

SPECIATION AND DIVERSITY ON TROPICAL ROCKY SHORES: A GLOBAL PHYLOGENY OF SNAILS OF THE GENUS *ECHINOLITTORINA*

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Abstract.—A phylogenetic approach to the origin and maintenance of species diversity ideally requires the sampling of all species within a clade, confirmation that they are evolutionarily distinct entities, and knowledge of their geographical distributions. In the marine tropics such studies have mostly been of fish and reef-associated organisms, usually with high dispersal. In contrast, snails of the genus *Echinolittorina* (Littorinidae) are restricted to rocky shores, have a four-week pelagic development (and recorded dispersal up to 1400 km), and show different evolutionary patterns. We present a complete molecular phylogeny of *Echinolittorina*, derived from Bayesian analysis of sequences from nuclear 28S rRNA and mitochondrial 12S rRNA and COI genes (nodal support indicated by posterior probabilities, maximum likelihood, and neighbor-joining bootstrap). This consists of 59 evolutionarily significant units (ESUs), including all 50 known taxonomic species. The 26 ESUs found in the Indo-West Pacific region form a single clade, whereas the eastern Pacific and Atlantic species are basal. The earliest fossil occurred in the Tethys during the middle Eocene and we suggest that the Indo-West Pacific clade has been isolated since closure of the Tethyan seaway in the early Miocene. The geographical distributions of all species (based on more than 3700 locality records) appear to be circumscribed by barriers of low temperature, unsuitable sedimentary habitat, stretches of open water exceeding about 1400 km, and differences in oceanographic conditions on the continuum between oceanic and continental. The geographical ranges of sister species show little or no overlap, indicating that the speciation mode is predominantly allopatric. Furthermore, range expansion following speciation appears to have been limited, because a high degree of allopatry is maintained through three to five branching points of the phylogeny. This may be explained by infrequent long-distance colonization, habitat specialization on the oceanic/continental gradient, and perhaps by interspecific competition. In the eastern Pacific plus Atlantic we identify five cases of divergence on either side of the Isthmus of Panama, but our estimates of their ages pre-date the emergence of the Isthmus. There are three examples of sister relationships between species in the western Atlantic and eastern Atlantic, all resulting from dispersal to the east. Within the Indo-West Pacific, we find no geographical pattern of speciation events; narrowly endemic species of recent origin are present in both peripheral and central parts of the region. Evidence from estimated divergence times of sister species, and from a plot of the number of lineages over time, suggest that there has been no acceleration of diversification during the glacio-eustatic cycles of the Plio-Pleistocene. In comparison with reefal organisms, species of *Echinolittorina* on rocky shores may be less susceptible to extinction or isolation during sea-level fluctuations. The species richness of *Echinolittorina* in the classical biogeographic provinces conforms to the common pattern of highest diversity (11 species) in the central “East Indies Triangle” of the Indo-West Pacific, with a subsidiary focus in the eastern Pacific and western Atlantic, and lowest diversity in the eastern Atlantic. The diversity focus in the East Indies Triangle is produced by a mosaic of restricted allopatric species and overlap of a few widespread ones, and is the result of habitat specialization rather than historical vicariance. This study emphasizes the plurality of biogeographic histories and speciation patterns in the marine tropics.

Key words.—Atlantic, Bayesian, biodiversity, Indo-West Pacific, speciation.

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Global gradients of species richness are among the most striking of biogeographic phenomena. Within the marine tropics there are marked longitudinal patterns, reflecting regional differences between ocean basins and gradients within them. The tropical oceans are divided into four principal biogeographic regions, Indo-West Pacific, eastern Pacific, western Atlantic, and eastern Atlantic. Species diversity within many taxonomic groups declines in this order, although for reef-associated taxa the western Atlantic is richer than the eastern Pacific (e.g. Briggs 1974; Vermeij 1978, 1996; Paulay 1997). Within the largest and most diverse of these regions, the Indo-West Pacific, there is a striking diversity focus in the central “East Indies Triangle,” encompassing the Philippines, Indonesia, and New Guinea. From this focus, species richness declines westward across the Pacific and, to a lesser degree, eastward across the Indian Ocean (Rosen 1984, 1988; Reid 1986; Kay 1990; Veron 1995; Crame 2000; Bellwood and Hughes 2001; Hughes et al. 2002). These patterns of regionality and diversity have changed over geological time. The pantropical Tethyan province of the Cretaceous

and early Cenozoic was disrupted by a sequence of tectonic events: the early Miocene collision of Africa with Europe, the northward movement of the Australian plate from the middle Miocene, the Pliocene uplift of the Isthmus of Panama and, throughout the Cenozoic, the continued widening of the Atlantic Ocean (Paulay 1997; Crame 2001; Vermeij 2001). As a result, the global center of marine diversity in the European Tethys was obliterated and, from the early Miocene, diversity increased in the East Indies Triangle to establish the modern focus there (Wilson and Rosen 1998; Vermeij 2001; Briggs 2003).

The modern patterns of species richness in the tropical oceans are the product of interactions between origination, extinction, and migration of species. Many hypotheses have been advanced, emphasizing one or a combination of these processes (reviews by Rosen 1984, 1988; Palumbi 1997; Paulay 1997; Bellwood and Wainwright 2002; Connolly et al. 2003). However, the primary interest has been speciation, not least because of a perceived paradox in the process as it occurs in the sea. Marine species often exhibit extensive geo-

graphical ranges and are potentially widely dispersed as pelagic larval stages (but for examples of limited realized dispersal of pelagic larvae see Barber et al. 2002; Gilg and Hilbish 2003; Taylor and Hellberg 2003). If this is so, populations should be large with high gene flow, and speciation by the classical model of divergence in allopatry should be infrequent and slow. Nevertheless, speciation is clearly not rare in the sea, as shown by the diverse suites of congeneric species that are most strikingly displayed in shallow-water tropical habitats (Palumbi 1994).

There are three major questions relating to speciation as it occurs in the marine environment. First, what is the prevailing mode of speciation? Many studies have supported the role of geographical isolation involving large-scale barriers (e.g. Colborn et al. 2001; Lessios et al. 2001; Meyer 2003), but divergence might also occur in sympatry (Knowlton 1993; Palumbi 1998; Vacquier 1998; Briggs 1999a), or require only transient allopatry (Hellberg 1998). Second, what are the geographical patterns of speciation? Allopatry may be achieved by vicariant division or by founder dispersal (Paulay and Meyer 2002); divergence across the Isthmus of Panama is a classic example of the former (Knowlton et al. 1993; Knowlton and Weigt 1998) and dispersal to isolated Pacific islands of the latter (Lessios et al. 2001; Paulay and Meyer 2002). In the Indo-West Pacific, speciation events might be concentrated at the periphery of the region (as suggested by center-of-accumulation models of the diversity focus; Ladd 1960; Jokiell and Martinelli 1992) or in the species-rich center (the center-of-origin model; Ekman 1953; Briggs 1999b) or scattered across the region (Palumbi 1997; Paulay 1997; Randall 1998; Wilson and Rosen 1998; Bellwood and Wainwright 2002). Third, how old are speciation events? Modern species may be the product of tectonic events during the Miocene and Pliocene, or alternatively of sea-level fluctuations during the glacio-eustatic cycles of the past three million years (McMillan and Palumbi 1995; Palumbi 1997; Benzie 1999; Bellwood and Wainwright 2002).

Molecular phylogenetics provides both an accurate reconstruction of the relationships between living species and estimates of their ages, which, in combination with known geographical distributions, yields an indirect record of speciation events (McMillan and Palumbi 1995; Palumbi et al. 1997; Hellberg 1998; Metz et al. 1998; Williams 2000; Colborn et al. 2001; Lessios et al. 2001; Kooistra et al. 2002; Meyer 2003). This method is most valuable when the following criteria are fulfilled. The sampling of species within the chosen taxonomic group must be as comprehensive as possible, to eliminate bias against rare species, to maximize the sample of reconstructed speciation events, and to calculate rates of speciation and extinction (Barracough and Nee 2001). The taxa sampled must not simply represent taxonomic species, but should be confirmed as evolutionarily significant units (ESUs; Barracough and Nee 2001). Geographical distributions should be known accurately. For inferences about global patterns it is clearly necessary to choose a group with representatives in all the world's oceans. So far, these criteria have only been fulfilled for small circumtropical clades of up to 10 species (Lessios et al. 1999, 2001; Colborn et al. 2001). Some large genus-level phylogenies are now being produced, but complete sampling has yet to be achieved (Lev-

inton et al. 1996; Kooistra et al. 2002; Meyer 2003; Bernardi et al. 2004; Lavery et al. 2004; Teske et al. 2004).

Our study group is the worldwide radiation of periwinkles of the genus *Echinolittorina*. This is a monophyletic group (formerly included in *Nodilittorina*, Williams et al. 2003) of 50 taxonomic species (Reid 2001, 2002a,b), distributed throughout the four tropical biogeographic regions of the global ocean and extending outside tropical latitudes only under the influence of warm currents or in enclosed seas (Fig. 1). Its members have internal fertilization, pelagic spawn, and planktonic larval development lasting up to four weeks (Reid 1989a, 2002b), permitting dispersal over distances up to 1200–1400 km (Reid 2002a). The duration of pelagic life and extent of larval dispersal therefore fall within the wide range reported for invertebrates and fish with pelagic development in shallow tropical seas, although both are considerably less than the maximum values for these groups (Brothers and Thresher 1985; Harrison and Wallace 1990; Kohn and Perron 1994; Emlet 1995). The species of *Echinolittorina* are among the most abundant macrofauna of the upper eu-littoral and supralittoral zones of rocky shores; substrates include basalt and limestone, but atolls and fringing reefs do not usually provide suitable habitats. They therefore contrast with the mainly reef-associated molluscs, echinoderms, and fish that have been the subject of comparable studies. Unfortunately, the fossil record of *Echinolittorina* is poor, as is the case for many organisms inhabiting high-energy shallow-water environments, but the oldest known species is *E. lozoueti* (Dolin and Pacaud 2000; as *Nodilittorina*) from the Middle Eocene of France.

Our aim is to examine the mode, geography, and timing of speciation in *Echinolittorina* and the resulting pattern of global species richness in this genus. We present a complete molecular phylogeny including all 50 recognized taxonomic species and an additional nine ESUs discovered by intensive worldwide sampling. This is, to our knowledge, the largest complete phylogeny for a circumtropical marine clade yet produced, and has been made possible by the abundance, accessibility, and resilience of these organisms. It is also the first for a clade restricted to intertidal rocky shores. We combine this with detailed distributional data for the 59 ESUs, and use the limited fossil record and major vicariant events to estimate a time scale. We show that patterns of distribution and diversity are the result not only of historical episodes of vicariance and dispersal, but also of habitat specialization on the oceanic-continental continuum.

MATERIAL AND METHODS

Sampling and Identification

Identification of the 50 taxonomic species of *Echinolittorina* (Reid 2002b; Williams et al. 2003) was based on taxonomic monographs (Rosewater 1981; Bandel and Kadolsky 1982; Reid 2001, 2002a), with nomenclatural changes as noted in the Appendix. To confirm these as ESUs, genetic variation was examined in at least two, and often more, individuals from the most distant available locations (Appendix). In most cases the taxonomic morphospecies were supported, appearing as tight clades in preliminary analyses, but the genetic data also suggested additional species. Usually, these

could be distinguished by small but consistent morphological differences (mainly in shells and penes). These additional species were designated by the traditional name and a letter (where “A” designates the name in its strict sense as determined by type material). In a few instances, morphological and genetic data were inconsistent. “Deep” molecular divergence (3–4% Kimura two-parameter divergence in COI sequence) was found without apparent morphological differentiation in *E. trochoides* A and B. Since these were reciprocally monophyletic with disjunct geographical distributions, they have been treated here as ESUs. Similar deep divergence (about 6%), but without disjunction, morphological differentiation, or clear reciprocal monophyly, was treated as intraspecific in *E. vidua*. Conversely, there were a few examples of morphospecies that showed incomplete sorting in some or all gene trees. In two cases (the two pairs *E. apicina*/*paytensis* and *E. dubiosa*/*tenuistriata*) their maintenance of morphological differences in microsympatry (Reid 2002a) persuaded us to accept these as species. By analogy, we also accepted the genetically close, but morphologically distinct, members of the following groupings as distinct species: *E. parcipicta*/*fuscolineata*; *E. punctata* A/B/*pulchella*; *E. ziczac* A/B; *E. millegrana*/*reticulata*. Further study of the boundaries between these species and their formal nomenclature will be reported elsewhere. We emphasize that in referring to these taxonomic units as “species,” we do not wish to make formal decisions concerning their appropriate specific or subspecific rank.

The 59 species of *Echinolittorina* included in this study are listed in the Appendix. Although multiple samples were taken for many species, a maximum of two sequences for each gene (and up to four for the variable *E. vidua*) are reported here. For 56 species two sequences of both cytochrome oxidase I (COI) and 12S rRNA genes were obtained and at least one of 28S rRNA. *Echinolittorina meleagris* B and *E. pulchella* are represented by 12S rRNA sequences alone, and *E. vermeiji* by one COI, one 28S, and two 12S sequences. All tissue samples and voucher specimens are deposited in the Natural History Museum, London.

As outgroup taxa we used the four known species of *Afrolittorina* and three representatives of *Littorina* (Appendix); these are members of the sister clade of *Echinolittorina* (Williams et al. 2003). Published sequences for 12S and 28S rRNA (Williams et al. 2003) and new, longer COI sequences were used for a single individual from each outgroup taxon.

