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The Namanereidinae (Polychaeta: Nereididae). Part 2, Cladistic Biogeography

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ABSTRACT. A cladistic biogeographic study of the Namanereidinae was undertaken to test whether the biogeographic patterns shown by the species can be explained by vicariance, and whether they support the conventional view of Pangaeian break-up and a hypothetical Tethys Sea. The Namanereidinae consists of two monophyletic clades, *Namalycastis* and *Namanereis*, members of which exhibit similar distribution patterns. If species of *Namalycastis* and *Namanereis* share a common history of fragmentation and diversification then their area cladograms should be congruent and congruent with the postulated sequence of geological fragmentation. Congruence between area cladograms and between taxon and area cladograms was assessed using the COMPONENT program (Page, 1993). Results indicate that the biogeographic patterns shown by species of both genera may be explained largely by vicariance. Rather than supporting the conventional view of Pangaeian break-up and a hypothetical Tethys Sea, the results are better explained by the expanding earth model (sensu Shields, 1976, 1979) which predicts that during the Jurassic Period the earth was substantially smaller, the Tethys Sea was much reduced (or absent) and the Pacific was essentially closed. The minimum age of the subfamily is thought to be about 200 My.

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The Namanereidinae are a rarely encountered group of polychaetes known for their remarkable adaptation to freshwater and semi-terrestrial environments. They are found in coastal regions of the tropics and subtropics (mainly) in a variety of habitats ranging from littoral areas (mangrove forests, amongst flotsam and jetsam etc.), riparian habitats, subterranean waters, even in leaf litter and phytotelmata (plant container habitats) (Glasby, this volume; Glasby *et al.*, 1990). The group was divided into five or six genera: the speciose *Lycastopsis* Augener and *Namalycastis* Hartman, and four monospecific genera, *Namanereis*

Chamberlin, *Cryptonereis* Gibbs, *Lycastilla* Solís-Weiss & Espinasa, and the poorly known *Lycastoides* Johnson. Some authors consider *Lycastopsis* to be a junior synonym of *Namanereis* (e.g., Hartman, 1959; Hartmann-Schröder, 1980). However, a taxonomic and phylogenetic revision of the group presented in this volume indicates that the 33 valid species in the subfamily should be divided between two monophyletic groups—*Namalycastis* and *Namanereis* (includes *Cryptonereis*, *Lycastilla*, *Lycastopsis* species), with the placement of *Lycastoides alticola* uncertain (Glasby, this volume).

In this study the biogeographic patterns exhibited by the Namanereidinae are investigated using cladistic biogeography. Area cladograms are constructed using component analysis (Nelson & Platnick, 1981; Page, 1990a) as implemented in the computer program COMPONENT (Page 1993). This program allows the assessment of the problems of redundant, missing, and ambiguous information between area cladograms. The pattern of area relationships of *Namalycastis* and *Namanereis* are compared and common biogeographical patterns sought. A general pattern is attributed primarily to vicariant events (viz. geological, climatological and oceanographic) that result in division of a group of species into two or more subunits. Non-conformity to a general pattern may be the result of dispersal, ecological variation or conformity to a different pattern (Humphries & Parenti, 1986).

The Namanereidinae were considered suitable for a cladistic biogeographic analysis because the dispersal capabilities of both larvae and adults are considered limited (see Discussion). Also, with the exception of a single species group, *Namanereis quadraticeps*, members of both genera show significant overlap in distribution. The subfamily is monophyletic (Fitzhugh, 1987; Glasby, 1991) as are the two genera: *Namalycastis*, defined by the presence of very short, conical antennae and posterior leaf-like dorsal cirri; and *Namanereis* by the presence of a tripartite pygidium and the absence of notosetae (Glasby, this volume). A cladistic analysis of relationships resulted in over 10,000 minimal-length trees, primarily due to an insufficient number of characters compared to taxa; however, it was established that all the trees belonged to the same island of trees (*sensu* Swofford, 1993) and therefore that branch swapping on any one of them would result in all minimal-length trees, given sufficient computing capacity (Glasby, this volume). Further, the characters employed in the analysis showed good agreement with one another ($ci = 0.55$) and a relatively high number of characters acted as synapomorphies ($ri = 0.81$).

A 50% Majority-rule Consensus tree was used as a starting point for the present analysis (Fig. 1). It was considered as the best alternative between two extremes: on the one hand selecting, *ad hoc*, a fully resolved (and shorter) tree amongst the set of 10,000 minimal-length trees and, on the other, attempting to summarise the information common to all 10,000 trees using a Strict (or Adams) Consensus trees, which resulted in a highly polytomous cladogram (fig. 5; this volume p. 20). The 50% Majority-rule Consensus tree represents clusters of taxa found in 50% or more of the minimal-length trees and is therefore the tree most similar, on average, to all minimal-length trees (Page, 1993). Unresolved polytomies were resolved arbitrarily by COMPONENT. This is not a problem for the *Namalycastis* clade since the only two polytomies occur at terminal nodes and the taxa involved were not used to infer biogeographic relationships; however, it may represent a limitation in the analysis of the *Namanereis* clade where the relationship between several species, including the clade of land-locked freshwater species, is unresolved (see Results).

There appear to have been no previous analytical studies of the historical biogeography of polychaetes. Salazar-Vallejo & Solís-Weiss (1992) employed cladistic methods to determine the relationships within the synelmine pilargids although the exact details of their method were not given. However, these authors acknowledged that their biogeographic analysis was “narrative” rather than analytical. Further, they employed *ad hoc* assumptions of the age of the common ancestor of the group and that the ancestor had a Tethyan distribution. The study of macellicephaline polynoids by Levenstein (1984) is another example of the narrative approach in which a Tethyan ancestor was also postulated.

The fossil record of the Nereididae is poor due to the very low fossilisation potential of the jaws (Colbath, 1986, 1988). Indeed according to Szaniawski (1974) there are no undisputed records of fossilised nereid jaws. Whether the Nereididae arose along with many other polychaete families during the Precambrian as has been suggested (e.g., Fauchald, 1974) or appeared later will probably never be answered by the fossil record alone. However, if the biogeographic patterns shown by the Namanereidinae are the result of vicariance then an estimate of the age of the subfamily may be possible by reference to the timing of major tectonic events. Further, we may ask whether the vicariant patterns support the conventional view of a single continent, Pangaea, fragmenting to form a northern landmass, Eurasia, and a southern one, Gondwana, separated by an hypothetical Tethys Sea, or provide support for less popular theories, such as the “expanding earth” (Carey, 1976; Owen, 1976; Shields, 1976, 1979) or Pacifica (Nur & Ben-Avraham, 1977, 1981) in which the Tethys Sea is essentially an artefact. If species of *Namalycastis* and *Namanereis*, representing partially sympatric higher taxa, share a common history of fragmentation and diversification then their area cladograms should be congruent and congruent with the postulated sequence of geological fragmentation.

Methods

Areas of endemism. Areas of endemism should contain at least two species having more or less congruent distributional limits (Platnick, 1991). In the marine realm a 10% or more level of endemism was regarded as sufficient to delineate a province (Briggs, 1974). Van Soest (1994) based his areas of endemism for recent demosponges on the provinces recognised by Briggs. The areas recognised in the present study (Fig. 2a,b) follow closely those identified by van Soest (1994) although they were modified slightly to bring them into line with the observed distribution of namanereidine taxa. These modifications included the recognition of a single Mediterranean-Black Sea region (rather than a separate eastern and western Mediterranean), an Indo-Pacific region (rather than separate Indonesian and Central Pacific regions) and an eastern Australian region (rather than separate northeastern Australian [= Solanderian] and southeastern Australian [= Peronian]) regions.

