

Biogeography of the genera of Naticidae (Gastropoda) in the Indo-Pacific

Alan R. Kabat

Division of Mollusks MRC-118, National Museum of Natural History, Smithsonian Institution, Washington, D. C. 20560 U. S. A.

Abstract: The biogeographic distribution of genera of the family Naticidae (Mollusca: Gastropoda) in the tropical Indo-Pacific is delineated and follows a pattern found in other marine molluscan families. Within the monophyletic clades "Naticinae" and "Sininae" the greatest Indo-Pacific species-level diversity is found in the western Indian Ocean and in Australia; with a marked eastward decline in biodiversity from Melanesia and Micronesia to Polynesia and Hawaii. At the generic level, the broad geographic distribution and lack of endemism precludes reconstruction of the vicariant history of these genera. The present-day distribution of species and genera is largely a function of larval dispersal, not of vicariant events.

The two questions for a biogeographical analysis are (1) "what are the patterns?" [descriptive biogeography] and (2) "how did the patterns come about?" [analytical or phylogenetic biogeography].

DESCRIPTIVE BIOGEOGRAPHY

The Naticidae is a cosmopolitan family of marine prosobranch gastropods, found burrowing in sandy habitats, usually in shallow, nearshore waters. There are about 260-270 Recent species in the family, which originated in the Triassic. The greatest species and generic diversity is in tropical regions, and the analyses here are based upon tropical taxa, with emphasis on the Indo-Pacific biogeographic region.

The phylogeny of the Naticidae (Kabat, unpubl.), although reasonably well-resolved for the Recent genera alone, does have several areas that require more research in order to resolve polytomies or less well-defined clades. In traditional classifications, four subfamilies have been recognized (*e. g.* Marincovich, 1977). One, the "Ampullospirinae" is actually a grade not a clade; as it is primarily found in Arctic and Antarctic regions, it is not further considered here. The second traditional subfamily, the "Polinicinae," is also a grade and the relationships of its genera remain less well-resolved. Although the "Polinicinae" includes several tropical genera, it was not analyzed in this study.

The remaining two traditional subfamilies do form monophyletic, well-defined clades, and are the focus of this study. The "Naticinae" has 15 genera (three now extinct), of which ten are found in Recent tropical regions. The

"Sininae" has five genera, all restricted to temperate-tropical regions.

First, consider the smaller Sininae. Fig. 1 shows the cladistic relationships of the five genera. Because the Sininae forms a monophyletic clade within the "Polinicinae" grade, its actual ranking (as a subfamily or tribe) is debatable. However, the "Sininae" does represent a monophyletic clade which is essential for this biogeographic analysis.

There are 50 Recent species of the Sininae (Table 1), among which 33 are found in the Indo-Pacific. The greatest specific and generic diversity is found in the Indo-Pacific, with a declining eastward gradient from the eastern Pacific to the western Atlantic and the least biodiversity in the eastern Atlantic. *Haliotinella* is an especially rare and cryptic naticid genus, whose three species are known from fewer than 20 specimens; its supposed absence in the eastern Pacific or even the eastern Atlantic may be a collecting artifact. When this geographic distribution is mapped onto the cladogram (Fig. 1), no apparent correlation with the position on the cladogram of the various genera is shown.

Now, to consider the more speciose subfamily Naticinae. Fig. 2 shows the cladistic relationships of the 12 Recent genera of this subfamily. However, two naticine genera are not found in tropical regions, and thus were not analyzed for the tropical species-level diversity in this study.

The species diversity of the ten genera of tropical Naticinae (Table 2) shows the highest specific diversity is found in the Indo-Pacific. In contrast to the Sininae, the Naticinae do not show a declining gradient from the eastern Pacific eastward to the eastern Atlantic; in fact, the gradient

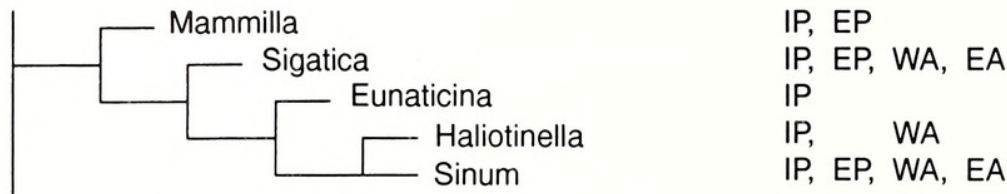


Fig. 1. Cladogram of the "Sininae" with the geographic distribution indicated for each genus. EA, eastern Atlantic; EP, eastern Pacific; IP, Indo-Pacific; WA, western Atlantic.

