

ENDEMISM: ORIGINS AND IMPLICATIONS

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ENDEMISM
CLADISTICS

ABSTRACT. – All taxa are endemic and occur in nested distributions at a range of spatial scales. Distinguishing endemics as either neoendemics or palaeoendemics may not be of practical value in analytical biogeography, but distinguishing extinction mediated endemics (cryptoendemics) from endemics which never had a significantly wider range (euendemics) would be useful for interpreting the history of geographic areas. Only cladistic phylogeny provides a tool for distinguishing these two types of endemic.

ENDÉMISME
CLADISTIQUE

RÉSUMÉ. – Tous les taxons sont endémiques et présentent des répartitions emboîtées selon les échelles spatiales considérées. La distinction de néoendémiques et de paléoendémiques parmi les endémiques peut ne pas avoir de valeur pratique en biogéographie analytique; en revanche, distinguer les endémiques dus à des extinctions (cryptoendémiques) par rapport aux endémiques qui n'ont jamais présenté de distribution significativement plus large (euendémiques) pourrait être utile pour interpréter l'histoire des aires géographiques. Seule, la phylogénie cladistique fournit un outil permettant de distinguer ces deux types d'endémiques.

ENDEMISM IN BIOGEOGRAPHY

Endemism has long been a central theme in biogeography, but it is often misinterpreted as referring only to "narrow" distributions, inferring that only some taxa are endemic. Hengeveld (1990) for example notes "it is hard to distinguish between endemic species and "wides"..." Lincoln *et al.* (1982) define an endemic as "restricted to a particular geographical region", a definition which can be seen to apply, quite correctly, to all organisms.

Since all taxa are endemic, it becomes necessary to categorise them on the basis of their range (extensive or restricted) and of their disjunction. Both range and disjunction are continua and depend upon the spatial scale (Table I, Fig. 1). The ranges of taxa vary from cosmopolitan through continental or ocean basin scales, to single sites. They all show some degree of disjunction, since populations, species and higher taxa are all separated from one another at some spatial scale. A taxon occurring uniquely in a local area might not be considered to have a disjunct distribution at a global scale. On the other hand it clearly could be considered to have a disjunct distribution on a local spatial scale. The decapod crustacean genus *Fredius* Pretzman, for example, is found only in

the Guianan lowlands of South America. When considered globally, this is not a disjunct distribution. Within the Guianan lowlands, however, the species are separated into four major basins, the Orinoco basin, the Essequibo-Cuyuni basin, the Atlantic basin and the Amazon basin (Rodriguez & Campos 1998), a clearly disjunct distribution. Disjunction can come about either through a vicariant event, or through jump dispersal. Vicariance may result from tectonic activity (plate movement, or orogeny), from eustasy or from local climate changes (often linked to tectonic and eustatic events). Jump dispersal occurs when propagules cross an intervening uninhabitable terrain to colonise a new area. This is difficult to discern as a naturally occurring event due to its relative rareness coupled with the short period of time over which scientific records have been kept. It may also be obscured by the frequency of human mediated transport (anthropochore dispersal).

Endemics then, can be classified hierarchically, consisting of a series of nested sets of areas of occupancy by taxa, the largest set of which, under current knowledge, is the entire world. If the biogeographic patterns resulting from multiple nested distributions can be shown to be statistically non-random, they demand a biogeographic interpretation. Some areas can be shown to have greater densities of species which are endemic to

Table I. – Classification of endemics with examples.

