
Towards a panbiogeography of the seas

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A contrast is drawn between the concept of speciation favoured in the Darwin–Wallace biogeographic paradigm (founder dispersal from a centre of origin) and in panbiogeography (vicariance or allopatry). Ordinary ecological dispersal is distinguished from founder dispersal. A survey of recent literature indicates that ideas on many aspects of marine biology are converging on a panbiogeographic view. Panbiogeographic conclusions supported in recent work include the following observations: fossils give minimum ages for groups and most taxa are considerably older than their earliest known fossil; Pacific/Atlantic divergence calibrations based on the rise of the Isthmus of Panama at 3 Ma are flawed; for these two reasons most molecular clock calibrations for marine groups are also flawed; the means of dispersal of taxa do not correlate with their actual distributions; populations of marine species may be closed systems because of self-recruitment; most marine taxa show at least some degree of vicariant differentiation and vicariance is surprisingly common among what were previously assumed to be uniform, widespread taxa; mangrove and seagrass biogeography and migration patterns in marine taxa are best explained by vicariance; the Indian Ocean and the Pacific Ocean represent major biogeographic regions and diversity in the Indo-Australian Archipelago is related to Indian Ocean/Pacific Ocean vicariance; distribution in the Pacific is not the result of founder dispersal; distribution in the south-west Pacific is accounted for by accretion tectonics which bring about distribution by accumulation and juxtaposition of communities; tectonic uplift and subsidence can directly affect vertical distribution of marine communities; substantial parallels exist between the biogeography of terrestrial and marine taxa; biogeographically and geologically composite areas are tractable using panbiogeographic analysis; metapopulation models are more realistic than the mainland/island dispersal models used in the equilibrium theory of island biogeography; and regional biogeography is a major determinant of local community composition. © 2005 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2005, 84, 675–723.

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INTRODUCTION

With the rise of interest in biodiversity and its regional structure over the last 15 years, biogeography has been attracting more attention than ever. Unfortunately, biogeographic methodology is still notoriously controversial. There are two main paradigms used in studying and interpreting distributions: traditional Darwin–Wallace dispersal (Darwin, 1859; Wallace, 1860, 1876; Matthew, 1915), in which taxa evolve at a point centre of origin and attain their range by physical movement out from there; and panbiogeography (Croizat, 1958, 1968a, b, 1975; Craw, Grehan & Heads, 1999; Crisci, Katinas & Posadas, 2003; Llorente *et al.*, 2003), in which taxa develop by

vicariance or allopatry over a region and there is no point centre of origin. Because Darwin–Wallace dispersal is so widely assumed in studies of the marine environment, this concept and alternatives are discussed below in some detail. Whittaker (1998) wrote that: ‘Historical biogeography has lately been rather polarized into two supposedly opposing camps, the dispersalist and vicariance biogeographers, each concerned with how disjunct distributions arise.’ However, the topic of the debate is rather more general than this – it is not just about disjunct distributions, but about how any speciation (and all other form-making and taxon-making) occurs, whether disjunct or not.

Panbiogeographic methodology involves the comparative study of as many distributions of unrelated taxa as possible and integration of these with tectonic

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history. It contrasts with methods used in dispersal biogeography in which the focus is on the study group and its ecology, especially its means of dispersal (Wilson, 1991). Panbiogeographic methods have been used to analyse distributions of reef fishes and marine macroalgae in the Pacific (Heads, 1983; Chin, Brown & Heads, 1991), marine and terrestrial organisms in south-east Asia (McManus, 1985), and marine triclad platyhelminths world-wide (Sluys, 1989). Hajdu (1998) analysed sponge distributions in a paper titled 'Toward a panbiogeography of the seas', and in a recent volume dedicated to Croizat, Aguilar-Aguilar & Contreras-Medina (2001) gave a panbiogeographic analysis of the marine mammals of Mexico.

FOUNDER DISPERSAL, VICARIANCE AND ECOLOGICAL DISPERSAL

CENTRES OF ORIGIN AND THE 'COMMON-SENSE' VIEW OF DISPERSAL

Darwin (1859) felt that each species begins by evolving at a point centre of origin from which it spreads out, and that the simplicity of this view 'captivates the mind' (cf. Heads, 1985). Most subsequent authors have also been captivated by this concept.

Ekman's (1953) comprehensive and lucid book on marine zoogeography is probably the single most influential work in the field – a great deal of contemporary work comprises timid variations on just a few of his themes. Ekman utilized Darwinian dispersal, arguing, for example, that 'Chance . . . plays a larger part in the possibilities of distribution for the fishes than for most other shelf animals', and that 'The longer the time the greater the part played by the so-called chance factor, that is to say, the interaction of unknown factors . . .' He relied on currents as means of dispersal, and explained faunistic boundaries, such as his famous 'East Pacific barrier' ('surmounted by very few species'), as 'barriers' to dispersal.

Veron (1995) argued that 'Dispersion (migration), the Achilles heel of vicariance, is of overwhelming importance in most corals' and that 'The presence of wide geographic disjunctures within the distribution ranges of species are of great biogeographic interest because they demonstrate the capacity . . . of corals to disperse over long distances.' Likewise, authors have asserted simply that 'Biogeography starts at the colonizing event' (Planes, 2002), and that island populations 'have certainly experienced a founder effect initially' (Planes & Fauvelot, 2002). Veron (1995) concluded tersely that 'Distribution patterns [in marine taxa] are the outcome of distribution by currents'. But is this 'common-sense' view actually true?

As George (1987) pointed out, it was discrepancies between theories of centres of origin, in particular how

one derived the centre of origin, that led to Croizat's development of the generalized tracks/vicariance approach. For example, authors such as Darwin (1859), Matthew (1915), Darlington (1957), Frey (1993) and Briggs (2003a) have assumed that the most advanced species occur at the centre of origin and out-compete the primitive ones which migrate away. In contrast, other dispersalist authors, such as Mayr (1942), Hennig (1966) and the modern phylogeographers (Avice, 2000), assume that the most primitive taxa occur at the centre of origin and it is the advanced ones which have migrated away ('Progression Rule'). (Nelson, 2004, noted that 'Hennig's rule is now reborn – as if it were for the first time – within phylogeography.') This is a fundamental split within the dispersalist school, but neither assumption is used in vicariance cladistics (e.g. Platnick, 1981; Nelson, 2004) or in panbiogeography.

Briggs (2000, 2003a) claimed that the pattern in which the 'apomorphic' species occur at marine centres of origin has been 'consistently displayed' in the Indo-West Pacific, but this is quite incorrect – a point centre of origin has been theorized countless times but it has never been 'displayed' or demonstrated as existing for any species, let alone being characterized by 'apomorphic species'. For traditional dispersalists such as Briggs, deducing which species are 'primitive' and which are 'advanced' in a genus, and so which evolved from which, are important procedures. However, panbiogeography and cladistics agree that while characters might be primitive or derived, taxa are generally not. The species in a genus are alternative recombinations of characters, and the species are derived from a common ancestor, not one from the other (Nelson, 2004).

Despite his adherence to Darwin–Wallace dispersal, as cited above, Veron (1995) concluded that 'The fundamental strength of Darwinian evolution, the most universally accepted and fundamental concept of Nature the world has ever seen, is its all-encompassing internal consistency . . . Yet the geographic basis of Darwin's evolution, his centres of origin, have been roundly rejected by most [coral] biogeographers'. Darwin's centres of origin theory, 'the first of the major theories of biogeography, is strongly refuted as a whole by present knowledge of coral species . . .' What are the alternatives to a Darwinian 'centre'?

VICARIANCE AND DISPERSAL

Scheltema (1995), a dispersalist, argued that 'the capacity for dispersal is not the sole condition which contributes to the geographic distribution of benthic species . . . there are also ecological constraints . . .' In this view, the centre of origin, capacity for dispersal and ecological constraints are the only factors govern-

ing distribution, and evolution (for example, allopatric speciation) has nothing to do with it. As indicated, dispersalists and ecologists often see dispersal as 'the movement of individuals away from a starting location' (Mora & Sale, 2002), but this is a very narrow interpretation and again overlooks the evolutionary component. Dispersal in the most general sense can be defined as 'any and all change of position' (Clements & Shelford, 1939) and in panbiogeography, dispersal, the process leading to distribution, can be brought about simply by evolution (i.e. vicariance) with no physical movement of individuals. In this concept, the distribution patterns emerge by development on a broad front, in the same way that the picture in a developing photograph or the veins in a leaf do, not by the movement of individuals or propagules out from an original parent pair at a point centre of origin. With respect to the spatial component of evolution, in panbiogeography a concept of 'dispersal' as physical movement from a centre of origin is replaced with one of vicariance mediated by tectonics, especially rifting, accretion, uplift and subsidence. This is not to say that dispersal does not occur; but it does not occur at random – the distribution patterns are too clear. In other words, taxa have moved together, in an orderly way, which presumably means over prior, totally different geographies. In many locally endemic taxa, dispersing stages almost certainly reach far outside the established range of the taxon but do not establish there. This is possibly due to competition from, for example, congeneric vicariants. But what is the process which led to the local endemism in the first place?

Vicariance is one of the main patterns and processes on which the panbiogeographic paradigm is based and along with Croizat's other concepts was for many years anathema to orthodox biology (e.g. Mayr, 1982). However, it is now one of the most common terms in biogeography and appears regularly even in journals which long opposed Croizat's work as a whole. While panbiogeography may not yet appear to have had much impact on marine biology, in several ways the field is moving towards a panbiogeographic view and in particular the key concept of vicariance is now well known. Indeed, in his study of coral distribution, Veron (1995) argued that vicariance biogeography was having the sort of impact on biogeographic concepts that equilibrium theory of island biogeography had had 20 years earlier. Bowen & Grant (1997) suggested that 'vicariance has been a dominant paradigm in biogeography for two decades'. This seems a little optimistic – most biogeography is still heavily dispersalist in orientation. But there are many signs of change.

The process that Mayr (1942) called 'allopatric speciation' is one particular case of the general process that Croizat called 'vicariant form-making'. This process does not necessarily involve formation of species

or indeed any taxa, as it may result only in sub-taxonomic character changes. Orthodox theoretical accounts of 'modes of speciation' usually cite the process, giving theoretical examples such as a new mountain range dividing populations as it rises and leading to the differentiation of new species. In these examples earth and life in general (not just one taxon) evolve *together*, and similar distributions would be expected in many taxa. Furthermore, there is no point centre of origin; each of the two or more segregates of the ancestor differentiates over a broad region.

However, in discussing actual examples of biogeographic patterns, instead of using vicariance as a 'default' explanation Mayr and his followers usually invoke a form of founder effect or jump dispersal, in which a taxon migrates across, for example, an already existing mountain range, and then, for no apparent reason other than 'chance', stops migrating. In this process earth and life evolve *independently*, and widely shared distribution patterns would not be predicted. In fact, as this concept of dispersal relies on 'chance', it cannot logically explain patterns of shared distributions among taxa, especially among those with totally different ecology and means of dispersal. As most distributions are demonstrably shared by many different organisms, this process can be ruled out a priori as a mechanism of dispersal. Nevertheless, dispersalists often invoke the most unlikely migrations, arguing that given enough time anything is possible. Thus, for dispersalist biogeographers, 'When all else fails, there is one final resort as explanation for distribution patterns: chance' (Kay, 1995). However, this concept of chance is very different from 'chance' in the sense of a mathematically calculated probability; it simply means 'the explanation is unknown' and is not in itself a scientific proposal.

In a typical example of a dispersalist approach (accepting vicariance in theory but not in practice), Whittaker (1998) wrote that 'The first step of this model [allopatric speciation] suggests a vicariant event (barrier formation), whereas, in the oceanic island context, the starting point will more commonly be dispersal across a pre-existing barrier, i.e. a founding population making chance landfall. But the idea is the same, gene flow is restricted after the founding event . . .' Again, this begs the question: why exactly does immigration and gene flow stop after the founding event? The only answer is 'chance'. Furthermore, Whittaker noted that 'It is particularly problematic that founding *events* (i.e. colonization) have been theorized to produce a variety of rather different founder effects . . . [italics in original], and that some authors have queried the significance of founder effects'. In fact, the whole field of founder effects is problematic. Tokeshi (1999) argued that 'data which can unequivocally be related to such peripatric speciation are not

easy to identify . . . the founder effect based on random genetic drift does not seem to be an effective means of speciation . . .'

Nei (2002) concluded that while the theory of speciation by the founder principle has been popular for the past 40 years, it is 'speculation, and there has been no empirical study of this hypothesis'. Recent studies of highly polymorphic MHC loci in Galapagos finches and cichlid fishes in African lakes have 'led to one of the most important findings in evolutionary biology in recent years: that speciation by the founder principle may not be very common after all.'

Palumbi (1994) concluded that 'it is unlikely that evolutionary models that rely on very small population sizes will explain a large fraction of speciation events among marine organisms with the potential for long-distance dispersal.'

ECOLOGICAL DISPERSAL

Ecologists generally use 'dispersal' to mean the ordinary, observable movement of plants and animals and their propagules (e.g. Clobert *et al.*, 2001; Bullock, Kenward & Hails, 2002). This process does not involve differentiation. 'Dispersal' in the sense of dispersalist biogeographers is a very different process, as it involves differentiation and speciation. Rosen (1988) gave an important review of reef coral biogeography and observed that: 'there is considerable confusion generated by different meanings of "dispersal" . . . It is particularly the question of "long-distance dispersal" in reef corals and other organisms . . . that highlights confusion in dispersalist explanations for distributions . . . Even if the widespread trans-Eastern Pacific pattern in modern reef corals is currently being maintained by long-distance dispersion . . . this would not necessarily explain how this pattern arose in the first place . . . The mode of speciation envisaged by advocates of centres of origin theories has never been made clear for reef corals . . . On the other hand, it has long been known that the basic features of reef coral distribution correspond broadly to those of other reef-associated and tropical marine organisms, especially mangroves, seagrasses and many larger benthonic foraminiferan, algal, molluscan, echinoderm, decapod crustacean and fish groups. A reasonable inference . . . is that these organisms share a similar biogeographical history.' He concluded that empirical analysis 'points to the importance of geotectonic events . . . newer ideas reflect a search for testable alternatives to the older ideas of an Indo-West Pacific centre of origin. In particular, hypotheses about vicariance . . . all merit further testing . . .'

The difference between ordinary range expansion (Croizat's 'mobilism') and the highly theoretical founder or chance dispersal has been highlighted by

many authors. For example, Liebermann (2003) referred to congruent, temporally correlated range expansion of many clades as 'geo-dispersal'. This term was coined to distinguish it from traditional (i.e. founder) dispersal, which is 'a very different process' and 'is by its very nature incongruent and not replicated in independent clades'.

Long-distance dispersal, in the simple sense of range expansion, not in the sense of founder effect dispersal (movement and then cessation of movement), explains similarities between biotas of different localities, not differences. Vicariance explains differences. If all taxa underwent chance dispersal, all taxa, even the slowest worms and molluscs, could theoretically spread all over the earth, at least in climatically favourable regions, in the geological time available. In fact, of course, the biota of the earth is highly divided geographically, with hardly any undifferentiated, cosmopolitan taxa. For example, a perusal of the world distribution records of the best-known group, the birds, shows this clearly. In the marine realm, many higher taxa (families and genera) of corals are widespread through the Indian and Pacific Oceans, as are many of the species. However, many genera and species of corals are restricted in one way or another and these are of special interest as they indicate evolutionary connections. Veron (2000) referred to the 'many thousands' of readily recognizable geographic subspecies of corals and these are also important indicators of putative genetic differentiation.

DISPERSAL AND GEOLOGY

In sum, both founder dispersal and vicariance are suggested by their proponents to bring about differentiation because of a break or cessation of movement of individuals and gene flow. Veron (1995) concluded 'dispersion (or migration), which increases distribution range, must alternate in time with the absence of dispersion, which allows vicariance to take place'. This idea of an alternation of mobilism and immobilism is pure panbiogeography. In founder dispersal the break is caused by 'chance'. In vicariance the break is caused by geological or other environmental change.

In practice, until the rise of molecular studies, dispersal biogeography characteristically ignored geology older than a million years or so. Events in the Pliocene and Miocene were usually regarded as almost inconceivably 'ancient' – a rather different time-scale from geology. This is because dispersal biogeography stresses, indeed, virtually relies upon, current and Quaternary ecology as the explanation for patterns. For example, in his classic work on the avifauna of New Guinea, Diamond (1972) overlooked the fact

that his large-scale Okapa–Karimui transect, which crossed the boundaries of many bird distributions, also crossed the major tectonic boundary in New Guinea (Heads, 2001a). Even when geology is considered, it is only to examine earlier (e.g. Gondwanic) landscapes and seascapes as possible avenues for migration from a centre of origin.

While panbiogeography involves close study of tectonics, palaeontology (along with genetics) has long been the most dispersalist of all the biological disciplines and is thoroughly permeated with the assumptions of that paradigm. For example, Rosen (1988) pointed out that ‘a biota first recognized from a particular horizon (T1) in a particular region (A) is often referred to as the “A biota”. This in itself seems reasonable, but when a similar, but not necessarily identical, biota is also recognized at a later horizon (T2) in another region (B), it is sometimes also referred to as the “A biota” . . . The reason for this seems to be because the younger biota is believed to consist largely of direct descendants of the A biota . . . The underlying assumption is that of dispersal, often from a supposed centre of origin (in this case region A), and clearly introduces bias into an apparently objective faunistic observation.’

PRACTICAL IMPLICATIONS OF THE CONCEPT OF DISPERSAL

If an author assumes founder effect dispersal, he or she will assume that only ‘chance’ processes are at work and that given enough time any distribution can develop. Thus there will be no point in looking for any correlation with anything except current ecology and little or no motivation for mapping and undertaking comparative analysis of distributions of taxa with different ecology. In fact, chance dispersal has usually been assumed and this has led to biological (including palaeontological) mapping lagging far behind geological (stratigraphic and tectonic) mapping. There is no biological equivalent of the mapping project assigned in many university first-year geology courses. A very high proportion of otherwise incredibly detailed monographs of taxonomic groups contain no distribution maps at all. This is particularly common in studies of marine groups, in which long-distance dispersal is even more universally accepted than in terrestrial taxa. It is impossible even to imagine a comparable regional geological study without maps.

Thus, if founder dispersal is assumed, that is usually the end of comparative biogeographic analysis. On the other hand, if vicariance is assumed, discussion and analysis can begin, as the author will want to compare the distributions of the taxa under immediate consideration with a wide range of others and also with aspects of tectonic history.

In fact, founder dispersal does not make sense as a process (it sometimes explains how taxa might get somewhere, but not why they would differ), nor does it make any sense of the patterns. Most aspects of most distribution patterns are simply ignored. In the corals, for example, discussion has nearly always focused on the patterns of taxonomic richness in different areas; individual distributions have hardly ever been mentioned let alone analysed. Good data on distribution are available (Hoeksema, 1989; Wallace, 1999a; Veron, 2000). However, many of the most obvious questions remain totally ignored: for example, how and why can a coral be endemic to Madagascar and Indonesia, and not be in the Red Sea or Australia? How can a coral surround W Indonesia and not be there, although a close relative is? Why are there so many endemic corals in Madagascar, the Red Sea, Sri Lanka, Japan and Hawaii, but virtually none in Queensland, New Caledonia or Fiji? Why do so many corals reach their eastern limits in Fiji and Hawaii and not occur in the south-east Pacific? None of these distributions makes any sense at all if dispersal is simply by movement and distribution is simply correlated with current environmental factors.

MOLECULAR BIOGEOGRAPHY

This approach, also known as phylogeography, is generally just a technically advanced form of founder dispersalism and is based on the same key concepts of centre of origin and means of dispersal. As Ebach & Humphries (2002) noted: ‘Phylogeography has reinvented dispersal biogeography . . . Phylogeography is limited in its perspective, as it has not overcome the logical hurdles already addressed in cladistic biogeographical methodology over the last two decades. Prior knowledge, it seems, is neither assumed nor necessary in phylogeography’. Nelson (2004) agreed: ‘Palaeontology of the past is revived in molecular systematics of the present, in the search for ancestors and centres of origin.’

Croizat (1977) regarded evolutionary development as ‘a function of (a) panbiogeography and (b) molecular biology’ and in their review of reef fish history Bellwood & Wainwright (2002) wrote that ‘The combination of fossil evidence, molecular systematics, and vicariance biogeography . . . offers an exciting avenue for future research.’ This is certainly true and the cladograms produced in many molecular studies are of tremendous interest.

Unfortunately, the vast majority of molecular results are interpreted using dispersalist theory and dubious clock calibrations (see below). An example of a dispersalist mode of reasoning that has been adopted uncritically by phylogeography is the assumption that

a 'basal' group is somehow primitive and ancestral, and occupies the centre of origin or ancestral area (cf. 'Centres of origin', above). For example, in the worldwide labrid genus *Thalassoma*, Bernardi *et al.* (2003) wrote that the Hawaiian *T. ballieui* and the Western Australian *T. septemfasciata* 'form a sister clade to all other studied taxa', but in the abstract, they wrote that these are 'ancestral species'. In the eelpouts (*Lycodes*: Zoarcidae), the long-tailed Pacific species are basal and it is claimed that 'this supports earlier theories of Pacific origin of the genus/family' (Møller & Gravlund, 2003). Basal lineages in *Ophioblennius* (Blenniidae) occur in the eastern Pacific/western Atlantic, 'strongly indicating that the genus evolved in this region' (Muss *et al.*, 2001). In fact, a 'basal' group is just the smaller of two sister groups. Both will have the same age and neither one is derived from the other. Other problems with phylogeography and the clock approach can be seen clearly in some examples.

The 14 species of eared seals (Otariidae) range widely around the Pacific and Southern Oceans, with largely vicariant distributions. *Callorhinus* (Canada – Japan) emerged as the basal clade in Wynen *et al.*'s (2001) molecular study and without any further explanation these authors proposed a classic Matthewian centre of origin for the family near Vancouver. This is presumably related to the basal position of *Callorhinus*, but as explained already, the 'basal' group is just a small sister group, not an ancestor, and there is no reason to assume that its range (or, in this case, part of its range) is the centre of origin. Wynen *et al.* suggested that the members of the family have subsequently colonized the rest of the range using their 'remarkable dispersal abilities'. However, some difficulties remain: 'it is difficult to hypothesize on the mechanisms leading to current distribution of *Arctocephalus philippii* [Juan Fernandez] and *A. townsendi* [California], straddling that of a less related species' – *A. galapagoensis* of the Galapagos. This is probably a very ordinary case of distribution by parallel arcs, with the inner arc held by *A. galapagoensis* and also *Zalophus* (Galapagos, Mexico). Other problems not addressed by Wynen *et al.* and not predicted for a group with 'remarkable dispersal abilities' include: why exactly is *Otaria* restricted to western South America, *Phocarctos* to islands south of New Zealand, and *Neophoca* to south-west Australia?