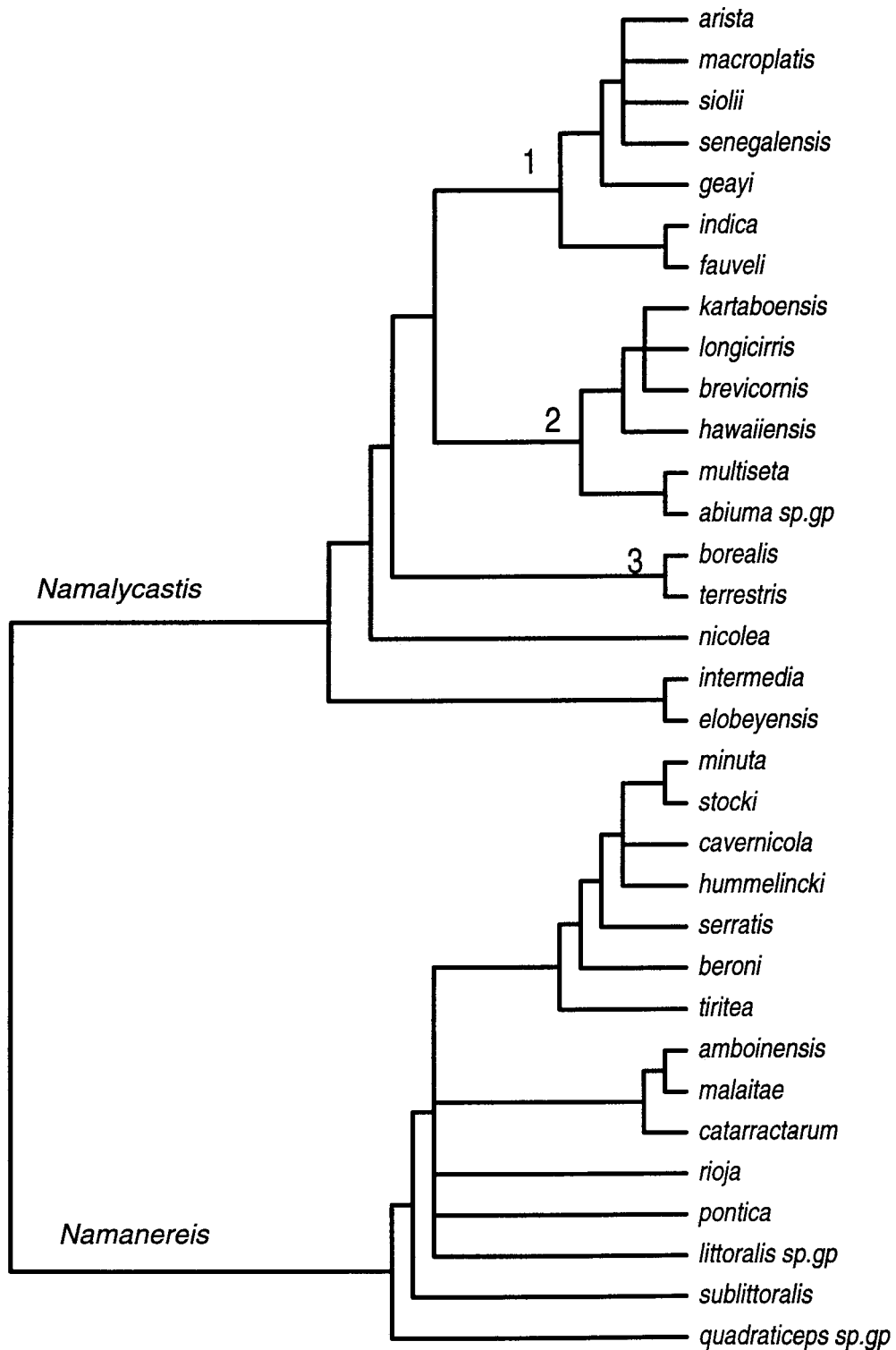


Figure 1. Phylogeny of the Namanereidinae (family Nereididae): 50% Majority-rule Consensus tree of 10,000 minimal-length trees (ci = 0.55, ri = 0.81) obtained in the study reported earlier in this volume. Percentages of minimal-length trees supporting a particular clade are indicated at each node.