DNA Extraction, Amplification, and Sequencing

DNA was generally extracted from ethanol-fixed mantle or columellar muscle, except in the case of small animals when both head and mantle, or the whole animal, were used. The extraction method was that of Winnepenninckx et al. (1993) with minor modifications. Tissue was blotted dry and soaked for up to 2 h in 0.01 TE buffer (0.001 M Tris-HCl, pH 7.5, 0.0001 M EDTA) to remove ethanol. Samples that had been dried or preserved in formalin were rinsed in several changes of buffer over two days. Tissue was placed in a microfuge tube containing 300 μ l of CTAB extraction buffer preheated to 60°C (100mM Tris HCl, pH 8.0, 1.4 mM NaCl, 20 mM EDTA, 2% weight/volume CTAB, 2% weight/volume

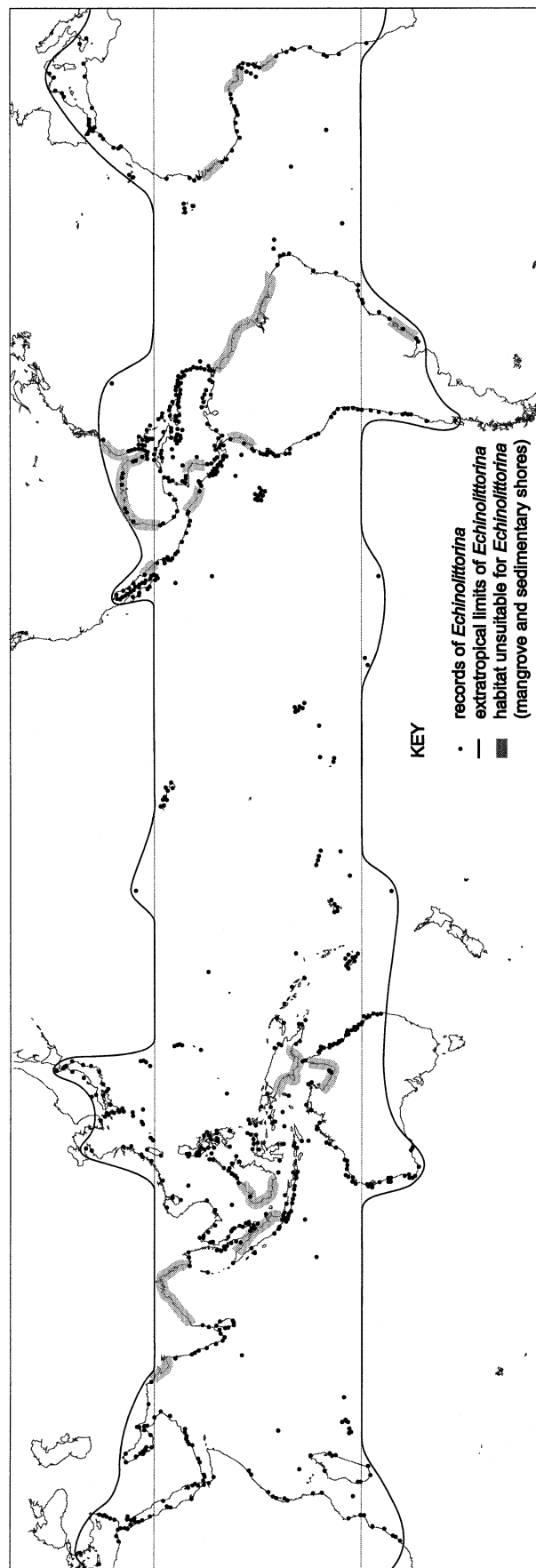


FIG. 1. Map of more than 3700 samples used to plot the distribution maps of *Echinolittorina* species in Figures 6 and 7. Heavy black lines correspond to the tropics and to the extratropical limits of the genus *Echinolittorina*. Large areas of unsuitable habitat (mangrove and sedimentary shores) are indicated by gray areas along coastlines.

TABLE 1. Forward (F) and reverse (R) polymerase chain reaction primers.

| Name | Sequence 5'-3' | Source |
|-----------------|-----------------------------------|--|
| 28S rRNA | | |
| LSU5 (F) | TAG GTC GAC CCG CTG AAY TTA AGC A | Littlewood et al. 2000 |
| LSU1600 (R) | AGC GCC ATC CAT TTT CAG G | Williams et al. 2003 |
| COI | | |
| LCO1490 (F) | GGT CAA CAA ATC ATA AAG ATA TTG G | Folmer et al. 1994 |
| COI RM1 (R) | GAA TAA CGT CGT GGT ATA CCT C | Designed from aligned littorinid sequences (this study) |
| COI vid 3' (R) | GCT GGG GGA AAA AAG TAA C | Designed to amplify <i>Echinolittorina vidua</i> (this study) |
| 12S rRNA | | |
| 12sa-L (F) | AAA CTG GGA TTA GAT ACC CCA CTA T | Modified from 12S-L1091 in Kocher et al. (1989), as in Palumbi (1996a) |
| 12SALint (F) | ACT AGG ATT AGA TAC CCT ACT ATT C | Williams et al. 2003; amplifies most <i>Echinolittorina</i> species |
| 12Sai-5' | AAA CTA GGA TTA GAT ACC CTA TTA T | Palumbi 1996a |
| 12Sa-H (R) | GAG GGT GAC GGG CGG TGT GT | Modified from 12S-H1478 in Kocher et al. (1989), as in Palumbi (1996a) |
| 12SAHint (R) | CGA GRG TGA CGG GCG ATG TGT GCA | Williams et al. 2003; amplifies most <i>Echinolittorina</i> species |

PVP 40,000 MW, and 0.2% β -mercaptoethanol added just before use), then macerated and incubated overnight at 60°C with 20 μ l of proteinase K (20mg/ml). Dried or formalin-preserved samples were incubated for several days with additional proteinase K. The tissue extract was then extracted at least twice with chloroform, precipitated with two volumes of ethanol in the presence of sodium acetate and finally resuspended in 0.01 TE buffer.

Portions of three genes were amplified and sequenced: mitochondrial 12S rRNA and COI, and nuclear 28S rRNA. These cover a range of evolutionary rates (Williams et al. 2003). Diluted total gDNA (15–80 ng) was used in polymerase chain reactions (PCR) to amplify approximately 1500 bp of 28S rRNA, 410 bp of 12S rRNA, and 1300 bp of COI. Reactions contained 0.1 μ M of a forward and reverse PCR primer (Table 1), 200 μ M of each dNTP, a gene-dependent concentration of magnesium chloride, 2.5 units of Qiagen (Valencia, CA) DNA polymerase (50 μ l reaction), one-fifth volume of "Q solution" and one-tenth volume of Qiagen buffer (10 \times). Magnesium chloride concentrations were 2.0 mM for 12S rRNA, 2.5 mM for 28S rRNA, and 3.0 mM for COI. Thermal cycling was performed with an initial denaturation for 3 min at 95°C, followed by 40 cycles of 45 sec at 94°C, 45 sec at a gene-specific annealing temperature, 2 min at 72°C, with a final extension of 10 min at 72°C. All temperature changes were ramped 1°C per sec. Annealing temperatures were 50°C for COI, and 52°C for 28S rRNA and 12S rRNA. Sequence reactions were performed directly on purified PCR products using a BigDye Terminator version 1.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, CA) and run on a 377 Applied Biosystems automated sequencer.

Sequences were verified by forward and reverse comparisons, except for some regions in 28S rRNA. Some 28S rRNA sequences showed intraindividual variation (heterozygous bases) and small (probably 1–2 bp) indels. In such cases, good sequence could be obtained from both forward and reverse reactions until a certain base was reached, and from

then on multiple (usually two) sequences were evident in both forward and reverse chromatograms. These regions were checked by multiple overlapping sequences in a single direction only. Some of this sequence was not used in analyses, as it was too variable to align unambiguously. Similar patterns of intraindividual variation in rRNA genes have been reported (Stothard et al. 2000; Bonnaud et al. 2002; Williams et al. 2003, 2004). All sequences have been deposited in GenBank (accession numbers for 28S rRNA: AJ623180–AJ623264, 12S rRNA: AJ623068–AJ623179, COI: AJ622946–AJ623067).

Sequence Analysis and Phylogeny Reconstruction

Sequences were edited using Sequencher (ver. 4.0, Gene Codes Corporation, Ann Arbor, MI). Sequences of ribosomal genes were aligned using Clustal X (Thompson et al. 1994, 1997; delay divergent sequence = 98%, gap-opening penalty = 15, gap-extension penalty = 5) with minor adjustments made by eye. Regions where the alignment was ambiguous were excluded from the analyses. Sites at which an insertion affected only a single individual were also excluded. Alignments of ribosomal genes have been deposited with European Bioinformatics Institute/European Molecular Biology Laboratory, and are available by anonymous FTP from ftp://ftp.ebi.ac.uk/pub/databases/embl/align/ or via SRS at http://srs.ebi.ac.uk, under accession numbers ALIGN_681, and ALIGN_682.

Prior to phylogenetic analyses, the concatenated sequences were tested to confirm that there was no significant heterogeneity of base frequencies ($\chi^2 = 83.5$, $df = 189$, $P = 1.00$). Pairwise distances between each taxon (including outgroups) were calculated for each gene and for the third codon position for COI. The inferred distance (Kimura's two-parameter) was plotted against the observed number of differences to investigate the level of saturation in each gene.

A phylogeny was constructed from each gene-sequence dataset and a combined dataset in which all three genes were

concatenated, using Bayesian methods (MrBayes ver. 3.0b4; Huelsenbeck and Ronquist 2001). Congruence among the three gene trees was assessed by looking for conflicting branches with greater than 95% support. In the Bayesian analysis, base frequencies were estimated, four chains were used (default temperature), and the starting tree was random. The general time-reversible (GTR) model was used, with gamma-distributed rate variation among sites approximated with four categories (α shape estimated) and allowing for invariant sites (GTR + Γ + I). For each dataset, this was the best model found using AIC criteria (MrModelTest ver. 1.1b performs hierarchical likelihood ratio tests of the nucleotide substitution models currently implemented in MrBayes; J. Nylander, www.ebc.uu.se/systzoo/staff/nylander.html). In the combined analysis, variation was partitioned among genes, gene-specific model parameters were used (all parameters were free to vary independently within each partition), and each gene was allowed to evolve at a different rate. The analysis for each dataset was run for 3.5×10^6 generations, with a sample frequency of 100. The first 15,000 trees were discarded, so that the final consensus was based on 20,000 trees. Each analysis was done three times, to confirm that independent analyses were converging on the same tree, and the final tree was computed from the combined accepted trees from each analysis (a total of 60,000 trees). Support for nodes was expressed as posterior probabilities (calculated by MrBayes) and as bootstrap support (data not partitioned; using maximum-likelihood [ML] GTR + Γ + I model, parameters estimated from MrBayes tree; 100 replicates and neighbor-joining [NJ] algorithms, distance estimated using ML; 10,000 replicates). For comparison, analyses of combined datasets were also performed using maximum parsimony (MP; using implied weighting, $K = 2$, heuristic search) and NJ (distance estimated using ML methods as above) algorithms (implemented in PAUP*; Swofford 2002).

Geographical Distributions and Mode of Speciation

Distribution maps were compiled from more than 3700 locality records, from personal collections, and from personally verified material in 16 major museums. The coverage of areas of suitable habitat is worldwide (Fig. 1), with relatively sparse records from only a few areas (Somalia, northwestern Sumatra, eastern Borneo, western Sulawesi, northwestern Luzon, northern New Guinea, southern Banda Sea, Solomon Islands, Vanuatu). Since all *Echinolittorina* species occupy similar high-shore habitats and are usually abundant, it is likely that collection at any one locality will detect most species present there. The distribution maps (see Figs. 6, 7) should therefore be examined in conjunction with the map of individual records (Fig. 1) to show areas of absence and the precision of range limits.

Numbers of sympatric species were counted in two ways, first as numbers of species within the classic biogeographic provinces (defined by Briggs 1974, 1999b), and second as numbers of species recorded at selected well-studied localities (an island or bay up to 50 km diameter).

If geographical range shifts following speciation are small, a phylogeny can be used to distinguish among different geographical modes of speciation (Barraclough and Vogler

1998). The percentage of range overlap between sister clades was plotted against average genetic distance (a proxy for evolutionary time). Clade relationships were determined from the topology of the combined-gene tree. Genetic distance was determined by branch length on the combined-gene tree and distances between clades were averages of all pairwise comparisons between their component species. Percentage of range overlap was defined as the area of overlap divided by the area of the clade with the smaller range (Barraclough and Vogler 2000). Areas of distribution could not be determined by planimetric methods, because of the difficulty of comparing linear ranges along continental margins with ranges on scattered oceanic islands. Instead, we took advantage of the high and relatively uniform worldwide coverage of our sampling points (Fig. 1). The percentage overlap was taken as the number of localities at which both clades occurred, divided by the total number of localities from which the more narrowly distributed clade was recorded. Multiple records within a single locality were counted only once.

Estimation of Ages of Nodes

Branch lengths were fitted to the Bayesian tree in PAUP* using ML and enforcing a molecular clock (using general time-reversible model with invariant sites and gamma-distributed rate variation among sites GTR + Γ + I; all parameters estimated from Bayesian tree). A likelihood ratio test showed significant variation between the rate-constant (clocklike) tree and the unconstrained tree from Bayesian analysis of the combined dataset ($\chi^2 = 562.5$, $P > 0.05$, $df = 63$). Therefore we transformed the Bayesian tree using nonparametric rate smoothing (NPRS; Sanderson 1997) as implemented in TreeEdit (ver. 1.0a10, A. Rambaut and M. Charleston, <http://evolve.zoo.ox.ac.uk>) with rate variation weighted across the root.

The conversion of the relative ages into actual dates requires at least one calibration point. The oldest fossil that can be assigned to the genus *Echinolittorina* is *E. lozoueti* (Dolin and Pacaud 2000), described from Biarritzian deposits of the Middle Eocene of France. This fossil is now assigned to the uppermost Lutetian stage and dated at 41 million years ago (mya; P. Lozouet, pers. comm.). Divergence times were calculated by scaling node heights to an age of 41 mya for the first node in the *Echinolittorina* clade. Two vicariant tectonic events were also used as independent calibration points. The closure of the Tethys Sea approximately 19 mya (Robba 1987; Vrielynck et al. 1997) was used to date the split between the Indo-West Pacific clade and its sister clade in the Atlantic and eastern Pacific. The rise of the Isthmus of Panama approximately 3.1 mya (Coates and Obando 1996) was used to date the youngest split between eastern Pacific and western Atlantic taxa, that between *E. riisei* and *E. apicina* + *paytensis*.