runs in the opposite, westward direction. There are two amphi-Atlantic species in this subfamily (along with two others in the genus *Polinices*); the eastern Pacific does not share any naticid species with the Indo-Pacific. In other words, the only trans-regional tropical naticid species are the four amphi-Atlantic species.

At the generic level, there is no gradient in generic diversity of the Naticinae in these regions, with six genera in the Indo-Pacific and eastern Pacific, seven in the western Atlantic, and five in the eastern Atlantic. Only two genera are truly endemic to one region: *Tanea* in the Indo-Pacific and *Cochlis* in the tropical eastern Atlantic. *Lunaia*, known from one species in the eastern Pacific, is a poorly defined genus and is potentially a synonym of another genus. *Carinacca*, which has one Recent species in the western Atlantic, was originally described as a fossil taxon from New Zealand. The geographic distribution of these genera is mapped onto the cladogram (Fig. 2); as with the "Sininae," there is no obvious pattern in the generic distribution in relation to the generic phylogeny.

The last component of the descriptive phase of this study comprises a species-level analysis of the tropical Indo-Pacific Naticinae. I have determined the distribution of the known species of this fauna, based primarily on examination of numerous museum records, and to a lesser extent on reliable literature records. Although the data are broken down by country and island group, for convenience

they are here combined into ten broad regions within the Indo-Pacific: western Indian Ocean [Africa to India and Sri Lanka]; southeast Asia [Burma to China, Indonesia, Philippines]; Japan (including the Ryukyus); Australia and New Zealand; western Melanesia [New Guinea and Solomon Islands]; eastern Melanesia [Vanuatu, New Caledonia, Fiji, Wallis and Futuna]; Micronesia [Marianas, Palau, Carolines, Marshall, western Kiribati]; western Polynesia [Tonga, Niue, Samoa, Tokelau, Phoenix]; eastern Polynesia [Cook and Line Islands, French Polynesia]; and Hawaii.

There are six genera of Naticinae in the Indo-Pacific fauna, comprising at least 52 species. Several rare species described from tropical Japan were not included here, as I have not seen any material, and the descriptions were not sufficiently detailed for me to determine whether these taxa were valid or junior synonyms.

The greatest species-level diversity is found in the western Indian Ocean and in Australia, with slightly lower numbers in southeast Asia. There is a decided eastward reduction in species diversity, from western Melanesia to eastern Melanesia and Micronesia, and even more so into Polynesia and Hawaii (Table 3). Note that these comparisons of regional diversity are *not* based on regions of comparable size, either overall or in suitable habitat area.

Of these 52 species, exactly half (26) are endemic to one of these broadly-defined regions. Most endemic

