoda, Bivalvia, and Cephalopoda. Proceedings of the Zoological Institute 187*: 1–203. [in Russian]

Harasewych, M. G., Adamkewicz, S. L., Blake, J. A., Saudek, D., Spriggs, T. & Bult, C. J. (1997*a*). Phylogeny and relationships of pleurotomariid gastropods (Mollusca: Gastropoda): an assessment based on partial 18S rDNA and cytochrome c oxidase I sequences. *Molecular Marine Biology and Biotechnology, 6(1)*, 1–20.

Harasewych, M. G., Adamkewicz, S. L., Blake, J. A., Saudek, D., Spriggs, T. & Bult, C. J. (1997*b*). Neogastropod Phylogeny: A Molecular Perspective. *Journal of Molluscan Studies 63(4)*, 327–351.

Haszprunar, G. (1988). On the origin and evolution of major gastropod groups, with special reference to the Streptoneura. *Journal of Molluscan Studies 54(4)*, 367–41.

Healy, J. M. (1988). Sperm morphology and its systematic importance in the Gastropoda. In W. F. Ponder, (Ed), *Prosobranch Phylogeny*, Proceedings of a Symposium held at the 9th International Malacological Congress. *Malacological Review, Supplement 4*, 251–266.

Healy, J. M. (1993). Transfer of the gastropod family Pleisiotrochidae to the Campaniloidea based on sperm ultrastructural evidence. *Journal of Molluscan Studies 59(2)*, 135–146.

Healy, J. M. (1996). Molluscan sperm ultrastructure: correlation with taxonomic units within the Gastropoda, Cephalopoda, and Bivalvia. In J. D. Taylor, (Ed), *Origin and Evolutionary Radiation of the Mollusca*. (pp. 99–113). Oxford: Oxford University Press.

Higgins, D. G., Bleasby, A. J. & Fuchs, R. (1992). CLUSTAL V: Improved software for multiple sequence alignment. *Computer Applications in the Biosciences 8*, 189–191.

Hillis, D. M. & Bull, J. J. (1993). An experimental test of bootstrapping as a method for assessing confidence in phylogenetic analysis. *Systematic Biology 42(2)*, 182–192.

Houbrick, R.S. (1981). Anatomy, biology, and systematics of *Campanile symbolicum* with reference to adaptive radiation of the Ceritheacea (Gastropoda: Prosobranchia). *Malcologia 21(2–3)*, 263–289.

Houbrick, R. S. (1988). Cerithioidean Phylogeny. In W. F. Ponder, (Ed), *Prosobranch Phylogeny*, Proceedings of a Symposium held at the 9[th] International Malacological Congress. *Malacological Review, Supplement 4*, 88–128.

Houbrick, R. S. (1989). *Campanile* revisited: Implications for Cerithioidean Phylogeny. *American Malacological Bulletin 7(1)*, 1–6.

Kay, E. A. (1996). Evolutionary radiations in the Cypraeidae. In J. D. Taylor, (Ed), *Origin and Evolutionary Radiation of the Mollusca*. (pp. 211–220). Oxford, Oxford University Press.

Kumar, S., Tamura, K. & Nei, M. (1993). *MEGA: Molecular Evolutionary Genetics Analysis*, version 1.0. The Pennsylvania State University, University Park.

Maddison, W. P. & Maddison, D. R. (1992). *MacClade, Analysis of Phylogeny and Character Evolution*. Version 3.05 Sinauer Associates, Inc., Sunderland, Massachusetts.

Morrison, J. P. E. (1954). The relationships of Old and New World Melanians. *Proceedings of the United States National Museum 103(3325)*, 357–394.

Philippe, H., Chenuil, A. & Adoutte, A. (1994). Can the Cambrian explosion be inferred through molecular phylogeny? *Development, 1994 Supplement*, 15–25

Ponder, W. F. & Lindberg, D. R. (1996). Gastropod Phylogeny — Challenges for the 90s. In J. D. Taylor, (Ed), *Origin and Evolutionary Radiation of the Mollusca*, (pp. 135–154). Oxford, Oxford University Press.

Ponder, W. F. & Lindberg, D. R. (1997). Towards a phylogeny of gastropod molluscs: an analysis using morphological characters. *Zoological Journal of the Linnean Society 119*, 83–265.

Ponder, W. F. & Warén, A. (1988). Classification of the Caenogastropoda and Heterostropha — A list of family-group names and higher taxa. In W. F. Ponder, (Ed). *Prosobranch Phylogeny*, Proceedings of a Symposium held at the 9[th] International Malacological Congress. *Malacological Review, Supplement 4*, 288–326.

Rosenberg, G., Kuncio, G. S., Davis, G. M., & Harasewych, M. G. (1994). Preliminary ribosomal RNA phylogeny of gastropod and unionoidean bivalve mollusks. In M. G. Harasewych & S. Tillier (Eds). *Molecular Techniques and Molluscan Phylogeny*, Proceedings of a Symposium held at the 11[th] International Malacological Congress. *The Nautilus Supplement 2*, 111–121.

Rosenberg, G., Tillier, S. Tillier, A., Kuncio, G. S., Hanlon, R. T., Masselot, M. & Williams, C. J. (1997). Ribosomal RNA phylogeny of selected major clades in the Mollusca. *Journal of Molluscan Studies 63(4)*, 301–309.

Salvini-Plawen, L. v. (1980). A Reconsideration of Systematics in the Mollusca (Phylogeny and Higher Classification). *Malacologia 19(2)*, 249–278.

