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Phylogenetic Relationships Among Calyptraeid Gastropods and Their Implications for the Biogeography of Marine Speciation

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Abstract.—Although calyptraeid gastropods are not well understood taxonomically, in part because their simple plastic shells are the primary taxonomic character, they provide an ideal system to examine questions about evolution in the marine environment. I conducted a phylogenetic analysis of calyptraeid gastropods using DNA sequence data from mitochondrial cytochrome oxidase I (COI) and 16S genes and the nuclear 28S gene. The resultant phylogeny was used to examine the biogeographic patterns of speciation in the Calyptraeidae. Parsimony and Bayesian analyses of the combined data sets for 94 calyptraeid operational taxonomic units and 24 outgroups produced well-resolved phylogenies. Both approaches resulted in identical sister-species relationships, and the few differences in deeper topology did not affect biogeographic inferences. The geographic distribution of the species included here demonstrate numerous dispersal events both between the Pacific and Atlantic oceans and across the equator. When parsimony is used to reconstruct the movement from the Pacific to the Atlantic oceans on the phylogeny, there are 12 transitions between oceans, primarily from the Pacific to the Atlantic. When the latitude is coded as north versus south of the equator, the most-parsimonious reconstruction gives the origin of calyptraeids in the north followed by 15 dispersal events to regions south of the equator and no returns to the north. Many clades of the most closely related species are either sympatric or occur along a single coastline. Closely related species can, however, occur in such divergent regions as Southern California and South Africa. There is little evidence for sister-species pairs or larger clades having been split by the Isthmus of Panama or the Benguela upwelling, but the East Pacific Barrier appears to separate the most basal taxa from the rest of the family. [Biogeographic barriers; *Calyptraea*; *Crepidula*; *Crucibulum*; cytochrome oxidase I; 16S; sympatric speciation.]

Geographic patterns of speciation in marine invertebrates are not well understood. However, the prevailing view of marine biogeography has been that of broad dispersal (e.g., Mayr, 1954). There are few obvious physical barriers to dispersal of mobile marine animals such as pelagic fish and plankton. For animals with sedentary benthic adults, high dispersal rates result from movement during a pelagic larval stage. Many species in most groups of marine invertebrates have free-living larvae that can spend from weeks to months or even years in the plankton. During this time, they are subject to passive dispersal via ocean currents and can be found thousands of miles from suitable adult habitat (Scheltema, 1986). Many other species lack planktonic larvae and are therefore expected to display limited dispersal. This difference in life histories (presence or absence of planktonic larvae) leads to different predictions about biogeography, population structure, and, therefore, patterns of speciation (e.g., Collin, 2001). Groups with high levels of larval or adult dispersal are expected to contain few species with large geographic ranges and little population structure (e.g., some fish: Bowen et al., 2001; Colborn et al., 2001; sea urchins: Lessios et al., 1999, 2001). Speciation in such groups is thought to come about as a result of barriers to dispersal (Mayr, 1954). The most often discussed barriers to dispersal for shallow-water marine organisms are (1) the Isthmus of Panama, which forms a land barrier between the Pacific and Atlantic Oceans, (2) the East Pacific Barrier, the great expanse (5,400 km) of the East Pacific Ocean between the Line Islands and Clipperton Atoll that provides no possible habitat for shallow-water organisms, and (3) the Benguela upwelling, an area of cold upwelling off the southern coast of Africa that is thought to prevent dispersal of warm-water organisms from the Indian Ocean to the Atlantic Ocean (Ekman, 1953; Briggs, 1961). Speciation due to vicariance across such barriers is expected to result in phylogenies with pairs of sister species or sister clades on each side of the barrier (Mayr, 1954). These events have been used to date divergence times of such clades (e.g., Lessios et al., 1999, 2001).

In groups lacking larval dispersal, it is reasonable to expect that smaller local barriers, such as a stretch of unsuitable habitat, could also act as barriers to dispersal and gene flow. Allopatric speciation due to such local barriers could result in a pattern of sister species occurring along a single shoreline if subsequent dispersal and extinction had not obscured the pattern. Similar patterns could also result from transient allopatry due to range shifts caused by climate change (Hellberg, 1998) or from sympatric speciation. Because many groups contain some species with direct development and limited dispersal potential and some with planktonic development and high dispersal, the distribution of species within a given group will likely show a combination of the effects of large and small barriers to dispersal.

Previous studies of marine species have seldom included examination of the biogeography of speciose clades throughout their ranges. Although patterns of speciation across several well-known barriers (e.g., the Isthmus of Panama or the biogeographic break in southeastern Florida) have been studied for species from many groups (e.g., Bert, 1986; Avise, 1992; Bermingham and Lessios, 1993; Knowlton and Weigt, 1998; Collin, 2001; Marko, 2002), these studies are often limited to the

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species that occur directly on either side of the proposed barrier, and few species from other regions have been included. This limit in scope results in a detailed picture of concordant patterns across diverse taxa but does not put these local patterns in the context of the worldwide bigeography of each group. Studies of worldwide phylogeny and distribution of marine fish and invertebrates usually contain few species, all of which have large, often transoceanic ranges (e.g., Lessios et al., 1999, 2001; Bowen et al., 2001; Colborn et al., 2001). Therefore, it is probable that species in these groups are the least likely to speciate due to anything but the most profound geographic barriers. Depauperate groups do generally show species separated by the major marine barriers.

The more geographically limited studies of speciose groups demonstrate that closely related species can cooccur and that species that occur in the same geographic region are often each others' closest relatives (e.g., Lee and Vacquier, 1995; Hellberg, 1998; Marko, 1998). From his study of species of Pacific *Tegula*, Hellberg (1998:1319) concluded that "all recent speciation within the genus has occurred along single coastlines" rather than across major barriers, which suggests that sympatric or transient allopatric speciation is likely in these groups. Unfortunately, the geographic sampling of *Tegula* in this study did not permit comparisons across some major barriers to marine dispersal. Because most samples came from the Northern or Eastern Pacific, the relative importance of such barriers could not be thoroughly assessed. Here, I present a worldwide phylogeny for the Calyptraeidae, a diverse and widespread group of shallow-water gastropods, and examine the geographic distribution of species to gain insight into the patterns of speciation along single coastlines versus across major barriers.

Calyptraeid gastropods, a family of sedentary filter-feeding marine limpets, have played a large part in our understanding of reproductive strategies in marine molluscs. They are tolerant of widely varying ecological conditions but generally occur in intertidal or shallow subtidal habitats. Unlike most groups of marine molluscs, their diversity is low in the Indo-West Pacific. They occur throughout the world's oceans with the exception of the Antarctic and Arctic. The genus *Crepidula* is probably the best studied group of calyptraeids, and a variety of species are commonly used in developmental (reviewed by Collin, 2003a), ecological (e.g., Matusiak and Fell, 1982; Loomis and VanNieuwenhuyze, 1985; Shenk and Karlson, 1986; McGee and Targett, 1989), and behavioral (Hoagland, 1978; Vermeij et al., 1987; Collin, 1995) research. These animals have been the major focus of research on protandrous sex change in marine invertebrates (e.g., Coe, 1942a, 1942b; Hoagland, 1978; Collin, 1995). *Crepidula fornicata* and *C. onyx* are well-studied examples of invasive exotic species in marine habitats (Carlton, 1979, and references therein; Deslous-Paoli, 1985; Woodruff et al., 1986; Sauriau et al., 1998). Despite the wide range of studies on the biology of these gastropods, the systematics and taxonomy of calyptraeids have received only moderate attention (e.g., Hoagland, 1977) compared with other groups of large-bodied, shallow-water gastropods (e.g., muricids: Kool, 1993; Marko and Vermeij, 1999; Vermeij and Carlson, 2000; *Conus*: Duda and Palumbi, 1999; littorinids: Reid, 1989). This lack of attention may be in part due to the widely accepted idea that calyptraeid shells, which are simple and extraordinarily plastic, may be of limited use for systematics. Researchers that have applied developmental and molecular methods to small groups of species within *Crepidula* (Gallardo, 1979; Hoagland, 1984, 1986; Collin, 2000, 2001, 2002a) and *Crucibulum* (Véliz et al., 2001) have demonstrated that sibling species, which differ genetically and developmentally, often do not show diagnostic differences in shell morphology. The discovery of these cryptic species has further complicated calyptraeid taxonomy.

Calyptraeid taxonomy has traditionally been based on shell morphology. The family usually includes slipper shells (*Crepidula* Lamarck, 1799; with a flat septum and posterior shell apex), cup and saucer limpets (*Crucibulum* Schumacher, 1817; with a cone-shaped shell and a cup-shaped septum), and hat shells (*Calyptraea* Lamarck, 1799; with a cone-shaped shell and flat septum). The generic and subgeneric assignments of species within the Calyptraeidae are contentious or uncertain and vary considerably among authors. *Crucibulum* and *Calyptraea* have not been revised since the 1800s (e.g., Broderip, 1834, 1835; Reeve, 1859). Some divisions in the family represent groups with distinctive shell morphologies (e.g., *Trochita*, *Bicatillus*, *Siphopatella*), but many represent groups from restricted geographic areas (e.g., *Maoricrypta* and *Sigapatella* from New Zealand). Acceptance of any of the proposed geography-based taxonomic groupings implies a belief that diversification occurs locally and that long-distance dispersal across ocean basins does not occur often. For example, *Maoricrypta* and *Sigapatella*, two genera that are restricted to New Zealand, cannot be distinguished from *Crepidula* and *Calyptraea*, respectively, on the basis of shell characters but have nevertheless been considered as separate groups based on locality. Several other proposed taxa such as the subgenera *Janacus* and *Gradicrepidula* and the genus *Bostrycapulus* occur throughout the world. If these taxa represent natural groupings, then worldwide dispersal and subsequent extinction must have been significant.

Materials and Methods

Taxon Sampling

DNA sequences were obtained from all calyptraeid species for which appropriately preserved tissue was available (Appendix 1). The sampling of *Calyptraea* and *Crucibulum* probably represents about 15–35% of the extant species. The 70 species of *Crepidula* sensu Hoagland (1977) represent a significant increase in the number of recognized species over the most recent taxonomic revision of the genus (only 50 valid species listed by Hoagland, 1977). A few of these species not listed by

Hoagland (1977) have been described or removed from synonymy subsequent to Hoagland's work, but the majority of the additional species have been detected too recently for formal taxonomic descriptions or revisions to have been completed.

Outgroups were selected on the basis of traditional notions about caenogastropod relationships. Hipponicids, trichotropids, and capulids have generally been considered close relatives of the calyptraeids (Broderip, 1834; Reeve, 1859; Hoagland, 1986; Bandel and Reidel, 1994). Because analysis of preliminary sequence data showed hipponicids to be surprisingly divergent from the other taxa, sequences were also obtained from species representing a variety of other "lower" caenogastropod families (Appendix 1). These outgroups were used in an attempt to identify the calyptraeid's closest sister family.

Because the taxonomy of calyptraeids is highly uncertain, many of the species designations used here are provisional (Appendix 1). The distinct species status of each operational taxonomic unit (OTU) that could not be clearly identified as a currently valid species was determined on the basis of morphological, developmental, and genetic differentiation from other similar samples. When two of these three criteria showed the OTUs to differ, they were considered to be distinct species. In many cases, it is not clear which existing name should be applied to which taxon (i.e., the original species description and type material are not adequate to identify a specific OTU). Therefore, I have used the following conventions. Cases in which several species fit the description of a named species but differ in locality have been indicated by appending the locality to the species name (e.g., *Crepidula excavata* Peru vs. *Crepidula excavata* Mexico). When a species was similar to but distinct from an identifiable named species, I indicate the similarity using "cf." (used here to imply morphological similarity only) or "aff." (used here to imply phylogenetic affinity and morphological similarity). In cases where I cannot associate the animals with named species I simply use "n. sp."