Range	Characteristics	Explanation	Example
Global (Holendemic)	Unlimited biogeographically, limited only by ecological and physiological tolerances.	Taxon with good powers of dispersal and colonisation (high competitive advantage) and with sufficient time for establishment.	<i>Gnathophyllum</i> (Fig. 1)
Conjunct broad (Euryendemic)	Broad, more or less continuous or contiguous distribution, limited by biogeographic barriers	Taxon expanding or contracting its range(s), or in quasi stasis or regressive (aging) taxon beginning to contract its range(s), or in quasi stasis	<i>Periclimenella</i> (Fig. 2)
Conjunct narrow (Stenoendemic)	Restricted more or less continuous or contiguous distribution limited by biogeographic barriers	Progressive taxon recently evolved yet to expand its range, or evolved <i>in situ</i> (phylogenesis) from a clade constrained historically by biogeographic barrier(s), or relict (old) taxon.	<i>Macrohectopus</i> (Fig. 2)
Disjunct (Rhoendemic)	Two or more widely disjunct distributions.	1. Vicariated taxon a) Euendemics, isolated by tectonic changes in geography b) Cryptendemics, isolated by extinction of intervening populations or taxa 2. Taxon jump-dispersed across a biogeographic barrier. a) Natural b) Anthropochore	<i>Globosolembos francanni</i> Reid Amphiatlantic (Cape Verde and Florida) Iguanidae New World + Madagascar/Fiji. Extinct in Africa <i>Bubulcus ibis</i> (L.) jump dispersed from Africa to South America in 1920's <i>Elminius modestus</i> Darwin Spread in 20 th century from New Zealand, ? Australia to Europe and South Africa



Fig. 1. – Schematic representation of the formation of endemic types.

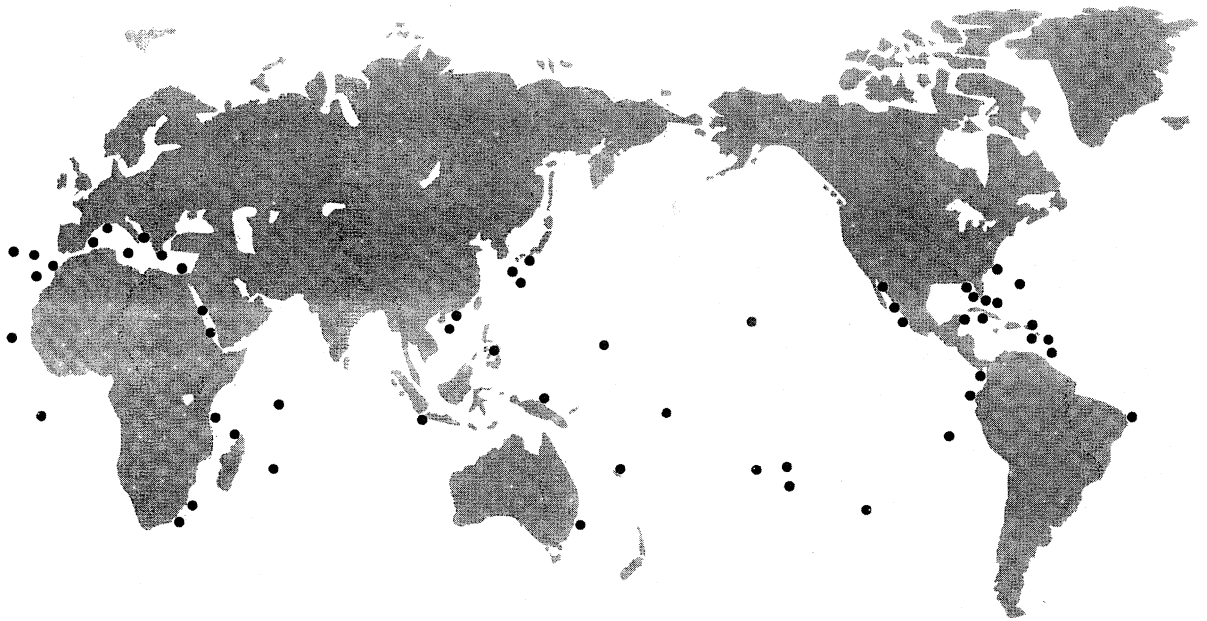


Fig. 2. – The distribution of the shrimp genus *Gnathophyllum* Latreille, a holoendemic.

themselves than have others. These have been described as “areas of endemism” and have formed the nucleus of much biogeographic classification. Areas of endemism are interpreted as areas of high endemism separated from other such areas by a decided gap. The gap may be defined as an area of low endemism between the two areas of high endemism e.g. the Sinaloan gap between the Cortez and the Mexican marine Provinces. Alternatively it may be defined as the region of co-occurrence of endpoints in species distributions (Hastings 2000).