Salvini-Plawen, L. v. (1991). Origin, Phylogeny, and Classification of the Phylum Mollusca. *Iberus 9*, 1–33.

Salvini-Plawen, L. v. & Haszprunar, G. (1987). The Vetigastropoda and the systematics of streptoneurous gastropods (Mollusca). *Journal of Zoology, London 211*, 747–770.

Salvini-Plawen, L. v. & Steiner, G. (1996). Synapomorphies and plesiomorphies in higher classification of Mollusca. In J. D. Taylor, (Ed), *Origin and Evolutionary Radiation of the Mollusca*. (pp. 29–51). Oxford: Oxford University Press.

Sitnikova, T. Y. & Starobogatov, Y. I. (1982). Content and Systematic Status of the group Architaenioglossa (Gastropoda, Pectinibranchia). *Zoologicheskii Zhurnal 61*, 831–842. [in Russian]

Smith, S., Overbeek, W. R., Woese, C. R., Gilbert, W., & Gillevet, P. M. (1994). The genetic data environment: an expandable GUI for multiple sequence analysis. *Computer Applications in the Biosciences 10*, 671–675.

Solem, A. & Yochelson, E. L. (1979). North American Paleozoic land snails, with a summary of other Paleozoic nonmarine snails. *U.S. Geological survey Professional Paper 1072*, 1–39.

Sorenson, M. D. (1996). TreeRot. University of Michigan, Ann Arbor.

Swofford, D. L. (1997). *PAUP, phylogenetic analysis using parsimony*. Versions 4.0.0d56 and 4.0.d57 (beta test versions). Laboratory of Molecular Systematics, Smithsonian Institution, Washington, DC.

Taylor, D. W. & Sohl, N. F. (1962). An Outline of Gastropod Classification. *Malacologia 1(1)*, 7–32.

Taylor, J. D., Morris, N. J. & Taylor, C. N. (1980). Food specialization and the evolution of predatory prosobranch gastropods. *Palaeontology 23(2)*, 375–409.

Thiele, J. (1929–1931). Handbook of Systematic Malacology. Part 1 (Loricata; Gastropoda: Prosobranchia). 1929. Part 2. (Gastropoda: Opisthobranchia and Pulmonata: Additions; Index). 1931. English translation, R. Bieler & P. M. Mikkelsen (Eds). 1992. Smithsonian Institution Libraries and The National Science Foundation, Washington, DC. Part 1, xiii + 1–625. Part 2, xiv + 626–1189.

Tillier, S., Masselot, M., Hevré, P. & Tillier, A. (1992). Phylogénie moléculaire des Gastropoda (Mollusca) fondée sur le séquençage partiel de l'ARN ribosomique 28S. *Comptes Rendus Academie de Science (Paris)* Series 3, *134*, 79–85.

Tillier, S., Masselot, M., Guerdoux, J., & Tillier, A. (1994). Monophyly of major gastropod taxa tested from partial 28S rRNA sequences, with emphasis on Euthyneura and Hot-Vent Limpets Peltospiroidea. In M. G. Harasewych & S. Tillier (Eds). *Molecular Techniques and Molluscan Phylogeny*, Proceedings of a Symposium held at the 11[th] International Malacological Congress. *The Nautilus Supplement 2*, 122–140.

Tracey, S., Todd, J. A., & Erwin, D. H. (1993). Mollusca: Gastropoda. In M. J. Benton (Ed), *The Fossil Record 2*. (pp. 131–167). London: Chapman and Hall.

Vaught, K. C. (1989). *A Classification of the Living Mollusca*. American Malacologists, Inc., Melbourne. 195 pp.

Wenz, W. (1938–1944). *Handbuch der Paläozoologie*. In O. H. Schindewolf (Ed). Band 1. Teil 1–7, pp. 1–1639, I–XII, 1–10. Berlin: Borntraeger.

Winnepenninckx, B., Backeljau, T. & de Wachter, R. (1994). Small ribosomal subunit RNA and the phylogeny of Mollusca. In M. G. Harasewych & S. Tillier (Eds). *Molecular Techniques and Molluscan Phylogeny*, Proceedings of a Symposium held at the 11[th] International Malacological Congress. *The Nautilus Supplement 2*, 98–110.

Winnepenninckx, B., Steiner, G., Backeljau, T. & de Wachter, R. (1998). Details of gastropod phylogeny inferred from 18S rRNA sequences. *Molecular Phylogenetics and Evolution 9(1)*, 55–63.

Appendix 1

Aligned partial sequences of the gastropod 18S rDNA gene corresponding to positions 60–515 of the 18S rRNA of *Onchidella celtica* as reported by Winnepenninckx *et al.* (1994:101). All sequences confirmed by at least two sequencing reactions in each direction. Ambiguous base assignments are noted using IUPAC symbols. Quotes (") represent gaps inserted during alignment.