Rate of Diversification

The NPRS-transformed tree was used to plot the log of the number of lineages against node height to show the diversification through time (using Genie, ver. 3.0; Pybus and Rambaut 2002). Many plots of lineages through time suffer from incomplete sampling within a clade. Although two spe-

cies of *Echinolittorina* are not represented in the combined-gene tree (*E. meleagris* B and *E. pulchella*), both were included in the 12S rRNA tree, allowing them to be included in the analysis. Using the topology of the 12S tree, nodes for these two species only have been arbitrarily assigned halfway along the branch of their sister species on the combined gene tree (Losos 1990; Barraclough and Vogler 2002).

Under a constant birth-death model we expect a straight line with slope $b-d$ (where b is speciation rate and d extinction rate), and an upturn in the number of lineages toward the present with slope b (Harvey et al. 1994; Nee et al. 1994; Pybus and Harvey 2000; Ribera et al. 2001; Barraclough and Vogler 2002). We used the γ -statistic of Pybus and Harvey (2000) to determine whether the phylogeny is consistent with a constant rate of both speciation (b) and extinction (d) through time. For a phylogeny with complete sampling of taxa and a constant rate of speciation, the statistic has a standard normal distribution (Pybus and Harvey 2000); significant departures indicate that nodes are too close to the root (negative values) or to the tips (positive values), compared with expectations of a constant speciation model (Pybus and Harvey 2000). We used the NPRS-transformed tree and, for comparison, the molecular-clock tree. The calculation was performed using a script in p4 (P. Foster, <http://www.nhm.ac.uk/zoology/external/p4.htm>).

RESULTS

Sequence and Gene Comparisons

Of a total 3052 bp of aligned nucleotide sequences, 103 bp were excluded from the analyses (63 bp of 1477 bp 28S rRNA, 40/377 bp 12S rRNA). Of the remaining 2949 bp of aligned sequence, 731 sites were variable, of which 661 were phylogenetically informative (108 informative sites of 1413 bp of included 28S rRNA, 113/337 bp 12S rRNA, 440/1199 bp COI). Plots of genetic distance versus observed distance for each gene (not shown) suggest that variation at most sites had not reached saturation. Third codon positions of COI sequences were retained in all analyses, because although all but eight of the third positions were variable, there was only modest evidence of saturation, and all except one of the variable third-position sites were informative. Recent studies (including one on littorinids, Williams et al. 2003) suggest that not only do third positions contain phylogenetic signal, but that in some cases inferences from them may be more reliable than from first and second positions (Stanger-Hall and Cunningham 1998; Sanderson et al. 2000). Bayesian estimates of relative rate of gene evolution differed between genes by two orders of magnitude with COI evolving the most rapidly (0.05:0.33:2.31 for 28S:12S:COI respectively). Likelihood analysis of COI codon site variation suggests that the relative rates of each codon position are 0.12:0.002:2.88. The rates of evolution of each gene in our analysis are estimated as follows: COI at 2.6% mya^{-1} (fossil calibration) and 4.8% mya^{-1} (Tethyan calibration), 28S rRNA 0.05% mya^{-1} and 0.1% mya^{-1} , and 12S rRNA at 0.4% mya^{-1} and 0.7% mya^{-1} .

Phylogenetic Analyses

Independent Bayesian analyses for each gene converged on the same or similar trees. Trees obtained from three runs of the 12S rRNA and COI data were not identical, showing small differences in topology of poorly supported branches. The well-supported clades identified in trees obtained by independent analyses of each gene were very similar (Fig. 2) and therefore sequences were analyzed in a single concatenated dataset. Multiple runs of this combined dataset converged on exactly the same tree except for two poorly supported nodes—the poorly supported monophyly of *E. radiata* and *E. arabica* A and B (PP = 31%), which was not found in one analysis, and *E. albicarinata* was sister to *E. parvipicta* + *E. fuscolineolata* in one analysis instead of *E. porcata* + *E. atrata* (PP = 41%; Fig. 3). The same clades were also identified in trees obtained using alternative tree-building methods (MP and NJ; results not reported). Both posterior probabilities and bootstrap support (NJ and ML) were high at most nodes.

All 26 Indo-West Pacific species of *Echinolittorina* appear in a single clade (posterior probabilities of 100% in 12S, COI, and combined trees, but not in the 28S tree; Figs. 2, 3). The relationships among the clades of eastern Pacific and Atlantic species are not clearly resolved (Fig. 3), reflecting incongruence among the three genes, but there was little support for their combination in a single clade. Topologies with a single eastern Pacific plus Atlantic clade were found in only 0.3% of trees in an unconstrained Bayesian analysis of the combined data and rarely in analyses of individual datasets (12S 14/60,000; COI 22/60,000; 28S 1/60,000). On the other hand, there is support for paraphyly of the eastern Pacific plus Atlantic clades in the COI gene tree (Fig. 2B) and weak support in the three-gene tree (Fig. 3).

Ages of Nodes

Estimates of ages of nodes are shown in Figure 4 using alternative calibrations based on the oldest fossil and on closure of Tethys (the former are 84% greater). Results from the calibration based on the age of the Isthmus of Panama were discounted, because they suggest that the genus is less than 9 my old, contrary to fossil evidence. These estimates are subject to four main sources of error: the use of an incorrect tree; rate variations that invalidate the assumptions of the method; use of an incorrect calibration point; and noise introduced from stochastic processes of substitution (Wikström et al. 2001). As in a previous study of littorinid phylogeny (Williams et al. 2003), the most important source of error for estimates of divergence times is likely to be the calibration point. Neither tree topology nor rate variation are expected to be major sources of error, because the topology of the combined-gene tree was robust to different methods of analysis and nonparametric rate smoothing does not assume rate constancy. Calibrations based on tectonic events often underestimate divergence times for which fossil evidence is available (Marko 2002). In addition, for COI the rate of evolution based on the fossil calibration is closer to published rates for molluscan taxa with better fossil records (0.7–1.2%, Marko 2002; 2.4%, Hellberg and Vacquier 1999). Therefore we favor the older (fossil) calibration.

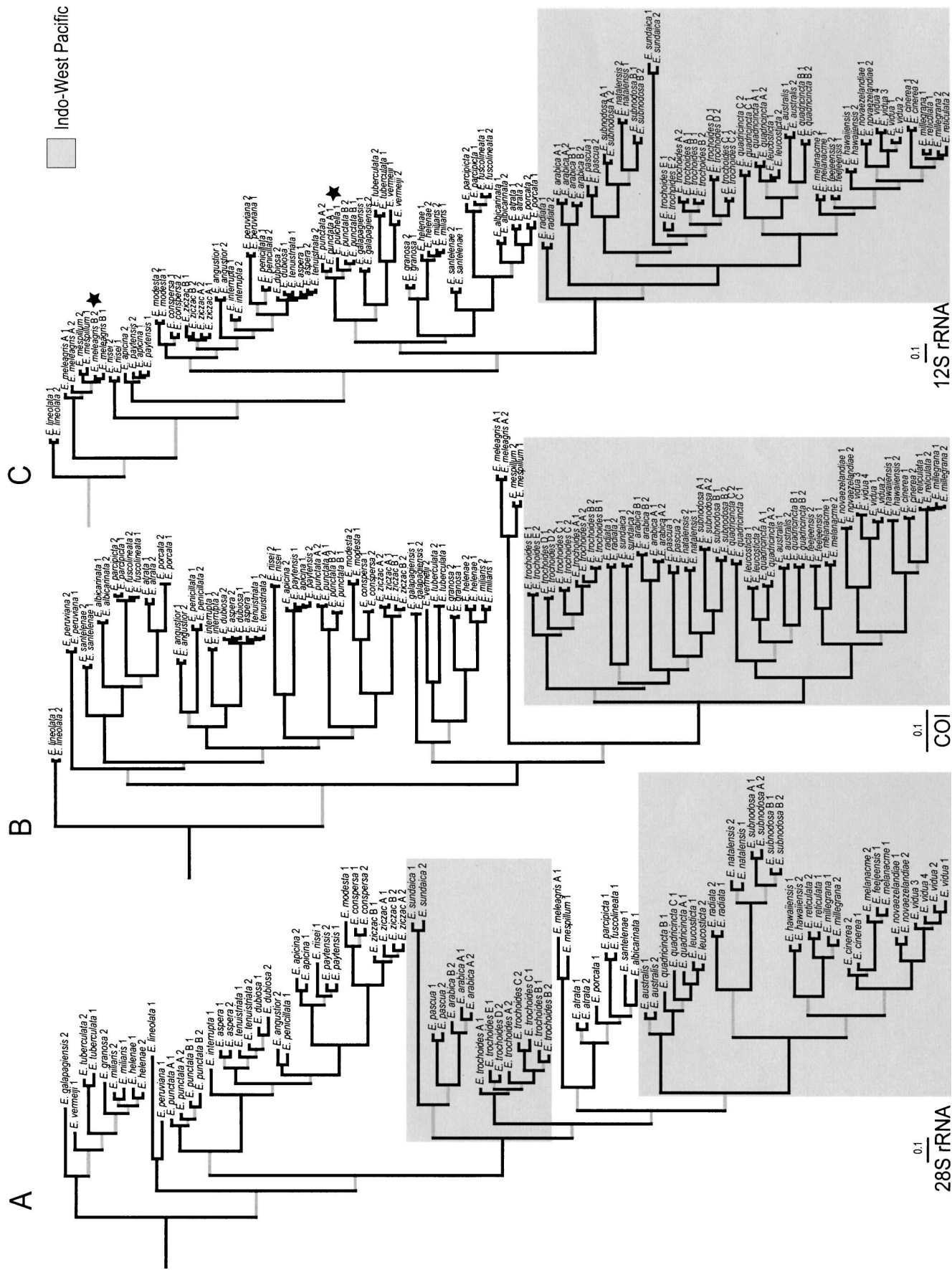


FIG. 2. Molecular phylogenies of *Echinolittorina* species produced by Bayesian analysis of individual gene-sequence datasets from 28S rRNA (A), COI (B) and 12S rRNA (C) genes. Outgroups have been removed from all trees. Branches with posterior probability (PP) <90% are gray, branches with PP ≥ 90% are black. Species from the Indo-West Pacific are enclosed in gray boxes.

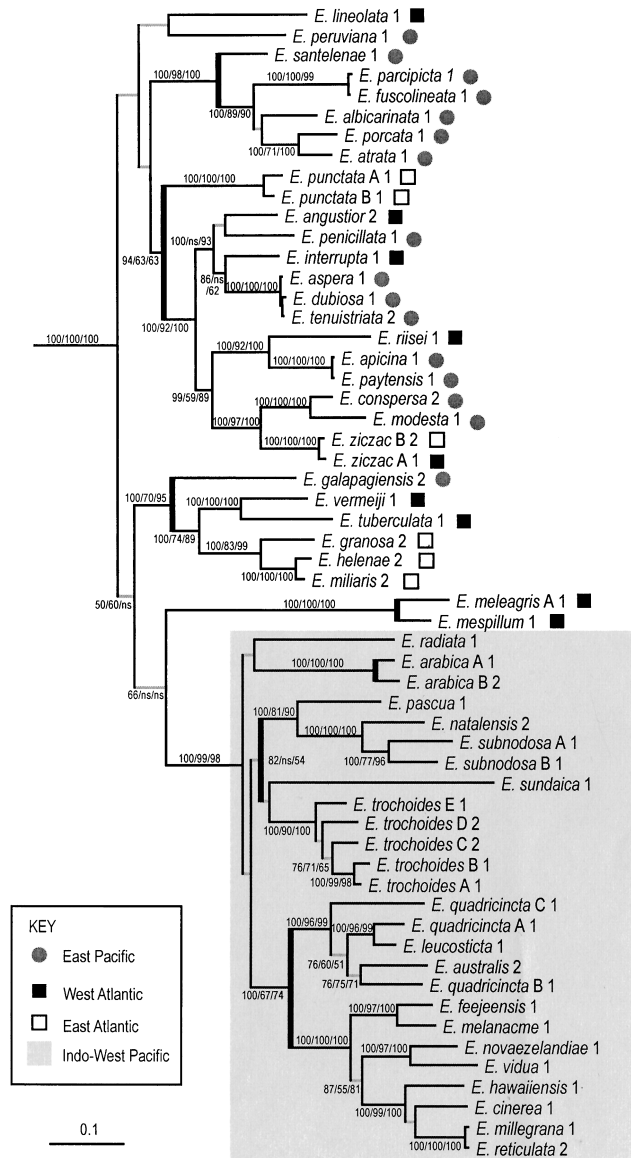


FIG. 3. Molecular phylogeny of *Echinolittorina* species produced by Bayesian analysis of concatenated gene sequences from 28S rRNA, COI, and 12S rRNA genes (outgroups removed from tree). Branches with posterior probability (PP) <90% are gray, branches with PP \geq 90% are black. Nodal support is posterior probability/bootstrap (neighbor joining using ML distance, 10,000 replicates)/bootstrap using maximum likelihood (100 replicates). Support values are only shown where at least two support values are >50%. Heavy vertical lines indicate the seven clades used in the overlap analysis (see Fig. 8). The Indo-West Pacific clade is enclosed in a gray box.

Rate of Diversification

The plot of lineages through time for *Echinolittorina* (Fig. 5) is slightly convex, lacking an upturn toward the present, suggesting that speciation rate has decreased over time (Harvey et al. 1994). This is confirmed by significant values of the γ -statistic of Pybus and Harvey (2000), -1.79 for the NPRS transformed tree ($P < 0.05$, one-tailed test, standard normal distribution) and also for the Indo-West Pacific clade alone ($\gamma = -2.02$, $P < 0.05$).

Geographical Distributions and Species Diversity

The geographical distributions of each *Echinolittorina* species are shown together with their phylogenetic relationships in Figures 6 and 7. Sister species are almost always allopatric, particularly in the Indo-West Pacific, and percentage overlap increases only slowly as more distant clades are compared (Fig. 8). Seven of eight sister-species pairs in the Indo-West Pacific are allopatric, whereas eight of 12 are allopatric in the eastern Pacific plus Atlantic (two of the 12 are not shown in Fig. 8; see figure legend). At 15 of 22 Indo-West Pacific nodes the sister clades were allopatric (68%) and at 17 of 28 in the eastern Pacific plus Atlantic (63%).