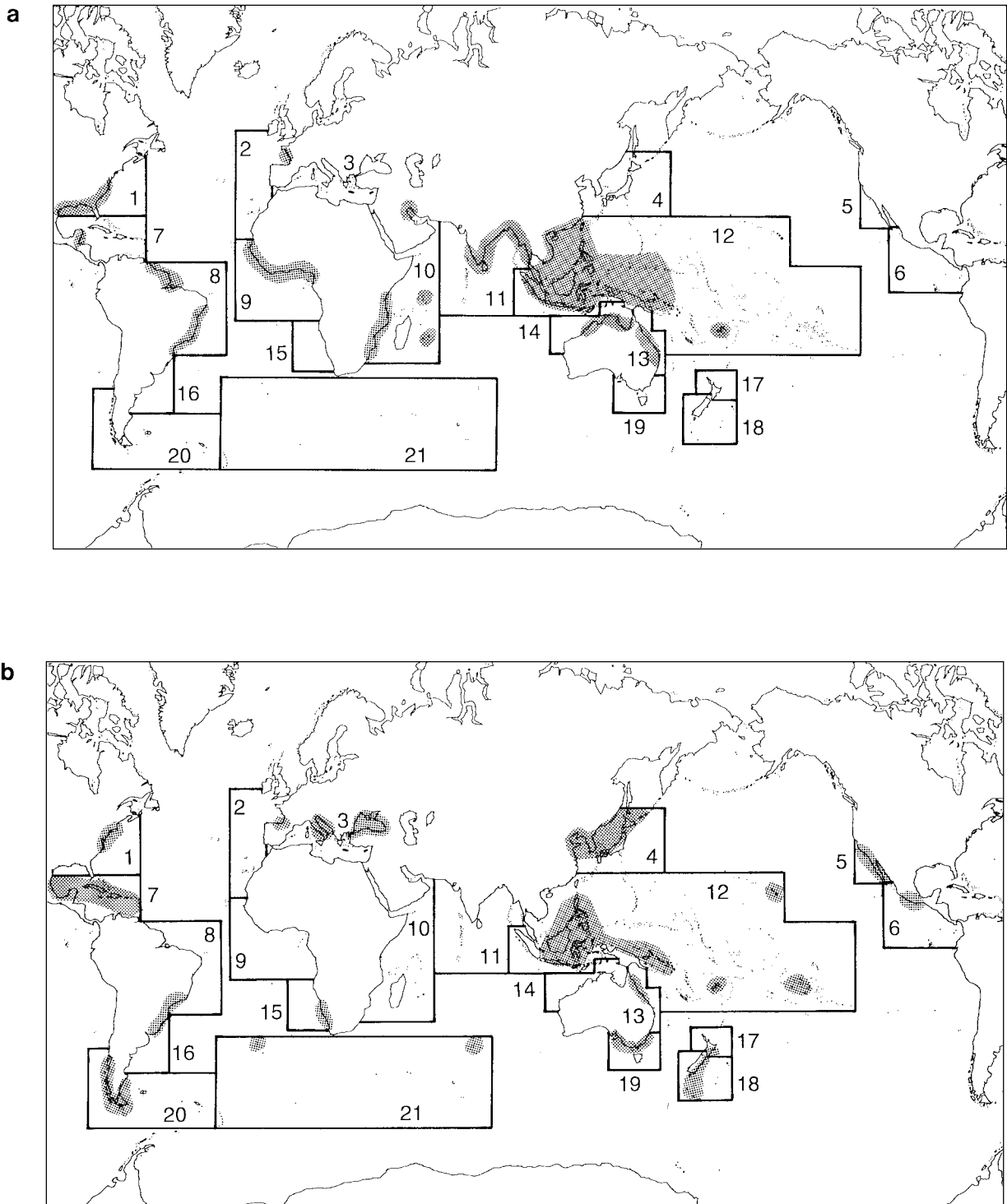


Figure 2. (a) Map showing the distribution of *Namalycastis* species and the areas of endemicism used in the present study. 1, Boreal West Atlantic (BORWESTATL); 2, East Atlantic (EATLANTIC); 3 Mediterranean-Black Sea (MEDBLACKSEA); 4, Japan-China area (JAPANCHINA); 5, Californian area (CALIFORNIA); 6, Central America (CAMERICA); 7, Caribbean (CARIBBEAN); 8, Brazil (BRAZIL); 9, West Africa (WAfrica); 10, western Indian Ocean (WINDIANOCEAN); 11, central Indian Ocean (CENINDIANOCEAN); 12, Indonesia-central Pacific (INDOPACIFIC); 13, eastern Australia (EAUSTRALIA); 14, northwestern Australia (NWAUSTRALIA); 15, southwest Africa (SWAFRICA); 16, southwest Atlantic (SWATLANTIC); 17, North New Zealand (NORTHNEWZEA); 18, South New Zealand (SOUTHNEWZEA); 19, Tasmanian area (TASMANIA); 20, Magellan area (MAGELLAN); 21, Subantarctic (SUBANTARCTIC). (b) Map showing the distribution of *Namanereis* species. Areas of endemicism as for part a.

Taxa included. Thirty namanereidine taxa in two genera, *Namalycastis* (16) and *Namanereis* (14) were included in the present analysis. Taxa excluded from the study were the poorly known species, *Lycastoides alticola* and *Namalycastis longicirris*, and two of the three species groups (*Namalycastis abiuma*, *Namanereis littoralis*) which both exhibited cosmopolitan distributions (Glasby, this volume). These species groups are potentially paraphyletic, or more precisely “metaspecies” (*sensu* Donoghue, 1985): each group may comprise two or more monophyletic species but autapomorphies have not as yet been identified. The inclusion of these species groups may mislead the cladistic biogeographic analysis under assumption 0 (widespread taxa and the areas in which they occur treated as monophyletic); however, the extent of the problem may be relatively minor (Crisp & Chandler, 1996). The other species group, *Namanereis quadraticeps*, has a circum-southern hemisphere cold-temperate distribution which does not overlap with other Namanereidinae. Therefore its inclusion would not unduly influence the outcome of the analysis (i.e. the equivalent of autapomorphies in a phylogenetic analysis).

Area cladograms. The computer program COMPONENT 2.0 (Page, 1993) was used to compute area cladograms, find consensus trees, analyse trees and to generate random trees. Species labels in the cladogram were substituted by the area(s) of endemism included in their distribution to produce unreduced area cladograms. Reduced area cladograms were computed separately for species of *Namanereis* and *Namalycastis*, and a general area cladogram was computed in a global analysis of all species. Most-parsimonious trees were computed using the NNI branch-swapping option and minimising the number of terminals (i.e. areas). Two of the three “standard” assumptions governing the treatment of widespread taxa and redundant areas were employed. Assumption 0 (Brooks, 1981; Wiley, 1987; Zandee & Roos, 1987) treats widespread species as if they (and the areas in which they occur) are monophyletic. The more flexible Assumption 1 (Nelson & Platnick, 1981) permits widespread areas (and their species) to be paraphyletic with the solution being found by congruence with the pattern shown by a second monophyletic group. Assumption 2 (Nelson & Platnick, 1981) permits both paraphyly and polyphyly as possibilities for widespread areas (and their species), and like Assumption 1 the solution is found by congruence with other groups. Assumption 2 is not implemented directly in COMPONENT and the manual method of editing the ranges of the widespread taxa as suggested by Page (1993) was considered too time consuming for the present data.

Comparing area cladograms. Tree-to-tree distances were compared between the two sets of reduced area cladograms in order to find cladograms in common (i.e. mutually consistent). The number of resolved and different triplets, or three area statements, was measured using the “d” measure: when $d = 0$, no triplets are resolved differently between two trees (i.e. the trees are mutually consistent). A randomisation test using the

Markovian model and minimum symmetric difference of triplets (SD_i) was used to test whether the observed degree of congruence between the reduced area cladograms could have been achieved by chance alone. The SD_i index measures the dissimilarity of two cladograms based on unshared three taxon statements (Page, 1993). Two sets of 40 random trees (maximum number using present computer hardware) were compared (one set with 7 terminal areas to simulate the *Namalycastis* area cladograms and the other with 13 terminals for those of *Namanereis*).

Reconciling taxon cladograms with area cladograms. Incongruence between taxon cladograms and resulting area cladograms can be explained by invoking the presence of unrecognised multiple lineages in the area cladogram (Nelson & Platnick, 1981; Page, 1993). The taxon cladogram can therefore be considered to be a subsample of the larger reconciled tree, which represents the complete taxon cladogram (Page, 1993). Species missing from an area represent putative species yet to be discovered or extinctions. They are estimated in the reconciled tree by the number of losses required to explain the distribution of the taxa. Other measures of fit between area cladogram and the taxon cladogram include the number of terminals added and duplications (number of times a duplication of a lineage has to be postulated to reconcile the two trees); duplications in a reconciled tree correspond to speciation by non-vicariant means (e.g., sympatric speciation) (Page, 1994).

In order to assess whether the fit between the area cladograms and the taxon cladogram(s) is greater than one would expect due to chance alone, the taxon cladogram was mapped onto a set of 1,000 randomly generated (Markovian distribution) area cladograms (Page, 1990a,b).

Results

Area cladograms. Relationships among areas in the unreduced area cladograms (Fig. 3a,b) are made ambiguous by widespread distributions (i.e. taxa occupying more than a single area of endemism) and redundant areas (areas harbouring more than 1 taxon). *Namalycastis* species having widespread distributions include *N. senegalensis*, which occurs on the northeast coast of South America and West Africa, and *N. brevicornis*, which occurs on the coast of Brazil and in the East Atlantic; however, its presence in the East Atlantic (Noirmoutier, France) is mainly of historical interest as the species has not been recorded there since the original description in the last century (Glasby, this volume; Gibbs & Saiz Salinas, 1996). Amongst *Namanereis*, *N. amboinensis* has a circum-subtropical distribution, *N. cavernicola* occurs in the Caribbean and Central America, *N. quadraticeps* is a widespread southern temperate species group and *N. tiriteae* is found in the Indo-Pacific and northern New Zealand. Redundant areas for the *Namalycastis* area cladogram are Brazil (7 species), Central Indian Ocean (3 species), Indo-Pacific (2 species), Boreal West Atlantic (2 species); those for *Namanereis* are the Caribbean (7 species) and the Indo-Pacific (5 species).