The first biogeographer to employ endemism as an analytical, rather than a descriptive tool, was probably Wallace (1876) who used the numbers of endemics as a measure of island age. He hypothesised that the more endemic species that occurred on an island, the more archaic that island was likely to be, the assumption being that older islands had experienced a longer period of time for the occurrence of phylogenesis.

Croizat (1958), developed a biogeographic methodology (panbiogeography) for transforming the recorded distributions of individual taxa into simplified pathways (tracks) and then combining several of these individual pathways into a summary (generalised track) which could be used to hypothesise the historical evolution of the biota concerned. This method has been further refined or applied by Page (1987), Craw (1989), Morrone & Lopretto (1994) and others. Meanwhile, Hennig (1966) developed a method for reconstructing phylogenies based on evolutionary descent. It was left to Nelson & Platnick (1981) to synthesise these two methods in their seminal book on cladistics

and vicariance. The use of cladistic methodology to answer biogeographic questions has been further developed in recent years by several authors, notably Humphries & Parenti (1986, 1999).

In cladistic biogeography, a phylogeny is first determined, after which, known distributions of the taxa in the phylogeny are superimposed upon the terminal nodes of the cladogram. It is the ancestor-descendent branching of a clade which indicates the sequence (although not the timing) of vicariant events and hence the relationship (and relative age) of each area. Areas of endemism are not a primary component of any data set analysed in cladistic biogeography and the number of endemics in a given area (*cf.* Wallace above) is irrelevant to any hypotheses of area relationships. In contrast, endemics have been used as the primary biogeographic data set in parsimony analysis of endemism (PAE) devised by Rosen & Smith (1988). PAE uses a cladistic method, but bypasses the requirement for a prior phylogenetic analysis. Taxa are treated as equivalent to characters and their distributions are the equivalent of character states. In cladistic terminology, taxa which occur in one place only are equivalent to autapomorphies, those occurring in all of the studied sites are equivalent to plesiomorphies and as in phylogenetic cladistics, neither have information content and are accordingly omitted from the analysis. Taxa occurring in some but not all of the areas under study (equivalent to synapomorphies) and which also lack an extrinsic distribution, are the only ones considered to have biogeographic information content in this method. The assumption in PAE is that two (or more) areas sharing endemic taxa are in