	10	20	30	40	50	60	70	80	90	100	
Diodora	TAAGTA"CAA	ACTCTCGCCC	AGTG"AAACT	GCGAATGGCT	CATTACATCA	GTTATGGTTC	CTTGGACGAT	ACCAT"CCTA	CTTGGATAAC	TGTGGTAATT	[97]
Astraea	TAAGYA"CAA	ACTCTAGCAC	AGTG"AAACT	GCGAATGGCT	CATTAGATCA	GTTATGGTTC	CTTAGATGAT	ACAAT"CCTA	CTTGGATAAC	TGTGGTAATT	[97]
Nerita	TAAGTT"CAA	ACTTTCACAT	AGTG"AAACC	GCGAATGGCT	CATTAGATCA	GTTATGGTTC	CTTAGATCGT	ACAACTC""A	CTCGGATAAC	TGTGGCAATT	[96]
Neritina	TAAGTA"CAA	ACCTTCACAT	GGTG"AAACC	GCGAATGGCT	CATTAGATCA	GTTATGGTTC	CTTAGATCGT	ACAACTCC"A	CTCGGATAAC	TGTGGCAATT	[97]
Cyclophorus	TAAGTT"CCA	ACCCTCGTAC	GGTG"AAACC	GCGAATGGCT	CATTAAATCA	GTCGAGGTTC	CTTAGATGAT	CCTTTACCTA	CTTGGATAAC	TGTGGTAATT	[98]
Neocyclotus	TAAGTT"CCA	ACCCTCGTAC	GGTG"AAACC	GCGAATGGCT	CATTAAATCA	GTCGAGGTTC	CTTAGATGAT	CCTTTTCCTA	CTTGGATAAC	TGTGGTAATT	[98]
Pomacea	TAAGTT"CAC	ACCCTCGTAC	GGTG"AAACT	TCATATGGCT	CATTAAATCA	GTCGAGGTTC	CTTAGATGAT	CCAAATC"TA	CTTGGATAAC	TGTGGCAATT	[97]
Marisa	TAAGTT"CAC	ACCCTCGTAC	GGTG"AAACC	GCGAATGGCT	CATTAAATCA	GTCGAGGTTC	CTTAGATGAT	CCATTTC"TA	CTTGGATAAC	TGTGGCAATT	[97]
Cipangopaludina	TAAGTT"CAC	ACCCTCGTAC	GGTG"AAACC	GCGAATGGCT	CATTAAATCA	GTCGAGGTTC	CTTAGATGAT	CCATTTC"TA	CTTGGATAAC	TGTGGTAATT	[97]
Campanile	TAAGTT"CAC	ACCCTTGTAC	GGTG"AAACC	GCGAATGGCT	CATTAAATCA	GTCGAGGTTC	CTTAGATGAT	CCATTTC"TA	CTTGGATAAC	TGTGGTAATT	[97]
Modulus	TAAGTT"CAC	ACCCTCGTAC	GGTG"AAACC	GCGAATGGCT	CATTAAATCA	GTCGAGGTTC	CTTAGATGAT	CCATTTC"TA	CTTGGATAAC	TGTGGTAATT	[97]
Cerithium	TAAGTTACAC	ACCCTTGTAC	GGTG"AAACC	GCGAATGGCT	CATTAAATCA	GTCGAGGTTC	CTTAGATGAT	CCATTTC"TA	CTTGGATAAC	TGTGGTAATT	[98]
Bacillaria	TAAGTT"CAC	ACCCTCGTAC	GGTG"AAACC	GCGAATGGCT	CATTAAATCA	GTCGAGGTTC	CTTAGATGAT	CCATTTC"TA	CTTGGATAAC	TGTGGTAATT	[97]
Annularia	TAAGTT"CAC	ACCCTCGTAC	GGTG"AAACC	GCGAATGGCT	CATTAAATCA	GTCGAGGTTC	CTTAGATGAT	CCAAATC"TA	CTTGGATAAC	TGTGGTAATT	[97]

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                         10         20         30         40         50         60         70         80         90        100
Littorina        TAAGTT"CAC ACCCTCGTAC GGTG"AAACC GCGAATGGCT CATTAAATCA GTCGAGGTTC C"TAGATGAT CCCAATC"TA CTTGGATAAC TGTGGTAATT [96]
Tectarius        TAAGTT"CAC ACCCTCGTAC GGTG"AAACC GCGAATGGCT CATTAAATCA GTCGAGGTTC CTTAGATGAT CCCAATC"TA CTTGGATAAC TGTGGTAATT [97]
Truncatella      TAAGTT"CAC ACCCTCGTAC GGTG"AAACC GCGAATGGCT CATTAAATCA GTCGAGGTTC CTTAGATGAT CCAAATC"TA CTTGGATAAC TGTGGTAATT [97]
Xenophora        TAAGTT"""C TCCCTCGTAC GGTG"AAACC GCGAATGGCT C"TTAAATC" GTCGAGGTTC CTTAGATGAT CCAA"TT"TA CTTGGATAAC TGTGGTAATT [92]
Cypraea          TAAGTT"CAC ACCCTCGTAC GGTG"AAACC GCGAATGGCT CATTAAATCA GTCGAGGTTC CTTAGATGAT CCAAATT"TA CTTGGATAAC TGTGGTAATT [97]
Fusitriton       TAAGTT"CAC ACCCTTGTAC GGTG"AAACC GCGAATGGCT CATTAAATCA GTCGAGGTTC CTTAGATGAT CCAAAT""TA CTTGGATAAC TGTGGTAATT [96]
Busycon          TAAGTT"CAC ACCCTCGTAC GGTG"AAACC GCGAATGGCT CATTAAATCA GTCGAGGTTC CTTAGATGAT CCAAACT"TA CTTGGATAAC TGTGGTAATT [97]
Oliva            TAAGTT"CAC ACCCTCGTAC GGTG"AAACC GCGAATGGCT CATTAAATCA GTCGAGGTTC CTTAGATGAT CCAAATT"TA CTTGGATAAC TGTGGTAATT [97]
Hastula          TAAGTT"CAC ACCCTCGTAC GGTG"AAACC GCGAATGGCT CATTAAATCA GTCGAGGTTC CTTAGATGAT CCAAATT"TA CTTGGATAAC TGTGGTAATT [97]
Aplysia          TAAGTT"CA" ACTGTCTCAC GGTGTAAACC GCGAATGG"T CATTAAATCA GTCGAGGTTC CTTAGATGAC ACGAT"CCTA CTTGGATAAC TGTGGCAATT [96]
Siphonaria       TAAGTT"CAC ACTGTCTCAC GGTG"AAACC GCGAATGGCT CATTAAATCA GTCGAGGTTC CTTAGATGAC ACGAT"CCTA CTTGGATAAC TGTGGCAATT [97]