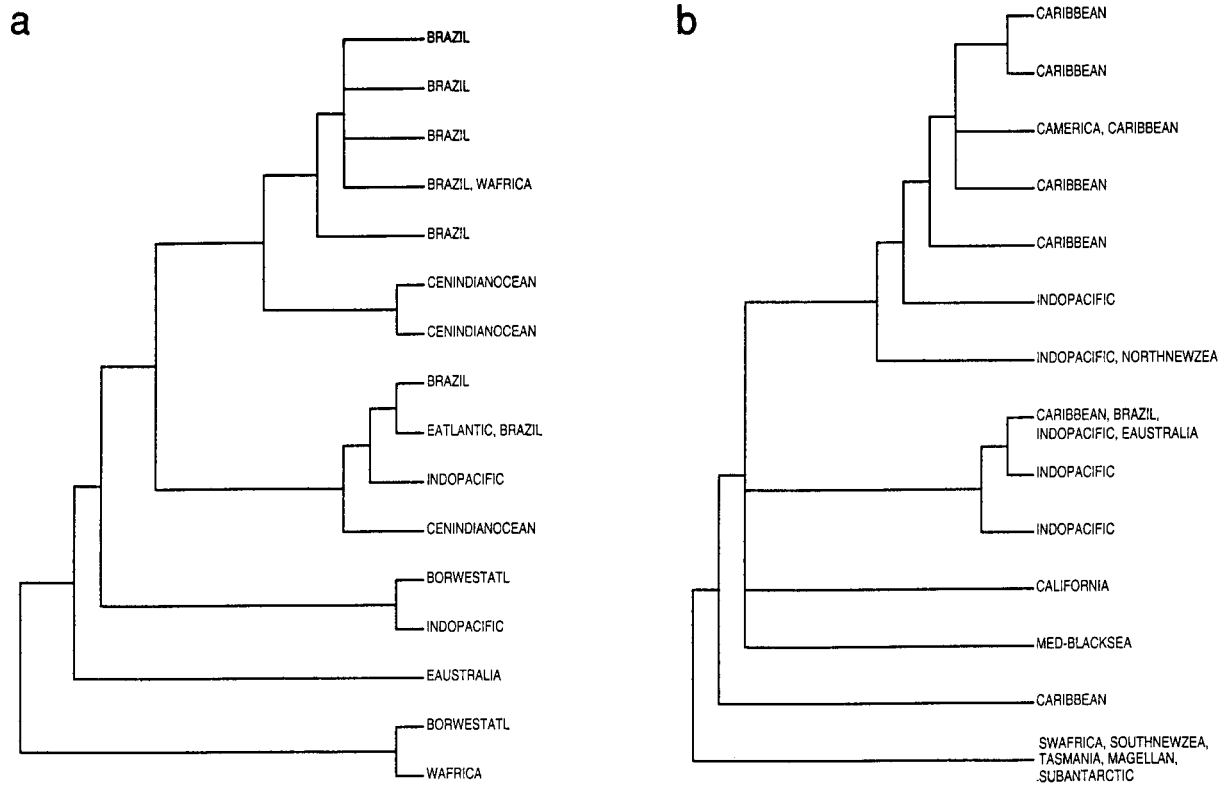


Figure 3. Unreduced area cladograms for species of (a) *Namalycastis* and (b) *Namanereis*.

A single reduced area cladogram with 7 areas of endemism was computed for *Namalycastis* species under both assumptions 0 and 1 (Fig. 4, Table 1). However, for *Namanereis*, under both assumptions, 1,000 minimal-length area cladograms were computed (calculation terminated), each having the same minimum value (36) and number of areas of endemism (13) (Table 1).

A pair-wise comparison of the single reduced area cladogram of *Namalycastis* with the 1,000 reduced area cladograms of *Namanereis*, under both assumptions yielded the following results:

Assumption 0: $d = 0$, $SD_t = 0.00$ for 402 pairs; $d = 1$, $SD_t = 1.00$ for 598 pairs.

Assumption 1: $d = 0$, $SD_t = 0.00$ for 335 pairs; $d = 1$, $SD_t = 1.00$ for 665 pairs.

An $SD_t = 0.00$ indicates that under both assumptions there is a considerable number of reduced area cladograms that are mutually consistent between the two genera (40% under assumption 0; 34% under assumption 1). The remaining comparisons are incongruent ($SD_t = 1$). A randomisation test indicated that the observed results lie outside those expected by chance (Fig. 5). While congruence between the area cladogram of two different groups is generally taken to indicate shared history of fragmentation and diversification, incongruence may result for many reasons. The fact that the two sets of area cladograms share only 3 areas of endemism in common may be a factor of concern. Clearly, further work needs to be done to better resolve the area relationships within *Namanereis* and preferably to identify a single area cladogram.

Table 1. Comparison of number of terminals added, minimal value and number of trees computed for *Namalycastis*, *Namanereis* and a combined analysis, each under assumptions 0, 1.

analysis	number terminals added	minimum value	number trees
<i>Namalycastis</i> (ass. 0,1)	7	19	1
<i>Namanereis</i> (ass. 0,1)	13	36	1,000 (overflow)
combined (ass. 0)	17	89	105
combined (ass. 1)	17	89	945

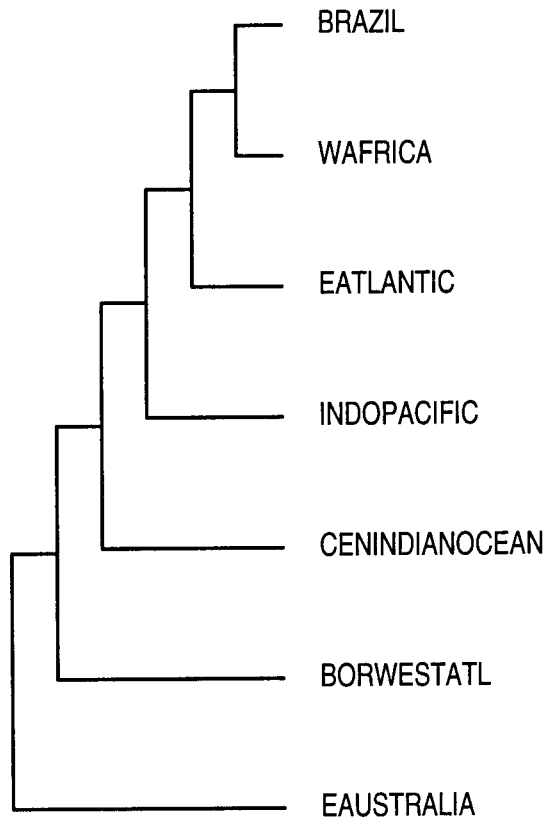


Figure 4. Reduced area cladogram for *Namalycastis* species.

Majority-rule Consensus area cladograms for *Namanereis* under both assumptions were computed in order to summarise the information on area relationships and to provide a single tree on which to map the taxon cladograms (Fig. 6a,b). The two consensus cladograms differ only slightly: under assumption 0, Brazil and the Indo-Pacific form a clade but the two areas are unresolved with respect to each other under assumption 1; also under assumption 0 the areas of the southern ocean, occupied by *Namanereis quadraticeps* species group, form a monophyletic group but the group is unresolved under assumption 1. Nelson consensus trees (*sensu* Page, 1993) for *Namanereis* differ only slightly from the Majority-rule trees: for the Nelson tree under assumption 0, the clade containing the southern ocean areas was fully resolved, (MAGELLAN ((SWAFRICA TASMANIA) (SOUTHNEWZEA SUBANTARCTIC))), apparently

unjustifiably considering that all information on the area relationships in this clade come from the one taxon, *Namanereis quadraticeps* species group; under assumption 1, the only difference between the two consensus trees was in the sister group relationship of Brazil and Indo-Pacific, which was collapsed in Majority-rule tree as only 48% of minimal-length trees had these as sister areas.