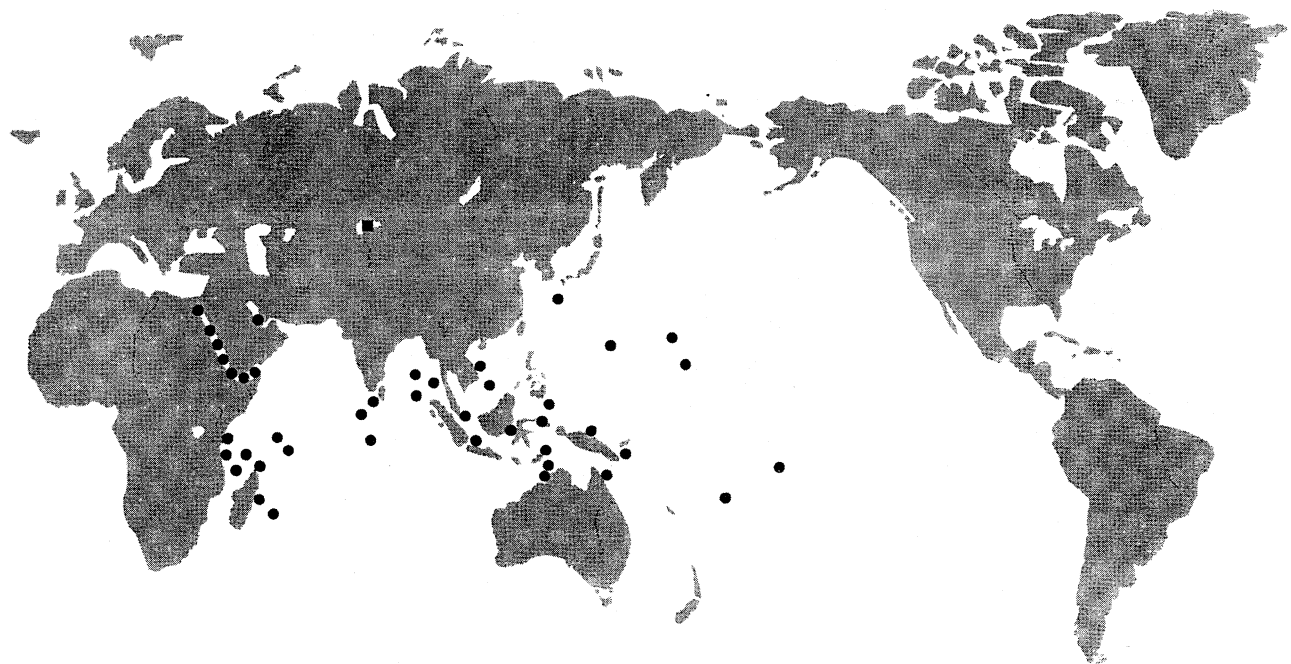


Fig. 3. – The distribution of the euryendemic shrimp genus *Periclimenella* Bruce (closed circles) and of the stenoendemic amphipod genus *Macrohectopus* Stebbing (closed square).

some way more “related” to each another, as a result of a lack of historical biogeographic barriers between them, than either is to any other area that does not share with them those same taxa. Humphries (2000), it should be noted, strongly criticises this method, asserting that, by bypassing taxic homology, it has corrupted the meaning of area homology. In PAE, the taxa are derived character states (synapomorphies) of the areas. Because PAE makes the inference that areas uniquely sharing taxa are more related one to another than to areas lacking these same taxa, it depends upon an assumption that extinction has not significantly modified the distribution patterns.

If a biogeographic analysis based on endemics is to be meaningful, it is necessary to distinguish between on the one hand, absent having never been present in the area (equivalent to symplesiomorphic in phylogenetic cladistics) and on the other hand, lost from the area i.e. extinct (equivalent to synapomorphic). Any analysis of endemics needs to be based entirely upon “synapomorphies”, which include both “present now” and “present once but now extinct”. Iguanid lizards, for example, occur among other places, in Madagascar and South

America, but not in Africa. Few biogeographers would posit a closer ancestral relationship between Madagascar and South America than between Madagascar and Africa. Iguanids almost certainly did occur in Africa but became extinct there (presumably through competition with more advanced agamid lizards). Thus, in cladistic terms, iguanids do occur in Africa but in modified form (they have been lost rather than having never been present). It could be argued that the same assumptions about “loss” are made in phylogenetic cladistics with regard to missing character states. However, data for falsifying a given hypothesis are more readily called upon in phylogenetic analysis. In a phylogenetic analysis, characters may be polarised by outgroup analysis, thus facilitating the identification of lost (rather than never evolved) states. PAE is not amenable to outgroup analysis. Clearly the outgroup would have to be an area outside the area of study which by the criteria set in PAE could exist only in the state “absent”. In addition, in phylogenetic cladistic analyses a number of unrelated character types may be analysed, allowing multiple corroboration, whereas PAE uses only one character type, the taxon.