The number of *Echinolittorina* species recorded within broad biogeographic provinces reaches a maximum of 11 in the East Indies Triangle; with 10 in the Western Pacific Ocean; nine in the Panamanian; and seven in East Indian Ocean, Caribbean, and West Indian provinces (Fig. 9A). However, the numbers of sympatric species at individual localities show a different pattern (Fig. 9B). In the Indo-West Pacific it only reaches six at three localities (northeast Taiwan, northeast Sulawesi, southwest Java), the result of slight overlap at the margins of distributional ranges, and four to five species is the rule throughout most of the East Indies Triangle. In the western Atlantic six or seven species are commonly sympatric, and in the eastern Pacific up to eight sympatric species are recorded. In the eastern Atlantic up to three species are sympatric. In central oceanic and peripheral localities (and the corresponding provinces) the numbers of species are low.

DISCUSSION

Classification and Phylogeny of *Echinolittorina*

Our study has added nine ESUs to the 50 taxonomic morphospecies of *Echinolittorina* (Reid 2002b, modified by Williams et al. 2003). The number of described morphospecies typically underestimates diversity in marine communities (Knowlton 1993; Bouchet et al. 2002), perhaps by as much as three to five times, even in well-studied groups (Knowlton and Jackson 1994). In these relatively well-known littorinids, molecular study has increased diversity by a modest 18%. Furthermore, the additional ESUs are allopatric sister lineages rather than cryptic sympatric species and so have no effect on estimates of sympatric species diversity. Similarly, molecular tools increased the species diversity of the taxonomically well-known Indo-West Pacific cowries by 36% (Meyer 2003). In each case these percentages are sensitive to decisions about the species status of genetically distinct lineages.

The only previous attempt to construct a phylogeny for these species was based on maximum-parsimony analysis of morphological characters of “*Nodilittorina*” (Reid 2002b). Resolution was extremely poor and failed to identify *Echinolittorina* as a monophyletic group. In a subsequent molecular analysis “*Nodilittorina*” was shown to be polyphyletic and *Echinolittorina* defined as a clade of seven exemplar species (Williams et al. 2003), as confirmed here for the entire genus. Some of the relationships reported here are consistent with morphological synapomorphies, but in general the group

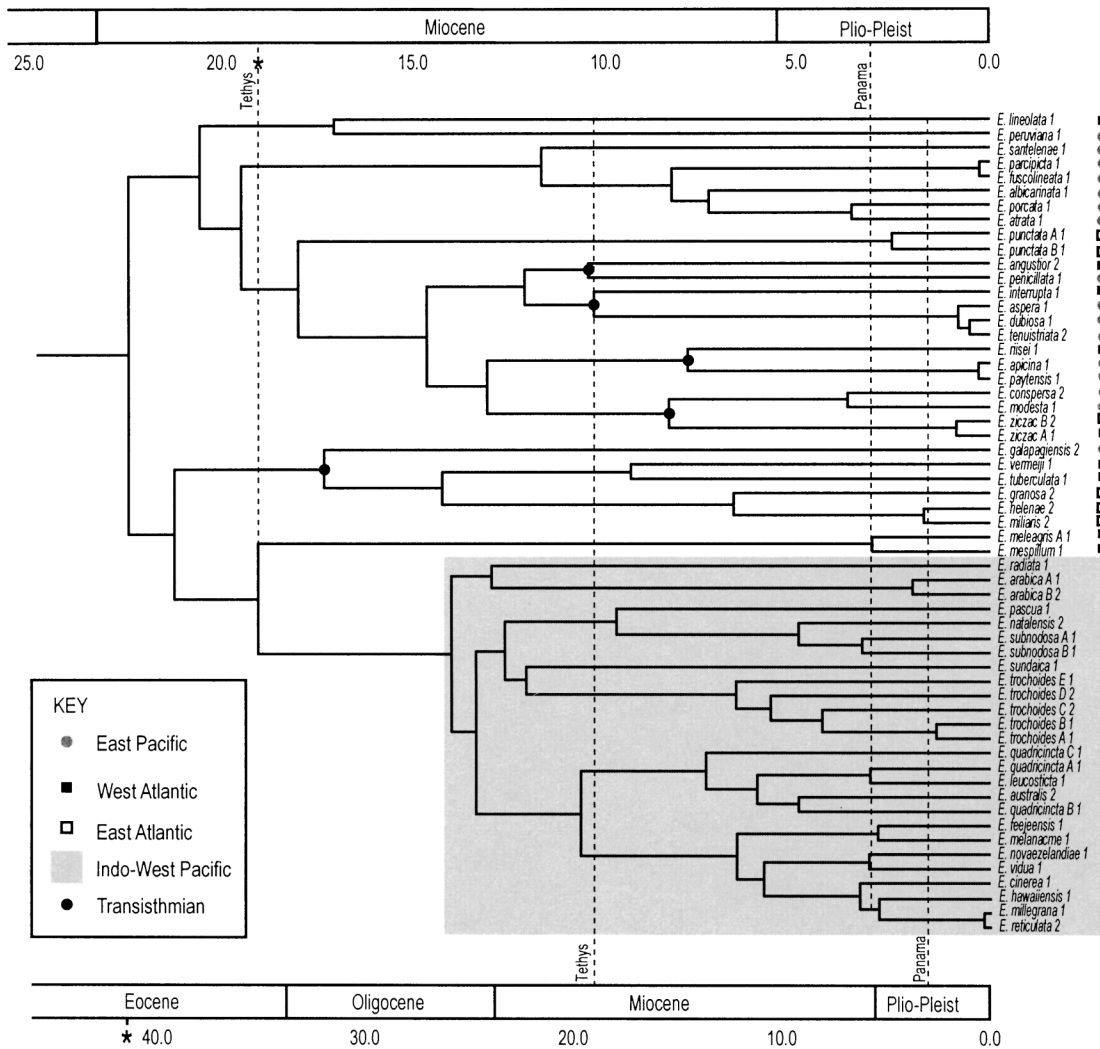


FIG. 4. Chronogram representing the Bayesian tree in Figure 3 transformed using nonparametric rate smoothing (Sanderson 1997). Two alternative time scales are given; the upper one is based on the assumption that the minimum age of the Indo-West Pacific clade is that of final closure of the Tethys Sea at 19 million years ago (mya); the lower scale is based on a minimum age of *Echinolittorina* equal to that of its oldest fossil (41 mya); the latter is preferred (see Results). Distributions of species in the principal tropical marine biogeographic regions are given. Dotted lines indicate vicariant events: final closure of Tethys (19 mya) and emergence of Panamanian Isthmus (3.5 mya).

shows high homoplasy of morphological characters (Williams et al. 2003).

Tethyan Biogeography

The only direct evidence of historical biogeography derives from the fossil record. The record of *Echinolittorina* is fragmentary and difficult to interpret in the absence of unequivocal morphological synapomorphies for the genus. The earliest known fossil is “*Nodilittorina*” *lozoueti* from the middle Eocene (latest Lutetian, 41 mya) of France (Dolin and Pacaud 2000) (reassignment to *Echinolittorina* based on close resemblance to modern *E. radiata*), establishing a minimum age for the genus and that it was present in the Tethys Sea. The next undoubted record of *Echinolittorina* is from the middle Miocene Paratethys area (as *Nodilittorina*; Reid 1989a). During the early Miocene, northward movement of the African plate brought about gradual closure of the Tethyan seaway

connecting the Mediterranean with the Indian Ocean. Three narrow, shallow channels persisted across Arabia until the late Burdigalian (about 18 mya; Vrielynck et al. 1997) and intermittent marine connections may have continued until the late Miocene (Robba 1987). For Tethyan groups, the expected phylogenetic consequences of this vicariant event are pairs of sister clades in the eastern Pacific plus Atlantic (or only eastern Atlantic) and Indo-West Pacific basins (Meyer 2003), as found in some molecular studies of marine groups of appropriate age (e.g. Streelman et al. 2002; Hrbek and Meyer 2003; Meyer 2003; Bernardi et al. 2004; Teske et al. 2004). However, the pattern in *Echinolittorina* is different, consisting of a single clade of all 26 Indo-West Pacific species and an arguably paraphyletic, basal, group of eastern Pacific plus Atlantic species. Furthermore, the estimated age of the Indo-West Pacific clade (based on the preferred fossil calibration) is 32.7 mya, preceding the final closure of the Tethys seaway.

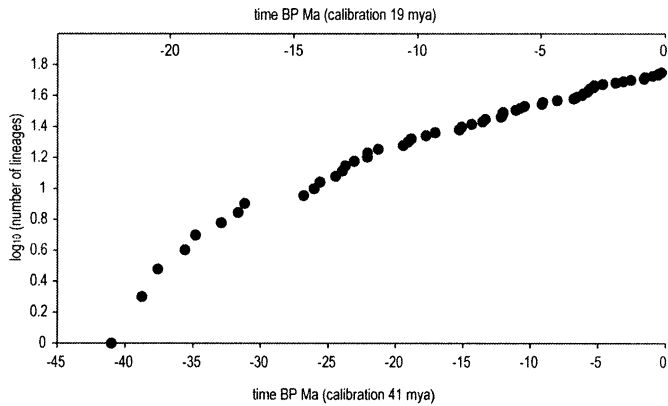


FIG. 5. Lineages-through-time plot for *Echinolittorina*. The x-axis is time before present (BP) using the NPRS branch lengths, scaled to two different calibration points, closure of Tethys at 19 million years ago (mya) (top axis) and earliest fossil *Echinolittorina* at 41 mya (bottom axis; see Fig. 4). The two species not represented in the combined-gene tree (*E. meleagris* B and *E. pulchella*) were included by using the topology of the 12S tree (nodes arbitrarily assigned halfway along the branch of their sister species on the combined gene tree; Losos 1990; Barraclough and Vogler 2002).

In the absence of a useful fossil record for *Echinolittorina*, explanation of these results remains speculative, because the contribution of extinction cannot be evaluated. If extinction has been insignificant, paraphyly of the eastern Pacific plus Atlantic clades is consistent with an origin of the genus in this region, expansion through the Tethys Sea and ultimate isolation of a single lineage in the Indo-West Pacific. A similar explanation has been proposed for eastern Pacific plus Atlantic paraphyly in *Uca* fiddler crabs (Levinton et al. 1996; for a similar pattern in loliginid squid, see Anderson 2000). The fossil record of a number of gastropod families indicates an Eocene origin in tropical America and later appearance in the Tethys Sea (Vermeij 2001). If, however, several lineages reached the Indo-West Pacific, Neogene extinctions in the eastern Atlantic (Paulay 1997) might have removed their sister taxa, resulting in apparent monophyly of an Indo-West Pacific clade older than the final Tethyan closure. Alternatively, loss of Indo-West Pacific lineages might have produced the paraphyly of eastern Pacific plus Atlantic clades. New fossil evidence and study of comparable global phylogenies are required to assess these alternatives.

Distribution and Dispersal of *Echinolittorina* Species

Before considering mechanisms of speciation in *Echinolittorina* it is necessary to review its capabilities for dispersal in relation to potential geographical barriers. The relation between developmental mode and potential for dispersal and colonization is complex (Palumbi 1995; Cunningham and Collins 1998; Benzie 1999), and even pelagic eggs and larvae may not disperse widely (Barber et al. 2002; Gilg and Hilbish 2003; Taylor and Hellberg 2003; but see Lessios et al. 2003, for an example of extreme dispersal). Direct observations of larval development in *Echinolittorina* are scarce. Pelagic egg capsules are known or predicted (from oviduct anatomy) in all species (Reid 1989a, 2002b). Only *E. hawaiiensis* has been successfully reared in the laboratory, showing a total plank-

tonic development time, from spawning to settlement, of 3–4 weeks at 25°C (Struhsaker and Costlow 1968). However, a similar duration of planktotrophic development can be predicted for all species from their uniform larval shells (Bandel and Kadolsky 1982; Reid 2002a; D. G. Reid, unpubl. data). The established ranges of *Echinolittorina* species are known with sufficient precision that extralimital occurrences can sometimes be identified, suggesting the maximum limits of dispersal. For example, in the eastern Pacific the mainland species *E. dubiosa* has once been found in the Galapagos Islands, 1200 km away, and *E. conspersa* can occasionally cross a gap of 1200 km of unsuitable mangrove habitat (Reid 2002a). In the Indo-West Pacific there is a single record of *E. trochoides* B in New Caledonia, 1400 km from Australia (D. G. Reid, unpubl. data). There are no records of Indo-West Pacific *Echinolittorina* species in the eastern Pacific (Reid and Kaiser 2001), so the ‘Eastern Pacific Barrier’ of more than 5000 km appears insurmountable. Even if larvae occasionally traverse distances of up to 1400 km, establishment of a self-sustaining population at such a distance must be very much rarer, because the founding population should be of sufficient density to ensure that mates can be found and to overcome the dilution of the resulting progeny during their own pelagic phase (Johannesson 1988; Paulay and Meyer 2002).

The evidence of dispersal suggests that distances of open water or unsuitable habitat of more than 1200–1400 km may be sufficient to isolate species. An unsuitable habitat includes areas without rock substrate, which is required by all *Echinolittorina* species, although there is no evidence for restriction to specific rock types such as limestone or basalt (Vermeij 1971; Reid 2002a; D. G. Reid, unpubl. data). For example, in the eastern Pacific three stretches of 370 to 1200 km of sedimentary shores delimit the ranges of species (Reid 2002a). Similar barriers appear to impose isolation on the northeast coast of South America and in West Africa, northwest India, and the Bay of Bengal (compare Fig. 1 with Figs. 6 and 7), in each case combined with outflows from great rivers that may lower salinity. The dispersal limit explains the restriction of island endemics to the Galapagos Islands, Ascension, St. Helena, Easter and Pitcairn Islands, and the Hawaiian Chain. Island groups may also be isolated by current flows, as in the Cape Verde Islands (De Wolf et al. 2000) and the Marquesas Islands (Planes and Fauvelot 2002). The genus is largely of tropical distribution (exceptions are *E. punctata* A and *E. peruviana*), so the temperate limits are presumably determined in some way by temperature. Cool upwelling on the Arabian Peninsula (Sheppard et al. 1992) may isolate *E. arabica* A and B.