Waters & Roy (2004) sought to explain the distribution of the starfish *Patiriella exigua*, which ranges from St Helena to south-east Australia and Lord Howe Island, a thoroughly standard Indian Ocean distribution which they claimed is 'unusual'. Because their cladogram for the populations is more complex than a simple Africa/Australia split they argued that the distribution cannot be the result of vicariance, an argu-

ment that panbiogeography has dealt with many times (e.g. Craw *et al.*, 1999, and references therein). For example, the distributions may be older than the geological events cited and/or the relevant geology may be more complex than a simple split. In fact, the genetic clades within the species show massive vicariance – Waters & Roy use the term 'marked phylogeographic structure' – 'evident across small geographic scales in Australia and South Africa', which basically means throughout the species' range. As the authors admit, this structure 'indicates that gene flow among populations may be generally insufficient to prevent the local evolution of monophyly'. In other words, dispersal is not important and vicariance is. In fact, the basal split in the species is between the Cape Town–Amsterdam Island populations and all the others. No explanation for this is given; Waters & Roy simply recite the usual argument that 'Organisms that possess strong migratory ability can undergo major range expansions through the colonization of new regions'. However, there is an important difference between what an organism can in theory do in terms of colonization and what it actually does in practice. In fact, any organism, given suitable ecology, can undergo massive range expansion, whether it has especially 'strong migratory ability' or not. For example, there are weedy species of snails, worms, etc., that have invaded very large areas. Conversely, many species with very high 'migratory ability', such as albatrosses and fruit bats, can in theory, but do not in practice, undergo rapid range expansion.

Despite all this direct evidence of vicariance, Waters & Roy (2004) concluded that 'small' genetic divergences between African and Australian haplotypes 'strongly suggest Pleistocene dispersal'. As pointed out by many authors, degree of divergence is not necessarily a guide to either the time involved in evolution or the age of that evolutionary event. Waters & Roy claimed that their study 'is one of the first to provide convincing evidence' and even 'compelling evidence' of long-distance rafting. But convincing or compelling to whom? Presumably the authors were convinced or they would not have argued for it, and whether the readers are convinced is surely up to them to decide.

Waters & Roy (2004) argued that 'Phylogeography has transformed biogeographic research, a field previously dogged by rhetoric and speculation, into a rigorous discipline centred on hypothesis testing (Wallis and Trewick, 2001)'. In fact, as Ebach & Humphries (2002), Nelson (2004) and others have indicated, there has been no transformation. The phylogeographers have confused technical advances with conceptual advances. Phylogeography is a new discipline only in its technical aspects; its theory and practice are not centred on hypothesis testing but on reiterating the

preconceptions of Matthew (1915) and the New York school. Its practitioners are unaware of this because they themselves are genetics technicians, not biogeographers, and have very little knowledge of that subject or its history.

Waters & Roy (2004) ended their paper with the observation that: 'Several recent phylogeographic studies have included statistical tests of dispersal hypotheses and have been published in high-profile biology journals' (references cited), as though the 'profile' of the journal should be used in assessing whether or not the conclusion makes sense.

In a study of the widespread sea-star genus *Coscina-asterias*, Waters & Roy (2003a) reached similar conclusions to those of their 2004 paper. Again, haplotypes exhibited 'strong phylogeographic structure', and again any hint that this is vicariance is carefully avoided. They write (Waters & Roy 2003b) that 'The "southern" clade of Australia is also represented in New Zealand, indicating Pleistocene oceanic dispersal'. They even made (2003a) the curious claim that the presence of 'related haplotypes' on Tasmania and New Zealand 'suggests that long distance dispersal is an important biogeographical process'. The assumption that degree of difference is proportional to time and that the calibration is reliable is made throughout the paper. Thus, what are supposedly 'shallow' genetic differences mean that vicariance can be 'clearly' rejected, and again the authors claim that their data provide 'strong' evidence that the distribution is attributable to long-distance dispersal. Waters & Roy (2003a) write, correctly, that while a number of studies use the final rise of the Isthmus of Panama as a means of calibrating molecular clocks, 'such clock calibrations should be treated with caution'. However, they themselves apply molecular calibrations derived from sister taxa isolated by the Isthmus of Panama. So much for their 'strong' evidence and 'clear' rejection of vicariance.

However, they also admit (2003b) that 'The fact that phylogenetic gaps in *C. muricata* are consistent with provincial marine biogeographical boundaries ... suggests a common underlying cause for interspecific and intraspecific biogeography.' They cite notolabrid and aplodactylid fishes with biogeographical discontinuities that are 'almost identical' to those of *C. muricata*, and also 'concordant phylogeographical and biogeographical provinces' in Australia and California. Concordant geography is actually found in taxa of all ranks, above and below species (Croizat, 1964) and the very important principle that it is due to a 'common underlying cause' forms the basis of panbiogeography.

In a molecular study of the world-wide family Calyptraeidae (Gastropoda), Collin (2003) suggested that 'geographic patterns of speciation in marine

invertebrates are not well understood', but in fact the patterns are well known, it is the mode of formation of the patterns which is not well understood. As argued here, this is because authors have relied on fundamentally flawed concepts of dispersal. In both its procedures and conclusions, Collin's work is a classic example of Matthewian phylogeography. For example, she wrote that the 'prevailing view' in marine biogeography is one of 'broad dispersal' and in the first paragraph alone cited Mayr (1954) as a key reference for different topics three times. Although Collin claimed that 'Previous studies of marine species have seldom included examination of the biogeography of speciose clades throughout their range', she failed even to mention classic work of this type by her Smithsonian colleague Springer (1982, 1988), presumably because it supports vicariance.

Following Matthew, she proposed a centre of origin of the Calyptraeidae in the Northern Hemisphere followed by 15 dispersal events to regions south of the equator, despite the fact that in her study the basal clade of the family comprises the two New Zealand genera *Maoricrypta* (incl. *Zegalerus*; also in south-east Australia) and *Sigapatella* and three southern Chinese species.

Collin suggested that the geographic distributions of the species she studied 'demonstrate numerous dispersal events', but of course these are theorized not demonstrated. She wrote: 'Calyptraeids show patterns of global movement (Fig. 7 [a cladogram]), and closely related species can occur half-way around the world from each other ... Long distance dispersal is evident in *Crepidipatella*, where *C. capensis* from South Africa is nested within a clade of species from Chile, and in *Trochita* where *T. calyptraeiformis* from Chile and Peru is nested within a clade of species from the northeast Pacific.' Leaving aside the question of the rather small sample of species in her study (15–35% of the total), it is simply not true that long-distance dispersal is 'evident' in these clades. Given the standard distributions it is probably not even likely.

At the start of her study Collin noted that many previously accepted groupings in the family occur in restricted geographic areas, but cannot be distinguished from other groups on the basis of shell characters (Collin does not mention other characters) and have been based merely on locality. For example, she cited *Maoricrypta* and *Sigapatella* from New Zealand, with shells indistinguishable from *Crepidula* and *Calyptraea*, respectively. She wrote that 'Acceptance of any of the [merely] geography-based taxonomic groupings implies a belief that diversification occurs locally and that long-distance dispersal across ocean basins does not occur often', which is logical. However, when her own study also found strong support for these two genera, she did not invoke local diversification and

limited long-distance dispersal, but instead reiterated centre of origin/dispersal theories.

PANBIOGEOGRAPHIC CONCEPTS APPEARING IN RECENT STUDIES

DATING TAXA

Dispersalists have often argued that the major geological changes, such as continental drift, that could have brought about vicariance are simply too old to have had any affect on the modern taxa, which are much younger. But are they really?

Fossils give minimum ages for groups

Establishing the age of taxa has traditionally been done using fossils; usually the fossil record has been taken at its face value and read literally, that is, the age of the taxon is equated with the age of its oldest fossil. For example, the oldest reported fossils of the widespread tropical alga *Halimeda* are Late Cretaceous (Kooistra, Calderón & Hillis, 1999) and so these authors cited 'the Cretaceous age of the genus'. The major problems with this approach are usually ignored and there is even a recent book titled '*The Adequacy of the Fossil Record*' (Donovan & Paul, 1998). Darlington (1957: 320) felt that the fossil record 'allows an almost magical view into the past' and Briggs (1974b: 249) used exactly the same words. This approach is what Croizat (1952) called 'the cult of the petrifact', and its adherents usually assume that the location of the earliest known fossil of a group is also the group's centre of origin.

The fossil record is sometimes admitted to be 'imperfect', but this is putting it very mildly. Rhodes (1979) wrote that about 91 000 species of fossils are known, but it is estimated that the total number of species that have lived in the geological past may be of the order of 500 million. More than half the classes of living organisms are unrepresented as fossils. Nebelsick (1996) concluded that 'fossil biodiversities must be regarded as underestimates even when dealing with organisms such as the sea-urchins which are well-skeletonized and have a long fossil record.' In most areas the land lacks not only fossils but also many geological strata and Smith (2001) observed that 'the rock record available for sampling is itself distorted by major systematic biases'. He suggested that taking fossil records of Phanerozoic diversity at face value was 'problematic' and argued for a more cautious approach.

New discoveries of fossils much older than the previously known oldest members of a group are made regularly. For example, molecular evidence suggested that vestimentiferan tubeworms (Pycnogonida) may be less than 100 m.y. old (Black *et al.*, 1997). However,

new fossil evidence subsequently indicated they are over 400 Myr old (Little *et al.*, 1997). Fossil loriform primates were previously known back to 20 Ma but fossils dated at 41–37 Ma were found recently (Seiffert, Simons & Attia, 2003). Crown-group salamanders were recently found in Middle Jurassic rocks, pre-dating the previous record by some 100 m.y. (Ke-Qin Gao & Shubin, 2003). Metatheria (marsupials and their relatives) were known back to 75 Ma, but a fossil dated at 125 Ma has been described by Luo *et al.* (2003). These new 'oldest fossils' are often regarded as of immense significance and reported in prestigious journals, and their location taken to represent a new centre of origin.

Discussing skates (see below), Last & Yearsley (2002) wrote that fossils 'often only constitute a minimal record of the age of the taxon', but in fact this is virtually always true; as Cunningham & Collins (1994) observed: 'fossil calibrations give minimum times of divergence [and] will yield overestimates of rates to the extent that cladogenesis precedes the first occurrence of identifiable descendant species'. Last & Yearsley (2002) concluded that given the relatively poor fossil record of skates and the 'complex biogeographical structure of the extant fauna the group is likely to be older than the fossil evidence suggests'. What the fossil record can do is give broad averages of level of organization through time. The names of the geological eras reflect the fact that Cainozoic (Phillips, 1841) members of a group (*kainos* = new) have a modern stamp and usually look rather different from Mesozoic (Phillips, 1841) and Palaeozoic (Sedgwick, 1838) members. But a literal reading of the details of the fossil record is bound to be misleading.

Purvis & Hector (2000) noted that new molecular phylogenies are 'pushing back the origins of many groups to long before their earliest known fossils . . . Many orders of mammals and birds are now thought to have originated long before the end-Cretaceous extinction . . . which was thought previously to have been the signal for their radiation . . . The puzzle is the absence of fossils'. Panbiogeographic analyses (e.g. Croizat, 1958, 1964) predict these earlier dates and the absence of fossils cannot really be regarded as a puzzle given the fragmentary nature of the fossil record.

The complete reliance of dispersal theory on a literal reading of the fossil record is shown clearly in a recent paper of Briggs (2003b). Much molecular work (summarized in Avise, 2000) has concluded that the global distributions of groups such as aplocheiloid fishes, cichlid fishes, ratite birds and parrots are the result of Mesozoic vicariance (Briggs calls it 'fractionation'). Briggs dismissed all these results, however, and concluded that they would be 'more meaningful' if they were 'better integrated' with the 'body of knowl-

edge that already exists', i.e. the literal reading of the fossil record.

Pacific/Atlantic divergence calibrations based on the rise of the Isthmus of Panama at 3 Ma are flawed

Occasionally authors admit the well-known limitations of using fossils and instead base ideas of age (and molecular clock calibrations) on interpretations of tectonics and biogeography. Unfortunately these are often very simplistic. For example, it is often assumed that vicariant populations on either side of the Isthmus of Panama began to diverge at c. 3 Ma, because that is the age of the final rise of the Isthmus. Muss *et al.* (2001) wrote that 'The Isthmus of Panama has been a boon to evolutionary studies of marine organisms', because it provides a 'robust framework' for evaluating divergence times. The rise of the Isthmus at 3 Ma is one of the most important dates in dispersal biogeography as it is supposed to mark the beginning of the 'Great American Interchange' of terrestrial faunas, one of the central pillars of dispersalist orthodoxy (Wallace, 1876; Stehli & Webb, 1985).

However, an original supporter of Matthew has written a telling critique of the 'Interchange' theory (Myers, 1966) and Croizat (1975) questioned the significance of the Isthmus of Panama, emphasizing instead the complex earlier geology of the Colombia–Central America region. Other geologists and biologists have also suggested much earlier isthmian links between North and South America in the late Mesozoic or early Cenozoic that may have led to Pacific/Atlantic isolation and differentiation of marine taxa. White (1986) suggested this for nearshore fishes, the two subfamilies of silversides (Atherinidae). Savin & Douglas (1985) also referred to many openings and closings of the Isthmus.

Rosen (1988) pointed out that although the differentiation of the main centres of endemism for reef corals, the Atlantic and Indo-Pacific, was often attributed to the Pliocene emergence of the isthmus, the emergence actually long post-dates faunal differentiation of reef corals (early Cainozoic – based on age of fossilization).

de Weerd (1990) commented that 'The Pliocene uplift of the Panamanian Isthmus is generally recognized as the vicariance event leading to sister-group relationships at both sides of the Isthmus . . . The conspecificity of the Brazilian and eastern Caribbean populations of *Millepora squarrosa* [a hydrocoral] does not fit very well with this timing, since the age of the Amazon–Orinoco barrier has been hypothesized . . . to be of Miocene age, thus older than the Isthmus. Glynn (1972, 1982) has presented the hypothesis that 'a restriction of flow across Central America occurred already before the rise of the Isthmus . . . It is suggested that the speciation of the ancestor of *M. squarrosa* and [its Indo-Pacific sister species]

M. platyphylla into these species has taken place before the rise of the Isthmus . . .'

Likewise, Knowlton *et al.* (1993) suggested that at least some of the trans-Panama species pairs of the snapping shrimp *Alpheus* may have diverged before the final closure of the Panama seaway, in a pattern of staggered rather than simultaneous isolation. Knowlton & Weigt (1998) estimated times of separation of trans-Panama pairs *Alpheus* ranging from 3 to 18 Ma for 15 species pairs. They assumed that the divergence of the pair with the least difference was due to Isthmus closure, but this pair, too, may have diverged earlier.

Based on fossil evidence of divergence a hypothesis of sequential vicariance was also proposed in the *Strombina* group (Columbellidae) of gastropods in the Caribbean and Eastern Pacific prior to 3.5 Ma; there was already substantial divergence at the subgeneric level at 5.0 Ma (Jackson *et al.*, 1993). Banford *et al.* (1999) suggested that divergence between Pacific and Atlantic members of Spanish mackerels (*Scomberomorus*: Scombridae) took place at around 6.3 Ma, again pre-dating the closure of the isthmus.

For trans-isthmian species of the muricid *Plicopurpura*, molecular data give a predicted time of divergence of between 5.6 and 11.4 Ma (Cunningham & Collins, 1994), 'consistent with the hypothesis that many geminate species [closely related species pairs] were divided long before the final closure of the Panama seaway'. Divergences that predate final seaway closure have also been recorded for geminate pairs of bivalve molluscs (Arcidae) dated at up to 30 Ma (Marko, 2002) and bryozoans (Cupuladriidae) dated at up to 11 Ma (Dick, Herrera-Cubilla & Jackson, 2003). Cunningham & Collins (1994) concluded that 'Paleontological and molecular data agree that the separation of taxa on either side of the Isthmus of Panama was not a singular event, as had previously been supposed, but most likely took place over millions of years'. This reasonable conclusion has been almost universally ignored by the many authors who continue to rely on the final closing of the Panama seaway to calibrate their molecular clocks. As Knowlton & Weigt (1998) concluded: 'Many past studies may have overestimated rates of molecular evolution because they sampled [trans-Panama] pairs that were separated well before final closure of the Isthmus'.

Muss *et al.* (2001) admitted that the Atlantic and Pacific species of *Ophioblennius* probably diverged prior to the closure of the Isthmus of Panama, but felt that because of this 'a geologically calibrated clock is unavailable'. This simply indicates the extremely narrow approach of many contemporary studies and the excessive reliance placed on this single feature. Of course there are many other geological features in the Pacific and Atlantic Oceans that could be used in calibrations, but for some reason never are.

Molecular clock calibrations are usually flawed

As Palumbi (1997) noted in a review of molecular biogeography of the Pacific, there are 'grave problems' with estimating the timing of species differentiation by molecular methods. As indicated above, the main problem is calibration: the clocks are usually calibrated using unrealistic correlations with palaeogeography or a literal reading of the fossil record. In a typical recent example, Leys, Cooper & Schwarz (2002) claimed that: 'Using a relaxed molecular clock calibrated using fossil carpenter bees, we show [sic] that the major splits in the carpenter bee phylogeny occurred well after the final breakup of Gondwanaland'. In practice, molecular clocks are usually calibrated simply by referring to other calibrations, often of distantly related taxa. Thus the whole literature is based on just a few key papers using fossils in the traditional way or simplistic ideas on palaeogeography and resembles a fragile house of cards. Despite this, many authors regularly exaggerate their findings. For example, in their abstract, Palumbi *et al.* (1997) asserted that Pacific *Echinomera* species 'have speciated within the past one to three million years', although in the text they wrote, more accurately, that the species show 'very low genetic distances [elsewhere they cited "substantial genetic differentiation"]', *implying* recent species formation' (italics added in both quotes).

Living coelacanth fishes (*Latimeria*) comprise one species around the Comoros (off Madagascar) and another species near Sulawesi, 10 000 km away. 'The coelacanth lineage has shown surprisingly few morphological changes through its 360 million year history and *Latimeria* is remarkably similar to its nearest fossil relative *Macropoma*, despite 80 million years of separation.' (Holder *et al.*, 1999). These authors discussed the geographic disjunction and wrote that 'Ideally, a wide range of systematic and ecological information would be used' to distinguish among the different possibilities. This is obviously the correct approach in comparative biology but the authors failed to follow their own advice and in particular neglected to establish whether the distribution was unique or a common pattern. Instead they focused entirely on *Latimeria* and a molecular clock approach. Although they admitted that 'the clock is difficult to calibrate because *Latimeria* has no close living relatives', they inferred that the two species separated at 1.8–11 Ma, with a 'best estimate' of 4.7–6.3 Ma. This approach left the problem unresolved: 'With no fossil record of the age or original geographic range of *Latimeria* it is difficult to postulate historical biogeographic explanations . . . no obvious physical barrier to dispersal between Sulawesi and the western Indian Ocean exists . . . [however] vast expanses of deep water are likely a barrier to dispersal of the adults . . .' They concluded that further living species may be

found and that genetic studies of these 'will help unravel the mysteries', but in the meantime the mystery stands. This study again epitomizes the narrow approach of much modern comparative biology; in fact, of course, the Comoros–Sulawesi disjunction is a standard track (e.g. the prosobranch *Cerithium gloriosum*; Houbriek, 1992), part of the general Madagascar–Indonesia track (e.g. the coral *Montipora orientalis*; Veron, 2000; vol. 1: 114). Springer (1999a) suggested that coelacanths were the result of vicariance events significantly earlier than those suggested by Holder *et al.* at 15–50 Ma, and as these authors admitted, this could be correct 'if slower rates of molecular evolution are considered'.

Quaternary events had minimal influence on distribution

Dispersalists have generally regarded the Pleistocene as the main era in which modern distributions and taxa formed. For example, a symposium volume (dedicated, appropriately enough, to Darwin and Wallace), concluded: 'It seems to be the general consensus that the vast uniformity of life that characterized the early Cenozoic, in both space and time, gradually changed to diversity throughout Tertiary time, in a grand crescendo that reached ecstatic proportions in the Pleistocene' (Hubbs, 1958). Recent authors agree. Lessios, Kessing & Pearse (2001) proposed that Indian Ocean/Pacific Ocean vicariance in marine taxa (discussed below) was due to Pleistocene changes in sea-level. They noted that this is the 'generally accepted explanation' and this is true; countless studies in marine biogeography invoke Pleistocene events to explain distributions.

In contrast, panbiogeography has always opposed the idea that Quaternary events such as the Pleistocene Ice Ages have had much effect on evolution or the main patterns of distribution, although they have caused range contraction and extinction. In particular, panbiogeography opposes the idea that modern distributions are the result of spread from small numbers of 'Ice Age refugia', whether in alpine plants (e.g. Heads, 1994, 2003) or montane birds (Heads, 2001a, 2002). The authors of many recent studies (e.g. Klicka & Zink, 1997; Stewart & Lister, 2001; Unmack, 2001; Wilf *et al.*, 2002; Church *et al.*, 2003) are now coming around to this idea, agreeing that the main aspects of diversity and distribution are much older than the Quaternary and that there were very many refugia during the Ice Ages that preserved the basic patterns, as in metapopulation theory (see below). In a similar example, the Pleistocene history of the Red Sea involved a hypersaline event which is often assumed to have wiped out most if not all the marine fauna. However, Ormond & Edwards (1987) observed that the presence of endemic fishes there without obvious

Indian Ocean counterpart species supports the contention that some Red Sea fauna survived. Righton, Kemp & Ormond (1996) argued that Red Sea endemic fishes may be considerably older than at first appears possible as they may have survived there through the Pleistocene in refugia of very limited extent.

Similarly, Woodland (1986) suggested that distributions of inshore marine fishes in the Indo-Australian Archipelago might be due not to Plio-Pleistocene changes in sea-level, but to the collision of Australia with south-east Asia at 25–20 Ma, and Kott (1985) suggested that Australia–South American ascidians are Gondwanic relics. Over the last 10 years or so, many molecular and other studies have likewise indicated that many marine taxa are older or much older than previously assumed in orthodox dispersal theory (e.g. Wallace *et al.*, 1991; Pandolfi, 1992; Anderson, 2000; Bellwood & Wainwright, 2002; George & Schminke, 2002; Last & Yearsley, 2002; Santini & Winterbottom, 2002; Williams, Reid & Littlewood, 2003). Even ecologists have found it necessary to expand their geological vocabulary beyond Pleistocene and Pliocene to include Miocene and even Oligocene. Future developments, especially refinement of dating, may mean they have to extend their horizons even further back, towards the time of origin of the ‘modern’ groups. As noted above, it is a simple matter of observation that Cainozoic taxa look modern, whereas Mesozoic ones do not. Thus, from the fossil record, the last phase of modernization of life was between the Mesozoic and Cenozoic, not between the Tertiary and Quaternary. The main patterns of modern distribution were probably being laid down at the same time as the modern forms were emerging.