In some cases, two geographically distant populations of the same species have been used as OTUs. Where they are genetically similar and no other evidence suggests their status as distinct species, it is likely that they are conspecific. However, the wide geographic separation between samples makes this conclusion uncertain. Therefore, I have considered these to be populations of the same species and are designated as "pop. 1," "pop. 2," etc., pending further study.

Vouchers from the same locality as the individuals used here have been deposited at the Field Museum in Chicago, the Academy of Natural Sciences in Philadelphia, and the Natural History Museum in London (Appendix 1). Additional ethanol-preserved or formalin-fixed material from various other localities is also deposited at these institutions. Where only a single individual was available, it has been deposited at the Field Museum. Sequences and alignments have been deposited in GenBank (Appendix 1).

DNA Sequencing

A 647-base pair (bp) fragment of mitochondrial cytochrome oxidase I (COI), 560 bp of mitochondrial 16S, and 450 bp of nuclear 28S genes were sequenced from the same individual from each species. DNA was extracted from ethanol-preserved tissue with a Puregene (Gentra Systems) or DNA Easy extraction kit (Qiagen), amplified using Ready-To-Go polymerase chain reaction (PCR) beads (Pharmacia Biotech), and the primers and PCR profile of Folmer et al. (1994) for COI, those of Palumbi (1996a; 16Sar-16Sbr) for 16S, and those of Park and O'Foighil (2000; D23F-D4RB) for 28S. PCR products were purified using standard GeneClean, Gelase, or spin-column protocols. Both strands were cycle-sequenced using the amplification primers and a fluorescent cycle sequencing dye terminator kit (dRhodamine, Big Dyes or New Big Dyes; Perkin Elmer) and sequenced on an ABI 377 automated sequencer. In many cases, multiple individuals of a single species were sequenced for other projects (Collin, 2000, 2001; in prep.), and little sequence divergence was detected within each species (0–3% in COI; 0–0.5% in 16S).

Analysis

Alignments.—Sequences were aligned and areas of ambiguous alignment were identified using the criteria for the first step of Lutzoni et al. (2000) using Sequencher 3.0. These criteria were used to strictly conserve positional homology, and therefore large regions of both 16S and 28S were considered to be ambiguously aligned (Table 1). Regions designated as ambiguously aligned were excluded from the subsequent equal-weighted parsimony and Bayesian analyses and were coded as unordered multistate characters for the weighted parsimony analysis. In general, areas with long gaps were treated has ambiguous, but indels of a single base were generally clearly aligned and therefore included as a fifth character state in subsequent analyses. Three separate alignments were created for this analysis: (1) an alignment for the ingroup taxa (i.e., calyptraeids) only, (2) an alignment for the ingroup and a small number of the closest outgroup taxa, including only trichotropids and capulids, and (3) an alignment including the ingroup and all the sequenced outgroups. Heterozygous bases occurred occasionally in the 28S sequences and were coded as ambiguous. Alignments from all three gene fragments were concatenated to create combined data sets that included all taxa for which two of three genes were successfully sequenced. Each analysis was repeated for combined data sets for all three alignments (ingroup only, ingroup plus small outgroup, and ingroup plus large outgroup) and on the separate data sets for each gene fragment (see Collin, 2002b). Independent analyses of these alignments were compared to determine the effects of distant outgroups not only on the rooting of the ingroup but also on the recovered topology within the ingroup.

Parsimony analyses.—Parsimony analyses were conducted using PAUP* 4.0b8 (Swofford, 2002). Heterogeneity of base composition among taxa was tested for by

TABLE 1. Summary of individual data sets.

	Data set			
	COI	16S	28S	Combined
No. bases sequenced	647	560	450	1657
No. bases ambiguously aligned, ingroup	0	156 (28%)	68 (15%)	224
No. bases ambiguously aligned, large outgroup	0	173 (31%)	116 (26%)	289
No. bases parsimony informative, ingroup	273 (42%)	108 (19%)	66 (15%)	447
No. bases parsimony informative, large outgroup	297 (46%)	174 (31%)	90 (20%)	561
Frequency A[a]	0.26	0.31	0.16	
Frequency C[a]	0.18	0.22	0.37	
Frequency G[a]	0.19	0.16	0.33	
Frequency T[a]	0.37	0.31	0.14	
No. taxa	93	87	91	94
No. characters	647	404	370	1417
Burn-in generations	100,000	100,000	200,000	100,000

[a]Excluding ambiguously aligned regions.

using the χ^2 test implemented in PAUP* for informative sites only and did not differ significantly for 16S and 28S data (see Collin, 2002b). However, COI did show significant heterogeneity among taxa (χ^2, $P < 0.01$). This heterogeneity did not appear to effect the results of the parsimony analysis beacuse the topology based on the LogDet analysis of the combined data set (not shown) did not differ from the results presented below.

Unrooted equal-weighted parsimony analyses were performed on each of the concatenated data sets using a heuristic search with tree bisection–reconnection (TBR) branch swapping, 1,000 random additions, saving two trees at each step, and maxtrees set to 1,000. This value of maxtrees was never reached. Gaps were treated as a fifth character state and areas of ambiguous alignment were excluded. Bootstrap support for each clade was assessed based on 500 bootstrap replicates with a heuristic search, TBR branch swapping, 10 random additions saving two trees at each step, maxtrees set to 1,000, and constant characters excluded. In addition to bootstrapping the concatenated data sets, data sets of each gene fragment were bootstrapped individually to gain some idea of the support provided by each data partition. Complete heuristic searches were not conducted on the data sets of individual gene fragments because the low levels of resolution and large numbers of most-parsimonious trees obtained from the 16S and 28S data sets made the time required for branch-swapping to reach completion prohibitive. Instead five trees were saved from each of 1,000 random addition replicates of a heuristic search to obtain a number of "short" trees. Branch swapping was then conducted on these 5,000 short trees.

Because equal-weighted parsimony methods do not take full advantage of the information contained in DNA sequences, a step-matrix weighted parsimony analysis was also conducted. Step matrices that weighted each nucleotide substitution by their relative frequencies (Felsenstein, 1981; Wheeler, 1990) were calculated for the first, second, and third positions of the COI codons and for the unambiguous regions of 16S and 28S fragments using STMatrix 2.2 (Lutzoni and Zoller, Duke University, Durham, NC, 2001). Ambiguous regions of the 16S and 28S sequences were each treated as a single unordered multistate character using Inaase 2.4b (Lutzoni et al., 2000) with transitions, transversions, and gaps all weighted as 1. Matrix weighting was not applied to the areas of ambiguous alignment because in many cases there were >60 separate character states for each region. Heuristic searches for the most-parsimonious trees and bootstrap analyses were conducted for the individual and concatenated data sets.

Bayesian analyses.—Bayesian analyses were conducted on all data sets from which ambiguous regions of the alignment were excluded. The appropriate model and starting parameters for Bayesian analysis were chosen for each of the data sets using the likelihood ratio test implemented in ModelTest 3.06 (Posada and Crandell, 1998, 2001) with the default settings and an α level of 0.01. Bayesian analyses using MrBayes 2.01 (Huelsenbeck, 2000; Huelsenbeck and Ronquist, 2001) were conducted for each data set (COI, 16S, 28S, and combined data for the ingroup only, the ingroup plus closest outgroups, and the ingroup plus all outgroups) using the model obtained from ModelTest 3.06 (TVM + I + G for all data sets except for 28S for which the model was TrN + I + G). The Bayesian analysis using 1 cold and 3 incrementally heated chains started from a random tree with a uniform (0, 10) prior for branch lengths and a uniform (0, 10) prior for the Gamma shape parameter. Invariant sites were retained in the sequences and their frequency was estimated using the "invgamma" setting with a uniform (0, 1) prior for proportion of invariant sites. Uniform priors were used because they are less likely to bias the estimated values. The Metropolis-coupled Markov chain Monte Carlo (MCMCMC) analysis was run five times for 1,000,000 generations for each data set, and the number of trees to be discarded as representing the "burn-in" period was determined graphically to be either 100,000 or 200,000 generations (Table 1). Majority-rule consensus trees for every 50th tree after the burn-in period were created using PAUP*, and consensus phylograms were created in MrBayes.

Combinability analyses.—Combinability of different data sets was assessed using the same logical framework

as the subsequent phylogenetic analyses. The incongruence length difference (ILD) test (Mickevich and Farris, 1981; Farris et al., 1994) was used to determine whether the COI, 16S, and 28S data sets had significantly conflicting signals prior to parsimony analysis. The ILD test was conducted with equal weighting prior to equal-weighted parsimony analysis and using the same step matrices as used in the subsequent weighted analysis. In all cases, the incomplete taxa and areas of ambiguous alignment were excluded. Five hundred replicates of the ILD test were conducted using a heuristic search, with TBR branch swapping, 10 random additions, saving two trees at each step, and maxtrees set to 1,000. Invariant sites were excluded following the recommendation of Cunningham (1997a, 1997b). Results of the ILD test should be treated cautiously (see Barker and Lutzoni, 2002; Darlu and Lecointre, 2002; Dowton and Austin, 2002).

Prior to phylogenetic analysis within a Bayesian framework, combinability was examined by comparing the support for each node from the Bayesian consensus tree from the three individual data sets. Because the percentage of trees in the consensus supporting a specific branch represents the posterior probability of the branch occurring in the most likely tree (if the model is correct), noncongruent groupings each with >95% support represent statistical conflict among the data sets.

Biogeography

Because the geographic range of many calyptraeids is not well known, detailed analysis of their ranges is difficult. Species included in this phylogeny were considered to be sympatric when I collected them in nearby localities (within a few kilometers) or when other detailed analyses of these species (e.g., Collin, 2000) demonstrated that they occurred in sympatry over a significant portion of their ranges. It is likely that coding species this way will underestimate the number of species that are sympatric over at least a portion of their ranges but should not affect the number of species pairs that are considered to occur along a single shoreline. I counted the number of sister-species pairs that are sympatric, that occur along a single coastline, and that are geographically distant and compared this number to the sequence divergence between the two sisters. In no cases did I include populations created by human-mediated disperal in the geographic range. There is no evidence to suggest that any of the samples used here were from outside their recent historic range.

To determine the frequency of large scale geographic dispersal, I traced the ocean (Atlantic/Pacific) and hemisphere (Northern/Southern) where each species occurs on the phylogeny. Equal-weighted parsimony was use to reconstruct the ancestral character states and count the number of transitions between oceans and hemispheres. Sisters or close relatives separated by major biogeographic barriers such as the Isthmus of Panama or the East Pacific barrier were identified by examining the phylogeny.

Maximum likelihood reconstructions of character state transitions (Cunningham, 1999; Pagel, 1994, 1999; Cook et al., 2002) between oceans and hemispheres were performed using DISCRETE (Pagel, 1999). I used a likelihood-ratio test to determine if a model with different frequencies of migrations from one ocean or hemisphere to the other and back (alpha and beta in DISCRETE) is significantly better than a model in which the frequencies of migrations back and forth are equal (alpha = beta in DISCRETE). For each character, the most likely model was used to reconstruct the likelihood of each character state at each internal node, using the local reconstruction option in the graphics menu in DISCRETE. Those nodes where the likelihoods of the two states differed by more than 2 log units were considered to provide significant support for one state at that node in preference to the other state (Pagel, 1999). The state at the root was not fixed.

RESULTS

Alignments

COI sequence data aligned easily with only a single codon indel in the *Vanikoro* species. There was evidence of saturation within the first and third position transitions but not for the other categories of substitutions. Within the ingroup, there were numerous small indels in the 28S gene, although the high G-C (Table 1) bias made the alignment of these indels strictly ambiguous. When the more distant outgroups were included, large regions of ambiguity were observed, resulting in the exclusion of 116 bp (Table 1). The 16S alignment for both the "ingroup only" and the "ingroup plus outgroups" were equally problematic. There were several large regions in which the sequences were not alignable, resulting in the exclusion of 28–30% of the sequence data (Table 1). Elimination of the outgroup taxa did not greatly improve the alignment. Examination of predicted secondary structure showed that the major features of 16S secondary structure are generally similar in all taxa examined here, with the exception of the hipponicids. Hipponicids had a large deletion relative to the other taxa in the area of the stem and loop region corresponding to positions 238–286 in this alignment.