There is one other set of environmental variables, less obvious than those listed above, but potentially just as important to an understanding of speciation and diversity patterns. In accounts of geographical distributions of tropical marine molluscs a distinction between continental and oceanic species has been recognized (Abbott 1960; Taylor 1971; Reid 1986; Vermeij 1987). Typically, continental species are those occurring on the nutrient-rich shores of continental landmasses and large, high islands, whereas oceanic species are found on oceanic islands in clear water of low productivity, but there is a spectrum between these extremes. Using a

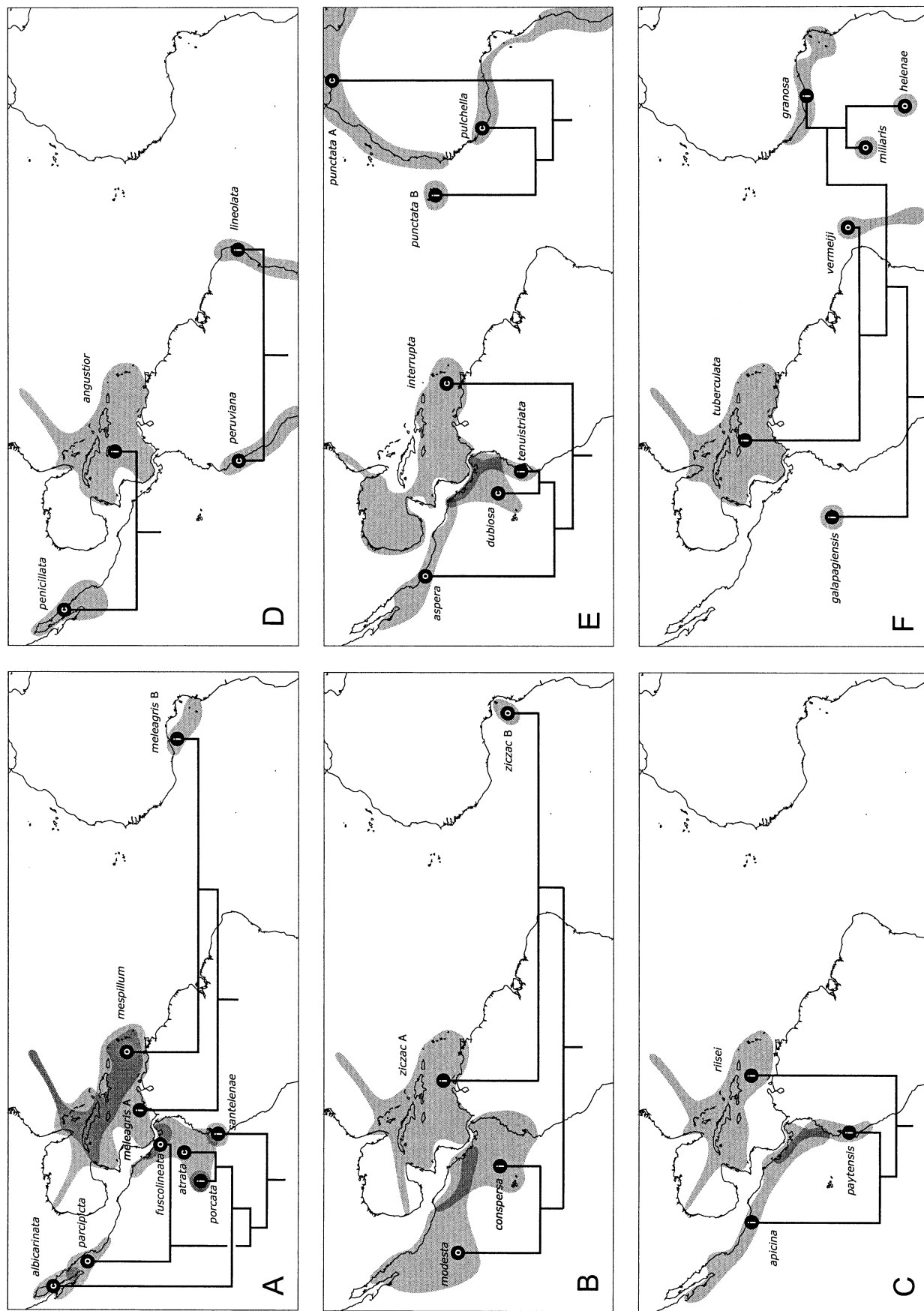


FIG. 6. Distributions and phylogenetic relationships of the *Echinolittorina* species of the eastern Pacific and Atlantic Oceans. The complete ranges of *E. lineolata*, *E. punctata* A, *E. pulchella*, and *E. peruviana* (which extend beyond the area of the map) can be read from Figure 1. For clarity, the single record of *E. fuscolineata* from Santa Elena Peninsula, Ecuador, has been omitted. The tree topologies are those of Figure 3 (and, for relationships of *E. mealegrisi* B and *E. pulchella*, Fig. 2C), but branch lengths have no meaning. See Figure 3 for branch support. Distributional areas are based on the records plotted individually in Figure 1, and the accuracy of distributional limits can be interpreted by reference to the density of sampling shown in Figure 1. Abbreviations: C, continental species; I, intermediate; O, oceanic species (see text).

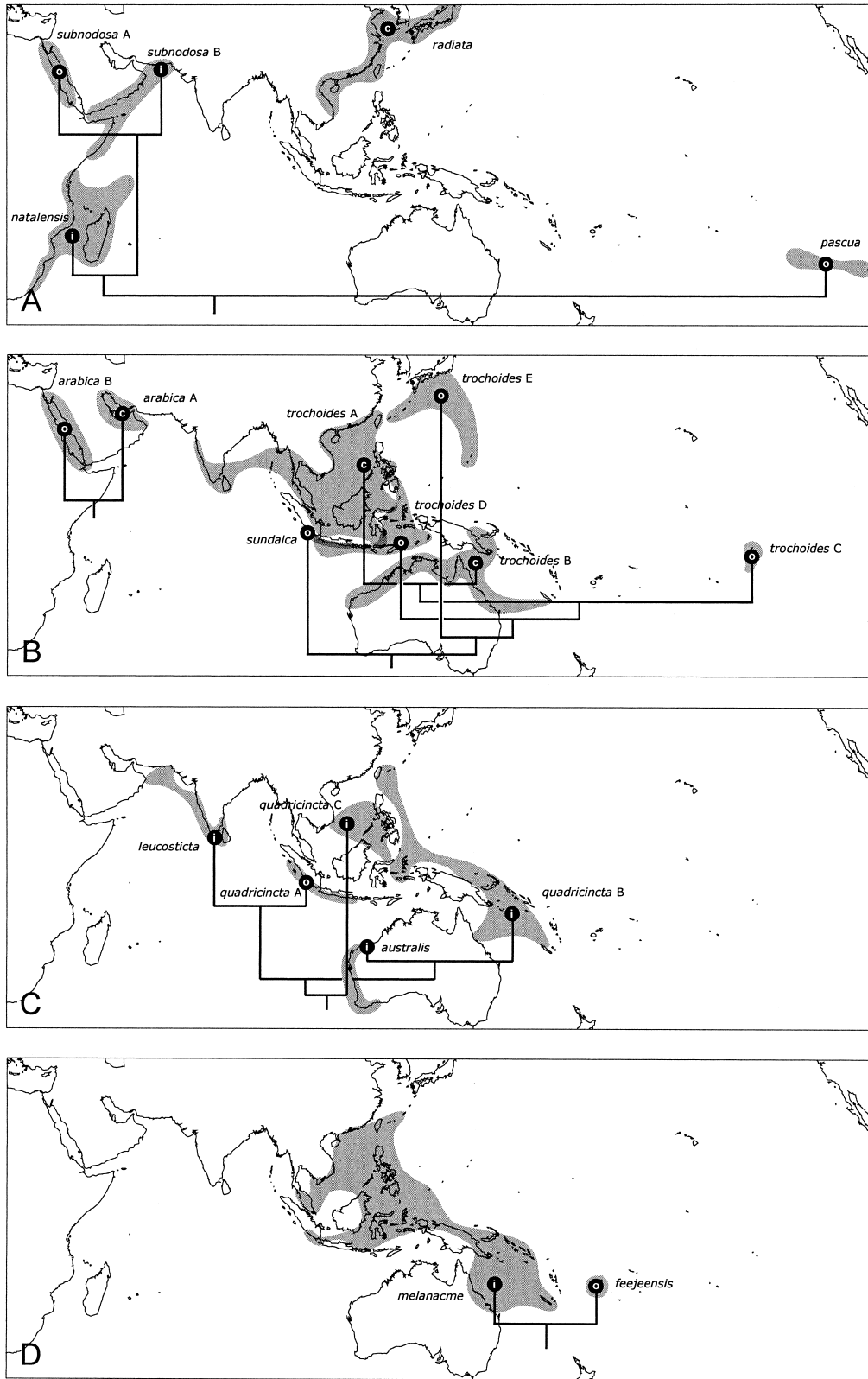


FIG. 7. Distributions and phylogenetic relationships of the *Echinolittorina* species of the Indo-West Pacific Ocean. The complete range of *E. radiata* (which extends beyond the area of the map) can be read from Figure 1. See Figure 6 for abbreviations and conventions.

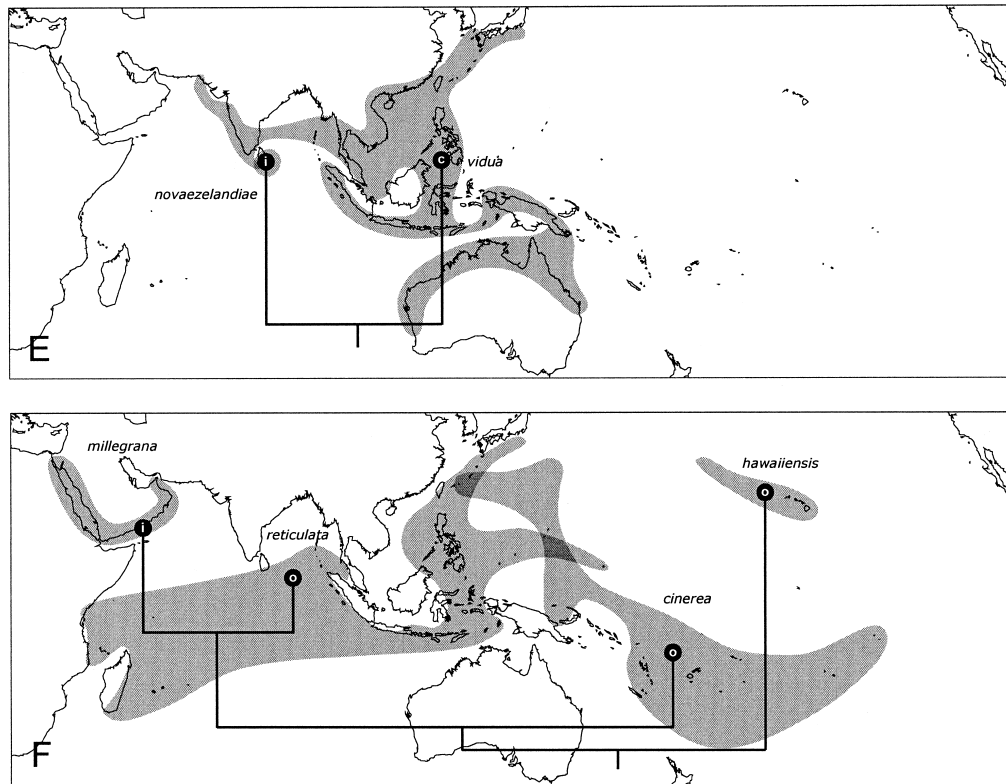


FIG. 7. Continued.

combination of geography, productivity maps (Rutgers University Primary Productivity Study; <http://marine.rutgers.edu/opp/>) and field observations (Reid 2001, 2002a; D. G. Reid, unpubl. data) the species of *Echinolittorina* can be classified as oceanic, continental or intermediate (Figs. 6, 7). Despite its subjectivity, this rough classification reflects striking differences in habitat and distribution. In the Indo-West Pacific, for example, *E. cinerea* is a typical oceanic species, restricted to the oceanic islands of Polynesia and the western Pacific (Fig. 7F). A species only slightly less oceanic is *E. reticulata*, found on islands in the Indian Ocean, touching the east coast of Africa in an area of low productivity and absent from the high-productivity shores of southeast Asia; it also occurs in the Philippines and northwestern Pacific, and the Indian and Pacific distributions are connected by a narrow corridor corresponding with the low-productivity areas of central Indonesia (Fig. 7F). A species of intermediate character is *E. melanacme*, reaching the high-productivity shores of the Southeast Asian mainland and the continental north-eastern coastline of Australia (Fig. 7D). Two continental species are *E. vidua* and *E. trochoides* A, both largely restricted to continental coasts and large islands, and extending even into nutrient-rich gulfs such as those of Tonkin and Thailand (Fig. 7B, E). These differences are mirrored at a local scale, for where *E. reticulata*, *E. melanacme*, *E. vidua*, and *E. trochoides* A inhabit the same area (e.g. Philippines and northern Sulawesi; D. G. Reid, unpubl. data) their relative abundance on a shore reflects local conditions of turbidity. There is no strong phylogenetic pattern to this attribute. Some clades are predominantly oceanic in character (e.g. the six species in-

cluding *E. galapagensis* and *E. helenae*; Fig. 6F), intermediate (e.g. the five species of the *E. quadricincta* group whose distributions form a mosaic, separated by continental areas; Fig. 7C), or continental (e.g. *E. trochoides* A and B; Fig. 7B) but there are also examples of sister species that differ (e.g. *E. arabica* A and B; Fig. 7B) and the five species of the *E. trochoides* clade form a mosaic of oceanic and continental species (Fig. 7B). It appears, therefore, that this trait is evolutionarily labile.

If there is a unifying explanation for the spectrum of oceanic/continental species, it remains elusive. Adult littorinids are seldom submerged, so an effect of nutrients or turbidity on larval development or distribution has been suspected (Reid 1986). In other gastropods there is a trend for reduction in duration (or even elimination) of the planktotrophic larval stage in continental species (Taylor 1971; Perron and Kohn 1985; Meyer 2003), but this is not the case in littorinids. A recent observation suggests that the littorinid *Littorina scutulata* can only develop in seawater enriched in dissolved organic carbon, but not in ocean seawater (L. Page, pers. comm. 2003). We suggest, therefore, that continental littorinids may prove to have a higher requirement for dissolved organic matter during their planktotrophic development than oceanic species, and that selection on larvae (Bierne et al. 2003) may limit the habitat range of adults at a range of spatial scales (for a similar suggestion in fish see Randall 1998). This process alone cannot explain the exclusion of oceanic species from continental habitats, and additional information on larval biology is desirable.