A panbiogeographic approach to dating marine groups

Despite the fact that the entire order Perciformes is generally accepted as Late Cretaceous based on the fossil record, Chao (1986) showed that the distribution of the Sciaenidae (croakers and drums) would best be explained by a Late Jurassic origin of the family. He suggested that a group ancestral to Sciaenidae was distributed through the Tethys and diverged, one to the west (pre-Atlantic) and one to the east (pre-Indo-Pacific). Bellwood & Wainwright (2002) took a similar approach. They wrote that ‘After fossils, the second line of evidence that may provide some indication of the age of reef fish is historical biogeography’. Freshwater fishes are usually assumed to be derived from, and thus to be younger than, marine groups. Bellwood & Wainwright gave a well-reasoned discussion of the family Cichlidae, found in rivers and lakes throughout South America, Africa, Madagascar and southern India. They wrote ‘Either they [cichlid ancestors] were associated with the land masses prior to separation,

cichlid origins thus being at least 100 Ma, or they maintained contact through extensive marine connections. The oldest cichlid fossil is from Africa, 46 Ma. At 100 Ma the origins of the cichlids would predate the earliest fossil of the family and that of any other extant perciform family by over 40 Ma’. Because of this, traditional authors such as Lundberg (1993) favoured a literal reading of the fossil record and so inferred trans-Atlantic dispersal, but Bellwood & Wainwright concluded instead that ‘Cenozoic trans-Atlantic dispersal seems unlikely given the clear regionalisation seen in the major cichlid clades . . . A much older origin for the Cichlidae and the perciformes must remain a possibility, with the Cichlidae being widespread across Gondwana prior to fragmentation . . . Recent biogeographic interpretations based on molecular phylogenies are consistent with these early origins . . . [and suggest that] several reef fish lineages (labrids, pomacentrids, acanthurids, and pomacanthids) were already established prior to Gondwana fragmentation (i.e. over 125 Ma) . . . It is almost axiomatic that the only surprise that the fossil record holds, in terms of the age of taxa, is that taxa are older than previously thought. Care must be taken therefore in ascribing minimum ages.’ Britz (1997) also disagreed with trans-Atlantic dispersal to explain fish distributions, suggesting instead that the origin of African – South American Nandidae dates back to the Late Cretaceous, before the separation of the two continents.

Bellwood & Wainwright (2002) integrated other palaeontological observations with this view. They pointed out that the morphology of marine fish species from Eocene (50 Ma) beds at Monte Bolca, Italy, ‘is almost indistinguishable from that of living representatives. These were not “primitive” precursors of modern forms . . . the level of preservation is such that in some cases pigment patterns can be seen, with striking similarities to living forms . . . On a dive along the coast of the Tethys Sea in the Bolca region 50 million years ago one would see a fish fauna little different from that in the tropics to-day . . . [this] highlights the stability of the taxonomic and morphological characteristics of tropical benthic marine fish faunas throughout the Cenozoic . . . Despite this, only 15 Ma earlier the perciformes are represented by only a few specimens of one species.’ Bellwood & Wainwright thus suggested that ‘the broad similarities in familial composition of modern [tropical] reef fish faunas may reflect an old shared history rather than recent colonization, and that familial differences between reef regions may be explained by subsequent events . . . Gondwanan fragmentation appears to have been a significant factor [also] in the biogeography of temperate fish taxa’. Here Bellwood & Wainwright cited freshwater and marine taxa distributed among South Africa, South America and Australia, for example Aplodactyl-

idae, Latridae, Congiopodidae, Cheilodactylidae, Labridae, Sciaenidae and Sparidae.

Molecular work by Farias *et al.* (1999) gave similar results. The phylogeny for Cichlidae was consistent with ancient vicariance associated with the break-up of Gondwanaland. Other freshwater groups with ancient origins include the characiform fishes (1200 species in 16 families), which occur in freshwater of South America and Africa. Ortí & Meyer (1997) identified three trans-Atlantic clades. All intercontinental distances were large by rDNA standards and interpreted as consistent with an origin by vicariance, caused by the separation of the two continents by continental drift at 90 Ma.

'MEANS OF DISPERSAL' DO NOT CORRELATE WITH DISTRIBUTION

Broad geographic distributions in marine organisms have often been correlated with the presence of a more or less long-lived pelagic larval stage. The need for dispersal is widely regarded as the principal factor selecting for a pelagic larva in reef fishes. Many early authors did express some concerns about dispersal in marine taxa; for example, Knox (1963) noted that the absence of many common and ubiquitous species of New Zealand shores from the nearby Chatham Islands, despite prolonged pelagic development and favourable currents, is 'puzzling'. But until recently, the fundamental importance of dispersal by currents was seldom seriously questioned. However, in his classic study of vicariance in Pacific shore fishes, Springer (1982) agreed with van Balgooy's (1971) observations on plant distribution in the Pacific by concluding: 'I cannot find a clear correlation between distribution and dispersal.' Even though lack of correlation between means of dispersal and distribution is a 'negative result' in the context of the dominant paradigm of Darwin–Wallace dispersal, and as such may be prejudiced against in publication (Browman, 1999), other studies have reached the same conclusion as Springer.

In species of angelfishes (Pomacanthidae), Thresher & Brothers (1985) found no direct correlation between geographic range size and either duration of the pelagic larval stage or adult body size. 'If anything, the relationship between larval duration and species distribution was negative, i.e. two Hawaiian endemic *Centropyge* species had larval durations among the longest of the species we examined, whereas the most widely distributed species examined, *Pomacanthus imperator*, had one of the shortest larval durations.' In contrast, *P. annularis* occurs only in a few island groups, even though these two congeners are 'virtually identical' in size and larval duration. The authors carefully examined these 'strikingly poor' correlations, and concluded that they are likely to be robust for the

family. They suggested that some other factor, such as relative specificity of recruitment sites, is as yet being overlooked 'or that historical factors are of paramount importance.' The latter idea is supported here. The authors continued: 'A predominance of historical factors would also imply that planktonic larvae are less effective for long-distance dispersal (i.e. between island groups) than is generally considered. Distributional boundaries that follow geological rather than hydrographic features have been reported for other reef fish families (e.g. Springer, 1982) and seem to support this point. It is also consistent with recent data suggesting larval retention close to reefs for some reef fish families' (this topic is discussed below). Thresher & Brothers also cited Atlantic gastropods (Scheltema, 1971) and Panamanian mangroves (Rabinowitz, 1978, pers. comm.) as other groups which show poor correlation between maximum duration of the larval or propagule stage and extent of distribution.

Thresher, Colin & Bell (1989) also found no correlation between breadth of a species' distribution and larval duration in the damselfishes (Pomacentridae).

Crosetti, Nelson & Avise (1994) felt that species with limited dispersal capability relative to the extensive ranges occupied are 'particularly enigmatic'. They studied the grey mullet (*Mugil cephalus*), distributed globally but normally confined to near-coastal waters. They found pronounced population genetic structure which was 'not necessarily anticipated', given the extensive migration of adults along coastlines and the lengthy planktonic larval stage. On the other hand, the spread of grey mullet to such remote islands as Hawaii and the Galapagos was hypothesized to have resulted either from 'nomadism' of adults or passive drift of juveniles, although direct dispersal pathways across the Pacific are 'somewhat difficult to envision'.

Even in foraminifera, Hayward, Hollis & Grenfell (1997) observed that New Zealand Elphidiidae include a number of taxa that are endemic to relatively small areas and 'for some reason have not dispersed widely.' While 43% of the elphidiids in the south-west Pacific are cosmopolitan, 27% are endemic to south-east Australia and 7% to New Zealand. Some are restricted to a single island group or local area of coast. Hayward *et al.* also noted striking absences of some species from, for example, the Chatham Islands 'despite the presence of suitable brackish environments'. They concluded: 'Why some elphidiids are widely dispersed and others are not is difficult to explain, as many of the locally endemic species occur in equal abundance and in the same habitats as those that are cosmopolitan'.

Marine mammals have a high capacity for dispersal, but mtDNA studies of the southern elephant seal (*Mirounga leonina*) revealed a high degree of geo-

graphic structure 'not correlated with dispersal ability' (Slade, 1997).

In their study of New Caledonian reef fish, Planes, Parroni & Chauvet (1998) 'expected to find substantial gene flow between the sampling sites', but in fact found a 'high degree of differentiation in two species' that was 'not consistent with what we expected ...' In addition, 'duration of the pelagic larval stage was not correlated with genetic differentiation'. These findings 'suggest that despite the fact that coral reef fishes have high dispersal potential and have previously been considered to consist of mainly large, panmictic populations, a number of species exhibit isolated populations with limited gene flow'.

Like many taxa of plants and animals world-wide, the reef fishes in the tropical eastern Pacific show a 'curious pattern' of wide-ranging species coexisting alongside congeners with exceptionally small ranges (Victor & Wellington, 2000). This huge variation in range means the area is a 'powerful testing ground' for biogeographic hypotheses about the group. Victor & Wellington examined the relationship between pelagic larval duration (PLD), the 'simplest proxy measure of dispersal ability', and size of species range for east Pacific wrasses (Labridae) and damselfishes (Pomacentridae). They argued that 'Few theories on the determinants of range in reef fishes would discount the importance of this feature of early life history', although they did not mention panbiogeography which discounts it completely. They wrote that 'Clearly an analysis of PLD should be the preliminary step in understanding the biogeography of fishes in this region', but this is only 'clear' in a Darwin–Wallace paradigm; in a panbiogeographic study the first step is comparison of many distributions. They proposed that 'If dispersal ability indeed plays a role in determining range then it would be expected that some relationship would be found between range and PLD'.

However, contrary to expectations, Victor & Wellington concluded that for both Labridae and Pomacentridae 'the correlation between measured PLD and range is non-existent'. In congeneric pairs of the fishes they studied, there is, if anything, an inverse relationship with local endemics having longer larval durations than widespread species. They described this finding as 'counter-intuitive', indicating their prior commitment to Darwin–Wallace dispersalism. In their discussion of the unexpected results, rather than regarding their work as a powerful test of dispersal biogeographic theory, which indeed it is, as they stated in the introduction, Victor & Wellington seemed reluctant to accept their own findings. In conclusion they simply suggested that 'There is, at present, no coherent theory explaining the complex biogeographic patterns exhibited by eastern Pacific reef fishes', although, again, they did not cite any alternatives to

dispersal theory such as panbiogeographic work. Their indictment of the dominant paradigm is even more severe when they state that 'the more data are gathered, the less clear the picture becomes'. This recalls the earlier conclusion of an influential dispersalist, who wrote that despite bird distributions being so well known, and despite his having discussed the topic with eminent ornithologists and having had access to Ernst Mayr's card-index, he still found the processes leading to bird distribution 'very hard to understand' (Darlington, 1957: 236). This is surely a strong argument for at least considering alternative world views of biogeography, but Darlington continued to insist that bird distribution is 'clearly' the result of dispersal and that continental drift 'if it occurred was evidently too long ago to affect bird distribution now'.

It is hardly surprising that Victor & Wellington (2000) seemed so reluctant to support their own results. For over a century the world's most distinguished biologists have always decreed that there is, or must be, a clear relationship between dispersal ability and distribution, as it is 'obvious'. Likewise, before the Scientific Revolution everyone accepted that the sun 'obviously' moves around the Earth. Victor & Wellington, trying to explain away their results, write that 'the documented arrival of vagrants from distant regions clearly indicates that many reef fish species do have long distance dispersal abilities.' But this is to confuse the different processes of range maintenance/expansion and differentiation (see above).

Other recent studies have concluded similarly to Victor & Wellington. For example, Glynn & Ault (2000) reviewed east Pacific corals and found that 'Unexpectedly, rafting [by larvae settling and growing on floating objects] has been observed in the genera of all restricted species, but only in two of the four genera of ubiquitous species'.

Bellwood & Hughes (2001) wrote that 'our understanding of regional scale patterns of biodiversity on coral reefs (and the processes underlying these patterns) has changed little since the seminal work of Stehli & Wells (1971).' However, although many diversity patterns have been established, 'the processes that shape these patterns remain elusive'. Families of reef fishes and corals show highly correlated geographic patterns of species richness 'even among families that differ markedly in life-history traits or larval duration'. Body size, longevity and larval type 'have surprisingly little impact on distribution patterns of species at a regional level ... The similarity in biodiversity patterns among corals and fishes indicate that the mechanisms that control the large-scale species composition of tropical reefs operate similarly across numerous taxa ... We found no significant correlation between reef type (oceanic versus continental) and taxonomic composition' (Bellwood & Hughes, 2001).

Robertson's (2001) work showed no difference between groups of small-island endemics and regional reef fish faunas in terms of the proportions of species that produce pelagic vs. demersal eggs, and no evidence that endemic species had relatively short larval durations. He concluded, 'island endemics do not have an unusual set of basic adult and larval characteristics ...'

Orthodox dispersalist phylogeography proposes that biogeographic boundaries form and are maintained as barriers to dispersal and to gene flow in general. However, this flawed concept results in an enigma – why are biogeographic 'barriers' crossed by some taxa but not others? For example, Lessios *et al.* (2001) regarded the split of *Diadema antillarum* into west and east Atlantic lineages as 'most puzzling', given that other sea-urchin genera show little differentiation between the two coasts, and *Diadema* shows lack of differentiation across other major 'barriers', but 'was divided by this relatively minor obstacle to migration'. (This approach leads to 'most puzzling' conclusions as it is predicated entirely on a concept of gene flow: cases of little or no population differentiation are interpreted as due to gene flow, and population differentiation is attributed to current 'barriers' to gene flow.)

Likewise, Lessios, Kane & Robertson (2003) found that the East Pacific barrier is 'remarkably unimportant' in the sea-urchin *Tripneustes*. 'Why larvae of Pacific *Tripneustes* should be so much better at dispersing than those of other Pacific sea urchins [which do not cross the barrier] is not clear, particularly in the light of the genetic subdivision of this genus in the Atlantic'.

Lessios *et al.* argued that 'species ranges by themselves cannot provide information on phylogenetic relations (e.g. Wallis & Trewick, 2001), and without information on the order of splitting between species, little can be said about speciation'. However, if they had looked beyond their narrow world view of molecular techniques and cladograms, and compared a few species distributions, perhaps they might have solved the mystery of *Tripneustes*. They would have found that taxa always conform to 'barriers' in some places but mysteriously 'cross' them in others. Thus, the whole concept of barrier can be put into question. Differentiation has less to do with what are supposed to be current barriers than with prior distribution of genetic potential and prior phases of vicariance which have resulted in some groups but not others fragmenting.

Jones, Caley & Munday (2002) also felt that 'The geographic range of a species should be related, at least in part, to its dispersal capabilities'. However, these authors' study of six coral reef fish families found 'no clear relationship' between pelagic larval

duration and range size. For example, the only damselfish lacking a dispersive larval stage, *Acanthochromis polyacanthus*, has a broad Indo-Pacific distribution greater than most confamilials with pelagic larvae. (The exceptional local variation in this taxon in eastern Papua New Guinea is discussed below.)

In molluscs, Swearer *et al.* (2002) cited work on 460 endemic molluscs of Easter Island, Hawaii, Kermadec Islands and the Galapagos (K. A. Selkoe, unpubl. data) showing that 'Overall, the presumed dispersal characteristics of endemic species and the total local molluscan fauna were indistinguishable'.

Bernardi, Findley & Rocha-Olivares (2003) studied the phylogeography of 12 fish species disjunct across Baja California Peninsula, and found that 'dispersal potential (inferred by pelagic larval duration) was a poor predictor of population structure between Gulf of California and Pacific populations'.

As few as one effective migrant moving between subpopulations each generation can hinder the genetic divergence of populations and prevent the fixation of an allele (Planes & Fauvelot, 2002). Swearer *et al.* (2002) wrote that 'Predictably, species whose larvae lack pelagic development ... often show gene frequency differences among populations ... However, genetic studies have also revealed some surprises. For example, copepods inhabiting high intertidal splash pools separated by as little as 10 km exhibit strong population subdivision, despite having larvae capable of pelagic dispersal (Burton, 1998) ... The larvae of the abalone are capable of moderate dispersal yet Jiang *et al.* (1995) found there are fixed mtDNA differences between populations of *Haliotis diversicolor* separated by just 10s of km. Reef associated fishes and stomatopods with even longer larval periods (weeks to months) can show genetic differentiation at similarly small spatial scales'. In these instances the degree of effective dispersal may be much more limited than would be expected 'based on assumptions of passive transport ... Over the long-term, larval retention may reproductively isolate populations and facilitate the formation of new species ... most closely related pairs of marine species often have abutting, or even overlapping, geographical ranges ...'

In the Caribbean goby *Elacatinus evelynae*, Taylor & Hellberg (2003) found that 'Despite evidence for extended pelagic larval duration, populations show strong phylogeographic structure between populations separated by as little as 23 km ... The simple assumption that extended PLD will result in broad dispersal is a faulty foundation for the management of fisheries resources and for understanding the geographic context of speciation in the sea.' Palumbi & Warner (2003) commented on these 'remarkably strong patterns'. They noted that 'for the better part of a century marine biologists have assumed ... that the

drifting eggs and larvae and rafting propagules of many marine species end up far from their homes . . .', and that Taylor & Hellberg 'help to overturn this notion'. Of course, like the wind-blown seeds of locally endemic alpine herbs on mountain ranges, some of the propagules must travel far, but the important fact is that they do not establish. The 'gobies join an increasing number of island species that have fine-scale genetic structure and low dispersal', and the 'conventional wisdom of marine biology [on larval distribution] may prove to be a coarse generalization' – if not worse.

Despite the observations cited here, distributions of taxa are still generally assumed to reflect means of dispersal. This has even carried into the biodiversity literature in which means of dispersal are used to infer estimates of biodiversity: taxa with 'good means of dispersal' are assumed to be more widespread and less diverse globally, and taxa with 'poor means of dispersal' are assumed to be more localized and therefore more diverse globally (Reaka-Kudla, 1997).

POPULATIONS OF MARINE TAXA MAY BE CLOSED SYSTEMS BECAUSE OF SELF-RECRUITMENT

What are the mechanisms that could enable the development of vicariance and endemism in marine faunas? Recent work suggests that many coral reef fish populations are 'closed' rather than 'open' systems, because a large amount of 'self-recruitment' takes place. This is very interesting as it could explain how speciation occurs in these taxa. Similar terrestrial examples are the surprisingly sessile populations of many birds.

Jones *et al.* (1999) successfully tagged pelagic larval stages in the marine environment and confirmed for the first time that pelagic larvae of reef fish return to their natal reef. Returning larvae may contribute substantially to local recruitment. Thus local populations of reef fish do not operate as 'open' systems, and Jones *et al.* 'challenge the assumption that long-distance dispersal is the norm for reef fish populations'. Cowen *et al.* (2000) also showed that larval retention occurs and that larval exchange rates in marine populations may be over-estimated. Montgomery, Tolimeri & Haine (2001) observed that although 'Fish larvae have long been considered passive particles at the mercy of ocean currents', in fact active behaviour and swimming to settlement habitat occur in reef fish larvae.

Discussing marine taxa, Warner & Cowen (2002) addressed the important questions: 'What is the source of recruits for any local population, and where do the young produced in a local population go? The answers to these questions are unknown for most widespread species with a pelagic larval phase. Proper marine management depends on knowledge in this area . . . Since most marine animals have a pelagic

larval stage, the paradigm thus far has been to assume extensive dispersal and massive export . . . To evaluate the appropriateness of this view we convened a Working Group [papers published in the volume with Warner & Cowen's article] . . . The entire group rapidly reached a consensus that evidence from a variety of fields indicated that local retention may be considerably more prevalent than previously thought, even in species with long larval durations. If such retention turns out to be a common feature of local marine population dynamics, this will require major reassessment of marine metapopulation models, fishery management schemes, marine reserve designs, and ideas about the mechanisms of marine speciation . . . The evidence for a surprising amount of local retention that we review here suggests that it is still an outstanding question whether marine populations should be managed as open . . . or closed . . .'

In marine mammals, Avise (2000) pointed out that even large, highly mobile species often show phylogeographic structure and regional assemblages (vicariance) due to 'self-imposed' limits on dispersal such as behavioural site fidelity. The question then becomes: what is the origin of this fidelity?

MOST MARINE TAXA SHOW AT LEAST SOME DEGREE OF VICARIANT DIFFERENTIATION

Although Ekman (1953) generally favoured Darwinian dispersal, he accepted vicariance in some cases. For example, while he attributed the close relationship between the Atlantic/East Pacific and Indo-West Pacific 'to long standing communication between the two . . . this is not to say that migration took place preponderantly from east to west. The relationship is due rather to the fact that both these faunas are descended from a more or less homogeneous Tethys fauna.' Likewise, 'To older zoogeographers the great similarities between the Mediterranean and Japanese fauna were a source of surprise. The discovery of the former extent of the Tethys Sea has solved this riddle'. As the former Tethys Sea diminished after the Eocene and Oligocene, the western part became more shallow, and the eastern part more brackish. Stenohaline marine animals such as corals and echinoderms died out, but those which thrive in brackish water, such as certain gastropods, survived.

Studies of vicariance received a boost in the 1970s when Gareth Nelson, Donn Rosen and Norman Platnick at the American Museum of Natural History gave strong support to Croizat's ideas (e.g. Croizat *et al.*, 1974). This led to a critical reappraisal of marine biogeography by a growing number of authors through the 1980s and 1990s.

McCoy & Heck (1976) and Heck & McCoy (1978) attributed distribution in corals, seagrasses and man-

groves to vicariance. Veron (1995) criticized their vicariance explanation for corals, but Glynn & Ault (2000) wrote that 'dismissal of this hypothesis seems unwarranted at this time . . . it is possible that some east Pacific coral species could be descended from Tethys relicts as suggested by Budd (1989)'. They cited the high proportion of endemism in east Pacific corals (e.g. *Pocillopora* sp. A, *Porites* sp. A, both known only from Clipperton Island, Revillagigedo Island and north Mexico) as lending support to a model of allopatric speciation.