Combinability Analysis

The ILD test showed no significant incompatibility among the COI, 16S, and 28S data sets for the ingroup or the ingroup and outgroup data sets in either equal- or matrix-weighted analyses ($P > 0.5$). The lack of significant incompatibility is possibly due to the lack of strongly supported resolution in the individual 16S and 28S data sets or the differing rates of evolution among the three genes (Dowton and Austin, 2002). Results of the ILD test should be treated cautiously (Barker and Lutzoni, 2002; Darlu and Lecointre, 2002). However general congruence between independent analyses of each gene supports a combined analysis of the data sets.

Comparison of the Bayesian support values for each node recovered by analysis of the separate data sets

showed only three significant differences (i.e., both conflicting nodes with >95% support) among data sets (circled in Figs. 1–3). Within the calyptraeids, the 28S data conflicted with the other two data sets in the placement of *C. aculeata* Florida and *C. aculeata* Cape Verde as sister to *Cruc. concamarata* (Fig. 1). The 16S and COI data sets conflicted only in the placement of *Bicatillus* plus *Siphopatella* as sister to *Cal. chinensis* in the 16S tree (Fig. 2) and to *Maoricrypta* in the COI tree (Fig. 3). The low number of well-supported (>95% on both trees) conflicting branches was due in part to the small number of well-supported branches in the 28S and 16S data sets, which limits the power to detect significant conflict.

Phylogenetic Results

The results of the parsimony and Bayesian analyses were largely similar (for details, see Collin, 2002b). All runs of the MCMCMC analysis for each data set converged on the same likelihood, showing that the analyses were not trapped in suboptimal areas of tree space. Matrix-weighted parsimony of combined data sets also converged on a single optimum.

Each gene provides a different level of phylogenetic resolution. The 28S has little variation and therefore provided little support for any topology when analyzed alone (Fig. 1). The 16S sequences evolves more slowly than do the COI sequences and thus provided more resolution toward the base of the tree (Fig. 2), whereas COI produced well-resolved clades toward the tips of the tree (Fig. 3). Combined data sets produced more highly resolved and better supported trees (Figs. 4, 5) than did the individual data sets. Generally, branches that received Bayesian support also received bootstrap support on the parsimony tree (Figs. 4, 5). There were more branches deep within the tree that received Bayesian support without parsimony support, but the relationships among the terminal taxa were well supported by both analyses.

Many of the taxonomic groupings currently recognized on the basis of shell characters do not reflect monophyletic groups. *Crepidula* and *Calyptraea* are not monopyletic and neither are the subgenera *Janacus* and *Grandicrepidula*. The following major relationships were supported by both the Bayesian and parsimony analyses (Collin, 2002b): (1) Calyptraeidae is a monophyletic family, (2) the same group of mostly west-Pacific taxa involving *C. chinensis, S. walshi*, *B. extinctorum*, and the calyptraeid species from New Zealand appeared in an unresolved three-way polytomy at the base of the calyptraeids, (3) the remaining calyptraeids appear in a well-supported monophyletic group, (4) a clade composed of the *Bostrycapulus*, *Crepipatella, Crucibulum*, and the Panamanian *Calyptraea* species is well supported, (5) the remaining species form a monophyletic *Crepidula* s.s. clade, which is sister to this clade, and (6) *Trochita* appears nested deep within this clade of *Crepidula* s.s. (Figs. 4, 5)

Outgroups

Trichotropids and capulids, the outgroups suggested by traditional taxonomy, have short branches in these analyses and consistently occur together as the sister clade to the calyptraeids (Fig. 6). The position of the root within the calyptraeids did not differ among the analyses using few or many outgroups. In all cases, the calyptraeids were rooted on a basal polytomy involving *C. chinensis*, *C. walshi, B. extinctorum*, and the calyptraeid species from New Zealand (Figs. 4, 5). Despite using rapidly evolving DNA sequences and a diversity of divergent outgroups, the outgroup relationships are fairly well resolved (Fig. 6) and shed light on the phylogenetic relationships of some poorly known caenogastropods.

Biogeography

The mapping of collecting localities on the tree showed evidence that calyptraeids disperse far and frequently (Figs. 4, 5). When parsimony was used to reconstruct the movement from the Pacific to the Atlantic Ocean on the Bayesian phylogeny, there was a minimum of 12 transitions between oceans. There could have been 12 independent migrations from the Pacific to the Atlantic (Fig. 7) or 10 from the Pacific to the Atlantic and 2 to from the Atlantic to the Pacific (in the ancestor of *C. philippiana* and the ancestor of the *C. williamsi* + *Trochita* clade). Calyptraeids also appear to cross the equator numerous times. When the ancestral condition is considered to be north temperate and tropical regions are considered ambiguous, there are nine independent migrations to southern temperate areas. When the latitude is coded as being north or south of the equator, the most-parsimonious reconstruction gives the origin of calyptraeids in the north followed by 15 dispersal events to the south and no reversals (Fig. 7). Of the southern temperate taxa, there were five independent southern migrations to Chile, one to the southwest Atlantic, two to the southeast Atlantic, and two to Australia and New Zealand. Slight variations in tree topology (e.g., Figs. 4, 5) and state weighting do alter the number of transitions, but the pattern of asymmetric transitions, predominantly to the south and to the Atlantic, are robust to such changes. Therefore the number of reconstructed changes should be viewed as a heuristic devise rather than an exact reconstruction of history.

Maximum likelihood analysis showed that transitions from the Pacific to the Atlantic were almost 4 times less likely than transitions from the Atlantic to the Pacific (alpha = 1.64; beta = 4.62) and transitions from the southern hemisphere to the north were twice as likely as migrations from the north to the south (alpha = 14.17; beta = 6.78). The two parameter model was significantly better than the model in which alpha = beta for transitions between oceans (LR = 9.09; critical value for χ^2 with $\alpha = 0.05$ and 1 df = 3.84) and between hemispheres (LR = 8.93; critical value for χ^2 with $\alpha = 0.05$ and 1 df = 3.84). The ancestral states could not be reconstructed with any confidence for any major clades deep within the phylogeny for either character; however two-thirds of the nodes toward the tip of the tree could be reconstructed for ocean with confidence and were in agreement with

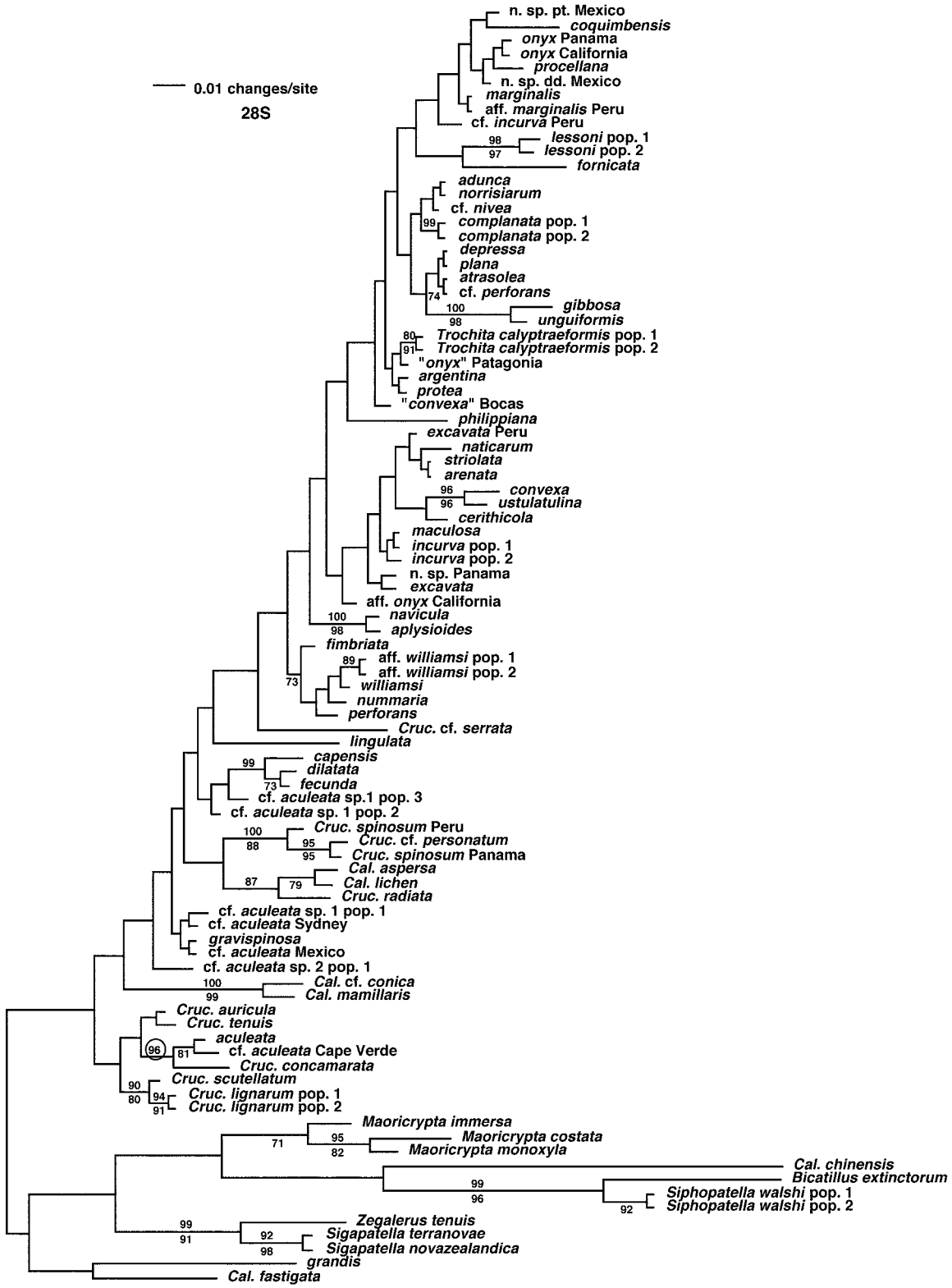

FIGURE 1. Consensus phylogram of the 80,000 trees retained from the five runs of the Bayesian analysis of the nuclear 28S gene sequences without outgroups. Numbers above the branches are posterior probabilities obtained from the consensus of all retained trees (only values >80% are shown). Numbers below the branches are bootstrap support from the matrix-weighted analysis (only values >70% are shown). Circled node with 95% support conflicted with supported nodes in trees from the 16S and COI data sets.

