Good morning Gondwana

Summary. Vicariance and dispersion both must be considered as possibilities for the fauna and flora of New Zealand and New Caledonia. Oligocene submersion, promoted by the geologists and several biologists, does not seem to have been total. Refuge stations must have existed in mountains and even in plains in some surrounding areas. From there the relicts must have radiated after the partial submersion. Certain “primitive” Chrysomelidae Eumolpinae (Bohumiljania spp.) are closely related to Patagonian genera. Their case is not unique among the terrestrial organisms of New Caledonia. How to explain the occurrence of Amborella in New Caledonia and of the tuataras in New Zealand, already very probably extinct elsewhere during the Paleogene?

Résumé. Bonjour Gondwana. La vicariance et la dispersion passive doivent être à la fois envisagées pour la faune et la flore de la Nouvelle-Zélande et de la Nouvelle-Calédonie. La submersion oligocène, envisagée par les géologues et certains biologistes n’a pu être que partielle, des stations refuges ont dû exister en montagne, même en plaine, en des lieux privilégiés, d’où s’est effectuée une radiation secondaire. Par exemple, certains Chrysomelidae Eumolpinae «primitifs» (Bohumiljania spp.) ont leurs plus proches parents en Patagonie. Ils sont loin de constituer des cas isolés parmi les organismes terrestres de la Nouvelle-Calédonie. Comment expliquer la présence d’Amborella en Nouvelle-Calédonie et des tuataras en Nouvelle-Zélande, alors qu’ils étaient déjà très probablement éteints ailleurs durant le Paléogène ?

Keywords: Vicariance, dispersal, Antarctica, Australia, New Caledonia, New Zealand, South America.

Introduction

That the huge supercontinent of Gondwanaland in the Southern Hemisphere remained undivided up to Cretaceous (130 to 140 Mya) and then got fragmented to form South America, Africa, Madagascar, Peninsular India, Australia, New Zealand, New Guinea, New Caledonia, and Antarctica, and that the resultant land masses, except the Antarctica, shifted northward (continental drift), or in brief the Gondwana Hypothesis is a well established palaeogeological concept (McLoughlin 2001). It has fascinated biologists throughout. The disjunct distribution of such organisms, as marsupials, ratites, pleurodires or side-necked turtles, lungfishes, and the araucarian gymnosperms, becomes meaningful in light of the hypothesis.

In recent past the following two controversies, related to the distribution of organisms in the lands of the Gondwanan origin, have been discussed in many communications, which have been cited in the subsequent discussion: 1) dispersal versus vicariance; 2) whether New Zealand and New Caledonia were fully or only partly submerged in Eocene-Oligocene period.

In context of the Gondwanan concept, by vicariance is meant fragmentation and consequent isolation of wide spread ancestral forms with breakup of the Gondwana supercontinent, as a result of which related forms inhabit lands of Gondwanan origin, and dispersal refers to spread of species by dispersal across stretches of water.

Dispersal versus vicariance controversy

1. Studies pointing to dispersal events

Balke et al. (2007) studied the diving beetle Papuadytes (Coleoptera: Dytiscidae) of New Caledonia and New Guinea through molecular phylogenetics, and compared them with the corresponding data for this genus from Australia and Indonesia. They inferred that the megadiversity, presented by the genus in New Caledonia has resulted from radiation in the Miocene, and that the basal form for this radiation arrived from Australia in two installments of dispersal, in 14 Mya (= million years ago) and 9 Mya, which is much after the suggested Paleogene (Oligocene) submersion. The authors pointed out several other instances of studies
Figures 1–3
1, land masses in the Southern Hemisphere, 140 Mya; 2, the Southern Hemisphere, 80 Mya; 3, the Southern Hemisphere, 60 Mya. All drawings from Isabel Sanmartin, summary, personal communication 2002, with permission. AP = Antarctic Peninsula; STR = Drake Passage; LHR = Lord Howe Ridge; NC = New Caledonia; NR = Norfolk Ridge; NZ = New Zealand.)
suggestions that the submersion and long distance dispersal of terrestrial forms across oceans has shaped the southern hemisphere distribution pattern.

Muriene et al. (2005) studied New Caledonia cockroach, Angustonicus, which belongs to the Tryonicae, through DNA molecular sequencing. Angustonicus occurs also in the Loyalty Islands and in the Ile des Pins. Tryonicae are present in Australia and New Caledonia too. From their study the authors inferred that “basal” species of this genus are in the Loyalty Islands, and that diversification of the genus in New Caledonia started less than 2 Mya ago. The recency of the diversification is suggestive of arrival of Angustonicus in New Caledonia through dispersal.

Arensburger et al. (2004) analysed DNA sequences in 14 species of cicadas from Australia, New Zealand, and New Caledonia. They concluded that the New Zealand cicadas form two well defined clades, one grouping with Australian taxa, and the other with New Caledonian taxa. Molecular clock analyses indicate that the NZ genera diverged from the Australian and the NC genera within 11.6 Mya, whereas NZ became isolated from other Gondwanan lands 82 Mya. Hence they concluded that the NZ forms resulted from radiation from NC and Australian forms, reaching the NZ through long distance dispersal across ocean.

Michael Heads (in a personal letter, dated 15th Nov. 2006, to the senior author) pointed out that New Caledonia, New Zealand, New Guinea, Philippines, and Fiji have each resulted from amalgamation of some terranes, many of which were of a deep sea origin with traces of volcanic material. Hence much of biota of NC and NZ is really not Gondwanan, “but belongs to central Pacific groups…”’. These constituents of the biota are “nearly always assumed to have arrived by long distance dispersal”.