                        110        120        130        140        150        160        170        180        190        200
Diodora          CTAGAGCTAA TACATGCACT TCG"GCTCCG ACCCT""""" """""""TT" CCC""""""" """""AAGGG GAAGAGCGCA TTTATCAGCC TCGAAGCCAG [171]
Astraea          CTAGAGCTAA TACATGCACT ATA"GCTCCG ACCCT""""" """""""TT" CGC""""""" """""GAGGG GAAGAGCGCG TTTATCAGT" TCGAAGCCAG [170]
Nerita           CTAGAGCTAA TACGTGCAAG AAA"GCTCTG AC"CT""""" """""""""" """""""""" """""CGCGG GAAGAGCGCT TTTATTAGT" TCAAAACCAA [163]
Neritina         CTAGAGCTAA TACGTGCAAG AAA"GCTCCG AC"CT""""" """""""""" """""""""" """""CGCGG GAAGAGCGCT TTTATTAGT" TCAAAACCAA [164]
Cyclophorus      CTAGAGCTAA TACATGCGGA CAA"GCTCCG ACCCG""""" """""""TT" "G"""""""" """""TTGGG AAAGAGCGCT TTTATTAGT" TCAAAACCAG [169]
Neocyclotus      CTAGAGCTAA TACATGCGGA CAA"GCTCCG ACCCT""""" """""""CT" C""""""""" """""GTGGG AAAGAGCGCT TTTATTAGT" TCAAAACCAG [169]
Pomacea          CTAGAGCTAA TACATGCAAA CCA"GCTCCG ACCCG""""" """""""""" """"GTGTCA CAG""CCGGG AAAGAGCGCT TTTATTAGT" TCAAAACCAG [174]
Marisa           CTAGAGCTAA TACATGCAAC CAA"GCTCCG ACCCG""""" """""""""" """"GTGTCA CAG""CCGGG AAAGAGCGCT TTTATTAGT" TCAAAACCAG [174]
Cipangopaludina  CTAGAGCTAA TACATGCCCA ACA"GCTCCG ACCCCGG"GC """""""TT" CGCGGT"T"" """""CGGGG AAAGAGCGCT TTTATTAGT" TCAAAACCAG [178]
Campanile        CTAGA"CTAA TACATGCGGA CCA"GCTCCG ACCCG""""" """""""""" """"GTGTCA AAG""CCGGG AAAGAGCGCT TTTATTAGT" TCAAAACCAG [173]
Modulus          CTAGAGCTAA TACATGCTGA CCA"GCTCCG ACCCT""""" """""""T"" """""""""" """""CGGGG AAAGAGCGCT TTTATTAGT" TCAAAACCAG [166]
Cerithium        CTAGAGCTAA TACATGCCAA CCA"GCTCCG ACCCT""""" """""""""" C""""""""" """""ACGGG AAAGA"CGCT TTTATTAGT" TCAAAACCAG [166]
Batillaria       CTAGAGCTAA TACATGCCAA CCA"GCTCCG ACCCT""""" """""""""" C""""""""" """""ACGGG AAAGAGCGCT TTTATTAGT" TCAAAACCAG [166]
Annularia        CTAGAGCTAA TACATGCCCA ACA"GCTCCG ACCCC""""" """""""TTT T""""""""" """""AGGGG AAAGAGCGCT TTTATTAGT" TCAAAACCAG [169]
Littorina        CTAGAGCTAA TACATGCCAA CCA"GCTCCG ACCCG""""" """""""TTA """""""""" """""CTGGG AAAGAGCGCT TTTATCAGT" TCAAAACCAG [167]
Tectarius        CTAGAGCTAA TACATGCCAA CCA"GCTCCG ACCTC""""" """""""T"" """""""""" """""CGGGG AAAGAGCGCT TTTATTAGT" TCAAAACCAG [166]
Truncatella      CTAGAGCTAA TACATGCCCA CCA"GCTCCG ACCCCGGCGC CGTTTCCTTT CGGGGGGGCA GTGGCCGGGG AAAGAGCGCT TTTATTAGT" TCAAAACCAG [195]
Xenophora        CTAGAGCTAA TAC"TGCC"A CCA"GCTCCG ACCCC""""" """""""T"" """""""""" """""CGGGG AAAGAGCGCT T"TAT"AGT" "CACAACCAG [156]
Cypraea          CTAGAGCTAA TACATGCCAA CCA"GCTCCG ACCCC""""" """""""T"" """""""""" """""CGGGG AAAGAGCGCT TTTATTAGT" TCAAAACCAG [166]
Fusitriton       CTAGAGCTAA TACATGCCTA CCA"GCTCCG ACCCC""""" """""""T"" """""""""" """""CGGGG AAAGAGCGCT TTTATTAGT" TCAAAACCAG [165]
Busycon          CTAGAGCTAA TACATGCCGA CCA"GCTCCG ACCCT""""" """""""T"" """""""""" """""CGGGG AAAGGGCGCT TTTATTAGT" TCAAAACCAG [166]
Oliva            CTAGAGCTAA TACATGCTGA CCA"GCTCCG ACCCC""""" """""""T"" """""""""" """""CGGGG AAAGAGCGCT TTTATTAGT" TCAAAACCAG [166]
Hastula          CTAGAGCTAA TACATGCCGA CCA"GCTCCG ACCCC""""" """""""T"" """""""""" """""CGGGG AAAGAGCGCT TTTATTAGT" TCAAAACCAG [166]
Aplysia          CTAGAGCTAA TACATGCTTC GCAAGCTCCG ACCCT""""" """""""""" """""""""" """""CGTGG AAAGAGCGCT TTTATTAGT" TCAAAACCAA [165]
Siphonaria       CTAGAGCTAA TACATGCTTT TGAAGCTCCG ACCCT""""" """""""""" """""""""" """""CGTGG AAAGAGCGCT TTTATTAGT" TCAAAACCAA [166]