Knox (1980) reviewed the biogeography of shallow-water benthic biota in the south-west Pacific and concluded that 'many biogeographers have been too ready to assume transoceanic dispersal as an explanation for contemporary distribution patterns'. Authors such as Briggs (1974a, b) 'tend to place too much weight on dispersal as the major, and sometimes exclusive, explanation . . . I would therefore urge that due consideration be given to alternative vicariance explanations'. Knox attributed the origin of many Oligocene molluscs in New Zealand to vicariance following the rifting opening of the Tasman Sea.

In an important review of marine biogeography in the Pacific, Kay (1980) wrote that 'Several recent biogeographers have shifted the frame of reference from dispersalist theory to the vicariance theory of Croizat (1958; Croizat *et al.*, 1974) . . . What is missing in the interpretation of Darwin–Wallace biogeographic theory is the sense of history in both a biological and geological context.' In other words, an adequate concept of time is lacking, as is an adequate concept of differentiation in space and the significance of locality. Kay concluded her paper by stating that modern theory and evidence 'provide a base for amplifying classic biogeographic theory [and giving] explanations for aspects of the distribution patterns that are not explained by Darwin and Wallace'.

Springer (1982) emphasized tectonic events in the determination of distribution patterns in shore fishes. He studied and mapped many taxa of reef fishes (and also land snails; Springer, 1981) restricted to the Pacific plate and relied heavily on vicariant events to explain the endemism and the striking faunistic breaks at the plate boundaries. One Pacific shorefish, *Siganus uspi* (Siganidae) (named after the University of the South Pacific), ranges in Fiji and New Caledonia, and Woodland (1983) asked the provocative question: 'Did this species evolve as Fiji became isolated from Tonga and the Melanesian Arc through sea-floor spreading during the last 9 million years . . . ?' In a classic, but seldom-cited, analysis Hocutt (1987) proposed that vicariant events were responsible for biogeographic patterns, especially endemism, in the Indian Ocean marine biota. In a study of the blennioid fish *Ecsenius*, Springer (1988) discussed Hocutt's work

and reached similar conclusions on vicariant events in the Indian Ocean. He also noted that the species of *Ecsenius* within a group 'usually exhibit sharply delimited distributions with respect to each other. For instance, one species of a group may have an extremely broad distribution with islandless voids of hundreds of kilometers separating its populations. Populations of the same species, however, may be separated from populations of another species in the same group at other islands by distances of only a few tens of kilometers. Such distribution patterns appear to be better explained by the tectonic history of the pertinent areas than by dispersal.'

Springer & Williams (1994) extended this reasoning with a discussion of the eight species of Salariaiini (Blenniidae) that occur in Hawaii. Five are endemic there but three occur throughout the Indo-Pacific. 'The high degree of isolation of the Hawaiian islands would seem to require that colonizing fishes be pelagic at some stage. Once reaching the islands, the operation of founder principle could result in the formation of endemics. But why not for all of the salariinins?' The authors suggested three possible solutions to the puzzle: different rates of evolution, different times of colonization and continual colonization by the three non-endemics. However, the last option raises another question: why are there only three wide-ranging salariinins present in Hawaii? Springer & Williams concluded that 'The causal factors contributing to Hawaiian Islands' endemism are undoubtedly complex and remain to be elucidated.' (The biogeography of Hawaii is discussed further under 'Metapopulation theory', below.)

Springer (1999b) has continued to investigate vicariant patterns in the blennioid genus *Ecsenius* in the south-west Pacific islands (Vanuatu, Fiji, Tonga, Samoa) and relate these to the geological history of the region, in particular the break-up of island arcs by sea-floor spreading. Arguing against dispersal, he suggested instead (Springer, 1989) that 'the species are acting like rocks . . . the major means of transport and separation of the species is by movement of the reefs (rocks) they inhabit'. His explanation (in Zug *et al.*, 1989) for the closer relationship of the shorefishes of Rotuma to those of Samoa than to those of Fiji uses similar tectonic argument.

Howes (1990, 1991) attributed the distribution of gadoid fish families such as Merlucciidae (southern parts of New Zealand, Africa, South America, north Atlantic and north-east Pacific) and Muraenolepididae (circum-Antarctic) to disruption of widespread distributions by vicariance rather than to colonization via 'elaborate routes' from the north. Grant & Leslie (2001) recently argued that vicariance cannot account for most of the disjunct distributions in *Merluccius* and that these are due to Pleistocene dispersal, but

this conclusion was based entirely on absence of early fossils and on a molecular clock calibration using the closure of the Panama seaway at 3–4 Ma. Grant & Leslie admitted there were problems with this calibration and extended the time of divergence between Atlantic and Pacific species to ‘as early as’ 4.5 Ma, but this is a negligible difference.

In invertebrates, the distribution of the belt-forming ascidian *Pyura praeputialis* in Australia and Chile (Antofagasta) was interpreted as a Gondwana relic by Kott (1985), and de Weerd (1989, 1991) attributed the Africa – South America and other Atlantic disjunctions in sponges to vicariance. (De Weerd’s study was discussed at length by Humphries & Parenti, 1999.) In the New World echinoid *Mellita*, Harold & Telford (1990) concluded that ‘long distance dispersal is an improbable explanation of disjunction’ and suggested instead that the species ‘have probably originated through vicariance of a wide-spread ancestral biota’.

Sluys (1989) gave a detailed global analysis of the marine triclade platyhelminths (infraorder Maricola). He used track analysis and concluded that several of the tracks are congruent with those well-established in the work of Croizat (1958, 1964) and others, e.g. Europe – North America; North Atlantic – eastern South America/Southern Ocean; South America – Australasia; Hawaii – south-east Polynesia (Marquesas etc.); New Zealand – western North America. Several tracks are repeated even within the Maricola, and Sluys quoted Croizat’s dictum: ‘Nature forever repeats’. He noted that vicariance is a better explanation for a general pattern than accidental jump dispersal and suggested that the distribution patterns are the result of ‘vicariant form-making’ mediated by plate tectonics, e.g. the separation of Laurasia and Gondwana, the rifting open of the Atlantic, and the break-up of Gondwanaland and Pacifica. The distribution of Gondwanaland taxa such as *Palombiella stephensoni* on South Africa, Tristan, Gough and New Zealand, and species of the panaustral *Synsiphonium* imply that there has often been ‘morphological stasis since the early Cretaceous’. Sluys observed that biological cladograms and geological cladograms of the break-up of Pangaea and Gondwana may be incongruent not because of dispersal, but simply because the taxa may have already undergone form-making prior to the break-up of Pangaea. In fact, this is probably the case for the triclads. (Sluys’ observations on old taxa on young islands are discussed below, under ‘Metapopulation theory’.)

For red algae of the Atlantic and Pacific, Guiry & Garbary (1990) proposed that species of Gigartiniaceae, Petrocelidaceae and Phyllophoraceae arose through vicariant events at several levels in different clades. Chin *et al.* (1991) attributed Pacific distributions in brown, red and green algae to vicariance.

In the widespread Indo-Pacific coral genera *Symphyllia* and *Coscinaraea*, Pandolfi (1992) found that the area relationships of the species show a marked congruence with the Cenozoic geological history of the region and he suggested successive isolation as an hypothesis explaining the evolutionary history of Indo-Pacific reef corals. In particular, ‘Vicariance events led to the breaking up of [broad Indo-Pacific distribution] first along a line at the junction between the West/Central and East Indian Ocean, then between the East Indian Ocean and the West/Central Pacific Ocean at the Indonesian Arc’. A similar pattern is found in the coral family Acroporidae (Wallace *et al.*, 1991) and the fish family Sparidae (Orrell *et al.*, 2002), in which ‘Results of biogeographic analysis suggested a strong vicariant explanation to structuring of genera . . . There were two areas of sparid evolution, eastern Indian Ocean-western Pacific and western Indian Ocean-Mediterranean/Atlantic. These species probably had a Tethyan Sea common ancestor.’

Vicariance has also been accepted as responsible for evolution in planktonic taxa. In the true jellyfishes, Hydromedusae (a class of Cnidaria), van der Spoel (1996) wrote that two faunal centres, one around Antarctica, the other around the Indo-Malayan Archipelago, had already become separated by Eocene time. ‘Splitting’ of an original continuous area ‘probably forms the vicariant event responsible for the development of [subclasses] Narcomedusae and Trachymedusae in the Antarctic waters, and of the Anthomedusae, Leptomedusae and Limnomedusae in the Indo-Malayan waters’.

Likewise, for krill (Crustacea, order Euphausiacea), van der Spoel, Pierrot-Bults & Schalk (1990) attributed general trends in the distribution of the genera to Mesozoic vicariance events involving ‘hydroplates’ of the ‘hydrotectonic system’.

van Soest (1998) concluded similarly for the salps and pyrosomas (Urochordata, Thaliacea): ‘the majority of thaliacean distributions arose during the Early and Middle Tertiary break-up of Laurasia and Gondwana and the later rearrangements of the continents.’

Knowlton (1993, cf. Klautau *et al.*, 1999) found that in many marine taxa ‘wide geographic ranges have been uncritically accepted as the natural consequence of potentially broad oceanic dispersal’, and a very large number of what were taken to be cosmopolitan, undifferentiated species are made up of two or more sibling species which are mostly regionally restricted. As Avise (2000) pointed out, these earlier assumptions about the significance of dispersal have had a ‘crippling’ effect on studies of marine ecology and evolution.

In the nudibranchs, Brunckhorst (1993) reported that the distribution of the six species of *Fryeria* ‘is interesting as each species appears to have a limited

geographical range with very little or no overlap with contiguous species': there is one species in each of the Mediterranean, the Red Sea, the tropical Indian Ocean, the Western Pacific, Micronesia and Guam. Brunckhorst suggested that the restricted range of the species 'may reflect a combination of factors including patterns of speciation, ocean currents, and availability of their specific food sponges', but only the first is accepted here.

In contrast with the ideas of Pandolfi (1992) and Wallace *et al.* (1991) cited above, Veron (1995) wrote that distribution ranges in Indo-Pacific corals 'are mostly so large that they can only be produced by long range dispersion.' However, Roberts *et al.* (2002) assessed marine biodiversity hotspots for tropical reef organisms (reef fish, corals, snails and lobsters) and found that 7.2% of coral species were 'range restricted'; fishes, snails and lobsters showed greater range restriction. The authors indicated that the relatively low fraction of restricted-range corals 'should be treated with caution because species were identified by morphology... Future studies may reveal much cryptic speciation'. As noted above, Veron (1995) himself accepted that thousands of geographic subspecies can be recognized in corals.

Myers (1996) attributed the high endemism of the Mediterranean amphipod fauna to the continued existence of a Tethyan fauna (despite frequent claims that the Mediterranean dried up entirely during the Miocene) rather than to successive waves of colonization from the Atlantic. This Tethys-relict explanation also explains the distributions of taxa such as *Rhinolabia*, known only from the Mediterranean and Papua New Guinea (Madang Lagoon).

Using the common concept of 'dispersal' often results in anomalies, and dispersalists often admit to finding 'surprises' in their studies. For example, Palumbi (1996) studied *Echinometra* sea urchins and found that 'The identity of the species found can change over surprisingly short geographic scales. For example, *E. mathaei* and *E. oblonga* are found together on Hawaii and on Niue. In Fiji, 1300 km to the west of Niue, there are also two species of *Echinometra*, but *E. mathaei* and *E. oblonga* do not occur. Instead, *E. sp. nov. A* and *E. sp. nov. C* are common... The result is a patchwork distribution of species'. This resembles Diamond's (1973) description of 'checkerboard' distribution in New Guinea birds. In fact, these are usually simple, standard patterns of vicariance repeated in many groups (Heads, 2002), but no explanation of these patterns is possible using chance dispersal.

In another study of these *Echinometra* species, Palumbi *et al.* (1997) did not mention vicariance but showed it clearly (in their fig. 6); all four taxa are in Okinawa and three are in New Guinea, but apart from

that, as the authors wrote, 'Regions for the four species are very different from one another, suggesting poor concordance in the processes generating population differentiation'. This 'poor concordance' is, of course, vicariance. For the different genotypes, there is no relationship between geography and dispersal (there is 'substantial scatter in the relationship of geographic and genetic distances'), a standard panbiogeographic observation for life in general. The authors concluded, accurately, that surface currents do not explain the 'patterns of gene flow' (more accurately, genetic structure – gene flow is inferred). However, their conclusions that 'These geographic patterns appear much less deterministic than in other well-known coastal marine systems and may be driven by chance and historical accident', and that the 'patchwork' pattern is 'affected strongly by random dispersal events' involving 'a few founder individuals' are unwarranted. For example, the New Guinea – Fiji connection in *Echinometra* sp. nov. A and sp. nov. C and the Fiji–Tahiti connection in sp. nov. C are thoroughly conventional tracks for both marine and terrestrial taxa, although Palumbi *et al.* did not cite any. (In the current literature, a biogeographic pattern often receives much more attention when it involves genotypes elucidated by recent, high-tech methods, than when it has been shown merely by traditionally studied species and genera. Scheltema, 1995, wrote that 'Biogeography is now at a turning point where new [molecular] techniques... will make it possible to address questions heretofore largely untractable', but this is incorrect; the questions were only intractable within the Darwin–Wallace paradigm, the same paradigm that forms the theoretical basis of phylogeography.)

Deep-sea fishes of the genus *Cyclothone* (Gonostomatidae) are perhaps the most abundant vertebrates on earth. Miya & Nishida (1997) studied mtDNA sequences in one circumglobal species, *C. alba*, and found large differences and five vicariant clades, three in the Pacific and one each in the Indian and Atlantic Oceans. They wrote that 'it seems surprising' that the three in the Pacific have not coalesced, and concluded that 'numerous questions remain unanswered...'

The East Pacific Rise and the north-east Pacific ridge systems were, prior to 56 Ma, one continuous system, but are currently separated by the on-land expression of the system, the San Andreas Fault. The deep-sea hydrothermal vent faunas of the East Pacific Rise and the north-east Pacific ridge are allied, but there are also considerable differences between them. Tunnicliffe (1988) and Van Dover (2000) argued that geological history supports a vicariance interpretation for this. At around 37 Ma the North American continent overrode the ridge, separating the two marine components and their faunas, with the two subassem-

blages subsequently diverging. Tunnicliffe, McArthur & McHugh (1998) also concluded that 'vicariance processes appear to be important' for the formation of deep-sea hydrothermal vent faunas in general. This seems reasonable, given the classic Pacific distributions of taxa such as the mite *Copidognathus papillatus* (no pelagic dispersal stage), restricted to hydrothermal vents on spreading ridges off Vancouver, at the Galapagos, between the Galapagos and Easter Island, and at Fiji (Lau).

As with marine taxa, 'The lack of morphological variation in many freshwater invertebrates over vast distances has been cited as evidence for their frequent long-distance dispersal. This scenario implies that vicariance will be an insignificant determinant of species distributions or diversity' (Taylor, Finston & Hebert, 1998). However, in the freshwater crustacean *Daphnia laevis* complex studied by these authors, variation in two mtDNA genes clearly indicated the existence of five morphologically cryptic, largely allopatric groups. The present-day distribution and phylogeography of the regional groups 'suggest the occurrence of both deep and shallow vicariance events'. However, Taylor *et al.* could not quite break with the old ideas and they felt that weak or no genetic differentiation over large geographic areas within each of the groups 'suggests' recent long-distance dispersal. Of course, lack of differentiation may simply mean there has been no cladogenic evolution in that area, not that there has been long-distance dispersal. Jamieson (1998) also undertook an explicitly panbiogeographic analysis of freshwater copepod distributions.

Benzie (1999) wrote that 'The genetic structure of widespread marine organisms is of particular interest because these species are expected to show little spatial variation given their high dispersal potential and the apparent lack of barriers to dispersal in the oceans (Briggs, 1974a). There is growing evidence, however, that widespread marine species can be highly structured genetically'. Likewise, Fosberg (1984) observed that 'contrary to the common belief, many of the [widespread] strand and even mangrove plants are not monotonously uniform over their vast ranges... [some] show striking differentiation and polymorphism'.

In *Halimeda* (calcareous Chlorophyta), Kooistra *et al.* (1999) accounted for the differentiation of the main clades in terms of vicariant events separating the west Pacific and the west Atlantic.

Guimarães (1999) discussed vicariant distributions in the serranid fish genus *Rypticus*, with a species on Revillagigedo Island (on the Pacific plate, off Baja California) having a sister species on mainland Central America, Cocos Island and Galapagos Islands (not on the Pacific plate). Guimarães attributed this pattern

to displacement of the Pacific plate, rather than to a 'dispersal' event and 'founder effect'.

Mayr (1954) observed that the species of the pantropical sea urchin *Eucidaris* 'illustrate geographic speciation almost diagrammatically'. Lessios *et al.* (1999) re-examined the genus and concluded that 'Although Mayr (1954) was more inclined to think in terms of dispersal, the allopatric species of *Eucidaris*, with adjacent ranges spanning in their aggregate the entire tropics, have always been consistent with the hypothesis of a circumglobal original common stock, which became fractionated by the closure of seaways and the formation of deep oceanic stretches... The first vicariance event in the history of extant *Eucidaris* was the isolation of the Indo-Pacific species from all others... The final definite split in *Eucidaris* occurred in the eastern Pacific', between *E. galapagensis* of Galapagos, Cocos Island and Clipperton Atoll, and *E. thouarsi* of the American mainland. 'There is no obvious extrinsic barrier to gene flow that could have caused this split... Even though currents could easily convey larvae between [the islands and the mainland] the two species do not appear to have invaded each other's ranges... Like many other marine species that are endemic to the Galapagos... *E. galapagensis* may have speciated because larvae reached the islands and then, for unknown reasons, were cut off from the mainland.' The absence of colonization of Galapagos by *E. thouarsi* is 'peculiar', as other mainland sea urchins do occur on the islands. Conversely, 'although it is hard to explain how larvae can cross the entire width of the Atlantic within their competent lifetimes, COI sequences of *Eucidaris* from the west coast of Africa are very similar to those of *E. tribuloides* from the Caribbean.'

Although the oldest present-day Galapagos islands are about 3 m.y. old, land vertebrates there 'appear to have been separated from their mainland ancestors for much longer than three million years... Thus, the time available for peripatric speciation of *E. galapagensis* is longer than the age of any extant island.' (cf. Grehan, 2001; 'Metapopulation theory', below).

In loliginid squids, Anderson (2000) found that the two basal clades are from Australia/New Zealand and Caribbean/Indonesia (i.e. Pacific). The terminal group involves three clades: (West Atlantic and East Pacific) ((East Atlantic) (Indo-West Pacific)). Anderson supported Brackoniec's (1986) conclusion that cladogenesis has been tightly correlated with continental drift and, in particular, vicariance events can be correlated with the widening of the Atlantic and the closure of the Tethys Sea.

Biologists have usually assumed that the populations of coral reef organisms in Indonesia are connected by strong ocean currents. However, Barber

et al.'s (2000) results for the stomatopod shrimp *Hap-tosquilla* indicated instead marked regional differentiation. Distinct populations are associated with old ocean basins, and Barber *et al.* stressed the importance of biogeographic history in explaining this. Although strong currents 'should facilitate dispersal of marine larvae', Barber *et al.* cited studies on fish and invertebrate larvae in the Caribbean and Australia (Jones *et al.*, 1999; Swearer *et al.*, 1999) that also showed 'a surprisingly small amount of movement, challenging the idea of a strict association between dispersal potential and realised movement between marine populations'.

Vallejo (2001) developed ideas of McManus (1985) on vicariance by basin isolation to explain patterns in Philippines coral reef gastropods, many of which show narrow ranges in the archipelago despite large areas of suitable habitat being present.

For polychaetes, Bhaud & Petti (2001) wrote that 'In spite of the probable ability of planktonic larvae of *Spirochaetopsis* to disseminate throughout the Atlantic Ocean, the benthic adults of each species cover only a limited geographical area . . . There is growing evidence that many marine species with large distribution areas, the so-called cosmopolitan species, are sibling species complexes that are in fact more subdivided than originally thought . . .' Bhaud & Petti concluded that 'The putative cosmopolitanism is probably the result of both inadequate morphological examination and the use of questionable ecological arguments linked to larval dispersal. Larval dispersal is often used to justify the conclusion that a species has a wide geographic distribution.'

Colborn *et al.* (2001) discovered several geographic clades in the bonefishes (*Albula* spp.: Albulidae). They proposed that 'dispersal is more restricted in the bonefish than the extended larval stage [references cited] would indicate, enhancing opportunities for allopatric speciation'. Although they noted that 'chance, long-distance dispersal has been proposed to explain micro-evolutionary structure in widespread marine species', they concluded instead that in *Albula* 'vicariant separation' is the main mechanism for species formation. Colborn *et al.* regarded *Albula* species as an 'evolutionary enigma', defying 'basic tenets of organismal evolution', as they represent an extreme example of morphological stasis over geological time and 'also defy expectations for larval dispersal'. The pelagic larval stage lasts about 2–6 months, 'at least twice the average for widely distributed reef fishes. Thus bonefishes should be world-class dispersers, but the genetic evidence argues to the contrary . . .'

Molecular studies of the trumpetfishes (*Aulostomus* spp.: Aulostomidae) indicated a simple, clear-cut pattern of pantropical vicariance (Bowen *et al.*, 2001), but the authors explained this by a convoluted history of

colonization routes, recent invasions and 'globe-spanning series of dispersal events'. Although there is notably low population structure across the entire Indian and Pacific Oceans, implying, for these authors, gene flow, the Ascension Island population is genetically distinct, implying little if any gene flow and thus constituting a 'dilemma'. The split between the Indo-Pacific *A. chinensis* and the Atlantic *A. strigosus* 'raises a subtle point about vicariance and dispersal models. Perhaps the divergence [of the two] was not due to a rare dispersal event that introduced Indian Ocean colonists into the Atlantic, but was caused by the vicariant sun-dering of a warm-water connection'. This is hardly a subtle point. The authors correctly inferred that 'the evolutionary consequences [of vicariance and dispersal] are indistinguishable' (this is hardly surprising as the models were proposed to explain the same phenomena), but incorrectly deduce that because of this 'dispersal and vicariance models are not always the stark alternatives they appear to be'. In any case, they concluded that the Atlantic species was 'a product of a recent invasion from the Indian Ocean'.

Writing on *Ophioblennius* (Blenniidae), Muss *et al.* (2001) concluded that 'distinctions between the biogeographic provinces of the Atlantic are not attributable solely to ecological idiosyncrasies of individual species, but to the presence of vicariant barriers that apply to most Atlantic reef fishes'.