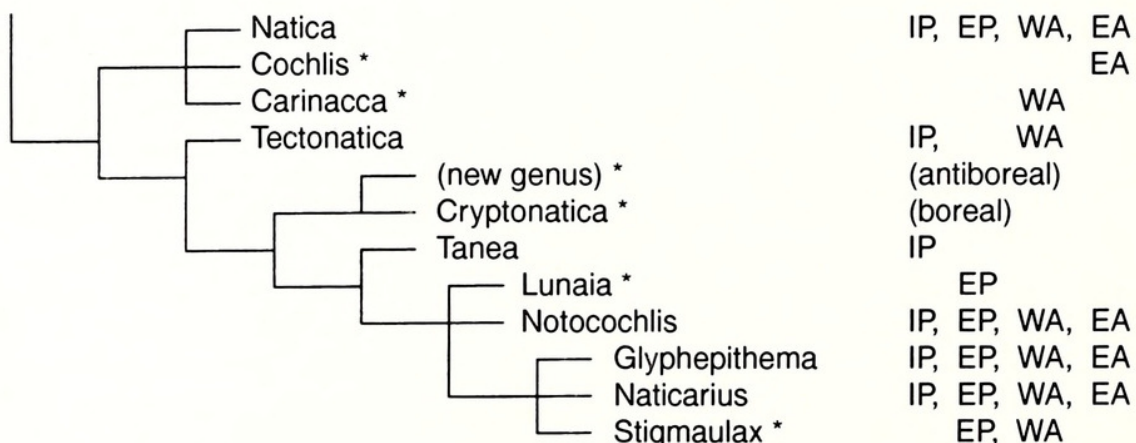


Fig. 2. Cladogram of the Recent genera of "Naticinae" with the geographic distribution indicated for each genus. EA, eastern Atlantic; EP, eastern Pacific; IP, Indo-Pacific; WA, western Atlantic; *, Recent genera *not* found in Indo-Pacific.

Table 1. "Sininae" (Recent), species diversity.

	Indo-Pacific	E. Pacific	W. Atlantic	E. Atlantic
<i>Mammilla</i>	9	1	—	—
<i>Sigatica</i>	6	1	2	1
<i>Eunaticina</i>	6	—	—	—
<i>Sinum</i>	10	6	3	2
<i>Haliotinella</i>	2	—	1	—
TOTAL	33	8	6	3

species are found in either the western Indian Ocean or in Australia (both tropical and warm-temperate); relatively few in the central Pacific proper. Most of the western Indian Ocean endemics are actually restricted to a quite smaller area within this region, such as the Persian Gulf or Mozambique and Natal. An alternative approach to analyzing endemism would be to start with corresponding species ranges and to define areas based on that rather than the "bottom down" approach used herein.

An analysis of the species found in more than one of these regions indicates that eight (15%) are found in two to four regions, nine (17%) in five to seven regions, and nine (17%) in eight to ten regions, including three being found in all ten regions.

A more detailed breakdown of species-level diversity, by genus, is shown in Table 4. The genera are listed in order of their appearance on the cladogram, with the oldest genus first, and the most derived last. For the five genera containing more than one Indo-Pacific species, there exists a west to east gradient in species number and in endemism. Table 5 lists the species and their distribution for each genus; the numbers in parentheses indicate species endemic to one region.

There are five species of Naticinae in Hawaii but only one (20%) is endemic. Although based on a small sample, this does agree with the results of Kay and Palumbi (1987) who found that of the 234 species of "Mesogastropoda" found in Hawaii, 49 (21%) were endemic to Hawaii. A nearly similar percentage (18%) of the "Neogastropoda" are also endemic to Hawaii; about twice as many "Archaeogastropoda" (39%) and Bivalvia (51%) species in Hawaii are endemics, but no explanation for this disparity among molluscan groups was offered by Kay and Palumbi (1987). G. Paulay (in litt., 15 July 1995) suggested that the former was due to the lack of planktotrophic development in most "archaeogastropods" while the endemism of the Bivalvia could be a taxonomic artifact of the monograph of Dall *et al.* (1938) which had numerous (over 130) supposedly new bivalve species endemic to Hawaii but many of which are actually known or probable synonyms of previously described species.

PHYLOGENETIC BIOGEOGRAPHY

With the descriptive data in hand, what are the possible explanations for the observed patterns? More importantly, what are the caveats that should be noted, or pitfalls likely to arise in such analyses?

1. At the species level, both groups analyzed have their highest biodiversity in the Indo-Pacific. The contrasting gradients in the four oceanic regions – eastward decline in the Sininae and westward decline in the Naticinae – do not suggest any simple pattern. It might be thought that these two clades had opposite "tracks" or biogeographic paths in their evolutionary history. A track analysis must be based on the actual taxonomic units that cross the boundaries between oceanic regions, in this case genera instead of subfamilies. One would need a phylogeny of species within a single genus to better address this problem.

2. At the generic level, the results are less conclusive. The eastward decline in generic diversity in the Sininae matches the similar decline in its species diversity. However, for the Naticinae, the generic diversity of all four oceanic regions is comparable (five to seven genera per region) and does not match the gradient of the species-level diversity. One also needs to know the relative ages of these two subfamilies: if the Naticinae is older, then there has been sufficient time for most of the genera to spread to all tropical regions.