                        210        220        230        240        250        260        270        280        290        300
Diodora          CCGGG"T""" """""""""" "C"GC""""" "AAGG""""" ""CCCGTCCA CCTTTGGTGA CTCTGGATAA CTGT"TGCGG ATCGCACGGC CCC""GAGCC [239]
Astraea          CCGGG"T""" """""""""" "C"GC""""" "AAGG""""" ""CCCGTCT" "CTTTGGTGA CTCTGGATAA CTCT"AGCGG ATCGCATGGC CTT""GAGCC [236]
Nerita           TCGGG"T""" """""""""" "C"GC""""" "AAGG""""" ""CCCGTCC" "GTTTGGTGA CTCTGGATAA CTTTGT"CTG ATCGCAGGGC CTC""GAGCC [229]
Neritina         TCGGGGT""" """""""""" "C"GC""""" "AAGA""""" ""CCCGTCC" "GTTTGGTGA CTCTGGATAA CTTTGTGCTG ATCGCACGGC CTC""GAGCC [232]
Cyclophorus      TCGGGGT""" """"""TT"" "CGGC""""" """""""""" ""TCCGTCC" ""TTTGGTGA CTCTGGATAA CTTTGTGCCG ATCGCATGGC CTC""GAGCC [235]
Neocyclotus      TCGGGG"""" """""CTT"" "CGGC""""" """""""""" ""TCCGTCC" ""TTTGGTGA CTCTGGATAA CTTTGTGCCG ATCGCATGGC CTC""GAGCC [235]
Pomacea          TCGGGGT""" """""CT""" "CGGC""""" """""""""" ""CCCGTCCC T"TTTGGTGA CTCTGGATAA CTTTGTGCCG ATCGCATGGC CTC""GAGCC [242]
Marisa           TCGGGGT""" """""CT""" "CGGC""""" """""""""" ""CCCGTCCC T"TTTGGTGA CTCTGGATAA CTTTGTGCCG ATCGCATGGC CTC""GAGCC [242]
Cipangopaludina  TCGGGGT""" """"""TT"" "CGGC""""" """""""""" ""CTCGTGC" ""TTTGGTGA CTCTGGATAA CTTTGAGCCG ATCGCATGGC CTC""GAGCC [244]
Campanile        TCGGGGT""T TGG""GTT"C "CGGC""CCG C""""""""" ""CTCGTCCC ""TTTGGTGA CTCTGGATAA CTTTGTGCCG ATCGCATGGC CTC""GAGCC [250]
Modulus          TCGG"GT""" """""TT""" "CGG"""""" """""""""" ""CCCGTCC" ""TTTGGTGA CTCTGGATAA CTTTGTGCCG ATCGCATGGC CTT""GAGCC [230]
Cerithium        TCGGGGT""" """""""""" "C"GC""""" """""""""" ""CCCGTCC" ""TTTGGTGA CTCTGGATAA CTTTGTGCCG ATCGCATGGC CTT""GAGCC [229]
Batillaria       TCGGGGT""" """""""T"" "C"GC""""" """""""""" ""CCCGTCC" ""TTTGGTGA CTCTGGATAA CTTTGTGCCG ATCGCATGGC CTT""GAGCC [230]
Annularia        TCGGG""""" T"""GT""C "C"CC"T"CG "TGGGTT""" ""CCCGTCC" ""TTTGGTGA CTCTGGATAA CTTTGTGCCG ATCGCATGGC CTC""GAGCC [243]
Littorina        TCGGG""""" CCC""GTTAA ACGG""T""" """""""""" """CCGTCCC """TTGGTGA CTCTGGATAA CTTTGTGCCG ATCGCATGGC CTC""GAGCC [237]
Tectarius        TCGGG""""" """""GT""A AC"CC""""" """""""""" ""CCCGTCC" ""TTTGGTGA CTCTGGATAA CTTTGTGCCG ATCGCATGGC CTC""GAGCC [231]
Truncatella      TCGAGG"""" ""GG"""""G GCGGC"TCGC GTTCGTTCCC T"CTCGTCCC T"TTTGGTGA CTCTGGATAA CTTTGTGCCG ATCGCATGGC CT"GTGAGCC [280]
Xenophora        "CGGGGT""" """""""""C "C"GC""""" """""""""" ""CCCG"CC" ""TTTGGTGA CTCTGGATAA CTTTGAGCCG ATCGCATGGC CTC""GAGCC [218]
Cypraea          TCGGGGT""" """""""T"C "C"GC""""" """""""""" ""CCCGTCC" ""TTTGGTGA CTCTGGATAA CTTTGAGCCG ATCGCATGGC CTC""GAGCC [231]
Fusitriton       TCGGGTT""" """""CT""" """G"""""" """""""""" ""CCCGTCC" ""TTTGGTGA CTCTGGATAA CTTTGTGCCG ATCGCATGGC CTC""GAGCC [228]
Busycon          TCGGGTT""" """""CT""" """G"""""" """""""""" ""CCCGTCC" ""TTTGGTGA CTCTGGATAA CTTTGTGCCG ATCGCATGGC CTC""GAGCC [229]
Oliva            TCGGGTT""" """""CT""" """G"""""" """""""""" ""CCCGTCC" ""TTTGGTGA CTCTGGATAA CTTTGTGCCG ATCGCATGGC CTC""GAGCC [229]
Hastula          TCGGGTT""" """""CT""" """G"""""" """""""""" ""CCCGTCC" ""TTTGGTGA CTCTGGATAA CTTTGTGCCG ATCGCATGGC CTC""GAGCC [229]
Aplysia          TCGTCGTCT" """""""""" "C"GCCGTT" "TTCGGGGGG GCGGCGTCCC ACTTTGGTGA CTCTGGATAA CTTTGTGCTG ATCGCATGGC CTTTTGTGCC [250]
Siphonaria       TCGCCGT"TG """"CCCTT" "C"GC""""" "AAGGGGGGT GCGGCGTCCC "CACTGGTGA CTCTGGATAA CTTTGTGCTG ATCGCATGGC C"C"TGCGCC [249]