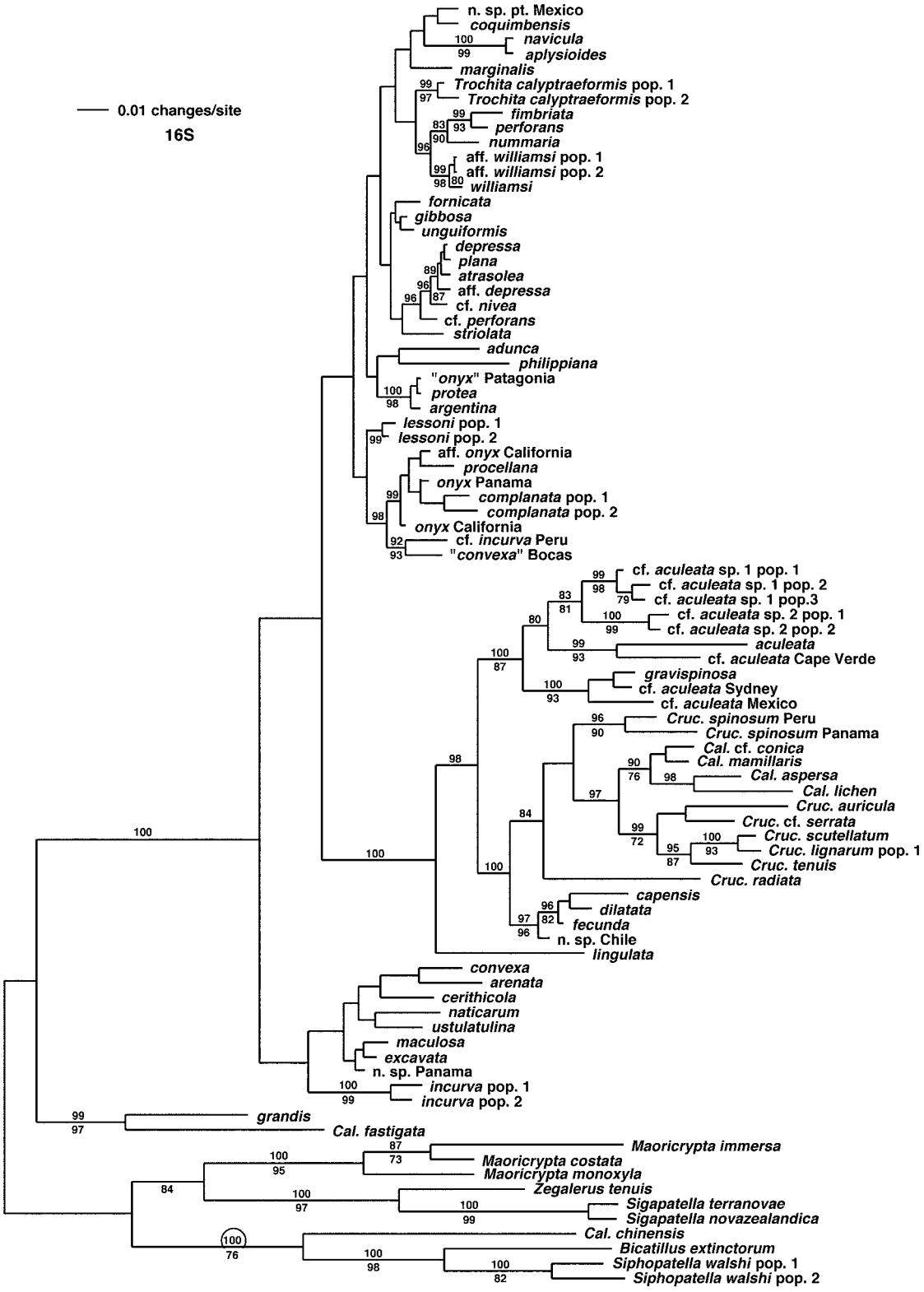

FIGURE 2. Consensus phylogram of the 90,000 trees retained from the five runs of the Bayesian analysis of the mitochondrial 16S gene sequences without outgroups. Numbers above the branches are posterior probabilities obtained from the consensus of all retained trees (only values >80% are shown). Numbers below the branches are bootstrap support from the matrix-weighted analysis (only values >70% are shown). Circled node with 95% support conflicted with supported nodes in trees from the 28S and COI data sets.

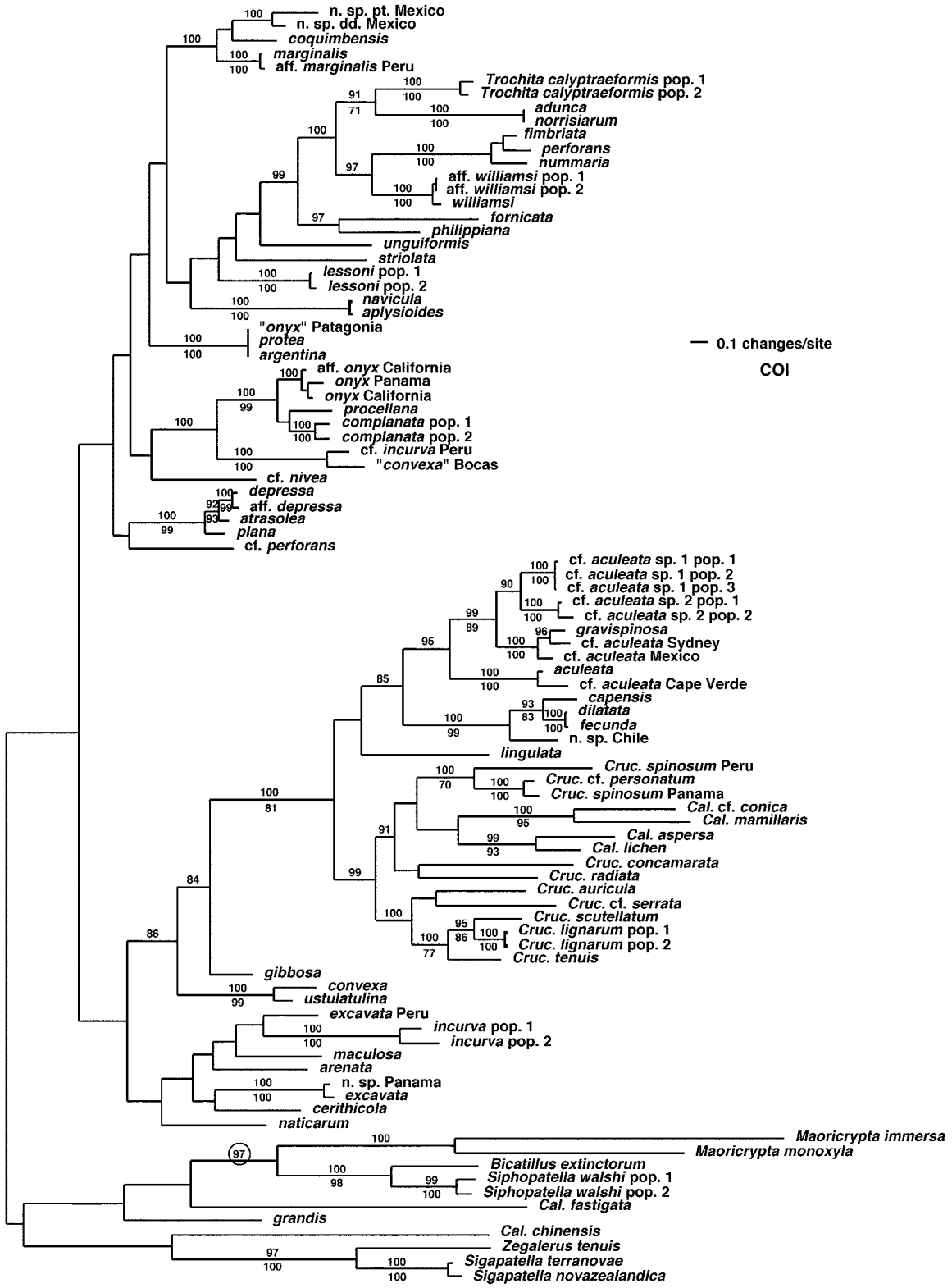

FIGURE 3. Consensus phylogram of the 90,000 trees retained from the five runs of the Bayesian analysis of the mitochondrial COI gene sequences without outgroups. Numbers above the branches are posterior probabilities obtained from the consensus of all retained trees (only values >80% are shown). Numbers below the branches are bootstrap support from the matrix-weighted analysis (only values >70% are shown). Circled node with 95% support conflicted with supported nodes in trees from the 16S and 28S data sets.

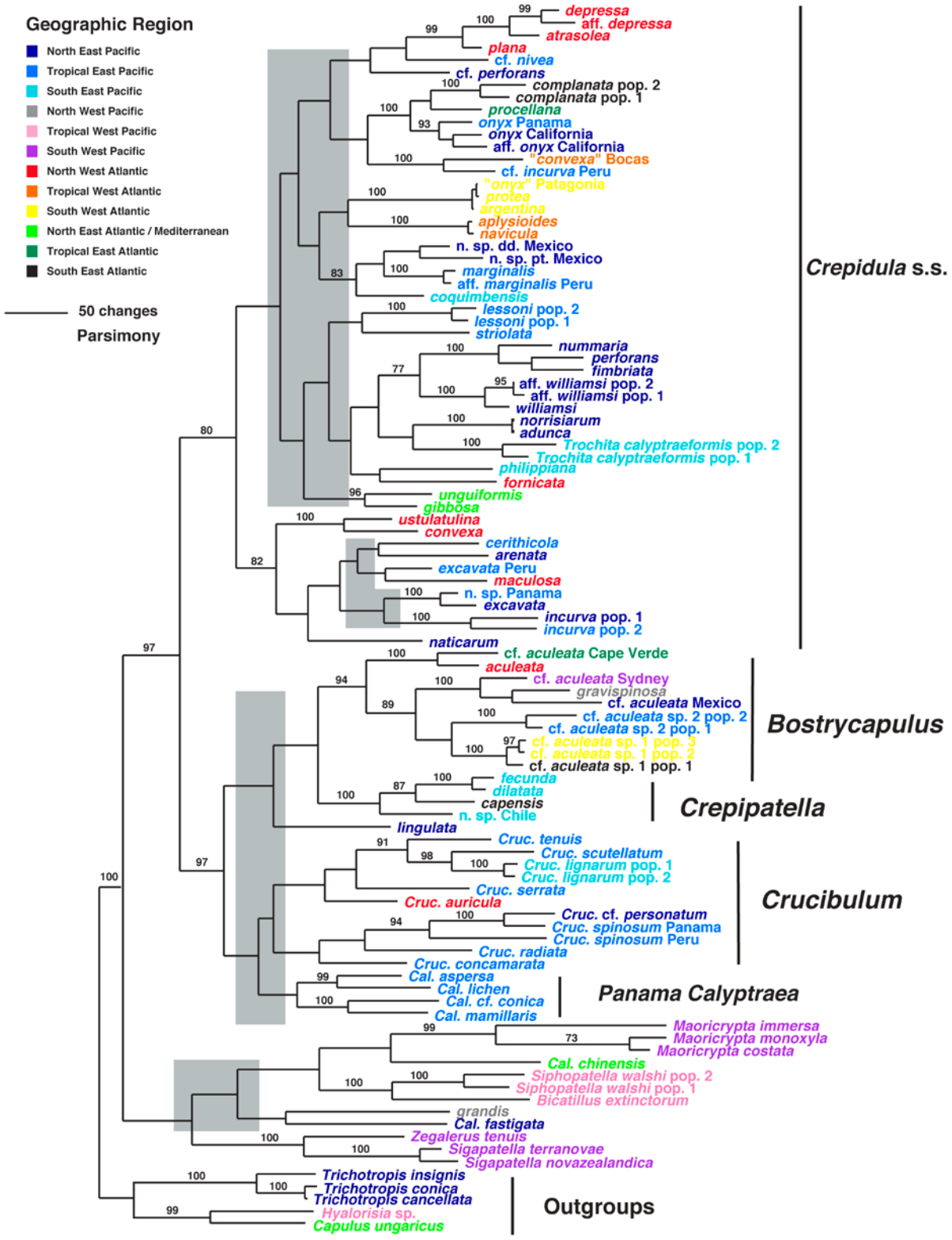

FIGURE 4. Phylogram of the most-parsimonious tree from the matrix-weighted parsimony analysis of the combined data set for the ingroup and the best outgroups. Numbers above the branches are nonparametric bootstrap support. Only support values >70% are shown. Taxonomic groups are labeled to the right, and taxon names are color coded to show the major ocean regions from which they were collected. Gray blocks highlight areas of poor support that conflict with the Bayesian estimate of relationships.