The dinoflagellates known as zooxanthellae are symbiotic in Scleractinia and other marine invertebrates and contribute to the corals' nutrition and calcification. Among the most important is the genus *Symbiodinium*. This was originally considered to comprise a single widespread species, but has subsequently been found to show marked geographic patterning, with some clades restricted to the Seychelles, some to Thailand and some to Sulawesi (Burnett, 2002).

In a study of coral reef biota, Santini & Winterbottom (2002) observed that 'With the discovery of plate tectonics, the concept of centres of origin has been strongly criticized and is now abandoned as an a priori explanation for current biotic distributions by many systematists. Adherents to panbiogeography and vicariance biogeography believe that vicariance is the most parsimonious, and the only testable, explanation for the majority of speciation events . . . According to this view, species do not have centres of origin; they were formed when the ancestral geographic range inhabited by an ancestral species was fragmented by vicariant events.' Santini & Winterbottom argued that 'Contrary to several previous claims . . . most lineages of coral reef fauna inhabiting the Indo-western Pacific region probably originated through vicariant events associated with, and following the break-up of Gondwana. A general pattern of biotic distribution that is

highly congruent with geological data shows that even if long distance dispersal and sympatric speciation may in some cases have taken place, they have probably not been the predominant mechanism of speciation in the clades examined'.

Bellwood & Wainwright (2002) commented that 'The similarities between the [distribution] patterns described in reef fishes and corals are striking . . . The two groups have markedly different life histories, approaching the extremes seen in marine benthic faunas. If the biogeographic patterns seen in fish and corals reflect a common mechanism, then the processes may be operating at the regional or ecosystem level and at large temporal scales. If this is the case, then one may expect to see congruent patterns in other benthic marine taxa.' They cited Springer's (1982) study on the Pacific plate fauna: 'Here fish and non-fish taxa appear to be closely linked to a specific continental plate. The nature of the barrier is unclear. Why do so many taxa with widespread or oceanic distributions and planktotrophic larvae not cross the plate margins? It is as if there is an invisible barrier in midocean [Springer, 1982, noted that prior topography may have been destroyed at subduction zones] . . . As with the pioneering work of Leon Croizat (Croizat *et al.*, 1974), it may be the simplest of patterns that provides the foundations for a quantum leap in our understanding of the nature of barriers in marine biogeography.'

Australasian skates are highly diverse and endemic (Last & Yearsley, 2002). There are 'striking' compositional differences between the faunas of New Zealand/New Caledonia and of Australia. The subfamily Arhynchobatinae is particularly speciose in the region and the New Zealand/New Caledonian fauna is dominated by undescribed supraspecific taxa and species. The Australian fauna, by contrast, although including many arhynchobatins is dominated instead by members of subfamily Rajinae and shows little overlap in species composition with the fauna of New Zealand and New Caledonia. The extant Australasian fauna 'appears to be derived from elements of Gondwanan origin, dispersal from the eastern and western Tethys Sea, and intraregional vicariance speciation . . . The Tasman Sea, which is thought to have divided Australia and New Zealand since the Late Cretaceous, has formed an effective barrier to the dispersal of obligate benthic fishes typified by most rays . . . the main ancient mechanism of derivation is almost certainly vicariance'.

Planes & Fauvelot (2002) wrote that 'general evidence of genetic homogeneity in marine organisms over large areas . . . and theoretical models of speciation seem opposed to the high diversity found in marine ecosystems and raise the question about the conditions that favour genetic divergence and specia-

tion in groups with planktotrophic larval dispersal . . . many marine taxa with high dispersal potential that were once thought to represent a single species spread over large areas are actually sibling species complexes . . .' They studied the genetic structure of *Acanthurus triostegus* (Acanthuridae), a widespread surgeonfish found through the Indian and Pacific Oceans. The female produces more than 100 000 eggs per year and the larvae are long-lived. Planes & Fauvelot emphasized that gene flow is a powerful cohesive force and so any significant divergence indicates at least a partial barrier to gene flow. They found a 'strong geographic pattern' in *A. triostegus* and the 'strong divergence between populations' is 'even more surprising considering the dispersal capabilities of surgeonfish larvae'.

In the gastropod family Littorinidae, the five members of *Austrolittorina* show a 'Gondwanan' distribution in Australia, New Zealand and South America. Williams, Reid & Littlewood (2003) concluded that 'Based on the morphological uniformity within this clade, relatively recent (Plio-Pleistocene) trans-Pacific dispersal events seemed a likely explanation, as proposed for numerous other congeneric marine taxa. However, molecular estimation of ages of divergence suggest an initial vicariance between Australian and South American lineages at 40–73 Ma, contemporary with the later stages of fragmentation of the Gondwanan supercontinent . . .'

Peijnenburg *et al.* (2004) attributed evolution of chaetognaths in European seas to vicariance. For reptiles, Turner (2004) found evidence of Cretaceous Gondwanan vicariance in crocodyliforms.

The damselfish *Acanthochromis polyacantha* is monotypic and over much of its Indo-Pacific range has a uniform dark-brown colour pattern. However, in Australia and New Guinea there are variations (Allen, 2003). In Milne Bay (Papua New Guinea) there are two basic patterns, dark brown and dark brown with a white tail. Allen (2003) wrote that the detailed distribution of the two main types is 'fascinating': between the Amphlett Islands (dark tail) and Sunday Island (white tail) and between Rossel Passage (dark tail) and Marx Reef (white tail) the two varieties are separated by only 20 km. Even in a single lagoon, fish at the eastern end of Rossel Lagoon have white tails, those at the western end have dark tails.

In cowries (Cypraeidae), Meyer (2003) found 'persistent, large-scale geographical structure [i.e. vicariance] in sister groups'. For example, *Cribrarula* has partitioned the entire Indo-West Pacific into local basins and peripheral endemics. In another example, *Notocypraea*, endemic in southern Australia, and *Cypraeovula*, endemic in southern Africa, are sisters, which 'suggests a Gondwanaland tie' (cf. Burgess, 1970: 19–20). Meyer concluded that 'Some researchers have claimed that post-speciational range expansions

have effectively erased the majority of geographical patterning by speciation in the Indo-West Pacific . . . Sister-group relationships revealed in the phylogeny refute this loss of geographical signal for cowries . . . The persistence of geographical signal of divergence events is remarkable'.

Darwin (1859) cited freshwater fishes found in New Zealand and other countries as examples of groups that have evidently dispersed across open ocean by 'unknown means'. Galaxiid fishes, some of which have a marine phase in their life cycle, are the classic example. They have been the topic of much debate between dispersalists (e.g. McDowall, 1964, 2002) who have argued for an Australian centre of origin followed by dispersal to New Zealand and South America, and panbiogeographers (Croizat *et al.*, 1974; Rosen, 1978) who favour vicariance of a widespread southern ancestor. Fortunately, this debate may be approaching a resolution, as a study of *Galaxias maculatus*, one of the world's most widespread freshwater fishes, found 'extremely strong intercontinental geographical structure', i.e. vicariance, with well-supported clades for Tasmanian, New Zealand and Chilean haplotypes (Waters, Dijkstra & Wallis, 2000). Waters *et al.* wrote 'This leads us to question the assertion that trans-Pacific dispersal is going on in this species . . . our data indicate that the dispersal powers of *G. maculatus* may be more limited than previously suggested' and 'a vicariant role in the divergence of eastern and western Pacific *G. maculatus* cannot be rejected'. Genetic divergences (implying maximum divergence dates of 36 Ma) 'may be consistent with a vicariance model'. For 40 years McDowall has argued strongly for a dispersal model of *Galaxias* biogeography, and so this study, in which he played 'a major role', represents a major reversal in the dispersal/vicariance debate.

However, the dispersalists have not yet become fully fledged panbiogeographers. Waters *et al.* (2000) also argued that the topology of the *G. maculatus* cladogram: (Tasmania, New Zealand) Chile, conflicts with 'the pattern of continental fragmentation' and so this means the Tasmania/New Zealand relationship is due to dispersal. Writing in a more popular publication less likely to be exposed to critical examination, Wallis & Waters (2003) even wrote that 'At first sight, this [Tasmania, New Zealand, Chile differentiation] might appear to support a Gondwanan explanation for their origin but this is not the case', contradicting Waters *et al.*'s more cautious and realistic statement that 'vicariance cannot be rejected'.

However, Waters *et al.*'s and Wallis & Waters' absolute faith in geology is naïve: they cite no geological publications, presumably because they think 'the pattern' is all worked out and agreed on. In fact the current geographic/political entities (Tasmania, New

Zealand, Chile) are not geological entities but geological composites, and there is no simple split sequence between them. The sequence and timing of accretion of the component terranes and their distinct biogeographic affinities are topics of current investigation and the ad hoc invocation of dispersal to explain apparent biological/geological incongruence in this region is unjustified. In fact, it is only cladistic biogeography that has predicted congruence between phylogeny and 'split sequences' of early (pre-terranic) plate tectonics; panbiogeographic work has criticized this assumption as simplistic (Hedges, 1999).

The dispersalist biogeography of Wallis and Waters resembles that of Wallace in most aspects, for example in basing biogeographic conclusions on theories from another field, geology, not on their own biological data. Their practice of privileging certain currently accepted theories from a field they have no expertise in means they can never make new predictions about either geology, as workers such as Wegener or Croizat did, or biology.

Even the way in which Waters *et al.* (2000) presented their data reflects their underlying commitment to dispersal. For example, in their abstract they point out that 'a lack of genetic structure among New Zealand samples suggests that marine dispersal [occurs within New Zealand]', and that 'marine dispersal is an important biogeographical mechanism for this species'. However, in the abstract they conspicuously avoid even mentioning their main finding, the 'extremely strong intercontinental geographic structure' among Tasmania, New Zealand and South America. Furthermore, in their paper lack of genetic structure is taken to imply dispersal, but extremely strong genetic structure is not necessarily seen as implying vicariance.

Berra *et al.* (1996) also worked on *Galaxias maculatus* and wrote that 'Significant genetic heterogeneity between populations *would be consistent with* a vicariant model, whereas its absence *would support* a dispersal model' (italics added). This also reveals the prejudiced stance of the authors: why would genetic heterogeneity not *support* vicariance and its absence *be consistent with* dispersal? In any case, when Waters *et al.* did subsequently discover strong vicariant genetic heterogeneity, they backtracked on Berra *et al.*'s prediction.

Ebach & Humphries (2003) contributed a useful, concise critique of dispersalism. McDowall (2004) responded that 'Interestingly, Ebach & Humphries (2003) do not seem to invest much effort in vicariance theories for the biogeography of albatrosses or oceanic sharks. And what of ferns, which seem to have massive capacity for spread . . .' In fact, Ebach & Humphries did not refer to albatrosses, sharks or ferns at all, but this omission is hardly 'interesting' as

their article was only three pages long. McDowall's implication that vicariance analysis of these groups is not possible because any biogeographic signal is obscured by chance dispersal is incorrect.

The vicariance biogeography of many ferns in New Zealand (Heads, 1990: figs 5a, 5d, 12b, 24a), the Malay Archipelago (Heads, 2003: 323, 345, 369, 390, 395, 415, 422, 425 and figs 82, 84) and New Guinea (Heads, 2001a: 900, 911, 913; Heads, 2001b: 72–73, fig. 9; Heads, 2002: 276) has been discussed elsewhere. I am not aware of any dispersalist interpretations for any of these patterns. The biogeography of Australasian skates is discussed above. Albatrosses and petrels roam very widely over the oceans using their normal means of survival, but this does not explain why they return to breed at sites which are as highly localized and as vicariant with related taxa as those of many passerines.

The seabird order Procellariiformes comprises the albatrosses, Diomedidae, and the petrels and shearwaters, Procellariidae. Harper (1978) suggested that 'petrels were evolving 80–90 million years ago in the Southern Hemisphere along the shores of a fragmenting Gondwanaland', and Olson (1978) noted that 'there appears to have been virtually no significant morphological evolution in the Procellariiformes since the middle Miocene'. The Diomedidae contain two main clades each with two genera (Nunn *et al.*, 1996), as follows. The species are listed here with their traditional circumscriptions (distributions are from Marchant & Higgins, 1990). Subspecies are not listed; many are treated by Robertson & Nunn (1998) as full species. Most are mutually vicariant.

Diomedea – the great albatrosses.

D. exulans: Indian Ocean: Prince Edward, Crozet, Kerguelen, and Heard. New Zealand: Macquarie, Auckland, Campbell, Antipodes. Atlantic Ocean: Tristan, South Georgia.

D. epomophora: New Zealand: Auckland, Campbell, Otago Peninsula, Chatham Island. These two species are a related pair. The distributions are largely vicariant, with overlap only on Auckland and Campbell Islands.

D. amsterdamensis: Amsterdam Island. This is quite vicariant with the other two species.

Diomedea s.s. is a southern group, most closely related to the north Pacific genus *Phoebastria*. This ranges from islands off Japan to Hawaii, the Galapagos, and islands off Ecuador. The two genera are thus vicariant. Croizat pointed out (1958: 2b: 929) that Diomedidae do not avoid the tropics (cf. *P. irrorata*) and so there has probably been extinction between New Zealand and Hawaii, on the track: Kermadecs, Tonga, Marquesas, Line Islands.

Phoebastria – the North Pacific albatrosses or gooneys.

P. albatrus: Izu Islands (off Honshu), Ryukyu Island (formerly), North Bonin islands, Bermuda (formerly – Olson & Hearty, 2003). The record from the Ryukyus is the only one for the family.

P. irrorata: Galapagos, La Plata Island (off Ecuador). This is vicariant with the three other *Phoebastria* spp.

P. immutabilis: Izu Island (formerly), Marcus, Wake, Johnston, West Hawaiian Island, Revillagigedo (off Mexico).

P. nigripes: Izu Island, North Bonins (formerly), Iwo Jima (Bonins), Marianas (Agrihan), Marcus, Wake, North Marshalls (Taongi), Johnston, West Hawaiian Island, islands off Baja California. There is considerable overlap with *P. immutabilis*, but there are significant additional records from the Bonins, Marianas, and North Marshalls, which all lie south of that species.

The second group in the family comprises *Thalassarche*, the mollymawks, and *Phebetria*, the sooty albatrosses.

Thalassarche melanophrys: Indian Ocean: Crozet, Kerguelen, Heard. New Zealand: Macquarie, Campbell, Antipodes. Atlantic Ocean: South Georgia, Falklands, Patagonian Islands.

T. cauta: Indian Ocean: Crozet, Tasmania. New Zealand: Snares, Auckland, Bounty, Chathams. This shows perfect vicariance with the last species in the Tasmania–New Zealand region, and overlaps globally only at Crozet.

T. chrysostoma: Indian Ocean: Prince Edward, Crozet, Kerguelen. New Zealand: Macquarie, Campbell. Atlantic Ocean: South Georgia, Patagonia. This range is similar to that of *T. melanophrys*, but *T. chrysostoma* does not occur on the Falklands, Antipodes or Heard, and does occur on Prince Edward.

T. chlororhynchus: Indian Ocean: Prince Edward, Crozet, Kerguelen, Amsterdam/St Paul. Atlantic Ocean: Tristan/Gough. This vicariates with all the other *Thalassarche* and *Diomedea* species on Amsterdam/St Paul and Tristan/Gough, lying to the north of the other Indian and Atlantic Ocean records.

T. bulleri: Snares, Stewart, Chathams, Three Kings. This overlaps with *T. cauta* on the Snares and Chathams, but is the only member of the family on Stewart and Three Kings, both important centres of endemism. The species distribution forms an outer arc around the New Zealand mainland (Heads, 1990:

fig. 6d). Many other groups show similar surprising links between the far north and far south of New Zealand, for example, the sandy shore bivalve *Paphies subtriangulata*, in which Kaitaia and Stewart Island forms are genetically similar (Smith, 1989).

Phoebetria fusca: Indian Ocean: Prince Edward, Crozet, Kerguelen, Amsterdam/St Paul. Atlantic Ocean: Tristan/Gough.

P. palpebrata: Indian Ocean: Prince Edward, Crozet, Kerguelen, Heard. Atlantic Ocean: South Georgia. New Zealand: Macquarie, Auckland, Campbell, Antipodes.

The distributions of these two species overlap only on Prince Edward, Crozet and Kerguelen, and overall are quite distinct, with *P. fusca* lying towards the 'Indian/east Atlantic side' (with additional records on Amsterdam/St Paul and Tristan/Gough, cf. *T. chlororhynchos*), and *P. palpebrata* lying towards the 'Pacific/west Atlantic side' (with records on Heard, around New Zealand and on South Georgia).

Phoebetria (like *Diomedea/Phoebastria*) is entirely absent from Patagonia and the Falklands, unlike *Thalassarche* which has two species there. *Phoebetria* is also notably absent from New Zealand north of Auckland/Antipodes, unlike *Thalassarche* which reaches Snares, Stewart, Chathams and Three Kings.

In sum, members of Diomedidae show striking vicariance at all ranks, from genera (e.g. *Diomedea* and *Phoebastria*) to many of the species, and nearly all the subspecies (not analysed here).

Ekman (1953) regarded penguins (order Sphenisciformes) as 'true marine animals', because they rely on water for dispersal. Thus he found it 'remarkable' that the genus *Megadyptes* is restricted to the comparatively small region of the New Zealand subantarctic islands (Macquarie, Auckland, Campbell, Snares, Stewart). *Megadyptes* is possibly most closely related to *Eudyptes*, which ranges on subantarctic islands of the Indian and Atlantic Oceans, but in the New Zealand region overlaps with *Megadyptes* only on Auckland and Campbell Islands. North of here, on South Island and Stewart Island, there is very precise vicariance between the two genera, with *Megadyptes* in the east and *Eudyptes* in the west (Oliver, 1974). Ekman recognized that the diversity of penguins is part of a more general problem: why is the Antarctic fauna 'so extraordinarily rich in species', and in particular, considerably richer than the fauna of the North Polar Sea? Ekman argued that a group of ordinal rank, like penguins, being endemic to the south 'throws light on the role played by this region as a centre of development'. This, of course, goes directly against the Holarctic centres dogma of Matthew, with northern derivation and 'waves of migration' southwards.

MANGROVE AND SEAGRASS BIOGEOGRAPHY IS BEST EXPLAINED BY VICARIANCE

It is often not realized that mangrove forests 'are as complex and as variable in makeup and evolutionary processes as any forest habitat.' (Duke, 1995). As noted above, McCoy & Heck (1976) attributed similar distribution patterns in corals, seagrasses and mangroves, in particular, regional patterns of generic richness, to vicariance. In mangrove floras, similar environments in different parts of the world have revealed strikingly different numbers of species. Considering these 'diversity anomalies', Ricklefs & Latham (1993) agreed that differences in local species richness might arise from the particular history and biogeographic circumstances of each region, quite apart from the contemporary local environment. Ricklefs & Latham described the situation in mangrove floras as 'one of the most enigmatic examples of diversity anomalies, with Malesia/Melanesia most diverse . . . it parallels similar differences in seagrasses and corals (McCoy & Heck, 1976)'. Ricklefs & Latham also cited differences between the mangrove floras of northern and southern New Guinea, and this is another pattern also seen in corals.

Ricklefs & Latham noted that many interpretations of the present distribution of mangroves 'incorporate tectonic conditions or events that predate the oldest [mangrove] fossils . . .', and that 'diversity anomalies may arise historically from region-specific differences in origin of clades . . . and their subsequent diversification . . . Extinction does not appear to have played a major role in the generation of the diversity anomaly . . .'

Duke (1995) argued that the centre-of-origin idea does not explain present-day mangrove distributions. The idea is 'based on a precept of exaggerated long-distance dispersal' and has led to 'often exaggerated claims of long-distance dispersal capabilities.' The importance of long-distance dispersal 'has been greatly over-rated'. For Duke, the distributions of mangroves are instead a 'direct result of movements in continental fragments described in the theory of continental drift'. Duke emphasized the importance of 'the formation of new intertidal habitat when continental landmasses break apart over millions of years'. The break-up of Gondwana would have created 'vast intercontinental estuaries, slowly changing from riverine swamps and flood plains to more marine conditions. The largest example was the division of Africa and South America . . .' Thus continental drift is the basis of his model – 'there appears to be no other explanation for the extant distributional ranges and disjunctions of most, especially polyspecific, genera. This being the case, we may find that some groups will extend back further than our present fossil records

indicate . . .’ Duke’s model of mangrove evolution also emphasized evolutionary stasis: ‘It is notable that taxa are remarkably conservative, changing very little over millions of years’.

Duke *et al.* (1998) found relatively low gene flow among populations of the mangrove *Avicennia*, which led to their ‘questioning assumptions that these widespread mangrove species achieve high levels of long-distance dispersal’. They recorded strong genetic structuring in *A. marina* which showed the ‘deconstruction’ of Australia also seen in terrestrial plants (Heads, 2003); south-west Australian populations are closer to south-east Asian and South African plants (Indian Ocean track) than to south-east Australian plants, which are closer to those of New Caledonia and New Zealand. Duke *et al.* cited determinations of *Avicennia* pollen from the Eocene of south-west Australia. They wrote that levels of divergence among the *A. marina* varieties ‘suggest’ they are of Pleistocene origin, but as indicated in this paper, degree of divergence is not a reliable guide to age of groups, especially when based on dubious calibrations. Duke *et al.* concluded that: ‘gene flow and dispersal of propagules is more limited than has been assumed for widespread mangrove species’.

Ellison, Farnsworth & Mertz (1999) also supported a vicariance hypothesis for mangroves, and so there is broad agreement among McCoy & Heck, Ricklefs & Latham, Duke *et al.* and Ellison *et al.* on a vicariance model.

Concerning seagrasses, Croizat (1958: vol. 2, 188–193) supported Setchell’s (1934) conclusion that the distribution of *Diplanthera* (= *Halodule*) and *Cymodocea* (both Cymodoceaceae) showed substantial parallels with those of land plants and were essentially relictual, resulting from early evolution in and around Tethys. Fortes (1988) noted that the fruits of most seagrass species are not buoyant and it is ‘extremely unlikely’ that seagrasses could disperse over long distances. ‘Paradoxically, *Enhalus acoroides* and *Posidonia* have buoyant fruits, but they have the most restricted worldwide distribution’. He concluded that the distribution of the species ‘favours vicariance as an explanation’. Larkum & den Hartog (1989) discussed seagrasses and agreed that the vicariance hypothesis has merit ‘in turning attention away from concepts based purely on present biogeography’. They agreed that an origin of seagrasses along the shores of Tethys (reaching westwards to the Caribbean) is reasonable. They also observed that seagrasses have no means of long-distance dispersal and again emphasized that genera with buoyant fruits (they cited *Thalassodendron* and *Posidonia*) have a restricted distribution. They cited *Heterozostera* in Australia (extant) and Chile (fossil) as evidence for an original Gondwanic distribution, and noted that ‘the evidence suggests

that seagrasses have remained largely unchanged for a long time (mostly since the Eocene).’