Distribution patterns similar to those classified here as oce-

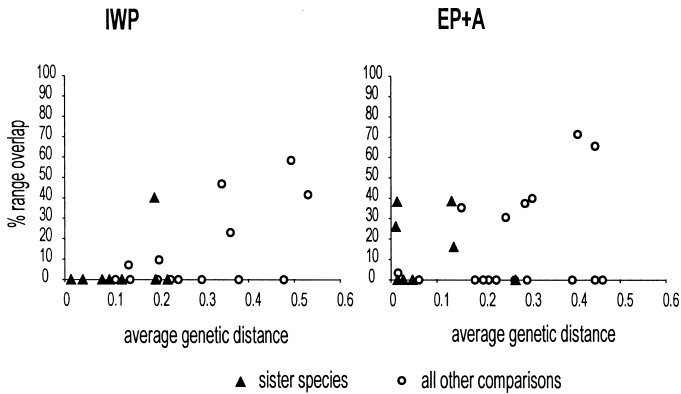


FIG. 8. Plot of the percentage of range overlap between sister clades of *Echinolittorina* against genetic distance (as a proxy for evolutionary time) in Indo-West Pacific (IWP) and eastern Pacific plus Atlantic (EP + A). Clade relationships are those of the combined-gene tree (Fig. 3). Only comparisons within clades with more than 90% support (posterior probability) were included (see Fig. 3). *Echinolittorina meleagris* B and *E. pulchella*, for which only 12S sequences were available, were excluded, resulting in loss of two datapoints for sister-species comparisons (both with zero range overlap).

anic or continental have been reported in a variety of taxa, suggesting that the distinction may be a general one. Besides littorinids (Reid 1986, 1989b, 1996) there are similar distributions in other molluscs for which detailed distribution records are available (Abbott 1960; Houbrick 1985; Meyer 2003). However, few authors have connected such distributions with the contrast between oceanic and continental habitats. In Indonesia, the mantis shrimp *Haptosquilla* shows three deeply divergent clades that have been interpreted as the result of geographic structuring by strong currents (Barber et al. 2002); however, their distributions correspond with those of *E. trochoides* A, B, and D, and these clades may prove to be distinct species with contrasting habitats. Springer (1982) documented the distributions of shorefishes and a range of marine invertebrates in the Indo-West Pacific and contrasted the distributions of "Pacific Plate endemics" with those of species on the adjacent continental lithospheric plates of the western Pacific and Indian Ocean. A vicariant hypothesis was proposed, but phylogenetic data do not support sister relationships between these two regions and the Pacific Plate endemics can simply be interpreted as oceanic species (Reid 1986; Paulay 1996). The distribution of the crab *Birgus* (Lavery et al. 1996) resembles that of *E. reticulata* (i.e. wide Indian Ocean and western Pacific areas connected by a narrow Indonesian corridor; Fig. 7F). Apparently disjunct Indian and Pacific distributions of fish species have been explained by vicariance (Springer and Williams 1990), but might reflect oceanic habitat (and possible inadequate sampling in Indonesia). The oceanic/continental distinction has not so far been reported in corals or reef fish (Wallace 1999; Bellwood and Hughes 2001).

Mode of Speciation

The boundaries delimiting the four tropical marine regions are obvious, but potential barriers to widely dispersing marine species within ocean basins are less clear. Nevertheless,

diversity within such clades is often high, casting doubt on the classic model of allopatric speciation (Palumbi 1994). The occurrence of broadly sympatric sister species has led to suggestions that sympatric speciation may play an important role in generating marine species diversity (Wallace et al. 1991; Pandolfi 1992; Knowlton 1993; Palumbi 1996b; Briggs 1999a; Williams 2000). Possible mechanisms of sympatric speciation include selection on gamete recognition proteins in broadcast spawners (Van Doorn et al. 2001) and habitat fidelity (Duffy 1996; Knowlton et al. 1992; Carlton and Budd 2002).

In *Echinolittorina*, most sister species in both the Indo-West Pacific (88%) and the eastern Pacific plus Atlantic (67%) are allopatric. Allopatry is largely maintained even through two or three (occasionally five) branching points (Figs. 6, 7, 8). Although there have been objections to using phylogenies to determine the mode of speciation (Losos and Glor 2003), this strong geographical pattern suggests that allopatric speciation dominates in *Echinolittorina*. This adds to the growing evidence that allopatric speciation is frequent in the sea, even in organisms with wide dispersal (McMillan and Palumbi 1995; Metz et al. 1998; McCartney et al. 2000; Colborn et al. 2001; Lessios et al. 2001; Kooistra et al. 2002; Meyer 2003).

The long-term maintenance of allopatry in *Echinolittorina* (also observed in cowries; Meyer 2003) implies limited range expansion following speciation, yet ranges must have expanded and contracted during eustatic cycles. For *Echinolittorina* the maximum dispersal distance may be only 1200–1400 km and, even across shorter gaps, successful colonization may be rare because of planktotrophic development. Nevertheless, allopatric ranges may be separated by gaps much smaller than this (e.g. *E. trochoides* A/B/D/E), and here habitat specialization along the continental/oceanic gradient may explain the maintenance of allopatry. It is not known whether interspecific competition may also play a part.

The spatial arrangement of coastlines and islands may itself influence the mode of speciation. The four tropical biogeographic regions show pronounced differences in coastal configuration. The Indo-West Pacific and western Atlantic are characterized by a two-dimensional array of islands and coastlines, whereas the eastern Pacific and eastern Atlantic each display one continuous north-south coastline with a few offshore islands and archipelagos. Speciation may be predominantly allopatric in each case, but on long coastlines allopatry is more likely to be transient, because of greater opportunities for postspeciation range extension, whereas geographical isolation should be more complete in island settings (Hellberg 1998). This prediction has not previously been examined in any circumtropical group and there is some support in *Echinolittorina*. We report only five examples of range overlap between sister species (Fig. 8): three on long coastlines (*E. modesta/conspersa* and *E. apicina/paytensis* on the eastern Pacific mainland, Fig. 6B, C; there is another case among *E. aspera/tenuistriata/dubiosa*, Fig. 6E, but branching order is not well resolved) and two on islands within dispersal distance of long coastlines (*E. atrata/porcata*, Fig. 6A; *E. vidua/novaezelandiae*, Fig. 7E). There is no overlap between sister species in the archipelagic setting of the central Indo-West Pacific, but nor is there any on the continuous coastline

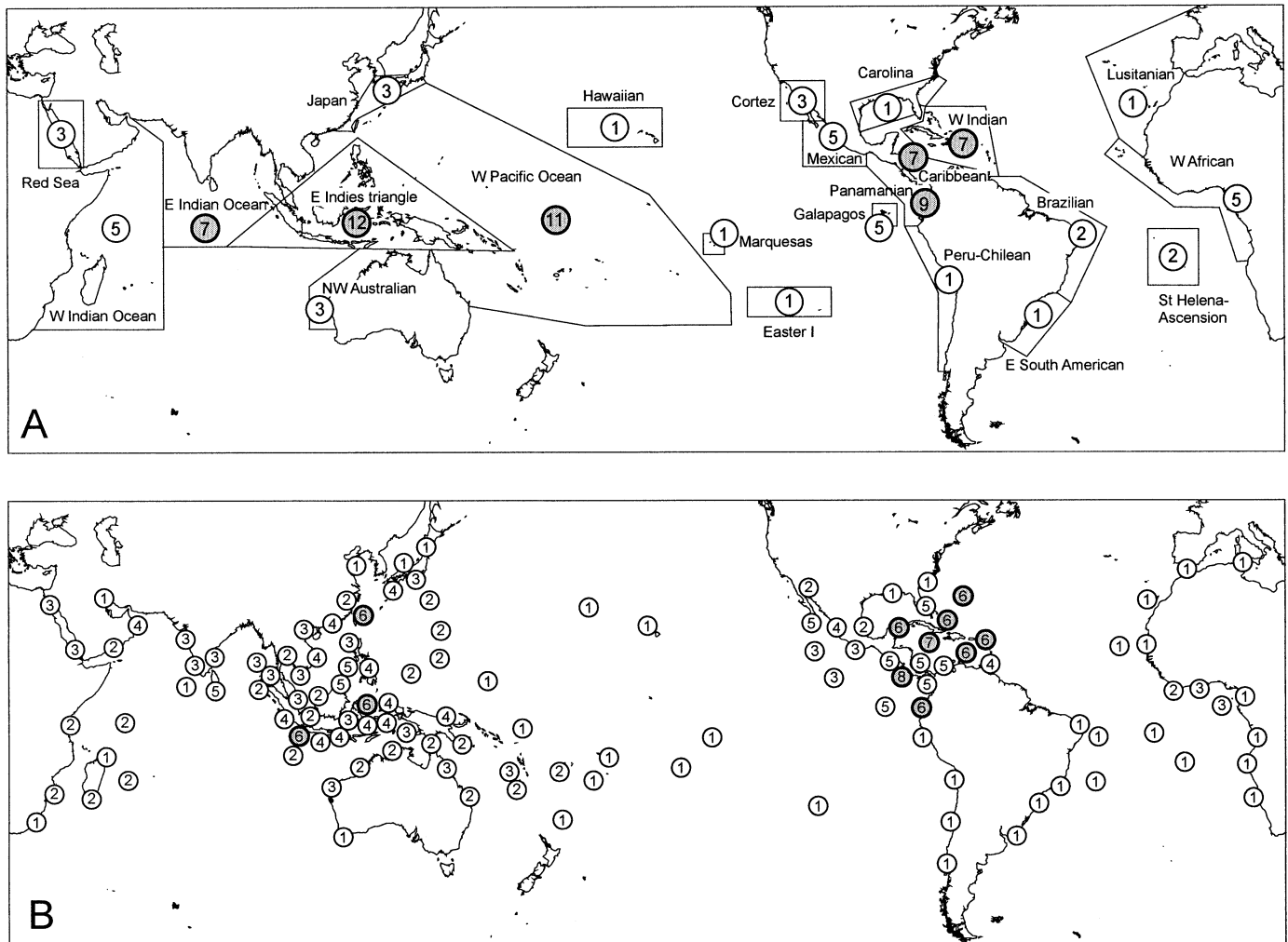


FIG. 9. (A) Numbers of *Echinolittorina* species occurring within broad biogeographic regions and provinces (as defined by Briggs 1974, 1999b; but with Indo-Polynesian province divided into East Indian Ocean, East Indies Triangle, and West Pacific Ocean). (B) Diversity of sympatric *Echinolittorina* species (maximum numbers of species recorded at selected well-studied localities). Shaded circles highlight six or more species.

of the eastern Atlantic or western Indian Ocean. Speciation on long coastlines can evidently occur rapidly, even if allopatry is more likely to be transient. For example, in the eastern Pacific the three most recent speciation events (*fuscolineata/parcipicta*, *tenuistriata/aspera/dubiosa*, *apicala/paytensis*) occurred at about the same time or later than the final closure of the Isthmus, whereas we have no evidence of speciation in the western Atlantic during this time. Studies of the gastropods *Strombina* (Jackson et al. 1996) and *Tegula* (Hellberg 1998) likewise show recent radiation in the eastern Pacific.

Geography of Speciation

Allopatric speciation can be the result of either vicariant or founder speciation. However, without knowledge of past distributions and of ages of potential barriers it can be impossible to distinguish between these processes. Furthermore, in the marine environment these two mechanisms can be considered as extremes of a continuum (Paulay and Meyer

2002). The classic example of a vicariant event in the marine realm is the closure of the Isthmus of Panama, dated at about 3.1 mya (Coates and Obando 1996). In *Echinolittorina* we have identified six cases of transisthmian divergence (Fig. 6), but all are of much greater age than this (Fig. 4). The four youngest (8–19 mya) involve continental and intermediate species, the oldest (16–32 mya) involves mainly oceanic species. Previous studies suggest that species from oceanic (and deeper-water) habitats were separated about 10 mya by the first effects of the shoaling of the isthmus, whereas those from mangrove habitats maintained the latest contact between the two oceans (Knowlton and Weigt 1998; Muss et al. 2001; Marko 2002; Dick et al. 2003). Even the most continental of *Echinolittorina* species occur on rocky shores of moderate to high energy and are absent from sheltered and muddy habitats, so divergences older than 3.1 mya could be expected. Nevertheless, our estimates are mostly older than the 5–10 mya range reported for other transisthmian pairs of rocky-shore molluscs (review by Marko 2002). If our estimates are

accurate, we may not be comparing true geminate pairs created by the rise of the isthmus. The eastern Pacific plus Atlantic has been profoundly affected by Pliocene extinctions (Paulay 1997; Vermeij 2001) that may have removed the true geminates (Marko and Jackson 2001). Alternatively, the transisthmian relationships may be the result of older episodes of differentiation unrelated to closure of the isthmus (Vermeij 2001; Marko 2002).

Within the Indo-West Pacific, vicariance has been invoked to explain pairs of sister species (and intraspecific clades) in the Indian and Pacific Oceans. Circulation between the two oceans has been progressively constricted by the northward movement of Australia and New Guinea since the middle Miocene (Kennett et al. 1985; Crame 2000) and there are examples of Indian/Pacific vicariance in corals that may be of this age (Pandolfi 1992; Wallace 1999). However, these phylogeographic patterns have generally been interpreted as the outcome of glacio-eustatic events in the past 3 my of the late Plio-Pleistocene (McMillan and Palumbi 1995; Williams and Benzie 1998; Benzie 1999). In *Echinolittorina*, however, we have identified no Indian/Pacific sister species pairs (some examples of shallow intraspecific differentiation will be described elsewhere), so it appears that sea-level fluctuations during the past 3 my have not resulted in speciation between these two oceans. The known cases of this phenomenon mainly concern reef-associated invertebrates and fish (Benzie 1999). The falls in sea level of 100–150 m associated with glacial maxima (Chapell and Shackleton 1986) resulted in a massive loss of shallow inner reefs and lagoons, exposing large areas of continental shelf in the western Pacific and reducing reefal habitats to narrow fringes (Potts 1984; Paulay 1990, 1996), so that both habitat loss and reduced circulation contributed to the isolation between the two oceans. We suggest that falls in sea level may have had less impact on the area of rocky-shore habitat suitable for *Echinolittorina*, or may even have increased it in some areas by exposing submerged islands. Vicariance can also result from regional extinction (Springer and Williams 1990; Briggs 1999c), and a possible example is discussed below.