                        310        320        330        340        350        360        370        380        390        400
Diodora          GGCGACGCGT CCATCAAATG TCTGCCCTAT CAGACTGT"C GATGGTAAGT "GCTATG"CT TACCATGGT" GATAACGGGT AACGGGG"AA TCAGGGTTCG [334]
Astraea          GGCGACGCAT CTATCAAGTG TCTGCCCTAT CAGACTGT"C GATGGTAAGT "GCTATG"CT TACCATGGT" GATAACGGGT AACGGGG"AA TCAGGGTTCG [331]
Nerita           GGCGA"GTAT CTTTCAA"TG TCTGCCC"AT CAATTT"A"" GATGGT"CGT "GATATG"CC TACCATGGT" TATAACGGGT AGCGGGG"AA TCAGGGTTCG [318]
Neritina         GGCGACGTAT CTTTCAAATG TCTGCCCTAT CAACTTTA"" GATGGTACGT "GATATG"CC TACCATGGT" TATAACGGGT AGCGGGG"AA TCAGGGTTCG [326]
Cyclophorus      GGCGACGCAT CTTTCAAATG TCTGCCCTAT CAAAT"GA"C GATGGTACGT "GATAGG"CC TACCATGTT" TACTACGGGT AGCGGGG"AA TCAGGGTTCG [329]
Neocyclotus      GGCGACGCAT CTTTCAAATG TCTGCCCTAT CAAAT"GA"C GATGGTACGT TGATAGG"CC TACCATGTT" TACTACGGGT AGCGGGG"AA TCAGGGTTCG [330]
Pomacea          GGCGACGCAT CTTTCAAATG TCTGCCCTAT CAAAT"GT"C GATGGTACGT "GATAGG"CC TACCATGTT" GACTACGGGT AACGGGG"AA TCAGGGTTCG [336]
Marisa           GGCGACGCAT CTTTCAAATG TCT"CCCTAT CAAAT"GT"C GATGGTACGT "GATAGG"CC TACCATGTT" GACTACGGGT AACGGGG"AA TCAGGGTTCG [335]
Cipangopaludina  GGCGACGCAT CTTTCAAATG TCTGCCCTAT CAAAT"GA"C GACGGTACGT "GATCTG"CC TACCGTGTT" GACTACGGGT AGCGGGG"AA TCAGGGTTCG [339]
Campanile        GGCGACGCAT CTTTCAAATG TCTGCCCTAT CAAATTGAAC GAGGGTACGT TGATAGGGCC TACCATGTTT GACTACGGGT AGCGGGG"AA TCAGGGTTCG [349]
Modulus          GGCGACGCAT CTTTCAAATG TCTGCCCTAT CAAAT"GA"C GATGGTCGGT "GATCTG"CC TACCATGTT" GGCTACGGGT AGCGGGG"AA TCAGGGTTCG [324]
Cerithium        GGCGACGCAT CTTTCAAATG TCTGCCCTAT CAAAT"GA"C GATGGTCGGT "GATCTG"CC TACCATGTT" TACTACGGGT AGCGGGG"AA TCAGGGTTCG [323]
Batillaria       GGCGACGCAT CTTTCAAATG TCTGCCCTAT CAAAT"GA"C GATGGTCGGT "GATCTG"CC TACCATGTT" TACTACGGGT AGCGGGG"AA TCAGGGTTCG [324]
Annularia        GGCGACGCAT CTTTCAAATG TCTGCCCTAT CAAAT"GA"C GATGGTACGT "GATCTG"CC TACCATGTTT AGCAACGGGT AGCGGGG"AA TCAGGGTTCG [338]
Littorina        GGCGACGCAT CTTTCAAATG TCTGCCCTAT CAAAT"GA"C GATGGTACGT "GATCTG"CC TACCATGTT" GGCAACGGGT AGCGGGG"AA TCAGGGTTCG [331]
Tectarius        GGCGACGCAT CTTTCAAATG TCTGCCCTAT CAAAT"GA"C GATGGTACGT "GATCTG"CC TACCATGTT" AACAACGGGT AGCGGGG"AA TCAGGGTTCG [325]
Truncatella      GGCGACGCAT CTTTCAAATG TCTGCCCTAT CAAAT"GA"C GATGGTACGT "GATCTG"CC TACCATGTT" GGCAACGGGT AGCGGGG"AA TCAGGGTTCG [374]
Xenophora        GGCGACGCAT CTTTCAA"TG TCTGCCCTAT CAAAT"GA"C GATGGTACGT "GATCTG"CC TACCATGTT" AGCAACGGGT AGCGGGG"AA TCAGGGTTCG [311]
Cypraea          GGCGACGCAT CTTTCAAATG TCTGCCCTAT CAAAT"GA"C GATGGTACGT "GATCTG"CC TACCATGTT" AGCAACGGGT AGCGGGG"AA TCAGGGTTCG [325]
Fusitriton       GGCGACGCAT CTTTCAAATG TCTGCCCTAT CAAAT"GA"C GATGGTACGT "GATCTG"CC TACCATGTT" AGCAACGGGT AGCGGGG"AA TCAGGGTTCG [342]
Busycon          GGCGACGCAT CTTTCAAATG TCTGCCCTAT CAAAT"GA"C GATGGTACGT "GATCTG"CC TACCATGTT" AGCAACGGGT AGCGGGG"AA TCAGGGTTCG [323]
Oliva            GGCGACGCAT CTTTCAAATG TCTGCCCTAT CAAAT"GA"C GATGGTACGT "GATCTG"CC TACCATGTT" AGCAACGGGT AGCGGGG"AA TCAGGGTTCG [323]
Hastula          GGCGACGCAT CTTTCAAATG TCTGCCCTAT CAAAT"GA"C GATGGTACGT "GATCTG"CC TACCATGTT" GGCAACGGGT AGCGGGG"AA TCAGGGTTCG [323]
Aplysia          GGCGACGCAT CTTTCAAATG TCTGCCCTAT CAAAT"GT"C GATGGTACGT "GATATG"C" TACCATGTT" TGTAACGGGT AACGGGGTAA TCAGGGTTCG [344]
Siphonaria       GGCGACGCAT CTTTCAAATG TCTGCCCTAT CAAAT"GT"C GATGGTACGT "GACATG"CC TACCATGTT" TATAACGGGT AACGGGG"AA TCAGGGTTCG [343]