More importantly, mapping the geographic areas onto the generic cladograms did not show any patterns as might have been predicted by theories of either traditional biogeography, or of cladistic (vicariance) biogeography.

To briefly review vicariance biogeography (Wiley, 1988), the keystone concept is that of vicariant events: geographic separations which serve to separate populations of one taxon leading to speciation, are shown by the geographic distribution of sister taxa. Vicariant phenomena can be extended to the analysis of higher taxa, such as genera or

Table 2. Tropical "Naticinae" (Recent), species diversity.

	Indo-Pacific	E. Pacific	W. Atlantic	E. Atlantic
<i>Natica</i>	13	2	1	5
<i>Cochlis</i>	—	—	—	2
<i>Carinacca</i>	—	—	1	—
<i>Tectonatica</i>	8	—	1	—
<i>Tanea</i>	13	—	—	—
<i>Lunaia</i>	—	1	—	—
<i>Notocochlis</i>	7	5	6 *	6 *
<i>Glyphepithema</i>	1	1	2	1
<i>Naticarius</i>	10	2	1	3
<i>Stigmaulax</i>	—	2	2	—
TOTAL	52	13	14 *	17 *

* includes two amphi-Atlantic species.

Table 5. Species distributions for the tropical Indo-Pacific Naticinae [geographic abbreviations as in Table 4]. An asterisk * indicates species endemic to one region.