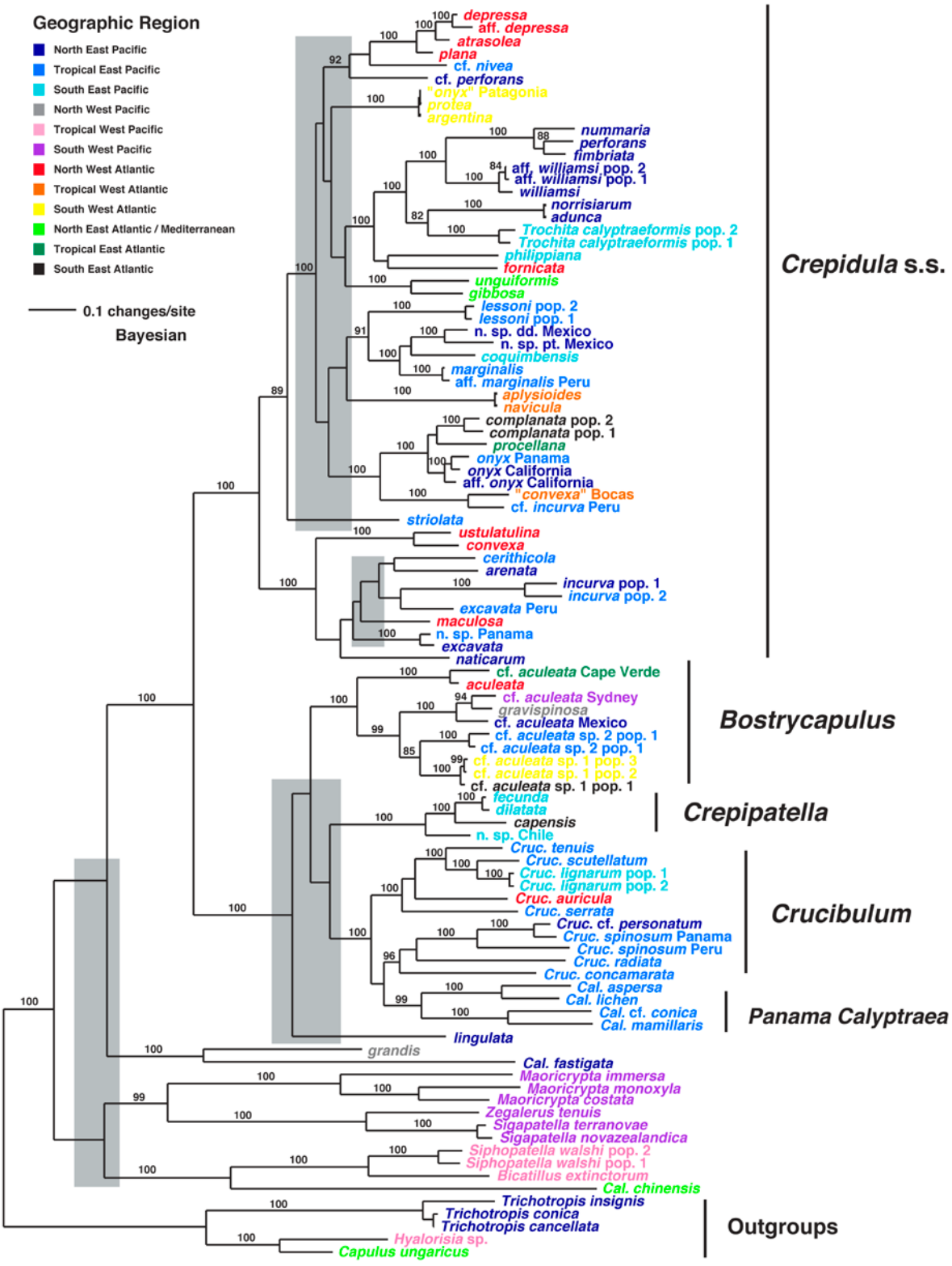

FIGURE 5. The consensus phylogram of the 90,000 trees retained from the five runs of the Bayesian analysis of the combined data set for the ingroup and best outgroup. Numbers above the branches are posterior probabilities obtained from the consensus of all retained trees. Only support values >80% are shown. Taxonomic groups are labeled to the right, and taxon names are color coded to show the major ocean regions from which they were collected. Gray blocks highlight areas of poor support that conflict with the weighted parsimony estimate of relationships.

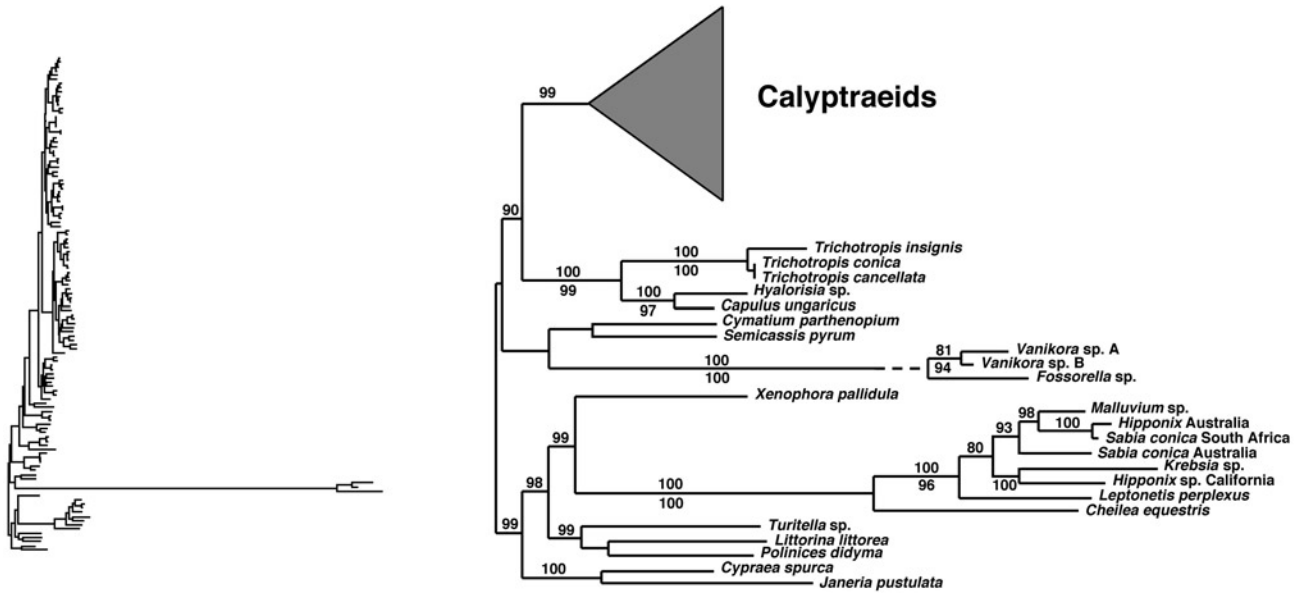

FIGURE 6. The relationships of outgroups used to determine the monophyly of the calyptraeids from the combined data set. Among these groups, capulids plus trichotropids is the closest outgroup for the calyptraeids. Numbers above the branches are Bayesian support, and those below the branches are bootstrap support. Vanikorids are a particularly long branch compared with the other outgroups (left).

the parsimony reconstruction. For only 10% of the nodes could hemisphere be confidently established.

Because the same species occur as sister species in both the Bayesian and parsimony analyses, the type of phylogenetic analysis does not effect the biogeographic patterns observed among sister-species pairs (Fig. 7). Of the 29 sister-species pairs recovered in the combined analysis, 11 are sympatric (Fig. 7). In addition to these sympatric species pairs, there are 10 clades of two or more species that occur along the same coastline and may overlap at the edge of their ranges (thick blue lines in Fig. 7). Comparisons of genetic divergence between sister species and their geographic proximity does not show any significant differences among sympatry, single shoreline, and distant groups (Fig. 8). Two of the sister-species pairs from the base of the tree are genetically distant and morphologically distinct and are not considered to be congeneric and were therefore excluded from the analysis (leaving 27 pairs). There is considerable variation in branch lengths in all three categories. However, the most genetically similar species pairs all fall into either the single shoreline or sympatric categories (Fig. 8). This suggests that the most recently diverged sister species are the most geographically proximate.

DISCUSSION

Biogeographic Barriers

Mapping geographic data on the phylogeny shows several surprising things about the distribution of calyptraeids (Figs. 4, 5, 7). Despite its fame as a biogeographic barrier that results in geminate species pairs, there are no sister-species pairs or sister clades of calyptraeids separated by the Isthmus of Panama. This lack may be due in part to the low diversity of calyptraeids in the Caribbean. The single species from the Panamanian Caribbean (*C.* "*convexa*" Bocas) is sister to a species from the tropical Peruvian coast. Therefore this pair could represent a geminate pair where the Pacific species has been lost from the Pacific coast of Panama or where an extant Pacific representative may not have been sampled in this study. The species from the Venezuelan Caribbean do not have close sisters in the Pacific and neither do the species collected from the Yucatan. Local extinction of species in the Panamanian Caribbean after the closure of the Isthmus (Vermeij and Petuch, 1986) could have obscured a regional pattern of geminate species. However, there is no evidence that such geminates existed, and the absence of extant relatives of Pacific species in the tropical Atlantic suggest that this is unlikely. There are also no deeper divisions in the tree that could be explained by the rise of the Isthmus of Panama. Such deep division would not be expected from the relatively recent (3.1 million years ago) formation of this barrier.

The origination of the Benguela upwelling, an older barrier (Miocene–Pliocene), could have separated *Crepidula porcellana* from Cape Verde and *C. complanata* from South Africa. However, the absence of samples from the mainland of tropical Africa makes it difficult to make a strong test of this possibility. All three known species of South African *Crepidula* were included in this analysis, but the African fauna is not well known, and it is likely that there are other unrecognized species. The extremely low calyptraeid diversity in the tropical West Pacific and Indian oceans makes it unlikely that there could be many species pairs where an African species is separated by the Benguela upwelling from a species in the Indian Ocean.