                        410        420        430        440        450        460        470        480        490        500
Diodora          ATTCCGGAGA GGGAGCATGA GAAACGGCTA CCACATCCAA GG"AAGGCAG CAGGCGCGCA AATTACCCAA TCTCGATACG AGGAGCTAGT GACGAAAAAT [433]
Astraea          ATTCCGGAGA GGGAGCATGA GAAACGGCTA CCACATCCAA GG"AAGGCAG CAGGCGCGCA AATTACCCAA TCTCGACACG AGGAGGTAGT GACGAAAAAT [430]
Nerita           ATTCCGGAGA GGGAGCATGA GAAACGGCTA C"ACATCCAA G""AAGGCAG CAGGCGCGCA ACTTACCCAC TCCTGGAACG GGGAGGTAGT G"CGAAAAAT [414]
Neritina         ATTCCGGAGA GGGAGCATGA GAAACGGCTA CCACATCCAA GG"AAGGCAG CAGGCGCGCA ACTTACCCAC TCCTGGTACG GGGAGGTAGT GACGAAAAAT [425]
Cyclophorus      ATTCCGGAGA GGGAGCATGA GAAACGGCTA CCACATCCAA GG"AAGGCAG CAGGCGCGCA ACTTACCCAC TCCTGGCACG GGGAGGTAGT GACGAAAAAT [428]
Neocyclotus      ATTCCGGAGA GGGAGCATGA GAAACGGCTA CCACATCCAA GG"AAGGCAG CAGGCGCGCA ACTTACCCAC TCCTGGCACG GGGAGGTAGT GACGAAAAAT [429]
Pomacea          ATTCCGGAGA GGGAGCATGA GAAACGGCTA CCACATCCAA GG"AAGGCAG CAGGCGCGCA ACTTACCCAC TCCCAGCTCG GGGAGCTAGT GACGAAAAAT [435]
Marisa           ATTCCGGAGA GGGAGCATGA GAAACGGCTA CCACATCCAA GG"AAGGCAG CAGGCGCGCA ACTTACCCAC TCCCAGCTCG GGGAGGTAGT GACGAAAAAT [434]
Cipangopaludina  ATTCCGGAGA GGGAGCATGA GAAACGGCTA CCACATCCAA GG"AAGGCAG CAGGCGCGCA ACTTACCCAC TCCTGGCACG GGGAGGTAGT GACGAAAAAT [437]
Campanile        ATTCCGGAGA GGGAGCATGA GAAACGGCTA CCACATCCAA GG"AAGGCAG CAGGCGCGCA ACTTACCCAC TCCTGGCACG GGGAGGTAGT GACGAAAAAT [448]
Modulus          ATTCCGGAGA GGGAGCATGA GAAACGGCTA CCACATCCAA GG"AAGGCAG CAGGCGCGCA ACTTACCCAC TCCTGGCACG GGGAGGTAGT GACGAAAAAT [423]
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	410	420	430	440	450	460	470	480	490	500	
Cerithium	ATTCCGGAGA	GGGAGCATGA	GAAACGGCTA	CCACATCCAA	GG"AAGGCAG	CAGGCGCGCA	ACTTACCCAC	TCCTGGCACG	GGGAGGTAGT	GACGAAAAAT	[422]
Batillaria	ATTCCGGAGA	GGGAGCATGA	GAAACGGCTA	CCACATCCAA	GG"AAGGCAG	CAGGCGCGCA	ACTTACCCAC	TCCTGGCACG	GGGAGGTAGT	GACGAAAAAT	[423]
Annularia	ATTCCGGAGA	GGGAGCATGA	GAAACGGCTA	CCACATCCAA	GG"AAGGCAG	CAGGCGCGCA	ACTTACCCAC	TCCTGGCACG	GGGAGGTAGT	GACGAAAAAT	[437]
Littorina	ATTCCGGAGA	GGGAGCATGA	GAAACGGCTA	CCACATCCAA	GG"AAGGCAG	CAGGCGCGCA	ACTTACCCAC	TCCTGGCACG	GGGAGGTAGT	GACGAAAAAT	[430]
Tectarius	ATTCCGGAGA	GGGAGCATGA	GAAACGGCTA	CCACATCCAA	GG"AAGGCAC	CAGGCGCGCA	ACTTACCCAC	TCCTGGCACG	GGGAGGTAGT	GACGAAAAAT	[424]
Truncatella	ATTCCGGAGA	GGGAGCATGA	GAAACGGCTA	CCACATCCAA	GG"AAGGCAG	CAGGCGCGCA	ACTTACCCAC	TCCTGGCACG	GGGAGGTAGT	GACGAAAAAT	[473]
Xenophora	ATTCCGGAGA	GGGAGCATGA	GAAACGGCTA	CCACATCCAA	GG"AAGGCAG	CAGGCGCGCA	ACTTACCCAC	TCCTGGCACG	GGGAGGTAGT	GACGAAAAAT	[410]
Cypraea	ATTCCGGAGA	GGGAGCATGA	GAAACGGCTA	CCACATCCAA	GG"AAGGCAG	CAGGCGCGCA	ACTTACCCAC	TCCTGGCACG	GGGAGGTAGT	GACGAAAAAT	[424]
Fusitriton	ATTCCGGAGA	GGGAGCATGA	GAAACGGCTA	CCACATCCAA	GG"AAGGCAG	CAGGCGCGCA	ACTTACCCAC	TCCTGGCACG	GGGAGGTAGT	GACGAAAAAT	[421]
Busycon	ATTCCGGAGA	GGGAGCATGA	GAAACGGCTA	CCACATCCAA	GG"AAGGCAG	CAGGCGCGCA	ACTTACCCAC	TCCTGGCACG	GGGAGGTAGT	GACGAAAAAT	[422]
Oliva	ATTCCGGAGA	GGGAGCATGA	GAAACGGCTA	CCACATCCAA	GG"AAGGCAG	CAGGCGCGCA	ACTTACCCAC	TCCTGGCACG	GGGAGGTAGT	GACGAAAAAT	[422]
Hastula	ATTCCGGAGA	GGGAGCATGA	GAAACGGCTA	CCACATCCAA	GG"AAGGCAG	CAGGCGCGCA	ACTTACCCAC	TCCTGGCACG	GGGAGGTAGT	GACGAAAAAT	[422]
Aplysia	ATTCCGGAGA	GGGAGCATGA	GAAACGGTTA	CCACATCCAA	GGTAAGGCAG	CAGGTGCGCA	ACTTACCCAC	TCCCGGCACG	GGGAGGTAGT	GA"GAAAAAT	[443]
Siphonaria	ATTCCGGAGA	GGGAGCATGA	GAAACGGCTA	CCACATCCAA	GG"AAGGCAG	CAGGCGCGCA	ACTTACCCAC	TCCCGGCACG	GGGAGGTAGT	GACGAAAAAT	[442]