MIGRATION IN MARINE ANIMALS IS BEST EXPLAINED BY VICARIANCE

Many marine animals show major, regular migrations. Some of the best known occur in seabirds, shorebirds, marine mammals and turtles. Dorst (1962) emphasized that ‘The origin of bird migrations is such an important question that it dominates all other aspects of ornithology’. He discussed theories on the origin of migration and wrote that for ‘some authors . . . migration routes reveal geographical conditions of another era’. Wolfson (1948) had suggested that continental drift was the stimulus for the more highly developed forms of migration, which evolved as follows:

- (a) before the advent of continental drift many birds were performing short flights between breeding and feeding areas;
- (b) with the onset of drift these areas diverged slowly;
- (c) the birds continued their use of these areas because of their well-developed homing instincts.

Wolfson (1948) wrote: ‘What tends to confuse the issue is the reasoning that the ends served constitute the causes of migration . . . Migratory behaviour . . . did not evolve into its highly developed forms because it served useful ends, but was the natural consequence of an inherent behaviour pattern responding to the drifting of continental masses. The “adaptive features” of migration, such as leaving an area with the approach of winter, are therefore the *result* of natural selection and *not the cause* of migration . . . If biologists have an adequate knowledge of the properties, requirements, and behaviour of organisms and have confidence in that knowledge, they can make a substantial contribution to our knowledge of the earth’s history. Thus, that the birds migrate along the routes indicated . . . seems to me to constitute prima-facie evidence for the drifting of the continents.’

Although green sea turtles (*Chelonia mydas*) live most of their lives in the ocean, adult females must return to land in order to lay their eggs. One population of green turtles leaves feeding grounds off Brazil every year to nest on beaches of Ascension Island in the mid-Atlantic Ocean 2000 km away. Carr & Coleman (1974) suggested that since the early Cenozoic certain turtles have inherited a tendency to swim a particular WNW–ESE path from Brazil to Ascension Island, swimming against the prevailing current for about 8 weeks. This migration route has developed gradually, as the Atlantic Ocean widened. Before continental drift, Ascension Island, or rather its precursors, lay much closer to Brazil. Continental drift

gradually (2 cm yr^{-1}) increased the distance between the turtles' feeding beaches and the nesting grounds and the turtles, driven by their homing instinct, have adapted to longer and longer migrations.

Croizat *et al.* (1974) discussed endemic crustaceans on Ascension Island with similar connections to Brazil and the Caribbean. They cited Tuzo Wilson's (unpubl.) suggestion that: 'Ascension is only the latest in a series of islands whose remains form scattered seamounts and ridges from Ascension Island to the Cameroons (the Guinea Rise) in one direction and in the other direction to the northeast corner of Brazil.' Likewise, Bonatti & Chermak (1981) concluded that 'Long segments of crust reached close to sea-level in the mid-Atlantic . . . it is likely that intense vertical tectonic motions occurred along the Romanche Transform Zone [just north of Fernando Noronha – Ghana] throughout the evolution of the Atlantic . . . shallow or emergent crust . . . may even have provided "land bridges" for faunal migrations . . .'

Bowen, Meyland & Avise (1989) (reported by Lewin, 1989) studied mtDNA of green turtles from the Ascension Island rookery and also from Florida and Venezuela rookeries. They found identifiable differences among the three rookeries. However, because these differences were relatively small Bowen *et al.* did not support Carr and Coleman's theory, and instead supported the standard dispersal theory that the 'separation occurred a few 10s of 1000s of years ago at most' (Lewin, 1989). Avise (2000) summarized molecular work on turtles and regarded Bowen *et al.*'s conclusion as a 'classic resolution' of a vicariance/dispersal controversy. However, the rate calibration for turtles has itself been controversial. The major split in green turtle phylogeny is between Atlantic/Mediterranean and Indo-Pacific clades. Bowen *et al.* (1992) regarded this as consistent with vicariant separation by the rise of the Isthmus of Panama at 3 Ma and they deduced evolutionary mtDNA rates from this calibration (writing, misleadingly, that the rates were 'revealed'). As indicated above, this is oversimplistic, and many authors regard the rise of this Isthmus as much too late to explain differences between Atlantic and Pacific groups. Avise *et al.* (1992) proposed an eight-fold decrease in evolutionary rate for turtles relative to the conventional rate for higher animals, but it may actually be even less, perhaps much less. In a group like turtles there may well be almost complete morphological as well as molecular stasis.

Young (1962) wrote that 'the migrations of fishes have attracted much attention, but are still imperfectly understood'. In the freshwater eels (*Anguilla*, c. 15 species) the adults live in estuaries, lagoons, coastal marshes, and freshwaters of lowlands and highlands. They migrate every year to spawn in oceanic waters. After spawning the adults die and the lar-

vae drift back to estuarine and freshwater habitats which they enter as juveniles. Adults are very rarely taken in the open ocean and the location of spawning grounds in the Sargasso Sea, off Bermuda, was only deduced in 1913 from the distribution of different sized larvae in the Atlantic. In 1977 the first direct evidence of adults occurring off the continental shelf was obtained when two were photographed on the sea-floor at about 2000 m depth near the Bahamas (J. S. Nelson, 1994).

The European eel (*A. anguilla*) and American eel (*A. rostrata*) are sister species and both migrate to adjacent breeding grounds in the Sargasso Sea. Europe is 3000 km away and Young (1962) described the migration as 'astounding', adding that 'no-one has yet discovered the factors that direct these movements'. Übisch (1924) interpreted the migrations as the result of continental drift. Croizat (1958: 1: 735–745), citing Bertin (1942), also attributed the eels' ontogenetic migration to phylogenetic migration that developed with the gradual geological widening of the Atlantic and regarded *A. anguilla* and *A. rostrata* as the by-product of the breaking apart of a common ancestor. Dietz & Holden (1973) wrote that *Anguilla* is 'Yet another animal [which] may be cited as proving continents drift'.

Anguilla species are widespread in the Indian, Pacific and North Atlantic Oceans, but are absent from the tropical and South Atlantic and the East Pacific. Croizat (1958) discussed the pattern and compared it with taxa of *Suaeda* (Chenopodiaceae) and *Gelochelidon* (Laridae). He attributed it to vicariant evolution along the 'Tethyan track'. Two molecular studies (neither citing Croizat) have given centre of origin/dispersal explanations for *Anguilla* but reached diametrically opposed conclusions for the distribution of the group, in particular the origin of the two Atlantic species. Lin, Poh & Tzeng (2001a, b) derived the Atlantic members by proposing a centre of origin in the south-west Pacific (as most species occur here) from which the ancestors of Atlantic eels migrated east across the Pacific and 'trekked across the central American Isthmus'. These authors suggested that the first divergence in *Anguilla* took place at 20 Ma. In contrast, Aoyama, Nishida & Tsukamoto (2001) proposed dispersal from a similar centre (Borneo, the location of the 'basal' species) westward to the Atlantic via the Tethys Sea. In this hypothesis, the eels' ancestor entered the Atlantic before 20–30 Ma, and Aoyama *et al.* proposed an origin of *Anguilla* at 50–60 Ma.

Migrating birds in the south-west Pacific may follow former, pre-drift coastlines (Hedges, 1990) and migrating marine mammals often strand or beach repeatedly at the same localities (McCann, 1964, referred to the 'coincidental distributional pattern' of strandings in

New Zealand). These phenomena may also be due to persistence of ancient biological movements in the face of major tectonic changes.

DIVERSITY IN THE INDO-AUSTRALIAN ARCHIPELAGO IS RELATED TO INDIAN OCEAN/PACIFIC OCEAN VICARIANCE

The triangle formed by Sumatra, the Philippines and New Guinea, in other words the region between Asia and Australia, is widely recognized as one of the world's major centres of diversity and endemism for both marine and terrestrial biota. Unfortunately, there is no widely agreed name for the region. Joseph Conrad called it the Eastern Archipelago; zoologists and marine biologists have termed it the East Indies, Southeast Asia, the Malay Archipelago, the Indo-Malay Archipelago, the Indo-Australian Archipelago (IAA), the Indonesian region, the Indonesian and Philippine region (IPR), the 'coral triangle', the West Pacific diversity triangle, and the Central Indo-Pacific (CI-P) hotspot, while botanists usually call it Malesia (i.e. Malaysia and Indonesia).

However, although it is agreed that the IAA is a centre of diversity for corals and reef taxa in general and also terrestrial groups (see below), it is often debated whether it is centre of origin, of overlap or of refuge. The first has been a 'particularly well-favoured explanation, apparently supported by the clear propensity for marine taxa to disperse during their pelagic larval stage.' (Veron, 1995). However, it has been criticized by many authors (e.g. Wilson & Rosen, 1998), and Benzie (1998), Wallace & Wolstenholme (1998), Gittenberger, Hoeksema & Gittenberger (2000) and Goud & Gittenberger (2000) have argued instead that the IAA has a composite fauna, with the diversity peak being caused by the overlap of Indian Ocean, Pacific Ocean and endemic taxa. For example, in the Siganidae (rabbitfishes), there are five pairs of sibling species with one member of each pair having an Indian-Ocean-centred distribution and the other a Pacific-Ocean-centred distribution (Woodland, 1983). In Indonesia, Barber *et al.* (2000) described 'southern' and 'northern' clades among populations of a mantis shrimp from 11 reefs in the Java and Flores Seas, which 'may be relics of [respectively] Indian and Pacific Ocean populations' (cf. the Malesian Ericaceae; Heads, 2003). Thus the IAA is probably not simply a centre of origin from which taxa have dispersed into the Pacific.

The terrestrial biota of the IAA has traditionally been assumed to 'result from the meeting and mixing of the floras and faunas from two major zoogeographic regions' (Benzie, 1998), these being Wallace's (1876) 'Oriental' and 'Australian' regions. Panbiogeography has never accepted these, but has instead accepted the

Indian, Pacific and Tethys Ocean basins as the main regions for terrestrial biota (Craw *et al.*, 1999). Marine biogeographers have never used the Oriental and Australian regions but have naturally used the Indian and Pacific Oceans.

Of the few genetic surveys of species in the Indian and Pacific Oceans, 'All have shown marked genetic differentiation of populations in the Indian Ocean from Pacific populations' (Benzie, 1998). For example, 'The genetic structure of butterfly fish and coconut crabs also show little variation within the Indian or Pacific Oceans but marked genetic differences between oceans'. These results 'are consistent with vicariant origins in oceans on either side of the SE Asian region, even within widespread marine species with long larval lives . . . These data provide further support for views that speciation of marine taxa did not occur within a centre of origin (SE Asia), but from successive isolation of populations outside this region (Wallace *et al.*, 1991; Pandolfi, 1992, 1993; Wallace, 1997).'

The starfish *Linckia laevigata*, renowned for its brilliant, royal blue colour, is continuously distributed through the Indo-west Pacific tropics. Populations from Thailand and South Africa, where an orange colour morph predominates, are significantly genetically differentiated from populations of the West Pacific and, to a lesser extent, from each other (Williams & Benzie, 1998). This is consistent with a major biogeographic boundary between the Indian and Pacific Oceans, and Williams & Benzie concluded that 'vicariant events have played an important role in shaping the broadscale genetic structure' of *Linckia*. Genetic studies also revealed a 'marked discontinuity' between Indian Ocean and Pacific Ocean (plus Western Australian) populations of the widespread crown-of-thorns starfish *Acanthaster planci* (Benzie, 1999). Again, the clades were congruent with two colour morphs. The Indonesian population is of special interest, as 11 of the specimens (localities not given) were grey-green and clustered with the Pacific Ocean group while two were blue and clustered with the Indian Ocean group.

Benzie (1999) concluded that all these examples 'strongly suggest that a vicariant event separated populations in each ocean'. None of the pairwise patterns of 'inferred gene flow' (actually, genetic similarity) conformed closely to present-day ocean currents. Benzie interpreted this to mean that genetic structure reflected 'sporadic long-distance dispersal where the effects of historical accident play an important role.' However, it may simply mean that genetic similarity is not due to present or recent currents or geography in general, but to much older conditions. The patterns of 'connectivity' in *A. planci* (e.g. Philippines-Vanuatu) are also similar to patterns seen in giant clams

(Benzie, 1998), discussed in the next section, as well as in many terrestrial taxa.

In a study of coral reef biota (Santini & Winterbottom, 2002), the Indonesian region, 'long stated to be a centre of origin' for most of the Indo-West Pacific marine fauna, appears as a very derived area in the general area cladogram. Santini & Winterbottom concluded that most of the lineages may have originated in the western Indian Ocean (Croizat's, 1952, 'African gate'), Australia, or the south-western Pacific (both comprising Croizat's, 1952, 'Polynesian gate'). They wrote that 'A series of events that fragmented an originally widespread biota seems to be highly congruent with geological events that caused the break-up of Gondwanaland.'

DISTRIBUTION IN THE PACIFIC IS NOT THE RESULT OF FOUNDER DISPERSAL

Distributions in the Pacific have always figured among the classic examples of long-distance dispersal. Kay (1980) observed that 'Most biogeographers have interpreted the distribution patterns exhibited by the biota of Pacific islands in terms of Darwin–Wallace biogeographic theory, a main assumption of which is that the biota of oceanic islands derives from [long distance] dispersal'. This might explain the western relations of most of the Pacific island biota, and the west–east attenuation of diversity. 'There remain, however, aspects of the distribution of the animals and plants of the Pacific that are not explained by traditional biogeographic theory: the occurrence of a recognizable Pacific biota, areas of endemism within the Pacific basin, disjunct distributions, and the diverse biotas of high islands compared with the sparse biotas of atolls . . .' As noted above, Kay concluded in favour of vicariance, as did Springer (1982) in explaining Pacific plate endemism in reef fishes. Springer emphasized the importance of the Pacific plate margins as geographic boundaries and Stoddart (1992) agreed that there is much support for this idea in the distributions of both marine and terrestrial biota. For example, the plate boundary (the Tonga Trench) lies just east of Tonga, and Stoddart noted that 'there is no more dramatic biogeographic boundary in the Pacific than that between the southern Cooks and the southern Tonga islands. The latter have mangroves and seagrasses, and a distinctly west Pacific aspect; the former lack them'.

Darwin (1859), Wallace (1860), Ekman (1953) and Darlington (1957) all assumed that Pacific biotas arose by long-distance dispersal from the Indo-Malay region. In the same tradition, authors such as Vermeij (1987) have described 'a west-to-east decline in diversity of shallow-water marine species across the Pacific, caused by the action of barriers to dispersal'. This

decline, 'from the continental regions of southeast Asia and Australasia across the tropical Pacific to the islands of Micronesia and Polynesia . . . is the consequence of the oceanic barrier, which effectively limits the eastward dispersal of planktonic stages'. Similarly, Palumbi *et al.* (1997) recorded greater genetic diversity in *Echinometra* populations from islands near Indonesia and less in the populations from the central Pacific. They inferred from this that there is 'low dispersal' here, and 'colonists to these island groups are rare'.

However, it has been overlooked by many authors that the eastward decline in diversity may instead be due simply to the eastward decline in the area of land and shallow water as one goes from the larger islands of Indonesia and Melanesia to the smaller islands of Polynesia. This point was made very clearly by van Balgooy (1971) for Pacific island floras. Even some marine algae may require high islands rather than atolls, and again, size is important. Discussing biodiversity in coral reef fish communities, Ormond & Roberts (1997) wrote that 'The species/area relationship has long been recognized by ecologists and it is surprising that it has been passed over by biogeographers so often'. Benzie (1998) concluded likewise: 'The fact that there is a reduction in species diversity eastwards into the Pacific does not mean there has to be dispersal of species eastwards from a [Indo-Malayan] centre of origin. It is possible, for example, that the smaller size of populations [around the small islands] . . . may result in a greater extinction of species in the Pacific'. Ladd (1960) also drew attention to the problem that eastward 'dispersal' across the Pacific from a supposed Indo-West Pacific centre was against prevailing ocean currents.

Benzie & Williams (1995) found that the 'main routes of gene flow' (i.e. gene similarity) in the Pacific giant clam *Tridacna gigas* do not run parallel with the major surface currents 'as might be expected', but cross them. This suggests that the genetic structure is the result of historical patterns of migration that no longer occur, rather than present-day dispersal. These findings raise fundamental questions concerning the origin and maintenance of genetic diversity in Pacific faunas . . . Benzie & Williams (1997) introduced their paper on *T. maxima* by observing that Darwin (1859) and subsequent authors have assumed that Pacific biotas arose by long-distance dispersal from the Indo-Malay region, whereas McCoy & Heck (1976), Kay (1980) and Springer (1982) supported vicariance. Up until now, genetic work 'has tended to support the traditional view' as little genetic differentiation had been found, but Benzie & Williams' own study showed highly significant regional differentiation, with 'routes of gene flow' (i.e. inferred routes of gene flow), again running perpendicular to main present-day ocean cur-

rents. Benzie & Williams admitted that these patterns are 'contrary to the expectations of long-range dispersal hypotheses'. The patterns are also shared with *T. gigas*, *T. derasa*, the pearl oyster *Pinctada margaritifera* (Benzie & Ballment, 1994) and several reef fishes (Springer, 1982), suggesting that these data reflect a 'fundamental pattern'. Nevertheless, in their summary discussion and their abstract, rather than supporting a vicariance model, Benzie & Williams argued that their patterns 'are consistent' with the traditional view. They did admit that 'the nature and timing of dispersal of marine species in the Pacific is clearly more complex than has been thought' and at one point in the text mentioned that 'a hypothesis of a more ancient origin . . . cannot be excluded', but did not follow this up.

In a subsequent paper, Benzie (1998) pointed out that 'widespread marine species have traditionally been viewed as having a high dispersal capacity . . . However, the notion that widespread species may not always reach their dispersal potential is increasingly recognized. A growing number of cryptic taxa within widespread species are being discovered . . . genetic studies [demonstrate] unexpected structure that is not consistent with dispersal by present-day ocean currents.' For example, 'The principal patterns of gene flow in all three [*Tridacna*] clam species were found to be parallel to the major island chains [from the Philippines to the Cook Islands] (following a NW–SE axis) and perpendicular to the major ocean currents flowing through the region (following a NE–SW axis) . . . it is clear that we do not understand the processes driving the origin and maintenance of marine diversity'. This NW–SE track across the central Pacific from east of the Philippines to south-east Polynesia is one of the most common of all Pacific distributions for plants and animals, both marine (e.g. the blennioid fishes *Cirripectes variolosus* and *C. fuscoguttatus*; Williams, 1988) and terrestrial (e.g. the warbler *Acrocephalus* subg. *Conopoderas*), and coincides with the atoll zone (Stoddart, 1992), probably because both relictual distributions and atolls form in areas of tectonic subsidence.

The clades in the surgeonfish *Acanthurus triostegus* discovered by Planes & Fauvelot (2002) have a geography that is quite standard: 'The Marquesas Islands are geographically close to the Tuamotu and Society Archipelagos but appeared genetically distant and were found genetically closer to the Hawaiian Archipelago . . . Currents have often been proposed to explain genetic differentiation in marine species, but analyses using present day currents have failed to find better relationships . . . These observations favour the hypothesis of biogeographic vicariance as an evolutionary process leading to the differentiation of the *A. triostegus* populations in the Hawaiian and Marquesas Archipelagos. A vicariant process is usually

supported by a congruent biogeographic pattern shared by several taxa and/or several independent genetic markers within a species . . . Congruence in the biogeographic distribution of some Hawaiian and Marquesan coral reef fish has been emphasized . . . (Springer, 1982; Newman & Foster, 1983; Randall, 1995). (Planes & Fauvelot could also have mentioned terrestrial groups such as the landsnail *Tornatellides* cited by Heads, 1983.) Likewise, Newman (1986) noted that despite being ill-equipped for long-distance dispersal as larval forms, Hawaiian barnacles show affinities with south and east Pacific taxa. This pattern is a 'fascinating exception . . . not readily explained by ordinary dispersal' and 'a vicariance explanation consistent with these facts would be welcome'. Planes & Fauvelot concluded likewise: 'Both genetic and biogeographic patterns favour the hypothesis of vicariant processes leading to the actual genetic structure'.

This seems more reasonable than the explanation of Lessios *et al.* (2001) for the two clades in the sea-urchin *Diadema paucispinum*, one in the Indian Ocean to Philippines – New Guinea vicariating with the other at Okinawa, Hawaii and Pitcairn/Easter (i.e. the standard Hawaii – south-east Polynesia track). Lessios *et al.* accounted for the pattern as the result of 'chance arrival of larvae' at Hawaii and Easter and inferred 'high rates of gene flow' between them. They also noted that the Hawaii – south-east Polynesia connection runs perpendicular to both the North and the South Equatorial Currents and that this is 'remarkable', indicating a 'tremendous capacity for dispersal'. This latter proposal would of course not account for the observed fact of vicariance: 'The expected genetic pattern after the removal of a barrier would be . . . remnants of differentiation coupled with leakage . . .' Lessios *et al.* concluded, reasonably, that 'despite . . . tremendous capacities of dispersal' *Diadema* provides 'a great deal of evidence in favour of allopatric evolution' and that 'ecological factors (physical tolerances or competition)' prevent vicariants from establishing themselves within the range of the other.

DISTRIBUTION IN THE SOUTH-WEST PACIFIC IS ACCOUNTED FOR BY RIFTING AND ACCRETION TECTONICS

The biota of the south-west Pacific includes many taxa with distributions difficult to explain using centre of origin/dispersal models or simple ecological correlation. As noted, Ekman (1953) found it 'remarkable' that a penguin genus, *Megadyptes*, should be endemic to the comparatively small region of subantarctic New Zealand. East of New Zealand, anomalous absences of marine taxa from the Chatham Islands are cited above (Knox, 1963; Hayward *et al.*, 1997). Marine distributions in northern New Zealand have also puzzled biol-

ogists. For example, Ayling & Cox (1982) described a group of inshore fishes with a 'rather limited' Tasman Sea distribution: rare on the Australian coast, abundant around Lord Howe and Norfolk Islands, moderately common in north-east New Zealand (eastern Northland, Poor Knights Islands, Bay of Plenty). They wrote that 'the reasons for the unusual distribution of these species is poorly understood'. The pattern has been illustrated by Croizat (1958: figs 252, 257).