Global analysis. When the two genera were analysed together under assumption 0, 105 area cladograms were computed with minimum values of 89 and 17 areas of endemism; under the less restrictive assumption 1, 945 trees were produced, each with the same minimum value and number of areas of endemism (Table 1). The global area cladograms computed under both assumptions 0, 1 were reconciled with the taxon cladogram. The fewer duplications, losses and additions for the global area cladogram under assumption 0 (Table 2) indicates that it is more congruent with the observed phylogeny. A Majority-rule area cladogram under assumption 0 is shown in Fig. 7. It shows no disagreement with the area cladograms computed separately for *Namalycastis* and *Namanereis*; it may therefore be taken as the best estimate of the area relationships for the present data.

A comparison of selected measures of fit between the taxon cladogram reconciled with those of randomly generated area cladograms (under assumption 0) indicates that the observed fit between area and taxon cladograms is better than would be expected by chance alone (i.e. vicariance is not refuted, Table 2).

Reconciling taxon cladogram with global area cladogram. By mapping the observed taxon cladogram onto the favoured Majority-rule Consensus area cladogram a number of discrepancies become apparent (Fig. 8). First, the relatively large number of duplications indicates that many speciation events within the Namanereidinae are the result of sympatry or some other non-vicariant mode. This is particularly true of *Namalycastis* species in the Brazil and West Africa areas and *Namanereis* species in the Caribbean. Second, the high number of areas with missing taxa suggests either that species have become extinct in these areas, or that these areas have been poorly sampled (i.e. further await discovery). The latter could certainly be true in places like the Indo-Pacific and West Africa, but extinction may be the better explanation in areas where

Table 2. Comparison of duplications, additions and losses in a reconciled analysis between the global area cladogram and taxon cladogram for the combined analysis under assumptions 0, 1 and between the taxon cladogram and 1,000 randomly generated trees.

analysis	duplications	added	losses
global area cladograms (ass. 0) × taxon cladogram	19	89	54
global area cladograms (ass. 1) × taxon cladogram	20	106	64
random area cladograms (ass. 0) × taxon cladogram	23–27	220–382 (mean 317, SD 37.6)	79–188 (mean 115, SD 14.3)

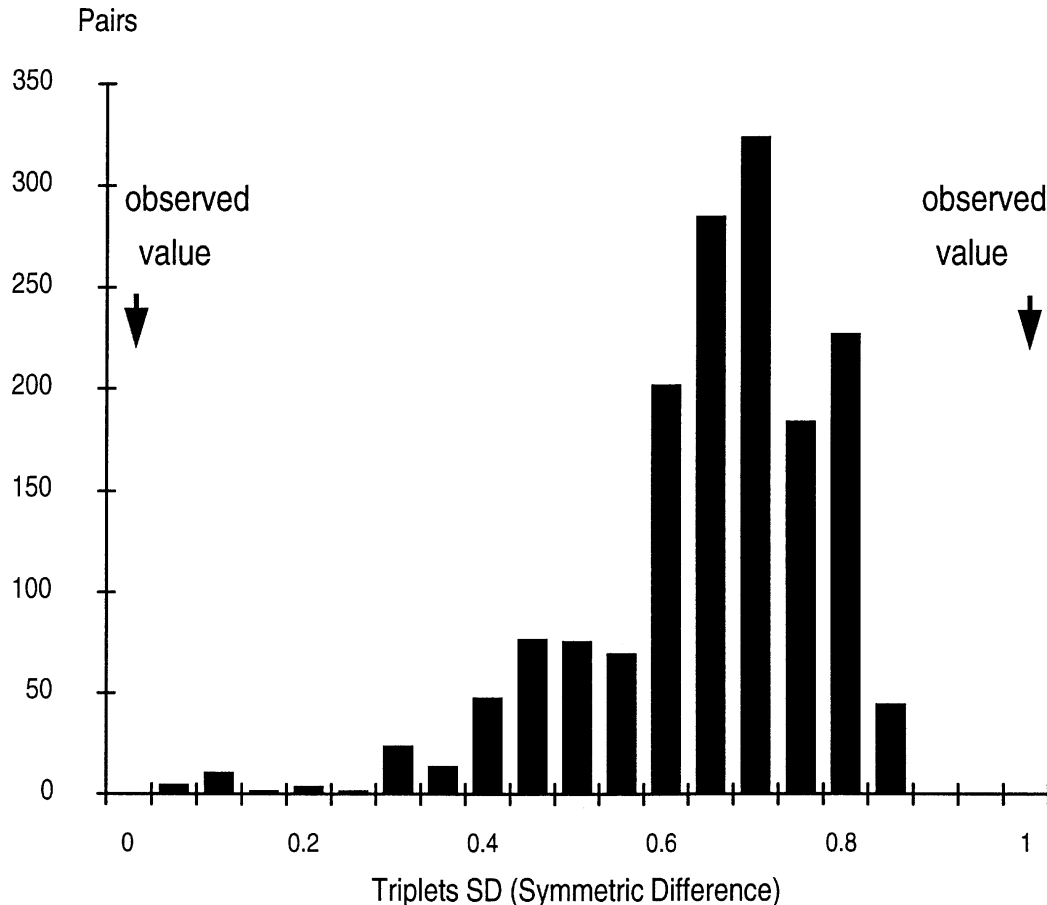


Figure 5. Comparison of observed and tree-to-tree distances (as measured by the symmetric difference of triplets, SD) between two sets of 40 randomly generated trees, one with 7 terminals and one with 13 terminals (see text for further explanation).

the namanereidine fauna is better known, for example the Caribbean. Unique components in area cladograms occur for a variety of reasons including failure of a population to divide in response to the formation of a natural barrier, extinction in one or more areas, and dispersal from one area to another.

Discussion

Congruence in biogeography has no simple interpretation: although it may be explained by the co-ordinated responses of taxa to a sequence of vicariant events, it may also be caused by ecological processes or co-ordinated dispersal (Page, 1988). There is no direct evidence for dispersal in the Namanereidinae and unfortunately nothing is known of larval development in the group; however, it is unlikely that larvae of namanereids are good dispersers—*Namanereis* species in particular exhibit very large, yolky eggs (300 to over 500 μ m) (Glasby, this volume) and larvae are therefore likely to be benthic or at least have a very short pelagic phase. Furthermore, members of both genera inhabit areas of freshwater and semi-terrestrial habitats where dispersal opportunities would be limited. The possibility of transport via dry ballast, including rocks, in the days of wooden sailing vessels has been suggested (Gibbs & Saiz Salinas, 1996) but the evidence is presently only circumstantial.

Dispersal via rafting of adults on floating materials (such as algae or coconuts), while a possibility, is not supported by any direct evidence. Nevertheless several widespread namanereidine taxa occur in conjunction with materials capable of being transported across the oceans meaning that dispersal in theory is possible for these species. *Namanereis littoralis* species group is often found in association with flotsam and jetsam cast up on beaches; and *Namanereis quadraticeps* species group occurs in the Southern Ocean which is influenced by west wind drift; members of the *Namalycastis abiuma* species group are found in association with coconuts cast up on the shore. Also the small body size and broad feeding capabilities of some *Namanereis* species in particular (Glasby, this volume; Glasby *et al.*, 1990) would be beneficial for a rafting strategy.