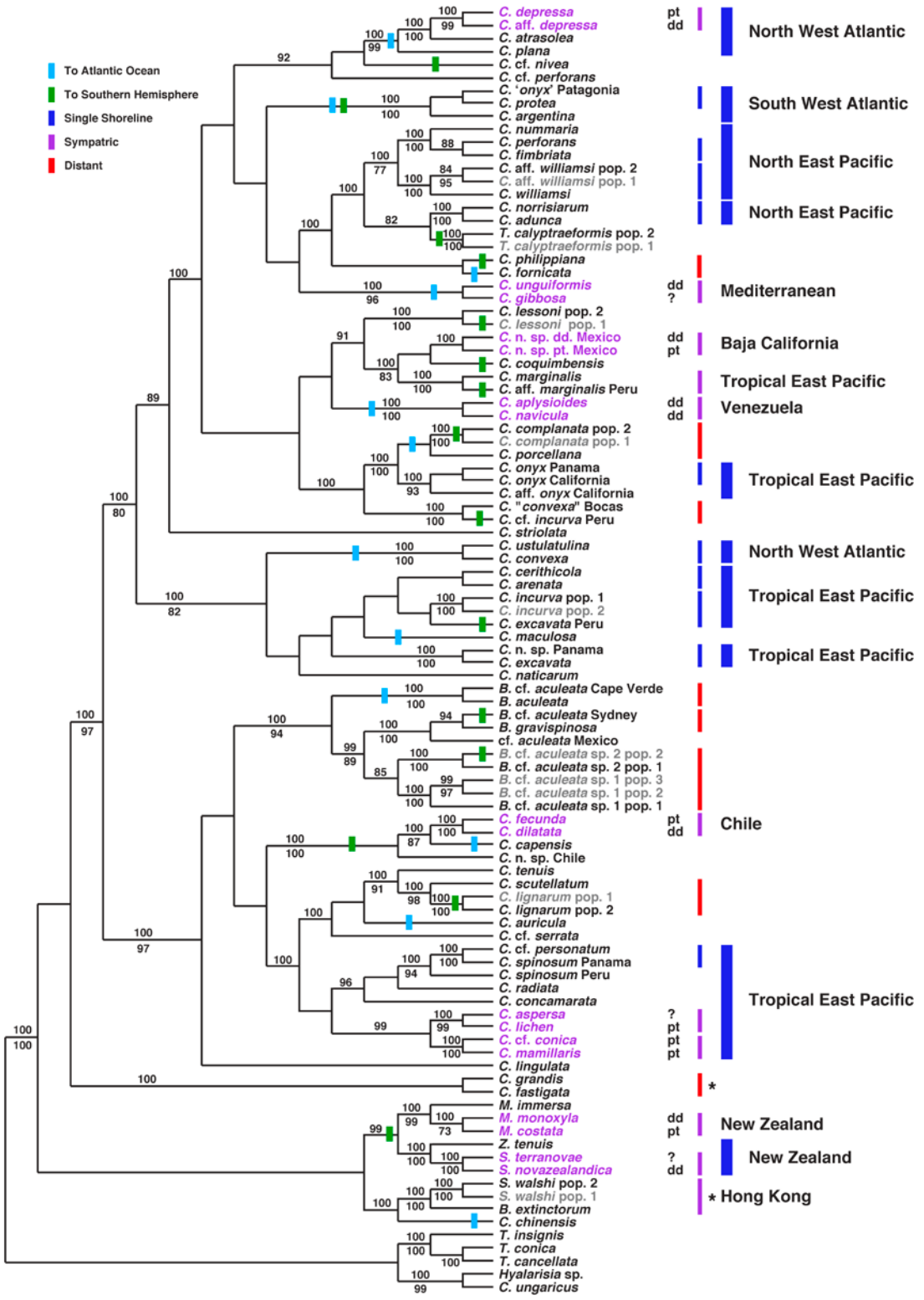

FIGURE 7. Calyptraeid phylogeny with topology as in Figure 5. Numbers above the branches are Bayesian support, and those below the branches are bootstrap support. Movement from the Pacific Ocean to the Atlantic Ocean is indicated with light blue bars across the branches. Movement across the equator from the Northern Hemisphere to the Southern Hemisphere is indicated with green bars. Sympatric sister species are indicated in purple. Cases where two individuals considered to be a single species were included are indicated by listing one of them in gray. Thick bars to the right highlight monophyletic groups that have radiated along a single shoreline. Thin lines to the right of the species names highlight the 29 sister-species pairs (purple = sympatric; blue = single shoreline; red = distant). Mode of development is indicated to the right of each sympatric species pair (dd = direct development or lecithotropic development; pt = planktonic feeding development). The asteriks indicate the two sister-species pairs that are not congeneric and were excluded from Figure 8.

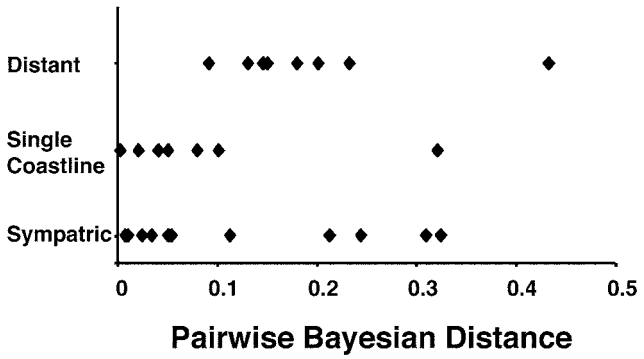

FIGURE 8. Plot showing the branch length divergence between sister species on the tree from the analysis of the combined data for sympatric pairs, pairs that occur along a single coastline, and pairs that occur in distant locations.

Likewise, no species pairs recovered in this analysis are separated by the East Pacific Barrier. However, the East Pacific Barrier does divide large clades on the tree; species in the basal clade of calyptraeids occur primarily in the western Pacific, but none of the *Crepidula* s.s., *Crucibulum*, or *Crepipatella* species occur there. This distribution supports the notion that the East Pacific Barrier is an ancient barrier to dispersal for calyptraeids but that it has not featured in more recent speciation events. The large expanse of deep water in the East Pacific is thought to have existed since the beginning of the Cenozoic (Grigg and Hey, 1992), which approximately fits the timing of the earliest fossil occurrence of "*Crepidula*" (most likely *Maoricrypta*) in the Cretaceous of New Zealand and the subsequent radiation of *Crepidula* s.s. in the rest of the world (Hoagland, 1977). The occurrence of *Bostrycapulus* species on both sides of the Pacific suggests, however, that the barrier is somewhat permeable to some calyptraeids, as it is to gene flow in some sea urchins (Lessios et al., 1998). Overall the lack of sister species or sister clades that are separated by obviously physical barriers suggests that most diversification of calyptraeids takes place within regions defined by such barriers and not across them.

Single Shorelines

If speciation or divergence in calyptraeids does not appear to be frequent across large barriers, how does it occur? The patterns reported here show that speciation is likely to occur along single coastlines, if not sympatrically. Comparisons of sister-species pairs show that 11 of 29 species pairs occur in sympatry and another 10 pairs occur along a single coastline (Fig. 7). The occurrence of 72% of the sister species in geographic proximity without large physical barriers separating them suggests that divergence occurs across small local barriers or possibly in sympatry. This result would be expected if most of the species examined here lacked a free-living larva and therefore had limited dispersal ability. However, examination of the mode of development of sister-species pairs shows that a number of them have planktonic larvae (Fig. 7). Calyptraeid larvae typically spend 2–4 weeks in the water column prior to settlement on a benthic substrate (Collin, 2003). This time in the water column appears to be adequate for dispersal of several kilometers along a shoreline, and species that have a 4-week planktonic period have been shown to have significantly less genetic population structure than species with direct development (Collin, 2001). This pattern of closely related species occurring along a single coastline or in sympatry suggests a peripatric or sympatric mode of speciation. However, the high levels of dispersal in species with larval development makes it unclear what mechanism could result in this pattern. Another possible explanation is transient allopatry, where range shifts due to climatic change bring populations into and out of sympatry (e.g., Hellberg, 1998). Unfortunately the fossil record of calyptraeids is not adequate to address this possibility. It is interesting to note that despite the common occurrence of small clades along a single coastline, there are no large radiations in a single region.

Although examples of radiations along a single shoreline or in a small region are not common among widespread depauperate groups, there are numerous examples in more speciose groups. Gastropods in the genera *Haliotis*, *Tegula*, and *Nucella* all show small radiations along the west coast of North America (Lee and Vacquier, 1995; Hellberg, 1998; Marko, 1998), as do strongylocentrotid sea urchins (Kessing, 1991). In the tropics, local radiations have occurred in *Synalpheus* shrimp (Duffy, 1996) and *Echinometra* sea urchins (Palumbi, 1996b), to name but a few. These examples include groups with long-lived feeding larvae (calyptraeids, strongylocentrotids, and *Echinometra*) and some with short-lived larvae (*Haliotis*) or direct development (*Nucella*). They also include groups where species are ecological specialists (*Synalpheus*) and those that are generalists (calyptraeids and *Haliotis*). Overall, speciation along a single shoreline appears to be common regardless of the group's ecological requirements or developmental characteristics.

Worldwide Movement

Calyptraeids show patterns of global movement (Fig. 7), and closely related species can occur half-way around the world from each other (Figs. 4, 5). For example, the *C. onyx* clade from California and Panama is closely related to *C. complanata* from South Africa. Long-distance dispersal is also evident in *Crepipatella*, where *C. capensis* from South Africa is nested within a clade of species from Chile, and in *Trochita*, where *Trochita calyptraeformis* from Chile and Peru is nested within a clade of species from the northeast Pacific. In *Bostrycapulus* cf. *aculeata* sp. 1, there is a possible case of very recent long-distance dispersal. This species has direct development and occurs along the east coast of South America from São Paulo to Patagonia and also in South Africa. COI sequence data show little variation, but it is clear that the animals from South Africa are derived from the South American animals (Collin, in

prep.). These results suggest that this direct developing species has somehow dispersed across the Atlantic quite recently.

When parsimony is used to reconstruct the movement from the Pacific Ocean to the Atlantic Ocean, there are 12 transitions between the oceans (Fig. 7). Calyptraeids also cross the equator numerous times. The most-parsimonious reconstruction of calyptraeid biogeography gives the origin of calyptraeids in the north followed by numerous dispersal events to the south of the equator. This scenario is most likely an overestimate of the evolutionary significant events (temperate species crossing the equator), because tropical species have been collected from north and south of the equator and inflate the number of apparent crossings. Because many calyptraeids occur in the tropics and there are no large exclusively temperate clades, there is no reason to think that the tropics pose a barrier to dispersal, as they may do for exclusively temperate groups. A number of southern temperate species occur nested within clades of northern temperate species, clearly indicating that such dispersal across the equator is common and that tropical intermediates do not always persist.

Effects of Taxon Sampling

Increased sampling could alter the results reported here in two ways. First, increased knowledge of species geographic ranges is likely to increase the levels of sympatry. This study recorded sympatry only in cases where sister species have been shown to co-occur. Cases where ranges inferred from few sampling localities are thought to overlap were not considered to be sympatric in this study. Increased sampling could easily show that these cases also represent sympatry. I use this conservative convention because the "well known" ranges of several species have turned out to be made up of several similar species that are not always closely related (e.g., *C. incurva* and *C. excavata*). Therefore, increased knowledge of species ranges will either not alter the results reported here or will increase the number of species reported to occur in sympatry.

Second, increased sampling of species could alter the sister-species relationships in the phylogeny. If most of the newly recovered sister species pairs occurred far from each other, the number of sympatric species pairs would be reduced. There is no reason to expect such a bias in additional sampling. In several cases where small clades of calyptraeids have been studied in detail, close relatives have been shown to occur in geographic proximity (Collin, 2001), and subsequent increased sampling in this study has not brought to light any species within these clades that are geographically distant. The genetically least divergent sister-species pair that has been studied in detail, *C. fecunda* and *C. dilatata*, co-occur along the entire coast of Chile. They cannot be distinguished morphologically, but they are developmentally different and can be distinguished on the basis of karyotypes and allozymes (D. Véliz, pers. com.). These two species are distinguished by <1% divergence in COI (R. Collin, unpubl. data), less than the interpopulation divergence in some other calyptraeid species (Collin, 2002). Because attempts at increased taxon sampling have failed to break up previously identified geographically proximate sister species, it seems unlikely that subsequent sampling will greatly change the results reported here, although I expect that some allopatric species pairs will be discovered.

Implications for Calyptraeid Evolution and Systematics

With the exception of the dendrogram of *Crepidula* based on shell morphometrics presented by Hoagland (1977), the results reported here provide the most inclusive species-level phylogenetic hypotheses for this genus. The present analysis contains more taxa than the two previous phylogenetic analyses of calyptraeids in general (e.g., 11 taxa and 112 morphological characters of Simone, 2002, and 5 taxa and 7 morphological characters of Bandel and Reidel, 1994). The phylogeny recovered here does not agree with the results of these previous studies, which were however generally poorly supported. The results supported here suggest the following revisions to the genus-level taxonomy of calyptraeids.

1. *Crepidula* s.s. should be used only to refer to the clade identified in Figure 4, which includes the type species, *C. fornicata*.
2. The subgenus *Janacus* does not refer to a monophyletic group within *Crepidula* and should be abandoned completely.
3. The subgenus *Grandicrepidula* as defined by McLean (1995) is not monophyletic and includes several species from the *Crepidula* s.s. clade in addition to the type species *Crepidula grandis*. *Grandicrepidula* could be retained as a genus-level name to refer to *C. grandis* and any other species that may be associated with it.
4. *Calyptraea* as currently used represents a polyphyletic group of taxa. The type species, *C. chinensis*, is not grouped consistently with any other species with similar shell morphology in this analysis.
5. *Cheilea* and other hipponicids should not be allied with the Calyptraeidae. On the basis of this analysis, a large indel in the 16S DNA sequence, and the paucity of convincing morphological synapomorphies uniting the hipponicids and calyptraeids (Collin, 2003b), it is likely that hipponicids are not any more closely related to the calyptraeids than are any of the other distant outgroups used here.
6. The New Zealand taxa *Maoricrypta* and *Sigapatella* (+*Zegalerus*) are both monophyletic and should be retained.