Cases of allopatric sister species in which ranges are strongly asymmetric in size and separated by wide areas of inhospitable habitat are examples of “classical founder speciation” (Paulay and Meyer 2002). *Echinolittorina* has a maximum dispersal distance of about 1200–1400 km, therefore endemic species on islands of similar or greater isolation than this are likely examples of founder speciation. In the Indo-West Pacific these include *E. feejeensis* and *E. hawaiiensis* (Fig. 7D, F). In the Atlantic there are six species on the central oceanic islands and in the Gulf of Guinea that (by a parsimony argument) are members of eastern Atlantic plus eastern Pacific clades (Fig. 6A, B). These are examples of founder speciation achieved by dispersal from west to east across the Atlantic. The faunistic affinity of Ascension, St. Helena, and the Sao Tome group with the western Atlantic has been observed in other groups (Vermeij and Rosenberg 1993; Joyeux et al. 2001; Wirtz 2003) and must be a consequence of both biogeographic history and similarity of oceanic habitat. Dispersal across the Atlantic from west to east is more common than in the reverse direction, and both paleontological (Vermeij and Rosenberg 1993) and phylogeographic (Muss et al.

2001) studies suggest that it has only taken place since the Pliocene as Atlantic circulation became stronger. The trans-Atlantic divergence of *Echinolittorina ziczac* A and B is estimated to have occurred in the upper Pliocene or early Pleistocene (1.1–2.0 mya, Fig. 4), and that leading to *E. meleagris* B is likely to be of similar age (genetic data available only for 12S; Fig. 2C). The third trans-Atlantic migration event, separating the eastern Atlantic clade of *E. miliaris*, *E. helenae*, and *E. granosa* from the pair *E. tuberculata* and *E. vermeiji*, took place earlier (14–27 mya, Fig. 4). In branching sequence this resembles the Atlantic clade of *Ophioblennius*, in which the pattern was explained by establishment of the Amazon River outflow (6 mya) and reorganization of Atlantic circulation resulting from shoaling of the Isthmus of Panama at about the same time (Muss et al. 2001), but our estimates of age are considerably older. It is becoming clear that founder speciation is more common in the marine realm than had previously been supposed (Colburn et al. 2001; Lessios et al. 2001; Meyer 2003).

In the Indo-West Pacific the geography of speciation events has been repeatedly discussed in explanations of the focus of diversity in the East Indies Triangle between the Philippines, Indonesia, and New Guinea (Rosen 1988; Palumbi 1997; Paulay 1997). According to the center-of-origin hypothesis, species originate within this central region and then expand their range outwards (Ekman 1953; Briggs 1974, 1999b, 2000, 2003). In contrast, the central region can be viewed as a “center of accumulation” for species that originated at the periphery of the Indo-West Pacific (Ladd 1960; Kay 1984; Rosen 1984; Jokiel and Martinelli 1992). These two hypotheses make different predictions about the location of recently formed species and their direction of spread. In *Echinolittorina* we have found evidence of speciation both in the central Indo-West Pacific and at its periphery. A number of narrowly endemic species are distributed around the periphery of the Indo-West Pacific, although not all these can be attributed to recent speciation events. Some (*E. millegrana* in Arabia, Fig. 7F; *E. hawaiiensis*, Fig. 7F; *E. trochoides* C in Polynesia, Fig. 7B; *E. feejeensis*, Fig. 7D) are terminal branches of the phylogeny and therefore the product of relatively recent divergence, as predicted by the center-of-accumulation hypothesis. However, others are relatively basal branches of the phylogeny (e.g. *E. pascua* in Easter Island, Fig. 7A; the pair *E. arabica* A and B in the Red Sea and Persian Gulf, Fig. 7B; and perhaps *E. radiata* in China and Japan, Fig. 7A) and represent ancient speciation events or even peripheral relicts (as predicted by the center-of-origin idea). We have no evidence of range expansion by peripheral species toward the center of the Indo-West Pacific; in fact, the long-term maintenance of allopatry between sister taxa suggests that range expansion may be very slow. It is possible that peripheral endemics are evolutionarily short-lived (Kohn 1980; Paulay 1990, 1997; Preece 1995). Endemic species are also present in the central region of the Indo-West Pacific and, once again, some are relatively basal (*E. sundaica* in Indonesia, Fig. 7B) whereas others, as predicted by the center-of-origin hypothesis, are terminal (*E. trochoides* A in southeast Asia, Fig. 7B; *E. quadricincta* A in western Indonesia, Fig. 7C). Speciation by a founder mechanism could account for cases of peripheral speciation, but divergence in

the central region is harder to visualize. It has been suggested that lowered sea level during Pleistocene glaciations might isolate the marine basins of Indonesia (McManus 1985; Wallace et al. 2000). Nevertheless, in *Echinolittorina* the distributions of the central endemics do not correspond with marine basins. Instead, as shown earlier, the mosaic of distributions of members of central-Indo-West Pacific clades (Fig. 7B, C) can be explained by habitat specialization on the oceanic/continental gradient and imply an ecological dimension to speciation (Schluter 2001). In summary, evidence from *Echinolittorina* adds to that from other studies and reviews (Palumbi 1996b, 1997; Palumbi et al. 1997; Paulay 1997; Wilson and Rosen 1998; Bellwood and Wainwright 2002; Bernardi et al. 2004) to suggest that speciation can occur throughout the Indo-West Pacific, as a result of diverse mechanisms.

Timing of Speciation

Despite an expectation of slow speciation in widespread marine organisms, there is evidence that eustatic and climatic oscillations during the late Pliocene and Pleistocene have been important causes of marine speciation, especially in the Indo-West Pacific (reviews by Palumbi 1997; Benzie 1999). The fossil record of several gastropod groups shows a pulse of species appearing at this time (Kohn 1990; Jackson et al. 1996; Kay 1996; Hellberg 1998). Molecular phylogenetic studies of small, closely related clades also show that sister species diverged in the last 1–5 my (e.g. McMillan and Palumbi 1995; Palumbi 1996b; Hellberg 1998; McCartney et al. 2000; Williams 2000; Lessios et al. 2001; Harrison 2004). However, a study of the large, family-level clade of cowries has found a wider range of ages of sister species without a pulse of speciation in the late Plio-Pleistocene (C. P. Meyer and G. Paulay, pers. comm.), and others have not detected speciation events in the past 3 my (Knowlton and Weigt 1998; Dick et al. 2003; Morrison et al. 2004). In *Echinolittorina* divergence times between sister species are mostly older than 5 mya (Fig. 4), although significant loss of sister species during Plio-Pleistocene extinctions (as in the eastern Pacific plus Atlantic, see Geography of Speciation, above) would weaken this conclusion. The plot of number of lineages versus time does not indicate a burst of recent speciation, but this analysis assumes constant extinction. Possibly the periodicity of Plio-Pleistocene climatic cycles may have been too rapid to promote speciation (Potts 1984; Roy et al. 1996; Williams et al. 2002). Furthermore, the rocky-shore habitat of *Echinolittorina* may have made it less susceptible than reefal species to isolation and local extinction during sea-level changes, and therefore less prone to speciation during the Plio-Pleistocene.

Extinction

In the absence of a good fossil record, there is no direct evidence of extinction in *Echinolittorina*. In general, post-Miocene extinction is believed to have been lower in the Indo-West Pacific than in the other regions of the marine tropics (Vermeij 1989, 1991, 2001; Paulay 1997; Meyer 2003). Pliocene extinctions were most severe in the western Atlantic and eastern Pacific, where respectively 32% and 15%

of genera went extinct, whereas none was lost in the Indo-West Pacific (Vermeij 1989). Some peculiarities of distributions in the eastern Pacific plus Atlantic are suggestive of extinction, such as the restriction of the *E. porcata* clade to the eastern Pacific and of the *E. meleagris* clade to the Atlantic (Fig. 6A), and the absence of geminate species across the Isthmus of Panama (see Geography of Speciation, above). In the Indo-West Pacific at least one pattern, the great distance (approximately 18,000 km) between *E. pascua* in eastern Polynesia and its sister clade of three species (*E. natalensis*, *E. subnodosa* A and B) in the western Indian Ocean (Fig. 7A), does imply extinction or reliction, for the distance is far too great to be explained by dispersal. The intervening region of the Indo-West Pacific is occupied by the five species of the *E. trochoides* group (Fig. 7B). The nodulose shells and supralittoral habitats of the *E. trochoides* and *E. pascua-natalensis* clades are so similar that competitive exclusion is suspected, leading to the extinction of the latter in the central Indo-West Pacific. This is the pattern predicted by Briggs (1999c) from his model of center-of-origin speciation in the Indo-West Pacific. As suggested earlier, the rocky-shore habitat may ensure that *Echinolittorina* is less vulnerable to extinction during sea-level changes than reefal species; during low sea-level stands, shallow inner reefs and lagoons are stranded and their inhabitants become extinct, whereas communities on outer reef slopes (and, by extension, rocky shores) persist (Paulay 1990, 1996; Planes and Galzin 1997).

Global Diversity Patterns

When presented as species richness in each of the tropical biogeographic provinces, the global diversity of *Echinolittorina* conforms to the familiar pattern (Fig. 9A): highest diversity near the equator, with a decline toward the temperate zones; a global maximum in the East Indies Triangle at the center of the Indo-West Pacific, with decline to the east and west; subsidiary foci in the eastern Pacific and western Atlantic; and lowest tropical diversity in the eastern Atlantic. Similar patterns have been repeatedly documented at a range of taxonomic scales (Briggs 1974, 1999b; Vermeij 1978, 1996; Rosen 1984, 1988; Reid 1986; Kay 1990; Veron 1995; Paulay 1997; Crame 2000; Bellwood and Hughes 2001; Hughes et al. 2002). When the distributional data for *Echinolittorina* are instead presented as the number of sympatric species within localities (Fig. 9B), the patterns within the eastern Pacific, western Atlantic and eastern Atlantic regions remain largely unchanged, because the distributions of individual species correspond closely with the biogeographic provinces. However, in the Indo-West Pacific the central diversity focus becomes much less marked, because the high number of species in the East Indies Triangle is the result not only of the overlap of a few widespread species, but of the presence of a mosaic of allopatric ones (Fig. 7). The area of shallow-water habitat in the central Indo-West Pacific is greater than elsewhere and on species-area grounds this alone should result in higher diversity (Crame 2000; Bellwood and Hughes 2001). Furthermore, the size and complexity of the Indonesian Archipelago should increase opportunities for isolation (leading to speciation) and for survival in refuges (reducing extinction) (McCoy and Heck 1976; McManus 1985;

Randall 1998; Bellwood and Hughes 2001; Santini and Winterbottom 2002). In contrast, we emphasize the diversity of oceanic and continental habitats in the central Indo-West Pacific. It is clear that habitat diversity is related to regional taxonomic diversity (Williamson 1988) and that the variety of habitats (reefs, lagoons, mangroves etc) in the central Indo-West Pacific contributes to its richness (Randall 1998). However, the significance of the oceanic/continental gradient *within* a broad habitat type (in this case the rocky shore) has not previously been pointed out. We suggest that this may prove to be important within other shallow-water habitats as species distributions become better known.

Few other groups have distributions known with sufficient accuracy to provide comparison. In contrast with our results, the central-Indo-West Pacific diversity focus for corals and reef fish is produced by the overlap of numerous widespread distributions and local endemism is low (Pandolfi 1992; Wallace 1999; Hughes et al. 2002). At the fringes of the Indo-West Pacific, reef fish are represented mostly by narrow-range endemics, whereas the corals of these areas are mainly widespread species (Wallace 1999; Hughes et al. 2002). Peripheral *Echinolittorina* are mostly narrow-range endemics, but include the widespread *E. cinerea* and *E. reticulata*; both patterns are also reported in cowries (Meyer 2003). Broad overlap between the ranges of Indian and Pacific Ocean endemics has been said to contribute to the species richness of the diversity focus of the central Indo-West Pacific (the center-of-overlap hypothesis; Ekman 1953; Woodland 1983; McMillan and Palumbi 1995; but see Connolly et al. 2003), but there is no evidence for this in *Echinolittorina*.

In contrast to the regional pattern of maximum diversity in the central Indo-West Pacific, local diversities of *Echinolittorina* are highest in the West Indian and Panamanian provinces (Fig. 9B). This unusual pattern is consistent with an origin of the genus in the eastern Pacific plus Atlantic, and is repeated in *Uca* with a similar biogeographic history (Levinton et al. 1996). This may be related to the general ecological principle that competition is more severe between closely related species (Barnes 2003). The Indo-West Pacific *Echinolittorina* species all belong to a single clade, whereas in both the West Indies and Panama the sympatric species are members of two or three clades of equal or greater age than the Indo-West Pacific clade. Although there is no direct evidence of interspecific competition among *Echinolittorina* species, the possibility is suggested by their grazing intensity and spatial zonation (Mak and Williams 1999).

Conclusion

As phylogenetic studies of marine groups accumulate, it is becoming clear that each has its own individual history, and that comparison and extrapolation must be done cautiously. When evaluating the generality of our findings in *Echinolittorina*, the important attributes of the group are, first, its age; the earliest fossil is of Middle Eocene date (41 mya), so that important episodes in its biogeographic history include possible origin in the tropical Americas, followed by vicariance in the Tethys Sea. Second is its rocky-shore habitat, which we suggest results in relative immunity to the effects of eustatic sea-level changes that appear to have

caused extensive speciation and extinction in reefal habitats in the Indo-West Pacific. Third is its potential for larval dispersal (a maximum recorded distance of 1200–1400 km), in the lower range of that documented for other marine groups with pelagic larval stages. This may contribute to the remarkable long-term maintenance of allopatry between sister clades, and the overall clarity of biogeographic relationships both between and within the tropical regions.

Our study is, to the best of our abilities, a complete account of the phylogeny and geographical distribution of an entire clade of 59 ESUs, giving a detailed picture of diversification within a worldwide radiation of marine invertebrates. Our results support the emerging view that speciation in the sea is predominantly allopatric, but that there is no prevailing geographical or temporal pattern. Rather, the observed distributions are the result of a plurality of mechanisms operating over different time scales.