	510		
Diodora	AACAATA"CG	GGACTCT	[449]
Astraea	AACAATA"CG	GGACTCT	[446]
Nerita	AACAATA"CG	GGACTCT	[430]
Neritina	AACAATA"CG	GGACTCT	[441]
Cyclophorus	AACAATA"CG	GAACTCT	[444]
Neocyclotus	AACAATA"CG	GAACTCT	[445]
Pomacea	AACAATA"CG	GAACT"T	[450]
Marisa	AACAATA"CG	GAACTCT	[450]
Cipangopaludina	AACAATA"CG	GAACTCT	[453]
Campanile	AACAATA"CG	GAACTCT	[464]
Modulus	AACAATA"CG	GAACTCG	[439]
Cerithium	AACAATA"CG	AAACTCT	[438]
Batillaria	AACAATA"CG	AAACTCT	[439]
Annularia	AACAATA"CG	GAACTCT	[453]
Littorina	AACAATA"CG	GAACTCT	[446]
Tectarius	AACAATA"CG	GAACTCT	[440]
Truncatella	AACAATA"CG	GAACTCT	[489]
Xenophora	AACAATA"CG	GAACTCT	[426]
Cypraea	AACAATA"CG	GAACTCT	[440]
Fusitriton	AACAATA"CG	GAACTCT	[437]
Busycon	AACAATA"CG	GAACTCT	[438]
Oliva	AACAATA"CG	GAACTCT	[438]
Hastula	AACAATA"CG	GAACTCT	[438]
Aplysia	AACAATAACG	GGACTCT	[460]
Siphonaria	AACAATA"CG	GGACTCT	[458]