One of the salient features of the area cladograms is the multiple sister group relationships between the Indo-Pacific and the Caribbean–Brazil–West Africa areas. These relationships are displayed by species in both namanereidine genera and therefore may be explainable by vicariant events. Broadly speaking, the Namanereidinae exhibit three types of distributions: amphi-Atlantic, amphi-Pacific and pantropical. The amphi-Pacific distribution includes regions as far east as Central America and the Caribbean since these areas were contiguous with the

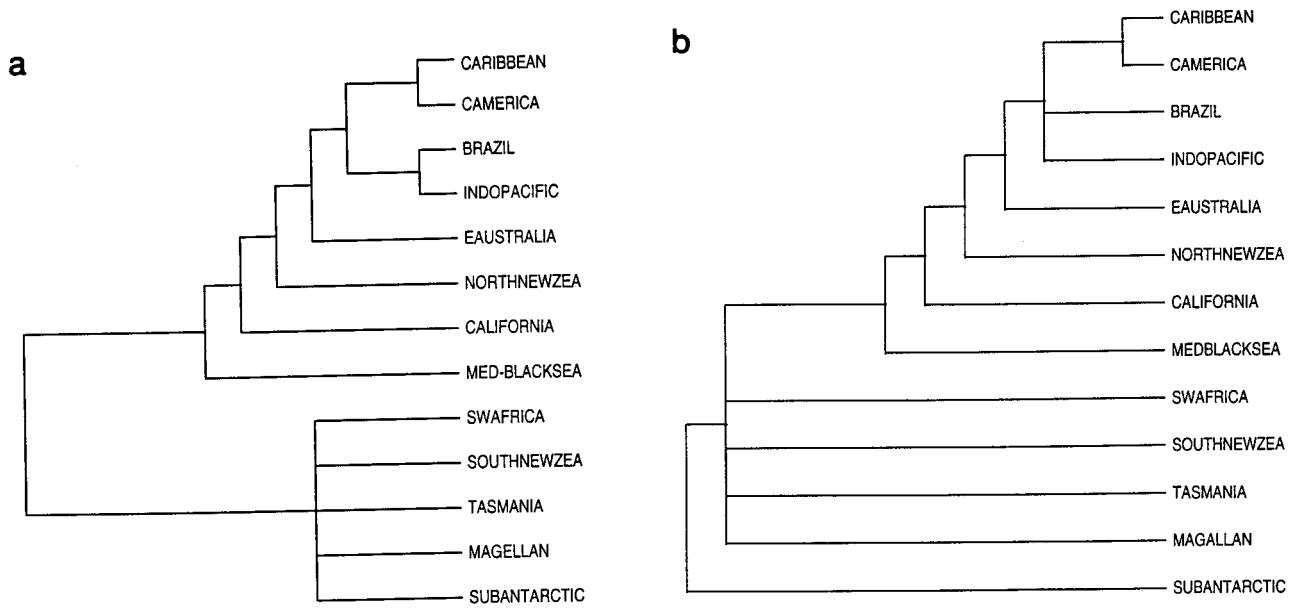


Figure 6. Majority-rule Consensus area cladograms for *Namanereis* species under (a) assumption 0 and (b) assumption 1.

eastern Pacific for much of the time between the late Jurassic (140 Ma) to the early Miocene (20 Ma) (Barron *et al.*, 1981; Smith *et al.*, 1981) when most speciation within the subfamily is likely to have occurred. Such a pattern of area relationships appears to be at odds with the conventional theory of continental drift involving a vast Tethys Sea separating the northern landmass (Laurasia) from the southern landmass (Gondwana) during the Jurassic (145–180 Ma). Under this theory it is generally considered that the Pacific formed an even wider ocean (Panthalassa or Eopacific) in Mesozoic times than it does now (i.e. a substantial barrier). Further, this model generally does not account well for amphi-Pacific sister group relationships, under a vicariance paradigm (Table 3). Of course, some form of co-ordinated dispersal could be invoked to explain the sister group relationships across the Pacific, but as explained above members of the group are not good dispersers.

Under the Pacifica model, proposed by Nur & Ben-Avraham (1977, 1981), an hypothetical continent, Pacifica, situated off eastern Gondwana began fragmenting and its pieces drifted northward in the early Mesozoic (225–180 Ma). The continental fragments (and their biotas) eventually collided with, and formed the allochthonous terranes of western North and South America, and northeast Asia. Although the model fits well the distribution of many Pacific basin biotas (see Nur & Ben-Avraham, 1981; Sluys, 1994, for examples) and therefore explains well amphi-Pacific and amphitropical distributions (Table 3), none of the *Namanereidinae* considered in the present analysis occur on the allochthonous terranes of the Pacific rim. The widespread species group, *Namanereis littoralis*, which was not included in the analysis occurs in both the western part of North America and northeast Asia, but it is not restricted to these areas. Therefore the Pacifica model, which resembles the conventional palaeogeographic model in

Table 3. Three common palaeogeographic models—Classical continental drift theory, Pacifica, and Expanding Earth (*sensu* Shields, 1979)—and their relative explanatory powers of biotic distribution patterns, based on a vicariance paradigm.

distribution type	Classical	Pacifica	Expanding Earth
amphi-Pacific Ocean	poor	good (only on allochthonous terranes)	good
amphi-Atlantic Ocean	good	good	good
amphi-Indian Ocean	good	good	good
amphitropical	poor	good (only in Pacific, on allochthonous terranes)	reasonable
pantropical	good	good	reasonable