	WIO	SeA	J	ANZ	WMel	EMel	Mic	WPol	EPol	Haw
<i>Glyphepithema</i>										
<i>alapapilionis</i> (Röding, 1798)	x	x	x	x	x	x	x	x	x	x
<i>Natica</i>										
<i>arachnoidea</i> (Gmelin, 1791)	x	x	0	x	x	x	x	0	0	0
<i>buriasensis</i> Récluz, 1843	x	x	x	x	x	x	x	0	0	0
<i>fasciata</i> (Röding, 1798)	x	x	0	x	x	x	x	0	0	0
* <i>forskali</i> Sowerby, 1825	x	0	0	0	0	0	0	0	0	0
* <i>ponsonbyi</i> Melvill, 1899	x	0	0	0	0	0	0	0	0	0
* <i>pulicaris</i> Philippi, 1852	x	0	0	0	0	0	0	0	0	0
* <i>pygmaea</i> Philippi, 1842	x	0	0	0	0	0	0	0	0	0
* <i>queketti</i> Sowerby, 1894	x	0	0	0	0	0	0	0	0	0
* <i>schepmani</i> Thiele, 1925	0	x	0	0	0	0	0	0	0	0
* <i>scutulata</i> Philippi, 1852	x	0	0	0	0	0	0	0	0	0
<i>stellata</i> Hedley, 1913	x	x	x	x	x	0	0	0	0	0
<i>tigrina</i> (Röding, 1798)	x	x	x	x	0	0	0	0	0	0
<i>vitellus</i> (Linné, 1758)	x	x	x	x	x	x	0	0	0	0
<i>Naticarius</i>										
* <i>collei</i> (Récluz, 1844)	0	0	0	x	0	0	0	0	0	0
* <i>concinna</i> (Dunker, 1860)	0	0	x	0	0	0	0	0	0	0
* <i>excellens</i> (Azuma, 1961)	0	0	x	0	0	0	0	0	0	0
<i>insecta</i> (Jousseaume, 1874)	0	0	0	x	x	0	0	0	0	0
* <i>lineozona</i> (Jousseaume, 1874)	0	0	0	0	0	x	0	0	0	0
<i>manceli</i> (Jousseaume, 1874)	x	x	0	0	0	0	0	0	0	0
<i>onca</i> (Röding, 1798)	x	x	x	x	x	x	x	x	0	0
<i>orientalis</i> (Gmelin, 1791)	x	x	x	x	x	x	x	0	x	0
* <i>philippinensis</i> (Watson, 1881)	0	x	0	0	0	0	0	0	0	0
<i>zonalis</i> (Récluz, 1850)	0	x	0	x	x	x	0	0	x	0
<i>Notocochlis</i>										
<i>cernica</i> (Jousseaume, 1874)	x	x	x	x	x	x	x	x	x	x
<i>gualtieriana</i> (Récluz, 1844)	x	x	x	x	x	x	x	x	x	x
* <i>insularis</i> (Watson, 1886)	0	x	0	0	0	0	0	0	0	0
<i>nipponensis</i> (Kuroda, 1961)	0	x	x	0	0	0	0	0	0	0
* <i>subcostata</i> (Tenison-Woods, 1876)	0	0	0	x	0	0	0	0	0	0
* <i>tranquilla</i> (Melvill and Standen, 1901)	x	0	0	0	0	0	0	0	0	0
* <i>zonulata</i> (Thiele, 1930)	0	0	0	x	0	0	0	0	0	0
<i>Tanea</i>										
<i>areolata</i> (Récluz, 1844)	x	x	x	x	x	x	x	x	0	0
<i>euzona</i> (Récluz, 1844)	x	x	0	x	x	x	0	0	0	0
* <i>hilaris</i> (Sowerby, 1914)	0	0	x	0	0	0	0	0	0	0
<i>lineata</i> (Röding, 1798)	x	x	x	x	x	0	0	0	0	0
* <i>luculenta</i> (Iredale, 1929)	0	0	0	x	0	0	0	0	0	0
<i>mozaica</i> (Sowerby, 1883)	0	0	0	x	x	x	0	0	0	0
<i>picta</i> (Récluz, 1844)	x	x	0	x	0	0	0	0	0	0
* <i>sagittata</i> (Menke, 1843)	0	0	0	x	0	0	0	0	0	0
<i>tabularis</i> (Kuroda, 1961)	0	x	x	x	0	0	0	0	0	0
<i>undulata</i> (Röding, 1798)	0	x	x	x	x	0	0	0	0	0
* <i>zelandica</i> (Quoy and Gaimard, 1832)	0	0	0	x	0	0	0	0	0	0
*new sp. 1	x	0	0	0	0	0	0	0	0	0
*new sp. 2	0	0	0	0	0	0	0	0	0	x
<i>Tectonatica</i>										
<i>bougei</i> (Sowerby, 1908)	x	0	0	x	x	x	x	x	x	x
<i>robillardi</i> (Sowerby, 1894)	x	x	0	x	x	x	x	x	x	0
* <i>simplex</i> (Sowerby, 1897)	x	0	0	0	0	0	0	0	0	0
* <i>shorehami</i> (Pritchard and Gatliff, 1900)	0	0	0	x	0	0	0	0	0	0
<i>suffusa</i> (Reeve, 1855)	x	x	0	x	x	x	x	0	0	0
* <i>tecta</i> (Anton, 1838)	x	0	0	0	0	0	0	0	0	0
<i>violacea</i> (Sowerby, 1825)	x	x	0	x	x	x	x	x	x	0
*new sp. 1	0	x	0	0	0	0	0	0	0	0

of endemism was in the western Indian Ocean and Australia, with significantly reduced endemism elsewhere in the Indo-Pacific (but note the caveat *re* defining the regions). Although there are several schemes for subdividing the Indo-Pacific into biogeographic provinces (*e. g.*

Kay, 1980; Dahl, 1984; Blum, 1989; Stoddart, 1992), none would allow us to have at least one endemic naticine species in each province. Even some very broadly defined regions, such as western and eastern Polynesia, do not have any endemic naticine species.

The "bugaboo" of larval dispersal is, in my opinion, the greatest barrier to biogeographic analyses of marine invertebrates. This intellectual barrier is probably even more important than the geographical barriers caused by the elevation of the Panama land bridge, or the closure of the Suez between the Mediterranean and the Red Sea, in reconstructing the biogeographic history of marine invertebrates!

We are all familiar, thanks to the studies of Scheltema and others presented in this symposium (*e.g.* Kohn, Bieler), of the remarkable abilities of the larval stages of marine invertebrates not only to cover vast distances, but also to maintain the genetic integrity of species across an oceanic region. It should come as no surprise to biogeographers that such dispersal can and often will make it impossible for us to delineate the vicariant events based upon a study of the current geographic distribution of taxa, as Gosliner (1994) has noted.