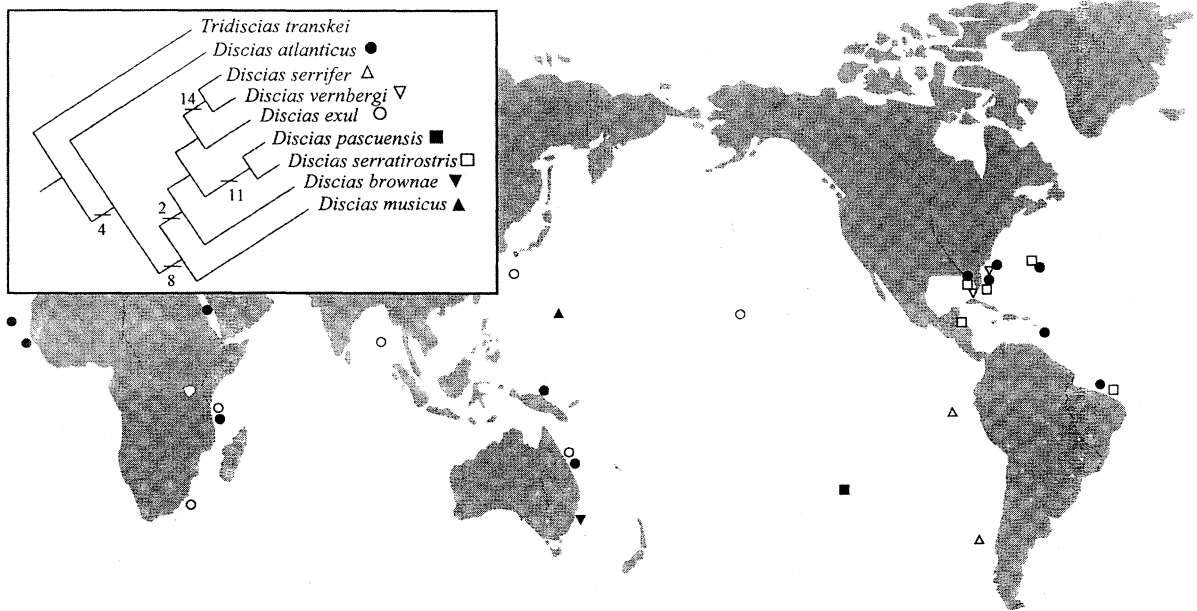


Fig. 4. – The distribution and phylogeny of the shrimp genus *Discias* Rathbun (for character matrix see appendix 1).

Vicariance biogeography then, based on phylogenetic cladistics, provides the most robust biogeographic technique, with the fewest assumptions. However, it requires well founded phylogenies which at this stage are missing for the vast majority of taxa. PAE may be flawed by its lack of an underlying phylogeny, but it can, if the signal is greater than the background noise, provide, in the absence of a sound phylogeny, a “rough and ready” technique for highlighting vicariant events, particularly when more than one level of the taxonomic hierarchy is used (see for example Myers 1991). The use of more than one taxonomic group may increase the confidence levels further, because it is parsimonious to assume that extinction events would not have affected distantly related taxa in an identical way. Differences in dispersal potential between taxa, however, need careful consideration, because such differences can strongly influence a hypothesis (see for example Myers 1993)

THE SPECTRE OF EXTINCTION

A taxon having a limited geographical range attributable to recency of origin (because theoretically there has been insufficient time for it to expand its range) has been termed a neoendemic. A taxon with a limited geographical range even though it has a considerable evolutionary age, i.e. a relict having undergone extensive extinctions, has been termed a