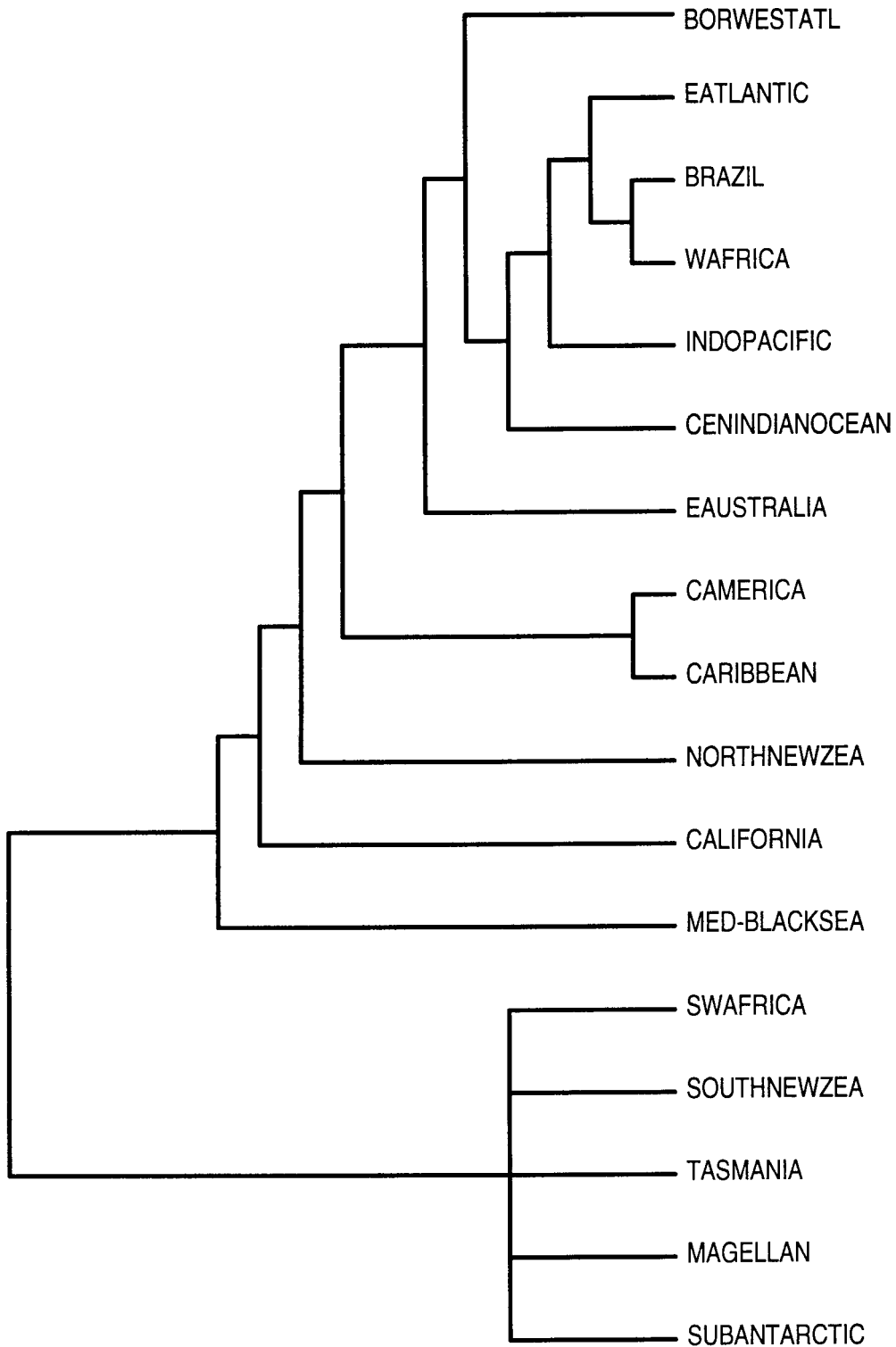


Figure 7. Global area cladogram for Namanereidinae under assumption 0.

terms of requiring the existence of an enlarged Pacific during the Jurassic, does not account well for amphi-Pacific and amphitropical distributions as displayed by the Namanereidinae.

In contrast the area relationships of the Namanereidinae

fit well the predictions of the expanding earth theory (Carey, 1976; Owen, 1976; Shields, 1976, 1979), although the various authors have different assumptions of the rate of earth expansion (from 60 to 80% of its current size during the early Jurassic, 200–180 Ma). The model that best

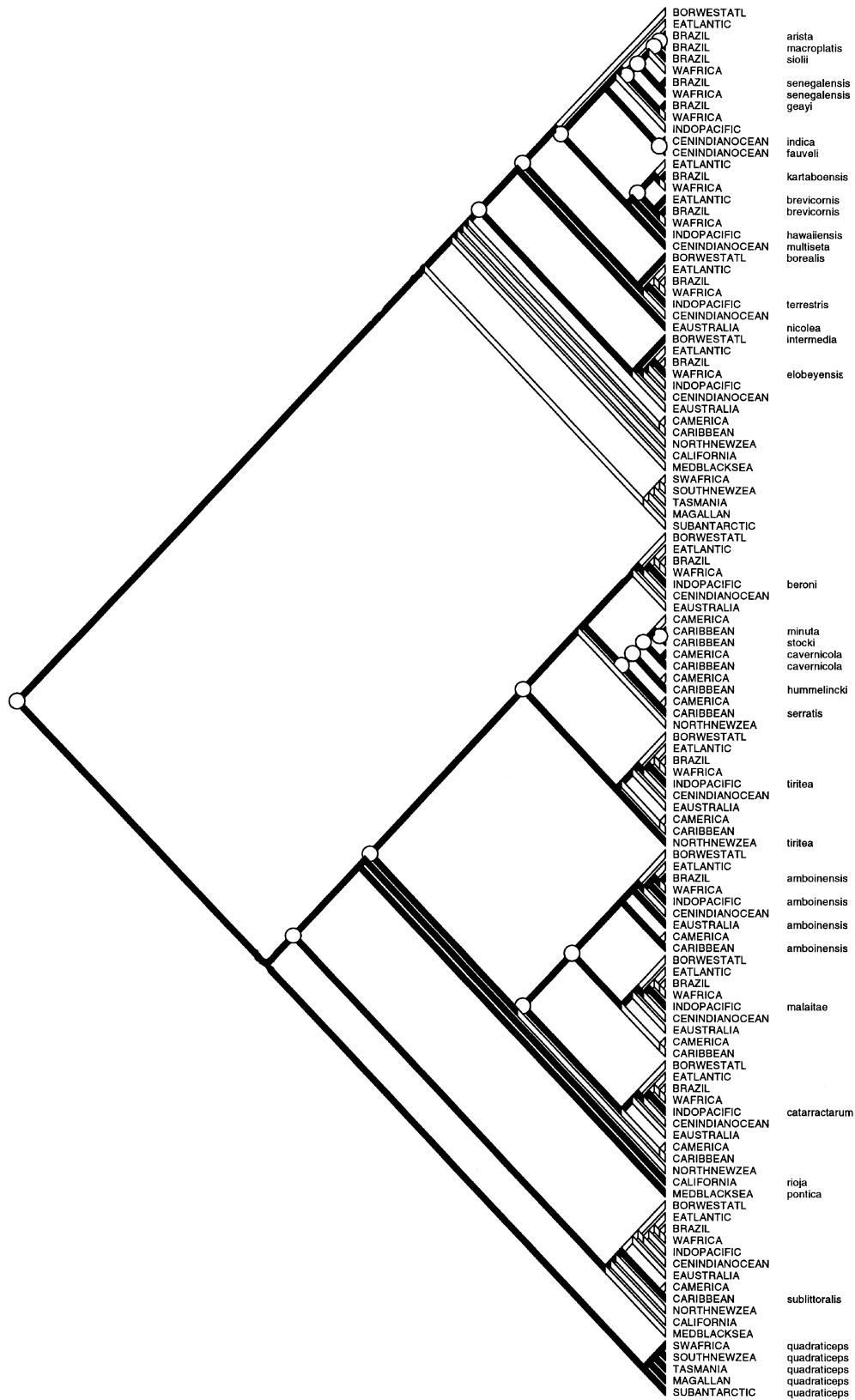


Figure 8. Taxon cladogram of Fig. 1 reconciled with global area cladogram (Fig. 7). Duplication events are indicated with a circle at the node, additions by hollow branches, and losses are the taxa missing from corresponding areas. See text for further explanation.