W. A. Nelson (1994) observed that 'Since the time of Laing (1895), New Zealand phycologists have expressed reservations about the explanatory power of dispersal as the prime influence shaping the composition of our algal flora'. Laing (1895) wrote that 'marine algae are not so widely distributed as might on first thoughts be imagined. Indeed, it might be supposed that the only limitations to their distribution would be due to unsuitable environment; but this is by no means the case. In spite of the great geological age of this class of plants, and their marine habitat, many of them are local in their distribution... the facts of distribution do not by any means favour the supposition that ocean-currents do [successfully] distribute living Algae broadcast on the shores which they wash'. He discussed the debate between Hutton (1872) and Wallace (1876), for and against land connections between Australasia and South America, and argued that the distribution of algae 'strongly favours a former greater land-connection', as Hutton suggested. For many years Laing continued to support Hutton against Wallace: 'Whatever the explanation of the present distribution of our seaweeds may be... the range of living forms cannot be accounted for on the supposition that the present land-masses have been permanent, i.e. the marine Algae in their present distribution tend to support such a belief in changing continental areas rather than negate it.' (Laing, 1927).

Describing the large brown alga *Lessonia adamsiae* endemic to the Snares, south of New Zealand, Hay (1987) wrote that 'the causes of such speciation are as enigmatic as are the reasons preventing *L. variegata* from colonizing the Snares and *L. adamsiae* from colonizing the mainland', but W. A. Nelson (1994) recognized that the vicariance analysis of the Lessoniaceae by Chin *et al.* (1991) was a 'very different view' from that of earlier dispersal studies. She concluded that 'The distribution of *Lessonia* [Southern Ocean plus Peru] and endemism in the New Zealand region suggests that the complex may have a vicariant eastern Gondwana origin'. Likewise, Nelson argued that the distribution of taxa such as *Ecklonia* [South Africa, Australia, New Zealand, north-west Pacific, north-east Atlantic, Oman] can be interpreted 'as ancient assemblages, with vicariant patterns developing as the links between northern and southern regions were

broken'. For the islands in the New Zealand region, 'neither proximity to the mainland, geological age of the island(s), or prevailing current systems are sufficient either singly or taken together, to explain the origins and composition of the extant floras. Craw (1982) suggested that the composite geological structure of New Zealand may be reflected in a composite biogeography...'. Heads (1990) developed a model of New Zealand biogeography which accounted for terrestrial and marine distributions as a result of rifting and accreted terrane tectonics.

Following this work other authors have accepted similar processes in other parts of the world and also in marine communities. Chin *et al.* (1991) cited circum-Pacific accretion of Pacifica terranes to explain circum-Pacific distribution of marine algae. Stevens (1997) found strong New Zealand - Mexico connections in his study of Jurassic ammonites. He discounted direct trans-Pacific migration, and considered possible alternative explanations. He noted that New Zealand is composed of a collage of tectonic blocks, some of which could have originated in the low latitudes of the Northern Hemisphere. The New Zealand and Mexican fossils both occur in terranes with a history of lateral displacement and may have formerly been more closely adjacent before 'long-distance travel of terrane units'. A second option involves expanding earth assemblages. Both alternatives 'might be considered unorthodox geological theory', but 'considering the vicissitudes endured by Wegener's Continental Drift theory... an open-minded approach should be adopted and judgement deferred *pro tem*'.

For Sauropterygian reptiles of the Triassic, Rieppel (1999) also suggested that trans-Pacific relationships of pistosaurs 'appear best explained as a consequence of vicariance due to the accretion of exotic terranes at opposite margins of the Pacific Basin'.

This process has also been invoked for more local areas in the Pacific. Marshall (1991) noted that the New Caledonian molluscan fauna in general is 'exceptionally rich' and also cited a 'remarkable' Pleistocene assemblage from Vanuatu. He described the seguenziid gastropod fauna of New Caledonia and found it 'exceptionally diverse', with 91% of the species endemic there. He proposed that 'Since the Melanesian arc is situated at current or former [convergent] boundaries of the Australian and Pacific lithospheric plates, species richness there is probably due at least partly to progressive accumulation of taxa transported on the plates'.

New Guinea is a geological and biological composite, formed from as many as 32 separate accreted terranes in the north juxtaposed to each other and to the northern margin of the Australian craton in the south of the island. Madang, in northern Papua New Guinea (PNG) on the accreted terrane section, is extremely

diverse for many marine taxa. For example, there are 536 opisthobranch species, the largest number from any equivalent area (Ghiselin, 1993), 150 octocorals (G. C. Williams, pers. comm., cited in Kohn, 2001), 31 comatulid crinoids (Messing, 1993), 39 fungiid corals, more than anywhere else (eastern Indonesia and the Philippines each have 37; Hoeksema, 1993), and 180 coral reef amphipods, 'likely' to exceed that of any other reef area (Thomas, 1993). The pantropical gastropod *Conus* has about 500 species and is possibly the most diverse genus of marine invertebrates. Röckel, Korn & Kohn (1995) indicated that at least 80 species occur on the Madang coast and Kohn (2001) recorded 36 species from a single reef there, far exceeding numbers recorded on any other reef. Thomas (1997) also noted unusually high species diversity there in polychaetes, cephalopods and algae, and wrote (citing D. Potts, pers. comm., 1994) that Madang Lagoon 'may prove to be the single most diverse site in the world for scleractinian corals'. At the eastern end of PNG, also on accreted terrane, Fenner & Turak (2003) recorded 418 coral species in Milne Bay Province alone, compared with 427 for all of Indonesia and 411 for all of the Philippines.

Kohn (2001) felt that the high diversity of so many disparate taxa on the north-east coast of PNG 'suggests one or more common environmental causes', but this is not accepted here. The fact that megadiversity of northern New Guinea taxa occurs in such a wide range of environments, including terrestrial habitats, indicates that the cause of the diversity is not related to the current environment but is due instead to historical factors. Thomas (1993) attributed the 'exceptional' biodiversity here to the invertebrate fauna being a 'composite formed by past geological events'. This was also accepted by Pandolfi (1993) in his explanation of New Guinea marine biogeography. Pandolfi argued that the high diversity of New Guinea marine taxa 'has been generally explained by a centre-of-origin hypothesis', but more recent workers have noted that that hypothesis is basically untestable (McCoy & Heck, 1976, 1983; Rosen, 1984). Pandolfi followed Springer (1982) and Rosen (1984) in relating present distribution patterns to past geological events in a vicariance model. In particular, Pandolfi (1993) gave an excellent review of terrane tectonics in New Guinea and its significance for marine biogeography that I regret not having seen when I wrote on terrane tectonics and terrestrial biogeography in New Guinea (Heds, 2001a, b, 2002, 2003). Pandolfi suggested that 'marine distribution patterns can best be interpreted by incorporating the geological history of the area under study. In New Guinean tectonics and biogeography, a striking coexistence of a tectonic zone composed of many independent parts [craton plus 32 terranes] with a marine biosphere of high diversity is

apparent'. Pandolfi suggested lateral displacement of whole faunas by plate tectonic motion: 'As the terranes neared and coalesced with each other and with Australia/New Guinea, an integration of biotas might have enriched diversity (Rotondo *et al.*, 1981; Rosen, 1984).'

Thomas (1997) supported this explanation for the diversity in north-east New Guinea, concluding that 'the composite marine fauna of the Madang Lagoon is the result of the accretionary process along the north coast of PNG... This docking process introduced a number of previously discrete biotic assemblages that then intermingled with established floral and faunal elements.'

Wallace (1997) discussed coral biogeography and wrote that 'There are indications that at least some of the distributions within the Indo-Australian arc follow terrestrial and freshwater biota in confirming relationships between the geological and biological evolution of the central Indo-Pacific.' She continued: 'Parenti (1991) agreeing with Heads (1990), argues that events in the late Mesozoic and the Miocene [actually Parenti and I only referred to the late Mesozoic] are likely to have played an important part in the evolution of modern taxa, an idea applied to corals and marine biota by Pandolfi (1992, 1993).' Parenti found that fishes, bugs, cicadas and bats have trans-Tethyan as well as Indian Ocean and Pacific Ocean origins, and this has resulted in the composite faunas of composite land masses such as New Guinea and Sulawesi. Wallace (1997, 1999b) proposed that areas such as the Togian Islands (central Sulawesi, Sula platform) and northern Halmahera (Moluccas) likewise show composite coral faunas related to terrane movement. She concluded that the high diversity of Indonesia's coral fauna is due to its complex tectonic history, in particular its geologically composite nature, with taxa of ultimately Indian Ocean, Pacific Ocean and Tethyan origin. As indicated above ('Diversity in the Indo-Australian Archipelago'), this is the same conclusion reached by other authors for terrestrial birds and plants in the same region.

Santini & Winterbottom (2002) discussed whether the Indonesian region is a centre of origin, or a 'centre of accumulation of diversity, with various taxa brought into contact by the collision of various tectonic plates and island arcs...'. They concluded in support of the latter: marine forms in the region 'appear to have been augmented by the accretion of island groups or terranes originating on the Pacific plate (e.g. parts of the Philippines, New Guinea, Halmahera)... The convergence on south-east Asia of so many continental and volcanic fragments and islands thus provided a melting pot for the creation of the highly diverse faunas we see in the region today... [Pandolfi's (1992)] overall conclusion that the diversity of south-east Asia

is mainly because of an amalgamation of faunas is congruent with our results.'

Carpenter & Springer (in press) document a global peak of shore fish diversity in the Philippines which they attribute to 'numerous vicariant and island integration events' there. The Philippines comprise at least three major island arc systems that were widely separated during much of the Cenozoic and each displaced over 1000 km to reach their current locations. The accretion of the archipelago could also have concentrated shorefish diversity.

TECTONIC UPLIFT AND SUBSIDENCE CAN AFFECT VERTICAL DISTRIBUTION OF MARINE COMMUNITIES

Although only a few of the 30 000 seamounts found worldwide have been investigated, their faunas are of special interest and show high endemism. For example, the vicariant distributions of the four roughies (Trachichthyidae) in New Zealand waters were mapped by Paulin (1979). In one, the orange roughy (*Hoplostethus atlanticus*), Haddon & Willis (1995) found that populations from the Puysegur Bank, south of New Zealand, and the Lord Howe Rise, west of New Zealand, had different body shapes, suggesting localized breeding groups on seamounts with little genetic interchange. How has this situation arisen?

Parin, Mironov & Nesis (1997) studied the seamount faunas of the Sala y Gómez and Nazca submarine ridges, east of Easter Island. The most pronounced feature is the endemism of invertebrates and fishes, which 'seems to be unprecedentedly high, even in comparison with the very high endemism of the nearshore fauna of the Hawaiian Islands . . . or Easter Island'. Parin *et al.* recognized that the process of formation of the faunas is the 'key problem' here. They felt that 'Such a high level of endemism might be attributed to the isolation of the ridges . . . but the problem is not so simple'. In explaining seamount endemism in this area Parin (1991) explicitly adopted Springer's (1982) ideas on tectonics and vicariant events.

George & Schminke (2002) studied the harpacticoid copepods of the Great Meteor Seamount west of the Canary Islands. They found 'pronounced endemism' and two distinct faunas, one on the plateau and one in the surrounding deep sea. On the plateau 'astonishing radiations' occur in groups such as Argastidae. The authors concluded that 'Owing to long isolation, the harpacticoid fauna . . . must, on the basis of present knowledge, be regarded as a distinct assemblage with only minor bathymetric and geographic exchange since the origin of the seamount (at least 50 million years ago . . .)'. Contrary to the idea that there is a constant step-by-step addition of deep-sea species to the fauna of the plateau, George & Schminke reached

the conclusion that 'the members of the plateau fauna with a deep-sea origin stem from ancestors that have been lifted up together with the seamount and that subsequently adapted to shallow-water conditions. Recruitment directly from the deep sea is negligible'. This is pure panbiogeography. For example, Craw *et al.* (1999: figs 2–4) showed how subsidence of basins can change a shallow-water benthos to a deep-water benthos, and that uplift can convert an intertidal community to a terrestrial one.

Stock (1977, 1993), Holsinger (1991, 1994) and Notenboom (1991) developed the idea that interstitial shore invertebrates such as amphipods have become stranded in freshwater subterranean habitats by passive vicariant events following tectonic uplift or marine regression. Several such stygobiont genera include both marine and freshwater species and have extremely limited dispersal capabilities. Stock (1993) also attributed vicariant horizontal distribution in these taxa to plate tectonic effects, especially the opening of the Atlantic and the closing of the Tethys.

Similar close relationships occur between many marine and freshwater fishes, but most authors have assumed that 'invasion' of freshwater habitats involves dispersal events. For example, Lovejoy & Collette (2001) writing on needlefishes (Belontiidae) admitted that their analysis 'makes the assumption that transitions between habitat types (and therefore dispersals) have occurred.' They wrote that a vicariance analysis would assume descent from a common ancestral species whose range included both habitat types, but this is not correct. In vicariance analysis ancestors are not necessarily single species (cf. Heads, 1985) and the ancestor may have been restricted to sea water before uplift changed conditions. Lovejoy & Collette argued that only a few needlefish species occur in both freshwater and marine areas, but whether it is species or larger monophyletic groups that occur in both is irrelevant in vicariance analysis.

Nelson (1984) addressed the same problem in marine/freshwater anchovies (Engraulidae) and accepted a vicariance model like that of Stock (1977) which, he argued, 'explains the development within South America of endemic freshwater species within taxa that are primitively marine. This model is one of environmental change from marine to freshwater conditions over a large area of western South America. The model is analogous to stream capture but on larger scale – here the "stream" captured is a large part of the E Pacific – and mediated not by erosion but by orogeny.'

As with the seamount faunas, the amphipods and the anchovies, it has been suggested that tectonics has directly affected the vertical as well as the horizontal distribution of mangroves. In Colombia (Chocó), Ricklefs & Latham (1993a) observed that uplifted man-

grove habitats may permit intermixing of more terrestrial, flood-tolerant (as opposed to salt-tolerant) vegetation. They noted that Croizat (1964) and others have suggested that mangrove taxa may have left descendants following uplift of mangrove habitat; certainly mangrove species of *Sonneratia* and *Pemphis* have sister taxa with restricted distribution at high elevations in Indomalaysia and Madagascar, respectively. Mepham & Mepham (1985) reported the presence of many mangrove taxa at upland sites and the inland and montane flora and fauna of Malesia and New Zealand can be interpreted in terms of derivation from mangrove and saltmarsh precursors (Heads, 1990, 2001a, 2003).

In the nudibranch genus *Phyllidiopsis* 'several cases of vicariance have been detected . . . Apparently two major vicariant events occurred between the tropical Indo-Pacific region and the Atlantic-eastern Pacific area first . . .' (Valdés, 2001). Two sister species are present on New Caledonia and Vanuatu, respectively, separated by a trench 6000–7000 m deep 'that might have caused fragmentation in the original range and subsequent speciation of the two'. Valdés extended this analysis to make the interesting observation that 'Vicariant events could also be involved in producing vertical distribution patterns . . . *P. shireenae* is found in the western tropical Pacific Ocean . . . , always in shallow waters down to 30 m depth'. However, its putative sister species, *P. crucifera*, also a western tropical Pacific species, is found off Futuna Island by a subduction zone where it occurs at a depth of 105–160 m.

SUBSTANTIAL PARALLELS EXIST BETWEEN THE BIOGEOGRAPHY OF TERRESTRIAL AND MARINE TAXA

Veron (1995) argued that 'Biogeographic concepts developed from terrestrial biota have very doubtful relevance to the ocean' and most other authors have assumed that this is true. However, the statement reflects a theoretical position deduced from dispersalist axioms rather than any empirical study. In the last section the intimate relationship between marine and freshwater communities was indicated and the migrations of eels between deep ocean basins and highland freshwaters was discussed. As Croizat (1958; vol. 2: 113) wrote: 'Lands constantly went up and down and so did seas; therefore, whatever once was of the mountains eventually came down, and whatever was of the shore eventually went up, fresh- and salt-waters forever mingling in the process and trading out life'. What about the relationship between marine and fully terrestrial biota?

Many obvious parallels among the distributions of marine and terrestrial taxa have been pointed out in panbiogeographic work on marine taxa (e.g. Croizat,

1958; vol. 1: 720–735 on seabirds, vol. 2: 917–931 on sea-birds, 1380–1387 on living and fossil marine bivalves, 1968a, b on mangroves, 1975: 89–97 on marine mammals; Heads, 1983; McManus, 1985; Chin *et al.*, 1991, Lourie & Vincent, 2004). In fact, panbiogeographic analysis can easily integrate records from marine and terrestrial, as well as fossil and living taxa. For example, the Triassic bivalve *Monotis* and the extant angiosperm *Coriaria* both have broad Pacific plus Tethys distributions that are strikingly similar (Heads, 1990: fig. 19) and the importance of Tethys distributions for terrestrial as well as marine biota in general has been a major theme of panbiogeography (Croizat, 1968a, b).

Croizat (1964) and Durham (1985) both suggested that biological disjunction along transform faults in the Caribbean was due to lateral movement on the transforms; Croizat used terrestrial liverworts to support his argument, Durham used echinoids (both mapped in Heads, 1990). In northern North Island, New Zealand, a similar parallel arcs pattern is evident in the biogeography of terrestrial plants and animals, and marine taxa such as barnacles (Heads, 1990: fig. 4).

There is tremendous opposition to the idea that marine and terrestrial patterns could be related. For example, in a submitted manuscript I mapped many New Zealand taxa, marine and terrestrial, which showed the Alpine fault disjunction. One of the referees accepted the main findings of the paper but insisted that the many marine examples be left out because 'they couldn't possibly have anything to do with the terrestrial pattern'. (I did manage to sneak one example, a red alga, into the published version of the paper; Heads, 1998. Other marine examples are cited in Heads & Craw, 2004.)

It is well known that many marine taxa have a broad Indo-West Pacific distribution, ranging from the west Indian Ocean to the west Pacific Ocean and absent in the East Pacific and Atlantic. It is perhaps less well known that many terrestrial plants have the same range. In a continuing series, van Balgooy (1963–1993) has mapped 43 such plant taxa, and countless other Indo-West Pacific affinities exist in land plants at different ranks. At a smaller scale, Roberts *et al.* (2002) found that restricted range species of reef taxa were clustered into centres of endemism 'like those described for terrestrial taxa'. In fact the actual centres are the same for both groups and so Roberts *et al.* listed centres of marine endemism together with their 'adjacent terrestrial biodiversity hotspots'. In particular the four marine groups studied (reef fishes, corals, snails, lobsters) all had primary centres in the Indo-Australian Archipelago, discussed above. This same area is well known to botanists as a centre of endemism (referred to by them as Malesia) and this is

the biological basis for describing its flora in a single work, the *Flora Malesiana* (van Steenis, 1948–).

COMPOSITE AREAS ARE TRACTABLE USING
PANBIOGEOGRAPHIC ANALYSIS

The Indo-Australian Archipelago, New Guinea and New Zealand are classic examples of areas that are composite, both biogeographically and geologically. How do the different methods of biogeographic analysis deal with such 'areas'? Although Veron (1995) criticized panbiogeography, he did not cite any main references on the subject, only brief commentary papers and Croizat *et al.* (1974). He suggested Seberg (1986) as a 'useful review' of panbiogeography, when in fact this paper is a very negative critique. However, Veron did make the valid point that panbiogeography is not 'necessarily over-ridden by its offspring, vicariance [cladistic] biogeography, as is widely supposed.' In particular, panbiogeography does not use the centres of endemism often employed in dispersal and vicariance-cladistic analyses, stressing instead that many of these traditional areas are composite. Lessios *et al.* (1999) observed that, 'Most of what we know about marine biogeography and barriers to dispersal for marine organisms has been based on the traditional approach of studying the number of species that are found in common in different geographic regions (e.g. Ekman, 1953; Briggs, 1974a; Vermeij, 1978, 1987).' In contrast, panbiogeography and geology do not recognize most current 'geographic regions' or areas as having any meaning, as most of them are composite, and do not use them in analysis. Likewise, panbiogeography and vicariance biogeography do not use numbers of species (or of any taxa) to establish any 'degree of difference' between areas.

In their important paper on the Indo-Australian Archipelago coral reef biota, Santini & Winterbottom (2002) emphasized that 'Composite areas do exist, and in fact they might actually be quite common in some parts of the world . . . with real datasets it can become a nightmare'. However, complex data sets need not be a problem if actual distributions, rather than a priori areas, are used in analysis. Santini & Winterbottom concluded their paper by suggesting that 'at least one new analytical approach needs to be developed. Current techniques only allow for a most parsimonious explanation of the entire dataset. Incongruent data are explained away as, for example, local extinction or dispersal. However, where areas are suspected of being the result of amalgamation of different biogeographic histories, we need to develop analytical techniques to recognize and treat them as such. We anticipate this as an essential tool that may allow us to tease apart the components of such complex areas of amalgamation as we propose for the Indonesian

region.' In fact, an effective analytical method for 'teasing apart' components of complex areas of amalgamation was well established by Croizat (1958). This method relies on analysing actual distributions rather than allocating them to 'areas of endemism' or 'centres of biodiversity' prior to analysis. Because of this, Croizat was able to 'tease apart' such complex areas as, for example, Sulawesi and New Guinea. The same method was applied to the Indonesian region in a study of the plant family Ericaceae (Heads, 2003). The family has almost 800 species in the region, most with distributions known in some detail, and this enabled a detailed analysis of Borneo, Sumatra and New Guinea, and their component terranes.

METAPOPULATION THEORY IS MORE REALISTIC THAN
LONG-DISTANCE DISPERSAL AND EQUILIBRIUM THEORY

MacArthur & Wilson's (1967) 'equilibrium theory' of island biogeography is a simple extrapolation from Darwin–Wallace dispersal biogeography, with founder dispersal from a mainland centre of origin playing a dominant role. In contrast, panbiogeography theory does not rely on a totally hypothetical mainland source or on equally hypothetical founder effect dispersal; instead it stresses normal migration among unstable local populations, any of which may go extinct, and regional persistence. Local populations come and go by ordinary means of survival and this 'metapopulation' approach (Hanski, 1998, 1999) is eminently panbiogeographic, although panbiogeography was cited neither in its formulation nor in its application.

Holloway (2003) insisted that panbiogeography is wrong to distance itself from the 'equilibrium theory' of island biogeography and quoted the Bible in support ('put aside childish things'), but this is hardly a convincing argument. Even Whittaker (1998), in a book heavily influenced by A. R. Wallace's work, agreed that 'equilibrium theory has been falsified many times . . .' Recently, a decline in the number of publications on MacArthur and Wilson 'island biogeography' in favour of metapopulation biology has been taken as evidence for a paradigm shift taking place (Hanski & Simberloff, 1997). Other evidence for the beginnings of a paradigm shift towards panbiogeography is given in this paper.