palaeoendemic (Engler 1882). Paleoendemism should, in theory, provide a signal of ancient biogeography provided that it is possible to distinguish real absences from extinctions. In practice, distinguishing endemics as either new or old may not be particularly informative in a biogeographic analysis. The limited distribution of neoendemism is assumed to be due to the fact that they have not yet had time to expand their ranges. This may not hold true for jump dispersers, which on entering a “new” area in which they have had no recent evolutionary history find vacant niches or poorly competitive residents (see Sax & Brown 2000). There is also, a spatial component (independent of the temporal component) of range expansion, i.e. the presence of biogeographic barriers, which cannot be ignored. Organisms trapped on an island (either a true island or a continental island) may be archaic (by definition palaeoendemism), but if they have had no opportunity during their evolutionary history to expand their range, they will give the same biogeographic signal as neoendemism. If, they have undergone *in situ* phylogenesis then the result will be a flock of taxa of variable ages. The age of a taxon is not critical; of importance is whether it once had a much wider range since modified by extinctions. Most species will have undergone some population extinctions in their evolutionary history, but it is necessary in most types of biogeographic analysis to be able to discern those species which have modified their distributions significantly through prior extinctions. Clearly the biogeographic interpretation of endemism depends upon the spatio-temporal scale of the analysis and the level in the taxonomic hierarchy. In the early Tertiary, adapid lemurs are known as fos-

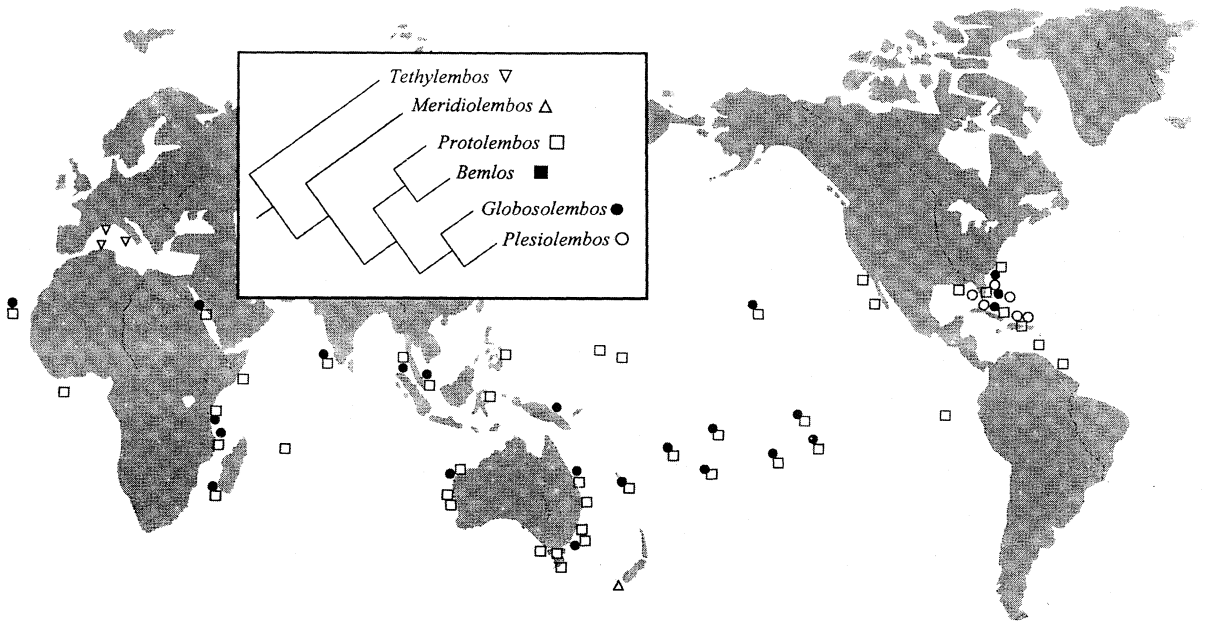


Fig. 5. – The distribution and phylogeny of the *Bemlos* clade (Amphipoda: Aorinae) (phylogeny from Myers 1988).

sils from America (Notharctinae) and Europe (Adapinae) (Hill 1953). At some stage Adapinae reached Madagascar where they have since undergone explosive phylogenesis, producing a high diversity of *in situ* endemic taxa. The Malgache lemurs can therefore be defined either as relict paleoendemics (the adapid clade) or as *in situ* neoendemics (the species of Lemuridae, Indridae and Daubentoniidae). Either definition is correct for a given context.