Conclusions

The prevailing view of marine speciation as primarily allopatric has been largely supported by studies of depauperate groups with worldwide distributions. The

patterns of speciation along shorelines in calyptraeids reported here are in accord with the results of other studies of species-rich groups of marine molluscs (Hellberg, 1998; Marko, 1998). Like the result of Hellberg's (1998) work with *Tegula*, the high frequency of sympatric sister-species pairs of calyptraeids shows that large geographic barriers are not necessary for speciation. Whether these patterns are the result of transient allopatry, microallopatry due to habitat partitioning, or sympatric speciation is currently unclear. Detailed studies of the genetics and ecology of recently formed species (e.g., Marko, 1998) along a single coastline could be a useful direction for further studies of speciation in marine molluscs.

The frequent movement of calyptraeids between oceans and across the equator has some important implications, not only for patterns of speciation, but also for the geographic design of taxon sampling in other studies. Such wide-scale movement results in a pattern where species from a single region of the world are unlikely to include each others' closest relatives. Therefore, if studies examining the relationships of species on either side of a putative barrier limit their sampling only to species from the region of interest, they will likely miss closely related species that occur in other regions. This bias could result in an overestimate of the number of sister-species pairs separated by the barrier and therefore an underestimate of speciation events that were not caused by geographic barriers. Until more widely distributed, species-rich groups have been examined, it will be difficult to determine the prevalence of this pattern of broad geographic movement.

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APPENDIX 1. Summary of taxa, vouchers and GenBank numbers for material used in this study.

Species	Authority	Locality	Voucher nos.[a]	GenBank nos. (COI, 16S, 28S)
Calyptraeidae				
Crepidula (*Bostrycapulus*)	Olsson and Harbison, 1953			
Crepidula aculeata	Gmelin, 1791	Mote Marine Lab, Lido Key, Florida, USA; 27°20′N, 82°42′W	ANSP A19745, FMNH282365, BM20010455	AY061792, AY061774, AF545921
Crepidula cf. *aculeata* Cape Verde		Calheta Funda, Sal Island, Cape Verde; 16°40′N, 22°03′W	FMNH282359	AY061776, AY061775,
Crepidula cf. *aculeata* Sp. 2, Pop. 1		Venado, Pacific Coast, Panama; 08°55′N, 79°38′W	FMNH282273, ANSP A19740, BM 20010452	AY061786, AY061770, AF545916
Crepidula cf. *aculeata* Sp. 2, Pop. 2		El Aubaz, Paita, Peru; 05°10′S, 81°10′W	ANSP A19746, FMNH282351, BM20010454	AY061785, AY061772, —[b]
Crepidula cf. *aculeata* Australia		Edwards Reef, Sydney, Australia; 33°51′S, 151°13′E	FMNH282302, ANM C400000	AY061793, AY061767, AF545914
Crepidula cf. *aculeata* Sp. 1, Pop. 2		Playa Orengo, San Antonio Oeste, Argentina; 40°53′S, 64°29′W	FMNH282297, ANSP A19744, BM20010456	AY061794, AY061764, AF545920
Crepidula cf. *aculeata* Sp. 1, Pop. 3		Gois Beach, Santos Bay, São Paulo, Brazil; 24°00′S, 46°21′W	FMNH282350	AY061779, AY061763, AF545915
Crepidula cf. *aculeata* Mexico		Bahía de La Paz, Mexico; 24°07′N, 110°24′W	FMNH282193, FMNH282194	AY061789, AY061789, AF545918
Crepidula cf. *aculeata* Sp. 1, Pop. 1		Wooleys Pool, Muizenberg, South Africa; 34°04′S, 18°20′E	FMNH282277, BM20010453	AY061780, AY061765, AF545919
Crepidula gravispinosa	Kuroda and Habe, 1950	Chijiwa, Nagasaki, Japan	FMNH282336	AY061783, AY061766, AF545917
Crepidula (*Crepipatella*)	Lesson, 1830			
Crepipatella capensis	Quoy and Gaimard, 1832–1833	Muizenberg, Cape Province, South Africa; 34°04′S, 18°20′E	FMNH282278	AF546053, AF545993, AF545924
Crepipatella dilatata	Lamarck, 1822	Corral Bay, San Carlos, Chile; 39°51′S, 73°27′W	BM20010461	AF546052, AF545992, AF545923
Crepipatella fecunda	Gallardo, 1979	Bahía de Coquimbo, IV Region, Chile; 29°59′S, 71°19′W	FMNH299425	AF546051, AF545991, AF545922
Crepipatella lingulata	Gould, 1846	Shady Cove, Friday Harbor, Washington, USA; 48°20′N, 123°01′W	FMNH282293, FMNH285019	AF546054, AF545994, AF545925
Crepipatella n. sp.		Totorelillo, IV Region, Chile	FMN282280	AF550491, AF550461, —
Crepidula (*Maoricrypta*)	Finlay, 1926			
Crepidula costata	Sowerby, 1824	Leigh, North Island, New Zealand; 36°10′S, 174°30′E	FMNH282294, FMNH282310	—, AF550462, AF550429
Crepidula (*Zeacrypta*)	Finlay, 1926			
Crepidula immersa	Angas, 1847	Edithburg, Yorke Penninsula, South Australia; 35°03′S, 137°26′E	FMNH282298	AF546024, AF545958, AF545881
Crepidula monoxyla	Lesson, 1830	Leigh, North Island, New Zealand; 36°10′S, 174°30′E	FMNH282305, ANSP A19732, BM20010467	AF546039, AF545978, AF545901
Crepidula (*Janacus*)	Mörch, 1852			
Crepidula argentina	Simone et al., 2000	Mar del Plata, Argentina; 30°00′S, 57°21′W	ANSP A19738, FMNH282346, BM20010457	AF546032, AF545969, AF545892
Crepidula atrasolea	Collin, 2000	Harbor Branch Oceanographic Institute, Florida, USA; 28°30′N, 81°20′W	FMNH282209, FMNH282213	AF178130, AF545966, AF545889
Crepidula coquimbensis	Brown and Olivares, 1996	Bahía de Herradura, Coquminbo, IV Region, Chile; 29°58′S, 71°21′W	FMNH282311	AF546046, AF545986, AF545909
Crepidula depressa	Say, 1822	Sanibel Marina, Florida, USA; 26°27′N, 82°02′W	FMNH282201, ANSP19187, FMNH282211	AF178147, AF545949, AF545872
Crepidula aff. *depressa*		Champotón, Campeche, Mexico; 19°23′N, 90°42′W	FMNH282318	AF387871, AF550479, —
Crepidula fimbriata	Reeve, 1859	Friday Harbor, Washington, USA; 48°20′N, 123°01′W	FMNH299426	AF546035, AF545974, AF545897
Crepidula lessoni Pop. 1	Broderip, 1834	Chumical, Pacific Coast, Panama; 08°30′N, 79°40′W	FMNH282271, BM20010465	AF546041, AF545981, AF545904

APPENDIX 1. Continued

Species	Authority	Locality	Voucher nos.[a]	GenBank nos. (COI, 16S, 28S)
Crepidula lessoni Pop. 2	Broderip, 1834	Zorritos, Peru; 3°45′S, 80°40′W	ANSP A19734, BM20010464	AF550514, AF550481, AF550453
Crepidula aff. *marginalis*	Broderip, 1834	Puerto Pizarro, Peru; 03°20′S, 80°15′W	FMNH299427	AF550489, —, AF550426
Crepidula cf. *nivea*		Puerto Pizarro, Peru; 03°20′S, 80°15′W	FMNH299428	AF550513, AF550480, AF550452
Crepidula nummaria	Gould, 1846	Santa Cruz, California, USA; 36°40′N, 122°02′W	FMNH282245	AF546018, AF545951, AF545874
Crepidula perforans	Valenciennes, 1846	Devonport Landing, Santa Cruz, California, USA; 36°40′N, 122°02′W	FMNH299407	AF550490, AF550460, AF550427
Crepidula cf. *perforans*		Santa Barbara, California, USA; 34°20′N, 120°01′W	FMNH282243	AF178155, AF545959, AF545882
Crepidula philippiana	Gallardo, 1977	Los Molinos, Chile; 39°51′S, 73°27′W	FMNH282349	AF546019, AF545952, AF545875
Crepidula plana	Say, 1822	Woods Hole, Massechuttes, USA; 41°30′N, 70°40′W	FMNH282207, FMNH282210, FMNH282214, FMNH282215	AF178120, AF545979, AF545902
Crepidula protea	d'Orbigny, 1841	Santos Bay, São Paulo, Brazil; 23°20′S, 46°25′W	MZSP32264	AF546021, AF545955, AF545878
Crepidula striolata	Menke, 1851	Rio Mar, Pacific Coast, Panama; 08°18′N, 79°50′W	FMNH282331	AF353123, AF545972, AF545895
Crepidula unguiformis	Lamarck, 1822	Italy	FMNH282344	AF178156, AF550455, AF550419
Crepidula williamsi	Coe, 1947	Santa Barbara, California, USA; 34°20′N, 120°01′W	FMNH282177, FMNH282178	AF546030, AF545967, AF545890
Crepidula aff. *williamsi* Pop. 1		Kodiak Island, Alaska, USA; 57°12′N, 153°24′W	FMNH287485	AF546038, AF545977, AF545900
Crepidula aff. *willisami* Pop. 2		Friday Harbor, Washington, USA; 48°20′N, 123°01′W	FMNH299429	AF546026, AF545962, AF545885
Crepidula s.l.	Lamarck, 1822 (in addition to *Janacus*)			
Crepidula adunca	Sowerby, 1825	Friday Harbor, Washington, USA; 48°20′N, 123°01′W	FMNH282185	AF546047, AF545987, AF545910
Crepidula cf. *aplysioides*	Reeve, 1859	Isla Margarita, Venezuela; 11°01′N, 64°03′W	FMNH293348	AF546022, AF545956, AF545879
Crepidula arenata	Broderip, 1834	La Paz, Mexico; 24°17′N, 110°17′W	FMNH282364	AF546023, AF545957, AF545880
Crepidula cerithicola	C. B. Adams, 1852	Punta Charmé, Panama; 08°30′N, 79°40′W	FMNH282332	AF388698, AF545953, AF545876
Crepidula complenata Pop. 1	Krauss, 1848	Langebaan Lagoon, Cape Province, South Africa; 33°04′S, 18°02′E	FMNH282295, ANSP A19748, BM20010462	AF546031, AF545968, AF545891
Crepidula complenata Pop. 2	Krauss, 1848	Kwazulu. Natal, South Africa	FMNH299430	AF550482, AF550454, AF550418
Crepidula convexa	Say, 1822	Wildwood Crest, Cape May, New Jersey, USA; 38°50′N, 74°59′W	FMNH282261, FMNH282262, FMNH282299, BM20010463	AF388726, AF545960, AF545883
Crepidula excavata Mexico	Broderip, 1834	Magdalena Bay, BCS, Mexico	FMNH282344	AF546034, AF545971, AF545894
Crepidula excavata Peru	Broderip, 1834	Puerto Pizarro, Peru; 03°20′S, 80°15′W	FMNH282339	AY169279, —, AY169280
Crepidula fornicata	Linnaeus, 1758	Woods Hole, Massechuttes, USA; 41°30′N, 70°40′W	FMNH282306	AF353129, AF545973, AF545896
Crepidula grandis	Middendorff, 1849	Japan	FMNH299421	AF546037, AF545976, AF545899
Crepidula gibbosa	Defrance, 1818	Port Lligat, Giroua	FMNH282356	AF550486, AF550458, AF550423
Crepidula incurva Pop. 1	Broderip, 1834	La Paz, Baja, Mexico; 24°17′N, 110°17′W	FMNH282179–FMNH282181	AF546028, AF545964, AF545887
Crepidula incurva Pop. 2	Broderip, 1834	Chumical, Pacific Coast, Panama; 8°30′N, 79°40′W	FMNH282333	AF546042, AF545982, AF545905
Crepidula cf. *incurva* Peru	Broderip, 1834	Zorritos, Peru; 03°45′S, 80°40′W	FMNH299431	AF546043, AF545983, AF545906