We emphasize that detailed distributional and ecological data are of great importance for biogeographic interpretation. For *Echinolittorina* species the rocky shore is not a uniform habitat, but is partitioned along an oceanic to continental gradient. Habitat specialization along this gradient may account for some patterns of large-scale distribution and contribute to the maintenance of allopatry. This may also be true in some other taxonomic groups and in other shallow-water habitats. There has been a tendency to interpret marine biogeographic patterns mainly in terms of historical barriers and present-day current flows, but we suggest that study of ecological specialization and larval biology will provide new insights.

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APPENDIX

Species of *Echinolittorina* and outgroups (*Littorina* and *Afrolittorina*) included in this study, with known geographical ranges of species and localities of samples. Totals are numbers of individuals sequenced to establish evolutionarily significant units (details to be reported elsewhere). Nomenclature of *Echinolittorina* species follows Reid (2002b), as modified by Williams et al. (2003), with the following exceptions. The name *E. biangulata* (von Martens, 1897) is replaced by *E. quadricincta* (Mühlfeld, 1824) (the latter incorrectly used for a species from India by Rosewater and Kadolsky 1981, but type locality, East Indian Sea, and figure indicate the species from Java and Sumatra); the valid name for the Indian species is *E. leucosticta* (Philippi, 1847). *Echinolittorina feejeensis* (Reeve, 1857) is divided into *E. feejeensis* sensu stricto from Fiji, and a widespread western Pacific species, *E. melanacme* (E. A. Smith, 1876). The name *E. trochoides* C replaces *E. "aff. pascua"*. To designate species within complexes, for which familiar names are not available, the letters A to E are used.

| Species | Range | Total no. | Sample location |
|--|---------------------------|-----------|--|
| <i>Echinolittorina</i> —East Pacific | | | |
| <i>E. albicarinata</i> (McLean, 1970) | Gulf of California | 3 | 1, 2: La Paz, Baja California, Mexico |
| <i>E. apicina</i> (Menke, 1851) | Mexico to Ecuador | 2 | 1: Playa Blanca, NW Costa Rica 2: Boca de Tomatlan, Puerto Vallarta, Mexico |
| <i>E. aspera</i> (Philippi, 1846) | Mexico | 2 | 1: Cabo San Lucas, Baja California, Mexico 2: Boca de Tomatlan, Puerto Vallarta, Mexico |
| <i>E. atrata</i> (C. B. Adams, 1852) | El Salvador to Ecuador | 3 | 1: Bahia el Hachal, NW Costa Rica 2: Punta Chocolatera, Santa Elena Peninsula, Ecuador |
| <i>E. conspersa</i> (Philippi, 1847) | El Salvador to Ecuador | 3 | 1: Ballenita, E of Salinas, Ecuador 2: Playa Manzanillas, NW Costa Rica |
| <i>E. dubiosa</i> (C. B. Adams, 1852) | El Salvador to Colombia | 2 | 1: Culebra I, Calzada de Amador, Panama 2: Manuel Antonio National Park, Costa Rica |
| <i>E. fuscolineata</i> (Reid, 2002) | El Salvador to Ecuador | 4 | 1: Manuel Antonio National Park, Costa Rica 2: Cabo Blanco, Costa Rica |
| <i>E. galapagensis</i> (Stearns, 1892) | Galapagos Is. | 2 | 1: Puerto Ayora, Santa Cruz, Galapagos Is. 2: Punta Estrada, Santa Cruz, Galapagos Is. |
| <i>E. modesta</i> (Philippi, 1846) | Mexico | 2 | 1: San Jose del Cabo, Baja California, Mexico 2: Puerto Vallarta, Mexico |
| <i>E. parcipicta</i> (Carpenter, 1864) | Mexico | 3 | 1, 2: Puerto Vallarta, Mexico |
| <i>E. paytensis</i> (Philippi, 1847) | Costa Rica to N Peru | 2 | 1, 2: Punta Chocolatera, Santa Elena Peninsula, Ecuador |
| <i>E. penicillata</i> (Carpenter, 1864) | Gulf of California | 2 | 1, 2: San Jose del Cabo, Baja California, Mexico |
| <i>E. peruviana</i> (Lamarck, 1822) | Peru, Chile | 2 | 1: Callao, Lima, Peru 2: Las Cruces, Santiago, Chile |
| <i>E. porcata</i> (Philippi, 1846) | Galapagos Is. | 2 | 1, 2: Puerto Ayora, Santa Cruz, Galapagos Is. |
| <i>E. santelenae</i> (Reid, 2002) | S Ecuador to N Peru | 2 | 1: Punta Chocolatera, Santa Elena Peninsula, Ecuador 2: Anconcito, Santa Elena Peninsula, Ecuador |
| <i>E. tenuistriata</i> (Reid, 2002) | Nicaragua to Ecuador | 2 | 1: Manuel Antonio National Park, Costa Rica 2: Punta Chocolatera, Santa Elena Peninsula, Ecuador |
| <i>Echinolittorina</i> —Atlantic | | | |
| <i>E. angustior</i> (Mörch, 1876) | Caribbean | 2 | 1: Caravel Beach, Grand Bahama, Bahamas 2: Jingle Beach, Priory, Jamaica |
| <i>E. granosa</i> (Philippi, 1848) | W Africa | 2 | 1: Praia das Sete Ondas, Sao Tome 2: W of Limbe, Cameroon |
| <i>E. helenae</i> (E. A. Smith, 1890) | St. Helena | 2 | 1: Jamestown, St. Helena 2: St. Helena |
| <i>E. interrupta</i> (C. B. Adams in Philippi, 1847) | Caribbean, Gulf of Mexico | 2 | 1: Colon I., Bocas del Toro, Panama 2: Lucea Bay, Jamaica |
| <i>E. lineolata</i> (d'Orbigny, 1840) | Brazil, Uruguay | 2 | 1: Araca Beach, Sao Sebastiao, Brazil 2: Natal, Brazil |
| <i>E. meleagris</i> (Potiez and Michaud, 1838) A | Caribbean | 2 | 1: Colon I., Bocas del Toro, Panama 2: Eight Mile Rock, Grand Bahama, Bahamas |
| <i>E. meleagris</i> B | Gulf of Guinea | 3 | 1: Annobon 2: Bom Bom I., Principe |
| <i>E. mespillum</i> (Mühlfeld, 1824) | Caribbean | 2 | 1: Priory, Jamaica 2: Eight Mile Rock, Grand Bahama, Bahamas |
| <i>E. miliaris</i> (Quoy and Gaimard, 1833) | Ascension I. | 2 | 1: Portland Point, Ascension I. 2: Boatswain Bird I., Ascension I. |
| <i>E. pulchella</i> (Dunker, 1845) | Sierra Leone to Angola | 1 | 1: Namibe, Angola |
| <i>E. punctata</i> (Gmelin, 1791) A | Mediterranean to Senegal | 3 | 1: Haifa, Israel 2: Agadir, Morocco |
| <i>E. punctata</i> B | Cape Verde Is. | 2 | 1: Mordeira Bay, Sal, Cape Verde Is. 2: Salamansa Bay, Sao Vicente, Cape Verde Is. |
| <i>E. riisei</i> (Mörch, 1876) | Caribbean | 3 | 1: Jingle Beach, Priory, Jamaica 2: Harrison Point Lighthouse, Barbados |
| <i>E. tuberculata</i> (Menke, 1828) | Caribbean | 3 | 1: Tulum, Mexico 2: Jingle Beach, Priory, Jamaica |

APPENDIX. Continued.

| Species | Range | Total no. | Sample location |
|---|------------------------------------|-----------|--|
| <i>E. vermeiji</i> (Bandel and Kadolsky, 1982) | Trindade I., Fernando do Noronha | 5 | 1, 2: Ilha de Cemeterio, Atol das Rocas, Brazil |
| <i>E. ziczac</i> (Gmelin, 1791) A | Caribbean | 2 | 1: Jingle Beach, Priory, Jamaica 2: Devonshire Bay, Bermuda |
| <i>E. ziczac</i> B | Gulf of Guinea islands | 2 | 1, 2: Praia das Sete Ondas, Sao Tome |
| <i>Echinolittorina</i> -Indo-West Pacific | | | |
| <i>E. arabica</i> (El Assal, 1990) A | Persian Gulf | 3 | 1: Haramal, Muscat, Oman 2: Ras Al-Khaimah Khor, United Arab Emirates |
| <i>E. arabica</i> (El Assal, 1990) | Red Sea | 2 | 1: Marsa Bareika, Sinai, Egypt 2: Eilat, Israel |
| <i>E. australis</i> (Gray, 1826) | SW Australia | 2 | 1: Beacon I., Houtman Abrolhos Is., W Australia 2: Rockingham, Perth, W Australia |
| <i>E. cinerea</i> (Pease, 1869) | W Pacific | 3 | 1: Chichijima I., Ogasawara Is., Japan 2: Pointe de Tapahi, Tahiti |
| <i>E. feejeensis</i> (Reeve, 1857) | Fiji | 2 | 1: Nadi, Viti Levu, Fiji 2: Crusoe's Retreat, Viti Levu, Fiji |
| <i>E. hawaiiensis</i> (Rosewater and Kadolsky, 1981) | Hawaiian Is. | 2 | 1: Waikiki, Oahu, Hawaii 2: Kaena Point, Oahu, Hawaii |
| <i>E. leucosticta</i> (Philippi, 1847) | India, Sri Lanka | 2 | 1: Kovalam, Kerala, India 2: Yala, Sri Lanka |
| <i>E. melanacme</i> (E. A. Smith, 1876) | SE Asia to New Caledonia | 11 | 1: Cape Pallarenda, Queensland, Australia 2: Hat Rin Beach, Ko Pha Ngan, Thailand |
| <i>E. millegrana</i> (Philippi, 1848) | Red Sea, Arabia | 10 | 1: Fujaira, United Arab Emirates 2: Hurghada, Egypt |
| <i>E. natalensis</i> (Philippi, 1847) | E Africa | 2 | 1: Dar-es-Salaam, Tanzania 2: Munster, Natal, S Africa |
| <i>E. novaezelandiae</i> (Reeve, 1857) | Sri Lanka | 2 | 1, 2: Mirissa, Sri Lanka |
| <i>E. pascua</i> (Rosewater, 1970) | Easter I., Pitcairn I. | 4 | 1: Ahu Vaihu, Easter I. 2: North Beach, Henderson I. |
| <i>E. quadricincta</i> (Mühlfeld, 1824) A | W Sumatra, S Java | 2 | 1, 2: Sukahujan, Malimping, Java, Indonesia |
| <i>E. quadricincta</i> B | New Caledonia, Moluccas, Taiwan | 3 | 1, 2: Kamenti, Kapataran, Sulawesi, Indonesia |
| <i>E. quadricincta</i> C | Sulu Sea | 3 | 1: Malapacao I., Palawan, Philippines 2: Mokupa, Manado Bay, Sulawesi, Indonesia |
| <i>E. radiata</i> (Souleyet in Eydoux and Souleyet, 1852) | Vietnam to Japan | 3 | 1: Cat Ba I., Ha Long Bay, Vietnam 2: Tsubaki, Wakayama, Japan |
| <i>E. reticulata</i> (Anton, 1838) | E Africa to W Pacific | 36 | 1: Ishigaki, Japan 2: Flic en Flac, Mauritius |
| <i>E. subnodosa</i> (Philippi, 1847) A | Red Sea | 2 | 1: Marsa Bareika, Sinai, Egypt 2: Hurghada, Egypt |
| <i>E. subnodosa</i> B | Arabia, Somalia | 6 | 1, 2: Masirah I., Oman |
| <i>E. sundaica</i> (Altena, 1945) | S Java, W Sumatra | 2 | 1: Surabaya, Java, Indonesia 2: Tanah Lot, Bali, Indonesia |
| <i>E. trochoides</i> (Gray, 1839) A | India, SE Asia | 40 | 1: Mandapam, Tamilnadu, India 2: Hat Rin Beach, Ko Pha Ngan, Thailand |
| <i>E. trochoides</i> B | N Australia | 18 | 1: Cape Pallarenda, Queensland, Australia 2: Watering Cove, Dampier, W Australia |
| <i>E. trochoides</i> C | Marquesas Is. | 10 | 1: Taihoae Bay, Nuku Hiva, Marquesas Is. 2: Tahuata, Marquesas Is. |
| <i>E. trochoides</i> D | S Java, Moluccas | 15 | 1: Bola, Buton I., Sulawesi, Indonesia 2: Senggigi, Lombok, Indonesia |
| <i>E. trochoides</i> E | S Japan, Mariana Is. | 6 | 1: Tsubaki, Wakayama, Japan 2: Mitsuiishi, Manazuru, Kanagawa, Japan |
| <i>E. vidua</i> (Gould, 1859) | India, SE Asia, Japan, N Australia | 65 | 1: Townsville, Queensland, Australia 2: Awung, Lombok, Indonesia 3: Araiike, Mitsune, Hachijo I., Japan 4: East Coast Park, Singapore |
| Outgroups | | | |
| <i>Afrolittorina acutispira</i> (E. A. Smith, 1892) | SE Australia | 1 | Sydney Harbor, Australia |
| <i>Afrolittorina praetermissa</i> (May, 1909) | SE Australia | 1 | Blackman's Bay, Tasmania, Australia |
| <i>Afrolittorina africana</i> (Krauss in Philippi, 1847) | South Africa | 1 | Mzamba, Transkei, South Africa |
| <i>Afrolittorina knysnaensis</i> (Krauss in Philippi, 1847) | South Africa | 1 | East London, South Africa |

APPENDIX. Continued.

| Species | Range | Total no. | Sample location |
|--|------------|-----------|-----------------------------------|
| <i>Littorina (Littorina) littorea</i> (Linnaeus, 1758) | N Atlantic | 1 | Koster Arch., Sweden |
| <i>Littorina (Littorina) plena</i> (Gould, 1849) | NE Pacific | 1 | Baker's Beach, San Francisco, USA |
| <i>Littorina (Neritrema)</i> <i>obtusata</i> (Linnaeus, 1758) | N Atlantic | 1 | Scilly Is., UK |