It would be particularly valuable to be able to distinguish between distributions mediated by extensive extinction, here referred to as cryptoendemics and those whose distributions have not been significantly altered by prior extinctions, here referred to as euendemics (see Table I). Indeed, without this knowledge, we may not be able to interpret areas of endemism effectively. In general, disjunct species are likely to be euendemics. If they had been isolated for considerable periods of time they would almost certainly have changed from their ancestors through anagenetic processes (selection or genetic drift). Endemic sister taxa and higher taxa represent *in situ* evolution (phylogenesis) from a common ancestor and may be euendemics or cryptoendemics. The higher in the taxonomic hierarchy the older the ancestral geographic relationship.

UNDERSTANDING ENDEMIC PATTERNS

If endemism is to be used as a primary database for any biogeographic analysis, it is necessary to be

certain that the areas under study are not paraphyletic. If endemic taxa in the areas under study were at one time distributed extrinsically and have only since become restricted to the areas under study (by extinctions in the extrinsic area), then the areas analysed are in fact paraphyletic. Any assumptions about biogeographic relationship would, in such a scenario, be fundamentally flawed. Even if the taxa concerned have never had an extrinsic distribution, they may once have been more widely distributed within the area (thus confounding the signal of area relationships) or may even have been cosmopolitan within the area (symplesiomorphic) so confounding any inferences of relationship.

It is clearly not possible to determine the real distribution of any taxon through its history, even with the existence of a fossil record. Phylogenetic analyses, however, provide insights that enable parsimonious decisions to be made between the claims of competing hypotheses.

Frequently some members of a taxon are stenoendemics whilst others are euryendemics. In such cases, a clade in which an ancestral taxon is widespread and the derived taxa have a restricted distribution will suggest a different history from a clade in which one or more of the derived taxa are widespread. The genus *Discias* Rathbun (Caridea, Disciidae), for example, is widespread across all world oceans (Fig. 4). Two species, *D. atlanticus* Gurney and *D. exul* Kemp are euryendemics, the former in all oceans, the latter in the Indo-west Pacific. Two species *D. serratiostris* Lebour and *D. serrifer* Rathbun are rhoendemics, the former in the western Atlantic, the other in the Eastern Pacific

and four *D. pascuensis* Fransen, *D. vernbergi* Boothe & Heard, *D. musicus* Holthuis, and *D. brownae* Kensley are stenoendemics. A phylogenetic analysis (Fig. 4) reveals that *D. atlanticus*, the widespread taxon, is ancestral whilst *D. pascuensis* for example – a species known only from Easter Island – is a more recently derived taxon. With these data, it is parsimonious to hypothesise that *D. pascuensis* is a stenoendemic whose ancestor arrived at some time in Easter Island and has not undergone significant extinction events elsewhere on a global scale. A similar scenario could be applied to the other stenoendemics, *D. serratirostris*, *D. serrifer* and *D. vernbergi*. The euryendemic *D. exul*, has spread widely in the Indo-west Pacific but has been unable to cross the ocean gap to the east Pacific, suggesting that the range expansion occurred after the development of that gap in the late Mesozoic (see Myers 1991). It is also reasonable to hypothesise that the extant distribution of *D. atlanticus* represents a distribution derived at a time in the past when the world was topographically different and colonisation of all the major oceans was still a possibility. A competing hypothesis could be that the ancestral *D. atlanticus* maintained a limited distribution over most of its evolutionary history and only recently spread rapidly to attain its present range. Such a jump-dispersal scenario is, however, less parsimonious since it requires two assumptions:

1. that the taxon had a restricted range through most of its evolutionary history and
2. that it underwent more recent jump-dispersal into all the major oceans.