Unlike many authors who have denied that there is a true Polynesian terrestrial flora, Philipson (1970) argued that plants such as *Meryta*, *Tetraplasandra* (both Araliaceae), *Fitchia* (Compositae), *Sclerotheca* (Campanulaceae), *Vaccinium* sect. *Macropelma* (Ericaceae), 25 endemic plant species on Rarotonga, and many others indicate that 'the southern Pacific islands must be credited with a flora specific to this region . . . Clearly land has been present for long periods in this

area of the Pacific because well-marked genera are endemic to it. The flora characteristic of this region could survive provided a few oceanic volcanoes projected above the sea at all times. Such oceanic islands characteristically rise and fall relative to sea-level so that they are precarious foot-holds for a flora, but collectively they form a secure base'. In this view, vicariants could also maintain their respective ranges in adjacent archipelagos, as long as new volcanoes and atolls constantly appear to replace vanishing ones. New individual islands will be colonized by ordinary, everyday movement, an observable ecological phenomenon which functions using ordinary means of survival.

This approach undermines the fundamental distinction that Wallace (1876) made between 'oceanic' and 'continental' islands. Oceanic islands, such as Hawaii, Easter Island and Ascension Island, have been assumed (e.g. Robertson, 2001) to have received their biota by chance long-distance dispersal from a distant source area, not from a now submerged island. However, in an important paper, Rotondo *et al.* (1981) gave a possible alternative to the founder principle in explaining Hawaiian endemism. They observed that different island chains formed by plate movement over hotspots would eventually join with others formed at other hotspots ('island integration') and used this idea to explain the Hawaii – south-east Polynesia connections in shore fishes and terrestrial taxa. (Newman & Foster, 1983, pointed out that the particular seamounts Rotondo *et al.* cited may not have been integrated with Hawaii as islands, but the general principle is valid.) Rosen (1988) found this a 'highly plausible' mechanism for 'isolation and regional vicariance amongst the many islands that rise from the Pacific floor'. (It has been pointed out that movement on geological formations, as in accreting terranes or island integration, is a form of 'dispersal', but apart from being over a million times slower than chance long-distance dispersal, it is an orderly process affecting all the members of communities in the same way and will give rise to analysable patterns, unlike founder dispersal.) Springer (1982) employed 'island integration' in discussing the Hawaiian reef fish fauna and Rowe (1985) (as cited by Rosen, 1988) adopted island integration in his discussion of the biogeography of Pacific asteroids.

Randall (1995) also suggested vicariant patterns to explain the origin of some of the inshore fish fauna of Hawaii and emphasized that some of the distributions can only be explained in terms of the geological history of the Pacific plate: 'The Hawaiian Islands have been forming intermittently over a relatively fixed site of volcanism for more than 70 million years (Rotondo *et al.*, 1981). As the Pacific Plate moved to the northwest, the islands of the Hawaiian-Emperor

chain eroded to reefs and ultimately subducted as seamounts under the Asian continent, but the resident fishes were able to disperse the short distance to the east to the newly emerging islands'. In an analysis of pontonid shrimps De Grave (2001) found Hawaii to be sister group to the rest of the Indo-West Pacific, and concluded that this 'is probably linked to its long geological history, as the Hawaiian – Emperor chain has been in existence since at least 70 Ma (oldest non-subducted seamount) . . .' Of course there may well have been older seamounts that are now subducted.

Hartley (2000) also used the idea of hotspot metapopulations when discussing the terrestrial plant genus *Melicope* (Rutaceae) which occupies, among other areas, 22 individual Pacific Basin islands. 'Most of them are less than 4 million years old, and the oldest (as far as known) dates to 8.6 Ma. The islands are mostly volcanoes of hotspot traces, however, and *Melicope* presumably could have occupied each trace for as long as its hotspot has produced a continuity of volcanic islands.'

Newman & Foster (1983) used similar reasoning in discussing the shore faunas of Easter Island and nearby Sala y Gómez, which both show a 'remarkably' high degree of endemism. The islands are very young (2.5 and 2 m.y. old) but the endemics appear to be relics stemming from older Indo-Pacific groups and are 'therefore potentially older than the island themselves.' (cf. Stock, 1993, on stygobiont amphipods of the Atlantic islands). Newman & Foster suggested a vicariance model for the origin of the fauna. An analysis of the numerous seamounts of the Sala y Gómez and Nazca ridges 'shows that most were once likely islands. It also indicates that there could have been a chronological continuity of shores among these islands for at least the past 29 Ma, . . . upon which the endemics of the region could have evolved and been perpetuated up to present times . . . [by] relatively local island-hopping'.

Likewise, discussing the notocthamaline barnacle *Rehderella belyaevi* of Pitcairn and Easter Islands, Foster & Newman (1987) wrote that 'the island age seems insufficient [to account for the distribution]. The lineage of this barnacle . . . must have involved a stock older than either Pitcairn or Easter Island. A solution has been sought in hypothesizing tectonic creation of islands near the East Pacific Rise at these latitudes for the last 30 million years (Springer, 1982; Newman & Foster, 1983). As erosion and subsidence drowned these islands, and as they moved apart to either side of the Rise by sea-floor spreading, the shore species dispersed to nearby, newly formed islands'. The populations on Pitcairn and Easter are moving apart as the seafloor spreads away from the East Pacific Rise. 'Survival of either population will depend

on the tectonic creation of new islands in the region before the existing ones are eroded and translated below sea level'. This analysis is pure panbiogeography, integrating ordinary ecological dispersal and tectonics, and not involving chance, long-distance dispersal.

Foster & Newman (1987) also considered where the stock of *Rehderella belyaevi* (Pitcairn and Easter Islands) came from in the first place. They gave a further vicariance explanation, based on the vicariant distribution of the subfamily members (Easter and Pitcairn, Central Pacific, south-east Australia, New Zealand, Chile): 'The notochthamalines could represent fragments of ancient southern ocean shore faunas which became isolated from each other during past tectonic events. Affinities with *N[otochthamalus] scabrosus* of South America tempt an east-to-west "tract" across the Pacific involving ancient Nasca Ridge archipelagos ...'

Sluys (1989) gave an interesting discussion of Hawaiian endemism in marine triclads and pointed out that it 'is not difficult to think of a scenario incorporating the break-up of Pacifica ... island integration ... and the process of escalator-dispersal (McKenna, 1983)' in which taxa survive more or less *in situ* by migrating from a sinking or eroding volcano onto a nearby younger one. Sluys noted that Croizat (1964) repeatedly stressed that old faunal elements occur on relatively young islands ('very new stratigraphy may harbour very ancient life') and invoked McKenna's (1983) 'tread-mill hypothesis', a variation of 'escalator-dispersal', to explain old fauna on Iceland, on the Mid-Atlantic Ridge. Likewise, he accepted a vicariance hypothesis to explain triclad distribution on the islands of the Southern Ocean; even though many of these are very young, most had forerunners, either other volcanic islands or ancient socles.

The most primitive members of three barnacle suborders are all associated with deep-sea hydrothermal springs: *Neoverruca* (Verrucomorpha) at the Marianas, *Eochionelasmus* (Balanomorpha) in the North Fiji Basin, and *Neolepas* (Scapellomorpha) on the East Pacific Rise. Yamaguchi & Newman (1990) wrote that 'at first glance ... [this] seems like a remarkable coincidence'. They cited theories for high endemism at hydrothermal vents, including the idea of a great age for the biota, 'although it is agreed that individual vents are ephemeral in space and time'. This would imply 'excellent dispersal capabilities' for the vent taxa, which is accepted here as it simply refers to 'means of survival' which permit a metapopulation to persist, not to 'chance dispersal' as a mechanism which generates new species.

On the Mid-Atlantic Ridge islands, the trumpetfish *Aulostomus strigosus* populations of Ascension and St. Helena share an endemic haplotype (Bowen *et al.*,

2001). This same affinity was also found by Muss *et al.* (2001) in *Ophioblennius* and they interpreted the pattern as due to colonization of Ascension from a centre of origin on St. Helena. However, it is extremely unlikely that there were never any other islands on the ridge and these may have been involved in preserving a Mid-Atlantic Ridge metapopulation with the endemic haplotype. Other fishes endemic to the Mid-Atlantic Ridge include *Pachycara* spp. (Zoarcidae) (Bischoito & Almeida, 2004).

In the eastern Caribbean, Roughgarden (1995) studied *Anolis* lizards and interpreted their distribution in a synthesis of ecology and plate tectonics. Two generalizations of 'island biogeography' turned out not to apply: the highest species diversity occurs on islands that are intermediate in size (not the largest) and intermediate in distance (not the closest) from 'source location'. 'Neither the area nor the distance effects are observed by this fauna. This foreshadows a deep role for plate tectonics ... The *Anolis* lizards may serve as "living strata ..."', and in fact fossil *Anolis* dated at 20 Ma, or possibly even 40 Ma old, from the Dominican Republic is 'indistinguishable' from extant Hispaniola species. (For discussion of life as a geological layer, see Heads, 1990, and Craw *et al.*, 1999.)

For Roughgarden, the Lesser Antilles faunas 'are not stages toward building up a large community, but are derived extractions from already existing large communities. Conversely, the assemblage of large communities, such as those on Cuba and Hispaniola, probably results from combining packages of species when tectonic blocks fuse to form a single island, rather than from the addition of single species, one by one ...' This view can be compared with those on accreted terrane tectonics in the south-west Pacific discussed above. Roughgarden concluded: 'An overall implication of plate tectonics for terrestrial ecology is that relatively fast-acting ecological interactions such as competition and predation are far from sufficient to explain the structure and composition of ecological communities. Instead, ecological communities are fashioned as much by relatively slow geological processes as by fast species interactions. We have thus come full circle. During the last two decades instances of fast evolution, on an ecological time scale, have been discovered. Now it is also clear that ecological change can itself be very slow, on an evolutionary time scale.' All this is pure panbiogeography.

In sum, both the metapopulation model and panbiogeography regard the distinction between 'oceanic' and 'continental' islands as biogeographically artificial and irrelevant (cf. Grehan, 2001). Many areas that are now continental (e.g. parts of Central America, New Guinea) were once oceanic or insular, and real islands are essentially similar to any other habitat islands,

such as mountain peaks, forest gaps, limestone outcrops or hydrothermal vents.

REGIONAL BIOGEOGRAPHY IS A MAJOR DETERMINANT
OF LOCAL COMMUNITY COMPOSITION

Ricklefs & Schluter (1993a) wrote that their book (Ricklefs & Schluter, 1993b) 'grew out of our conviction that the discipline of community ecology would benefit from a broadening of its paradigms. Ecological studies of the past thirty years have presumed that interactions among populations within small areas are the fundamental forces regulating community structure. However, this paradigm failed to solve one of the monumental problems of biology: the origin and maintenance of global patterns of biodiversity . . . disparities were often found in the number of species present in similar environments in different parts of the globe, hinting that larger scale processes were also at work and might even dominate local ones. Until recently, community ecologists largely ignored such vexing disparities. Indeed, from the 1960s to the 1980s ecology largely spurned its sister disciplines of systematics, biogeography, and palaeontology and the insights they provided into the larger-scale processes and historical events that have influenced species richness. By the late 1980s, however, the intellectual climate of ecological study was changing. The failure of the local-process paradigm to achieve a consensus on the causes of diversity opened the door for fresh approaches.'

Likewise, McPeck & Miller (1996) observed that 'Community ecologists are beginning to examine how present-day species diversity is influenced by macroevolutionary and biogeographic processes . . . While most ecologists are mindful that evolution is important in shaping community structure, the general role of evolution is often ignored when considering the ecology of specific communities . . . However, ignoring evolution leaves many fundamental questions about community structure unanswered. For example, where did the collection of species we see coexisting today come from in the first place . . .?'

In their study of coral species richness Cornell & Karlson (2000) concluded that 'biogeography can be at least as important as local ecology in explanations for richness variation among different locations . . . understanding community assembly will require more focus on macroevolutionary processes.' For example, in less speciose regions of the Indo-Pacific, 'local richness was extremely sensitive to regional effects which accounted for fully 95% of explained variation in local richness . . . The results imply that local environment can modify local richness, but it does not set its upper limit'. This was an early conclusion of Croizat (1964). In panbiogeography, ranges of groups are interpreted as shaped primarily by the original evolution of the

group, not by intrinsic factors such as means of dispersal or physiological capabilities, or by extrinsic factors such as interactions with other groups and aspects of the physical environment. Ecological factors may eliminate a group from a certain area or site, but they do not determine why a group is in the areas it is in to begin with. Authors often feel that ecology plays a crucial role in determining evolution and biogeography. However, if the location of marine communities can be affected by plate movement and their depth by processes such as uplift and subsidence, biogeography may instead determine ecology.

EVOLUTION IN SPACE AND TIME IS A FUNCTION OF
GENETIC POTENTIAL

Ekman (1953) took a broader view of speciation than most Anglo-American neo-darwinists. After discussing speciation by divergence, he wrote that 'We must also take into account the possibility of another way in which species may originate, namely parallel development. It is conceivable that two populations of the same parent species . . . have developed on parallel lines . . . [eventually] parallel development has produced morphological identity.' Orthogenetic evolution may also lead to extinction: through mutations 'the organism becomes adapted ("preadapted") to new environmental conditions . . . On the other hand changes in the germ plasm and the environment may become unfavourable to the species and lead in time to its extinction.' This view has important implications for a panbiogeographic synthesis of evolution in space, time and form.

Differing locations of groups are due to different locations of ancestral genetic potential.

Why are some groups present or diverse in some areas and less so or absent elsewhere, while other groups show the reverse pattern? Authors sometimes suggest this is due to different powers of dispersal or different rates of evolution in different areas. However, it may be that there was simply more genetic potential in different groups in different areas (cf. Schwabe & Warr, 1984; Levin, 2001). When the last major phase of modernization in plants and animals took place (for most groups in the late Mesozoic) some groups evolved many species in one area, while others evolved more in a second area. As an example, Adler *et al.* (1995) found large differences between levels of endemism in birds and those in skinks of the Pacific Islands. The islands of the central Pacific, east of Fiji (on the Pacific plate) have an avifauna exceptionally rich in endemic species (Adler, 1992), even if the bizarre, recently extirpated birds of areas like Hawaii are omitted from consideration. The bird faunas of Hawaii and Marquesas are nearly completely endemic, while the

skinks there show no endemism. On the other hand, the skink fauna of New Caledonia (south-west Pacific; Australian plate) has much more endemism than the bird fauna. Adler *et al.* concluded that these results 'presumably' reflect the relative dispersal powers of the two groups and consequently rates of evolution. They suggested that differences may also be due to 'unknown' local ecological interactions. Confusingly, 'Despite the extremely limited capacity of skinks for active overwater dispersal, these lizards have managed to colonise virtually every archipelago and isolated island in the tropical Pacific [although there is no endemism there] . . . [thus] skinks must have relied primarily upon chance events . . .'

By relying on presumptions, chance dispersal and unknown ecological factors, Adler *et al.* avoided confronting the possibility that birds may well have had an early ancestral base and centre of genetic potential in the central and east Pacific (east of Fiji) that the ancestors of skinks may never have had, and that current differences may simply be a result of different Mesozoic main massings of the ancestral forms. In other words, the current patterns have little if anything to do with the current groups, their current ecology or current geography. There are no fossils or even rocks older than 150 Ma in the central Pacific, so whether it was mainly land or sea then is highly speculative, but there was undoubtedly something there.

In another example, Larkum & den Hartog (1989) considered the seagrasses. Australia has the highest number of species (18) of any continent, and about one-third of all known species are endemic there. The south-west is especially rich. Sixteen species and two endemic genera are restricted to the temperate zone of Australia, but in 'striking contrast' New Zealand has only two species. These authors wrote that 'two explanations are possible': either the Australian species arrived after the separation from Gondwanaland, or east Australia and New Zealand lost more species through extinction. However, a third possibility seems much more likely: there was an original Indian Ocean centre of evolution which did not involve east Australia/New Zealand. There was always more diversity in the west, from a seagrass precursor stage right through to the modern flora. Thus, different taxa are diverse in different areas not because they have dispersed there, or because the ecology is most suitable there, but because their ancestral genetic potential was greatest there.

Different degrees of differentiation between groups are due to their differing genetic potential, not their age or rate of differentiation

Palumbi (1997) wrote that congruent geographic patterns at different taxonomic levels suggest that either '1. different taxa were affected at different times or 2.

a single event affected [different] taxa in markedly different ways'. The second is accepted here as correct.

It was well established prior to the modern molecular work that the degree of differentiation between two taxa is not proportional to the time elapsed since their last contact. Evolution may well occur in bursts during which an ancestral complex is modernized rapidly followed by long periods of stasis (Croizat, 1964). Neither is the degree of divergence proportional to the rate of evolution in the two taxa, and so divergence may instead be related to the genetic potential for change in the ancestors of the two.

Thus in a phase of evolution, one group may 'dissolve' into new genera (or equivalent genetic divergence), another, along the same 'track' may give rise to species, another to barely distinguishable cytotypes. All may have the same distribution. For example, the New Guinea – New Caledonia track skirting Australia is held by many terrestrial taxa of different rank as well as many coral species. The same track may be the result of, say, events that took place at about 50 Ma, with the subfamilies taking 3 m.y. to evolve, the genera 2 m.y., and the species 1 m.y. After this phase of evolution, morphological and genetic stasis may have set in. The different ranks and genetic divergences are neither proportional to the age of the groups (all about 50 m.y. old) nor the rate of evolution – they may have all evolved at about the same rate. The difference is due to the genetic potential for evolution that each group held in the region prior to the phase of evolution.

Avice (2000) emphasized that the boundaries of traditional marine 'faunal provinces' may represent historical as well as ecological breaks. He also noted that these boundaries often delimit ranges of species as well as groups below the rank of species. In fact, it has long been known that most important biogeographic boundaries, or nodes, delimit ranges of groups with a very wide range of taxonomic divergence. Probably every group differentiated at a node has a different degree of divergence (Hedges, 2004). Phylogeographers interpret these as due to differing ages of differentiation and so need to postulate a huge number of separate dispersal or vicariance events to explain a single node. Panbiogeography instead interprets the situation as *prima facie* evidence that a vicariance event will result in the differentiation of many groups, each to a different level of divergence. Only a single vicariance event is needed.

Cladistic homoplasy in character distribution is widespread in all groups and indicates that parallel evolution is one of the main modes of evolution. Parallel molecular evolution (by, for example, molecular drive, Palumbi, 1994; Craw *et al.*, 1999) means that DNA sequences of taxa will stay the same distance apart as they evolve. Traditionally, of course, genetics usually assumes instead that any genetic similarity is due to

gene flow, even when this is problematic. For example, the 'puzzling' conclusions of Lessios *et al.* (2001) were cited above (under 'Means of dispersal') and these authors also found 'some remarkable instances of high gene flow between very distant areas'.

It has often been assumed that marine taxa are widespread and undifferentiated, whereas terrestrial forms obviously exhibit much local endemism. This apparent difference was attributed to different means of dispersal. It now appears that many widespread marine taxa also show vicariance, often in the form of geographic genotypes that show relatively small differences. In both panbiogeography and cladistics 'degree of difference' is seen as an inadequate basis for comparative studies and no essential difference is seen between a cosmopolitan family of many vicariant genera and species, and a cosmopolitan species of many vicariant cytotypes. In other words, taxa of the same rank but in different groups, such as a genus of ascidian and a genus of angiosperm, cannot realistically be assumed to have similar 'degree of divergence', despite the claim of the 'biological species concept' that the species is special.

CONCLUSIONS

Panbiogeography predicts an intimate connection between the evolution of earth and life. This might seem unlikely to some readers, who may also feel that geological evidence is 'harder' and more reliable than biological distribution data. But it should be recalled that biogeographic evidence played a crucial role in Wegener's argument for continental drift. Tunnicliffe *et al.* (1998) wrote that 'In retrospect, it appears amazing that Wegener's 1924 deductions of shifting continents met with such summary rejection by geologists, while gaining acceptance from biologists'. However, orthodox biogeography, led by Simpson and Mayr (direct intellectual descendants, via William Diller Matthew, of Darwin and Wallace) soon re-established itself against continental drift and instead strongly supported continental stasis, until the majority of geologists themselves accepted drift in the 1970s.

In another example, North America appears stable and unitary, but on the basis of biogeographic analysis Croizat (1961; cf. Craw *et al.*, 1999: 154) made the novel prediction that it was composed of eastern and western sectors that were originally separate. (Liebermann, 2003, erroneously attributed the idea to palaeobiogeographers, including 'real visionaries', writing in the 1980s.) This prediction was confirmed in subsequent geological studies, which showed that the accreted terranes along the western margin of the continent contain different biotas that may have travelled great distances. As Liebermann (2003) suggested, 'it is conceivable that some elements of the modern terres-

trial biota of North America may represent forms that arrived rafted on terranes'. As indicated above, this may also be true for marine biota. Why is biogeographic evidence routinely ignored when it was so successful in predicting continental drift, the hybrid structure of North America, and many other phenomena? Again, this is probably because of preconceptions about 'chance dispersal'.

It is especially important to justify and undertake panbiogeographic analysis of marine taxa as they hold so much vital biogeographic information. As yet, this is largely untapped simply because chance, founder dispersal has been almost universally assumed. Now that it is beginning to look less likely, distributions may be looked at more closely and even analysed comparatively. Perhaps the most valuable terrestrial groups for biogeography are the birds, as they and their distributions are so well known. Along with seabirds, however, lichens, lizards and invertebrates also have heuristic value as they have such high 'coefficients of survival'. If a former landmass is currently represented by a last relic, a small rock stack in the sea, it will be members of these groups, along with the reef taxa, which serve to reveal its history. Any terrestrial mammals, forest trees, passerines and so on will have long gone extinct. Thus the biota of reefs and seamounts has a special interest.

Unjustified assumptions about dispersal have important practical implications, for example in estimating biodiversity levels (taxa with apparently good means may actually include much allopatric differentiation) and in the management of marine communities (populations of taxa with apparently good means of dispersal may not actually operate as open systems). In biogeographic practice, assuming chance dispersal removes much of the motivation for mapping and comparative studies, apart from having obvious implications for the theory of evolution and speciation.

One of the main problems in identifying tropical taxa, whether on a reef or in a rainforest, is the huge diversity. In practice this means one often tends to jump too quickly to conclusions, overlooking certain possibilities. The critique of founder dispersal is counter-intuitive and even an experienced panbiogeographer, let alone a dispersalist, may find it surprising to learn that there is so much local endemism in, for example, corals or foraminifera. What is the explanation for this? The sea is full of surprises and, again, in developing our ideas we should always proceed with caution and avoid jumping to conclusions.

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