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APPENDIX 1. Continued

Species	Authority	Locality	Voucher nos.[a]	GenBank nos. (COI, 16S, 28S)
Crepidula maculosa	Conrad, 1846	Panacea, Florida, USA; 30°00′N, 84°30′W	FMNH299368	AF546048, AF545988, AF545911
Crepidula marginalis	Broderip, 1834	Venado, Pacific Coast, Panama; 08°55′N, 79°38′W	FMNH282272	AF546033, AF545970, AF545893
Crepidula naticarum	Williamson, 1905	Santa Barbara, California, USA; 34°20′N, 120°01′W	FMNH282176, ANSP A19731, BM20010468	AF546029, AF545965, AF545888
Crepidula navicula	Mörch, 1877	Morrocoy, Venezuela	FMNH293349	AF546040, AF545980, AF545903
Crepidula cf. *navicula*		Bocas del Toro, Panama; 09°20′N, 82°15′W	FMNH282355	AF546036, AF545975, AF545898
Crepidula norrisarum	Williamson, 1905	Santa Barbara, California, USA; 34°20′N, 120°01′W	FMNH282173–FMNH282175	AF550487, —, AF550424
Crepidula onyx	Sowerby, 1824	Santa Barbara, California, USA; 34°20′N, 120°01′W	ANSP A19741, BM20010469	AF546025, AF545961, AF545884
Crepidula dd. *onyx*[c] Santa Barbara		Santa Barbara, California, USA; 34°20′N, 120°01′W	FMNH299432	AF550485, AF550457, AF550422
Crepidula aff. *onyx* Panama		Venado, Pacific Coast, Panama; 8°55′N, 79°38′W	FMNH299420	AF546020, AF545954, AF545877
Crepidula cf. *onyx* Argentina		Playa Orengo, San Antonio Oeste, Argentina; 40°53′S, 64°29′W	FMNH282287, ANSP A19739, BM20010471, BM20010472	AF546017, AF545948, AF545871
Crepidula porcellana	Lamarck, 1822	Calheta Funda, Sal Island, Cape Verde; 16°40′N, 22°03′W	FMNH282337	AF546044, AF545984, AF545907
Crepidula ustulatulina	Collin, 2002	Dzilam de Bravo, Yucatan, Mexico; 21°20′N, 88°55′W	FMNH282316	AF388700, AF545950, AF545873
Crepidula n. sp. pt.[d] Mexico		La Paz, Mexico; 24°17′N, 110°17′W	FMNH282195–FMNH282197	AF546045, AF545985, AF545908
Crepidula n. sp. dd. Mexico		La Paz, Mexico; 24°17′N, 110°17′W	FMNH282198–FMNH282200	AF550484, —, AF550421
Crepidula n. sp. Panama		Islas de las Perlas, Panama; 08°30′N, 79°02′W	FMNH299433	AF550483, AF550456, AF550420
Crucibulum	Schumacher, 1817			
Crucibulum spinosum Peru	Sowerby, 1824	Santa Maria, Peru; 12°20′S, 76°45′W	BM20010478, FMNH282345	AF546057, AF545997, AF545928
Crucibulum spinosum Panama	Sowerby, 1824	Venado, Panama; 08°55′N, 79°38′W	FMNH299404	AF546058, AF545998, AF545929
Crucibulum cf. *personatum*		La Paz, BCS, Mexico; 24°17′N, 110°17′W	FMNH282279, ANSP A19743, BM20010479	AF550492, —, AF550430
Crucibulum scutellatum	Wood, 1828	Chumical, Pacific Coast, Panama; 08°30′N, 79°40′W	FMNH299405	AF546056, AF545996, AF545927
Crucibulum lignarum Pop. 2	Broderip, 1834	Bahia de Herradura, Region IV, Chile; 29°58′S, 71°21′W	FMNH282304	AF550497, —, AF550435
Crucibulum lignarum Pop. 1	Broderip, 1834	Ancud, Chiloe, Chile; 41°53′S, 73°50′W	FMNH299434	AF550496, AF550465, AF550434
Crucibulum concamaratum	Reeve, 1859	Islas de las Perlas, Panama; 08°30′N, 79°02′W	FMNH299298	AF550495, —, AF550433
Crucibulum auricula	Gmelin, 1791	Champotón, Campeche, Mexico; 19°23′N, 90°42′W	FMNH2994000	AF550494, AF550464, AF550432
Crucibulum radiata	Broderip, 1834	Venardo, Pacific Coast, Panama; 08°55′N, 79°38′W	FMNH299399	AF546059, AF545999, AF545930
Crucibulum cf. *serrata*	Broderip, 1834	Islas de las Perlas, Panama; 08°30′N, 79°02′W	FMNH299435	AF550493, AF550463, AF550431
Crucibulum tenuis	Broderip, 1834	Vanardo, Pacific Coast, Panama; 08°55′N, 79°38′W	FMNH299436	AF546055, AF545995, AF545926
Calyptraea	Lamarck, 1799			
Calyptraea aspersa	C. B. Adams, 1852	Islas de las Perlas, Panama; 08°30′N, 79°02′W	FMNH282342	AF546060, AF546000, AF545931
Calyptraea chinensis	Linneus, 1758	O'Grove Bay, Spain	FMNH299392	AF546064, AF546004, AF545935
Calyptraea cf. *conica*		Venado, Pacific Coast, Panama; 08°55′N, 79°38′W	FMNH299437	AF546063, AF546003, AF545934
Calyptraea fastigata	Gould, 1846	Friday Harbor, Washington, USA; 48°20′N, 123°01′W	FMNH282221	AF546065, AF546005, AF545936

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Species	Authority	Locality	Voucher nos.[a]	GenBank nos. (COI, 16S, 28S)
Calyptraea cf. *lichen*		Venado, Pacific Coast, Panama; 08°55′N, 79°38′W	FMNH282300	AF546067, AF546007, AF545938
Calyptraea mamillaris	Broderip, 1834	Punta Charmé, Pacific Coast, Panama; 08°30′N, 79°40′W	FMNH282363	AF546066, AF546006, AF545937
Trochita	Schumacher, 1817			
Trochita calyptraeformis Pop. 1	Born, 1778	Bahía de Herradura, IV Region, Chile; 29°58′S, 71°21′W	ANSP A19737, BM20010476	AF546050, AF545990, AF545913
Trochita calyptraeformis Pop. 2	Born, 1778	Santa Maria, Peru; 12°20′S, 76°45′W	BM20010475, FMNH299424	AF546049, AF545989, AF545912
Bicatillus	Swainson, 1840			
Bicatillus extinctorum	Lamarck, 1822	Changi Point Beach, east of Singapore; 01°15′N, 103°39′E	FMNH299402	AF546061, AF546001, AF545932
Sigapatella	Lesson, 1830			
Sigapatella terraenovae	Peile, 1924	Leigh, North Island, New Zealand; 36°10′S, 174°30′E	FMNH282366	AF550498, AF550466, AF550436
Sigapatella novaezelandiae	Lesson, 1831	Portabello, South Island, New Zealand	FMNH282186–FMNH282189, ANSP A19733, BM20010480	AF546068, AF546008, AF545939
Siphopatella	Lesson, 1830			
Siphopatella walshi Pop. 2	Reeve, 1859	Hong Kong; 22°20′N, 114°00′W	FMNH299401	AF546027, AF545963, AF545886
Siphopatella walshi Pop. 1	Reeve, 1859	Changi Point Beach, east of Singapore; 01°15′N, 103°39′E	FMNH299403	AF550488, AF550459, AF550425
Zegalerus	Finlay, 1926			
Zegalerus tenuis	Gray, 1867	Omaha Bay, North Island, New Zealand; 36°10′S, 174°30′E	FMNH282309	AF546062, AF546002, AF545933
Capulidae	Montfort, 1810			
Capulus ungaricus	Linné, 1767	Koster, Sweden; 58°52′N, 11°05′E	FMNH299395	AF546070, AF546010, AF545941
Hyalorisia sp.		New Caledonia	SMNH16891	AF550501, AF550468, AF550439
Trichotropidae	Gray, 1850			
Trichotropis cancellata	Hinds, 1843	Friday Harbor, Washington, USA; 48°20′N, 123°01′W	FMNH282220, FMNH285018	AF546069, AF546009, AF545940
Trichotropis insignis	Middendorf, 1849	W. Yukon Island, Kasitsna Bay, Alaska, USA; 59°31′N, 151°30′W	FMNH299438	AF550499, —, AF550437
Trichotropis conica	Møller, 1842	NW Hesketh Island, Kasitsna Bay, Alaska, USA; 59°30′N, 151°31′W	FMNH299439	AF550500, AF550467, AF550438
Hipponicidae	Troschel, 1861			
Hipponix sp. Australia		Lizard Island, Australia	University of Michigan Collection	AF546073, AF546013, AF545944
Hipponix sp. California		Jalama, California, USA; 34°29.7′N, 120°29.8′W	FMNH299406	AF550512, AF550476, AF550449
"Sabia conica" South Africa		Park Rynie, Kwazulu-Natal, South Africa; 30°19′S, 30°44′E	FMNH299397	AF546076, AF546016, AF545947
"Sabia conica" Australia		Edithburgh, Yorke Peninsula, South Australia; 35°03′S, 137°26′E	FMNH282246, ANSP A19750	AF546074, AF546014, AF545945
Cheilea equestris	Linné, 1758	Louisiodes Archipelago	FMNH299396	AF546072, AF546012, AF545943
Krebsia sp.		New Caledonia	SMNH33624	AF550511, AF550475, AF550448
Malluvium sp.		New Caledonia	SMNH16893	AF550510, AF550474, AF550447
Leptonetis perplexus	Suter, 1907	New Zealand	FMNH282289	AF546075, AF546015, AF545946
Vanikoro sp. 1		New Caledonia	SMNH16892	AF546071, AF546011, AF545942
Vanikoro sp. 2		Baie de Chantal, New Caledonia	SMNH33639	—, AF550478, AF550451
Fossorella sp.		Baie de Chantal, New Caledonia	SMNH33638	—, AF550477, AF550450

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Species	Authority	Locality	Voucher nos.[a]	GenBank nos. (COI, 16S, 28S)
Other outgroups				
Xenophora pallidula	Reeve, 1842	New Caledonia	SMNH16888	AF550503, AF550469, AF550441
Cypraea spurca verdensium	Melville, 1888	Sal Island, Cape Verde; 16°40′N, 22°03′W	UF289544	AF550504, AF550470, AF550442
Janneria pustulata	Solander, 1786	Venado, Panama; 08°55′N, 79°38′W	FMNH282341	AF550507, AF550472
Cymatium parthenopeum	von Salis, 1793	Sal Island, Cape Verde; 16°40′N, 22°03′W	FMNH282347	AF550502, —, AF550440
Turitella sp.		Langebaan Lagoon, Cape Province, South Africa; 33°04′S, 18°02′E	FMNH299410	AF550505, —, AF550443
Semicassis pyrum	Lamarck, 1822)	New Zealand	FMNH299394	AF550508, AF550473, AF550445
Polinices didyma	Röding, 1798	Taiwan	UF282591	AF550509, —, AF550446
Littorina littorea	Linné, 1758	Long Island, New York, USA	FMNH282334	AF550506, AF550471, AF550444

[a] Abbreviations for institutions follow Leviton et al. (1985), with SMNH-Swedish Museum of Natural History and ANM-Australian National Museum. Numerous additional lots from other localities have also been deposited at these institutions.

[b] Sequences for these fragments could not be obtained.

[c] dd = direct development.

[d] pt = plankfonic feeding.