The vicariant hypothesis requires only one assumption, that it became widespread during a period in history when barriers to its dispersal were not significant.

An alternative pattern is illustrated by a phylogeny of the *Bemlos* clade of aorid amphipods (Fig. 5). Two genera, *Bemlos* Shoemaker and *Globosolembos* Myers are euryendemics, occurring throughout the tropical oceans of the world and extending into the warm temperate of Australia. Ancestral taxa *Meridiolembos* Myers and *Tethylembos* Myers are stenoendemics restricted to the Mediterranean and New Zealand respectively. The most parsimonious hypothesis is that *Tethylembos* and *Meridiolembos* are antitropical relicts of an ancient flock of taxa most of which were driven to extinction within the tropics by competition with derived taxa now represented by the widespread tropical genera *Bemlos* and *Globosolembos*. The sister taxon of *Bemlos* (*Protolembos* Myers) and of *Globosolembos* (*Plesiolembos* Myers) are stenoendemics. They may be either ancestral or derived with respect to their euryendemic sister taxon.

If a taxon is composed of several narrow rhoendemics, these may be either vicariants, or

relicts of a once more widely distributed clade. Again, a phylogenetic analysis can help to illuminate the spatial parameters of the ancestral clade.

The genus *Parisia* Holthuis consists of six species, four in Madagascar and two in Australia. The two Australian species share a number of character states and appear to be more closely related to each other than either is to the Malagasy species (Williams 1964). No cladistic analysis has yet been performed on this genus but if the above relationships are confirmed, there is an orderly relationship between phylogeny and distribution. Under these circumstances there is no reason to hypothesise other than that each clade evolved *in situ*, after a vicariant event had first divided the ancestral taxon. An alternative to this pattern would be realised if a phylogenetic analysis revealed that the closest sister of a taxon was not its nearest geographic neighbour. The barnacle genus *Chthamalus* Ranzani may be an example of this. The two species *Chthamalus montagui* Southward and *C. stellatus* (Poli), sympatric along north-east Atlantic shores are apparently not sister taxa (Dando & Southward 1980). *C. stellatus* is thought to be more closely related to two species from the west Atlantic, viz. *C. angustitergum* Pilsbry and *C. bisinuatus* Pilsbry, whilst *C. montagui* is thought to be more closely related to Pacific species such as *C. challengerii* Hoek and *C. dalli* Pilsbry. Unfortunately no cladistic analysis has been carried out on *Chthamalus* to support the relationships suggested by morphological and electrophoretic studies within the genus. Three possible explanations, other than a falsified phylogeny, exist for such a phylogenetic relationship:

- 1) They may have been euryendemics which subsequently underwent extensive extinction to leave a geographically unordered pattern of relicts in widely separated localities.
- 2) Tectonic activity may have altered the earth's geography to such an extent that the extant distributions can only be understood by plotting them onto a map of ancient topography
- 3) Jump dispersal may have occurred.

CONCLUDING COMMENTS

Higher taxa above the genus level generally have little biogeographic information content. In the main, families are cosmopolitan, although this may hold less for plants. Genera tend to be more narrowly endemic and species are frequently stenoendemic. Endemism originates in three different ways:

- 1) by extinction of populations in part of their range.
- 2) by range restriction through biogeographic barriers (after anagenesis or phylogenesis)

3) by jump dispersal followed by anagenesis or phylogenesis.

Whilst no known technique can distinguish absolutely between these different routes to endemism, phylogenetic cladistics provides the best method on which to erect a parsimonious hypothesis.

With an awareness of the importance of preserving the Earth's biodiversity comes the need not only to determine which areas contain large numbers of species unique to them, but also how such areas of endemism originate.

An appreciation of the complexity of origins of endemics and of the alternative routes to narrow endemism may improve our understanding of how areas of endemism have come about.

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