For the family Naticidae, there is little or no adult dispersal of biogeographic relevance. However, the majority of tropical species whose development is known or can be inferred from protoconch size have planktonic larvae. Direct development, or the hatching of benthic juveniles, is documented primarily for cold-water species and I have predicted its occurrence for several tropical species with restricted ranges (endemic to a small region) based upon their large protoconch sizes. Some other endemic tropical naticid species may have lecithotrophic, or short-dispersing larvae, although this needs to be documented from study of the egg masses themselves. In contrast, most of the widespread tropical naticid species, including all four tropical amphi-Atlantic naticids, are known to have planktonic development, usually documented as planktotrophic (*e. g.* Thorson, 1940; Bandel, 1976).

If all naticids had direct development, or at least short-term lecithotrophic development, then their dispersal abilities would be significantly restricted, and it would be easier to reconstruct the vicariant history of this group. However, the admixture of all three modes of larval development within a single genus would result in dispersal patterns confounding the original vicariant patterns. Again, it must be emphasized that vicariant theory was based primarily on non-marine organisms with limited dispersal capability. I seriously question whether we can apply cladistic biogeography to marine invertebrates, at least to those groups with high larval dispersal ability or those that are readily dispersed by rafting.

There is one study on marine organisms, the fish family Chaetodontidae (Blum, 1989) for which satisfactory vicariant analyses could be conducted, as not only were the species-level relationships reasonably well known, but also there were sufficient numbers of endemic species among

the regions. Nonetheless, most of the "barriers" which Blum recognized (1989: fig. 11, table 2) were based on only one or (seldom) two to three pairs of sister taxa, which may not be statistically significant considering the large numbers of tropical species (over 110) in this family. Indeed, Blum (1989: 10) stated that "almost all of the sister groups ... are broadly sympatric ... Thus most of the geography associated with early chaetodontid evolution has been obscured by subsequent dispersal." These problems will recur with other marine taxa. It might seem that one should avoid biogeographic conclusions based upon a small and carefully selected subset of a group, yet such a group (containing allopatric species) may allow reconstruction of the vicariant history prior to subsequent dispersal.

McMillan and Palumbi (1995) recently performed a molecular analysis on two of Blum's species groups in the Chaetodontidae. Their results from these two species groups, carefully chosen to include only allopatric species, showed fairly recent speciation events potentially attributable to Pleistocene glacio-eustatic sea level changes (see also Paulay, 1991).

I now briefly discuss whether the Naticidae fits into Springer's 1982 model of "Pacific Plate Biogeography" which was based primarily upon an analysis of the distribution of shorefishes, but also drew upon several invertebrate groups. Springer (1982) claimed that the margin of the Pacific plate represented a significant dispersal barrier, and thus a source of endemic species. For the Naticidae, at least, these results are not confirmed. Most widely-distributed species have dispersed right across the western (Asian) margin of the Pacific plate, as might be expected from the prevailing oceanic currents which naturally bear little relation to the distribution of tectonic plates on the ocean floor itself. Furthermore, most endemic naticid species are found neither within the Pacific plate itself, nor on its margin, but rather in the western Indian Ocean, or along the Australian continental shelf, both areas at some remove from the Pacific plate. Indeed, not a single species among the Naticinae is a "widespread Pacific plate endemic" and the sole species restricted to the Pacific plate is endemic to Hawaii.

In conclusion, this paper has demonstrated a number of biogeographic patterns based upon the descriptive biogeography of the genera and species of tropical Naticidae. However, explaining these patterns in a cladistic or vicariance context remains quite problematical, for several reasons which are equally applicable to most taxa of marine organisms. Although seemingly a "negative result" this does indicate the limited utility of such biogeographic theories, and suggests that an entirely different approach to reconstructing the geographic history of marine taxa is needed.

ACKNOWLEDGMENTS

I thank Gustav Paulay for inviting me to participate in the Island Biogeography symposium. Travel costs were supported by the research fund of the National Museum of Natural History, Smithsonian Institution. Gustav Paulay and an anonymous reviewer kindly critiqued the manuscript.

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Date of manuscript acceptance: 8 February 1996



Kabat, Alan R. 1996. "Biogeography of the Genera of Naticidae (Gastropoda) in the Indo pacific." *American malacological bulletin* 12, 29–35.

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