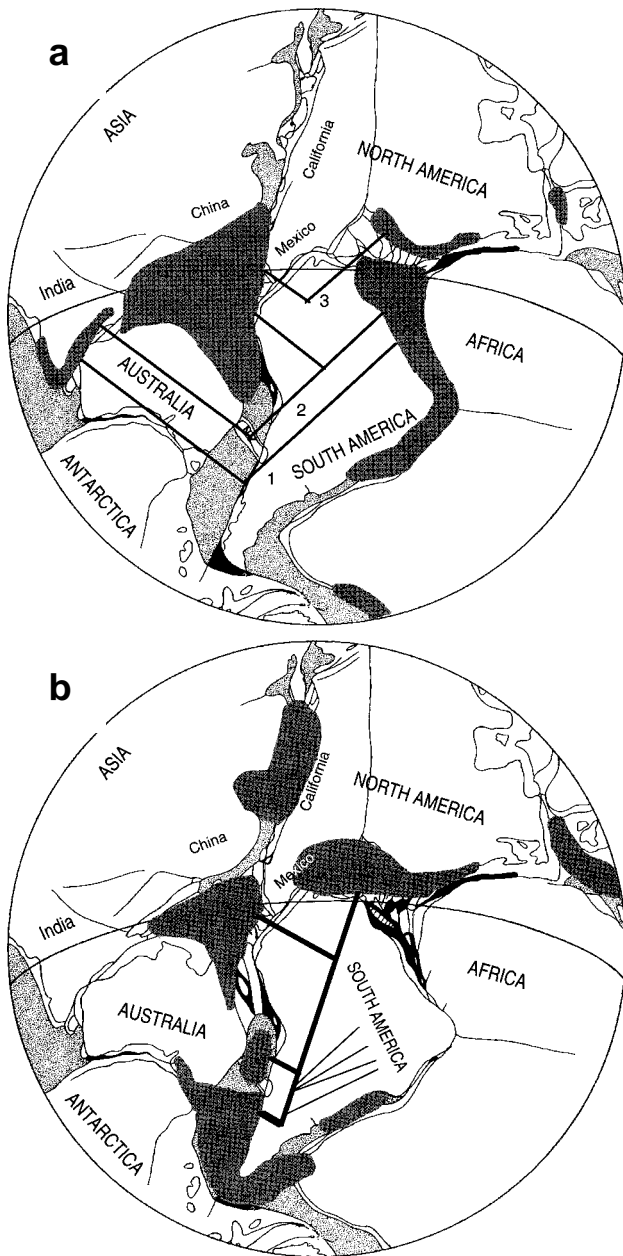


Figure 9. Pacific region of Pangaea during the Jurassic as hypothesised by Shields (1979) (after Matile [1990]) together with present-day distributions of sister groups as indicated in Fig. 1. (a) *Namalycastis* clade excluding the species group *N. abiuma* (southeast Africa) and the aberrant record of *N. brevicornis* (western France). (b) *Namanereis* clade excluding the species group *N. littoralis* (northeast Asia, western North America, southeastern South America, eastern Atlantic-Mediterranean).

explains the biogeography of the Namanereidinae appears to be the one proposed by Shields (1976, 1979) in which the continents of the early Jurassic fitted together tightly, with the Pacific almost closed and the tropics of Asia and the Americas in close proximity (Fig. 9a,b). The south Pacific is thought to have begun forming in the late Jurassic

(Shields, 1979). The general pattern of speciation within the Namanereidinae appears to concur with this sequence of geological events, although the more complex pattern of speciation within *Namalycastis* is difficult to reconcile precisely with the timing of geological events predicted by the model. Within *Namalycastis* three amphi-Pacific sister group relationships can be identified (Fig. 9a), each indicating close links between areas that are now widely separated. It is postulated that the ancestor of *Namalycastis* was widespread throughout the tropical regions in the early Jurassic and that speciation was facilitated by the subsequent rifting of the Pacific, particularly in the equatorial region. By contrast, early speciation within *Namanereis* occurred in southern latitudes with latter events occurring in what is now the Indo-Pacific and Caribbean areas (Fig. 9b). It follows then that the stem species from which all Namanereidinae were derived had a wide distribution along the continental margins of both the tropics and southern (emerging) Pacific. The major series of geological events beginning in the Jurassic, including rifting in the Pacific, under the expanding earth model provides a plausible vicariant speciation mechanism for the Namanereidinae. Further, it would imply that the namanereidine ancestor should be at least 200 My, although an older age is possible.

Vicariance by rifting appears to be an important method of speciation within the Namanereidinae, especially in historically tectonically-active areas such as the Indo-Pacific and Caribbean. Ross & Scotese (1988) have characterised these areas (Gulf of Mexico-Caribbean region and Southeast Asia) as interplate zones, in which tectonic evolution is controlled solely by the interactions of the major plates around them. Other vicariant mechanisms such as changes in sea level and uplifting of coastal areas may also have been important, especially for the more recent speciation events and in the Indo-Pacific and Caribbean. The freshwater *Namanereis* species in the Caribbean show many similarities in modern day habitat with stygobiontic amphipods; in this group vicariance by marine regressions was considered an important factor in isolating inland populations (Stock, 1980, Notenboom, 1991). The sympatry of related species in both the Caribbean (7 *Namanereis* species) and the Brazil area (7 *Namalycastis* species) may either be due to a multiple speciation event following the formation of a barrier, or that speciation occurred allopatrically, but later species dispersed from the original environment.

In more recent times (Miocene-Pleistocene), glacial activity is thought to be the cause of the disjunct species distributions displayed by many amphi-Pacific polychaete species. Uschakov (1971) identified, conservatively, 25 species that exhibit amphi-Pacific distributions, including four species in the Nereididae. As noted by this author the disjunct distributions are best explained by glacial activity—interglacials saw these species having a wider, contiguous, distribution throughout the northern part of the Pacific as well as on either side of the Pacific, but the onset of glacial periods saw ranges contract and the species being driven out of northern waters thus resulting in the present distributions. A similar process might explain the present-day distribution of the *Namanereis quadriceps* species

group in the southern hemisphere. Like the *N. quadriceps* complex, many of the amphi-Pacific boreal species mentioned by Uschakov may be shown with further study to have significant intraspecific genetic differences.

The present results show elements of compatibility with a recent biogeographic study using Parsimony Analysis of Endemicity (Rosen, 1988) of demosponges (van Soest, 1994), but in two other cladistic biogeographic studies (Hajdu, 1995; van Soest & Hajdu, 1997) the resultant area cladograms, which are based on different methods and assumptions, could not be reduced by the authors to single general area cladograms. Therefore comparisons with these studies are probably not useful at present, but they do serve to highlight the significant problems that exist with the methodology and in reconciling area cladograms based on different marine groups. The PAE cladogram of van Soest (1994: fig. 17) supports the monophyletic grouping of the eastern Atlantic–West Africa–Brazil–Caribbean–Indo-Pacific–central Indian Ocean, although there are differences in the branching order of other areas. Further, the “cold water” assemblage in van Soest’s (1994) area cladogram shows an amphitropical sister group relationship, which as explained earlier cannot be explained well by reference to the traditional Pangaeon break-up model (Table 3).

It has been said that in general pantropical groups tend to concur with the theory of Pangaeon breakup whereas amphitropical groups do not (Humphries & Parenti, 1986). For example, the present pantropical distribution of corals, seagrasses and mangroves is thought to be best explained by the existence of widely distributed ancestral tethyan biotas (McCoy & Heck, 1976). Although the Namanereidinae may be regarded as essentially pantropical in distribution, subgroups display other types of large scale distributional patterns (amphi-Pacific, amphi-Atlantic). Amphi-Pacific generalised tracts in particular provide a critical test of competing palaeogeographic models. It would be premature to use the area relationships derived from this study to test the various competing models given the uncertainties that exist in phylogenetic relationships within the group. Nevertheless this analysis demonstrates, I hope, the potential cladistic biogeography holds to critically evaluate competing theories of palaeogeography, none of which, according to Sluys (1994), is fully compatible with all geologic and biogeographic data. Also, it provides an objective and testable way in which to estimate the age of a group, information of particular value for those lacking a good fossil record.

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