2. Studies suggesting vicariance

In view of such instances of studies, bringing out the role of dispersal, one should not underestimate the role of vicariance in the southern context. It may be reasonably imagined that, if a chunk of land breaks away from the Gondwana, it may inherit a part of a wide spread archaic species on the motherland, and the archaic form may radiate into endemic forms in isolation in the thus formed land mass. The resulting species would obviously be of vicariant origin.

Sanmartin & Ronquist (2004) cladistically analysed a large data set of 54 animal and 19 plant phylogenies, including marsupials, ratites, and southern beeches. They found that the cladistic tree for animals shows a good congruence with a tree depicting the geological sequence of the Gondwana breakup, but not the tree for plants. This situation suggests that vicariance played a significant role in shaping the disjunct distribution of animals, but not so much of plants. Perhaps the reason for this is that plants produce stages, such as seeds and spores, resistant to sea water, and, therefore they got dispersed, crossing oceans, more successfully than did animals.

Brundin (1965) extensively studied chironomids in lands, which are of the Gondwanan origin. He worked out phylogenetic relations among different chironomid groups following Hennig’s method. He inferred, that “The conclusion is inescapable that the transantarctic relationships developed during a period when the southern lands were directly connected with each other”. He found the sequence of breakup of Gondwana, as suggested by the phylogenies of the chironomid midges, agreeing well with the sequence as per the present opinion in Geology.

C. Jones et al. (2006) and Worthy et al. (2006) reported fossil remnants of a non-flying archaic mammal in the South Island of New Zealand, belonging to the middle Miocene. This has been the first record of a native nonvolant mammal from NZ. The fossil form has been inferred as representing a ghost lineage, distinct from monotremes and eutherians. Its presence in the NZ has been inferred by the authors as of vicariant origin for the following reasons: 1) the preserved femur of the NZ mammal has nothing to suggest that it was a good flier or swimmer; 2) in southeast Australia a fairly diversified and rich fossilized mammalian fauna has been recorded in Oligocene to Pliocene deposits, but nothing like the NZ mammal has been found so far; 3) the NZ, by 65Mya, was >1000 km away from Australia, Antarctica and South America.

M. Jones et al. (2008, 2009) report a sphenodontine (Reptilia: Rhynchocephalia) from the Miocene of New Zealand. It seems improbable that, if New Zealand was completely submerged at the Oligocene-Miocene boundary (25–22 Mya), an ancestral sphenodontine would have colonized the reemergent landmass of NZ via ocean rafting from some unrecorded and extinct Miocene population. According to earlier authors, the transoceanic capabilities of modern Sphenodon are questionable. All these facts very much reduce the possibility of a terrestrial “archaic” mammal or reptile reaching NZ by dispersal from the lands around.

According to M. Jones (pers. comm.), evidence for or against total submersion of Zealandia is scant.

Heads (2006) studied past and extant distribution of Nothofagus, with special attention to species massings. He said that “The vicariant main massings of the four subgenera are compatible with largely allopatric differentiation and no substantial dispersal since at
least the upper Cretaceous…, by which time the fossil record shows that the four subgenera had evolved.”, and also, “Global vicariance at family level suggests that Nothofagaceae/Nothofagus evolved largely as the South Pacific/Antarctic vicariant in the breakup of a world-wide Fagales ancestor.”

Conran et al. (2009), have discussed biogeography of orchids, and have inferred “The restriction of most of the Earina complex… as well as of the basally divergent Australasian Dendrobium lineages…. to New Zealand, New Caledonia and continentally derived Pacific islands indicates an early radiation into Zealandia prior to this subcontinent becoming largely submerged during the middle Cenozoic supporting Brieger’s and Chase’s suggestions that vicariance has been important in the family, despite apparently rapid, relatively recent radiation at the species level…”.

Swenson et al. (2001) attempted to unravel the problem of Nothofagus biogeography (with special reference to the subgenus Brassospora) by cladistics, using both morphological criteria as well as nucleotide sequences. They said that “New Caledonia has complicated geological origin which probably confounds a simple understanding of its biogeography. The presence of the subgenus Brassospora on the island is a riddle that is beginning to be answered. We suggest that the migration route to New Caledonia included some form of ancient land link to New Zealand…”. Here again probability of vicariance is being inferred.

Hyriidae are unionoid mollusks with a disjunct Gondwanan distribution. Graf and Foighil (2000) have analysed a nuclear ribosomal DNA (28S rDNA) of Hyriidae of Australia, New Zealand and South America, and have compared the data, thus obtained, with those for other unionoids. The two main inferences, reached by them: 1) origin of Hyriidae predated the break up of the Gondwana land, and 2) the New Zealand Hyriidae are relics and not colonizers.

Gheerbrant & Rage (2006) have pointed out that the continent of Africa was first to break away from the supercontinent of Gondwana. It has remained isolated from mid-Cretaceous to early Miocene. During isolation Africa was inhabited by vicariant west Gondwana taxa. New Caledonia had also a Gondwanan past, as discussed here elsewhere. Whether it was totally flooded at the Oligocene, or not, seems much debatable. Some relics, such as Bohumiljania spp., because of their size, could not have been reasonably imported with the wind. Moreover Bohumiljania is missing in Australia while the two related genera: Hornius and Stenomela are there in South America. Persistence of related Gondwanan biota on both sides of the Pacific is in favor of vicariance.

Sequeira & Farrell (2001) studied through DNA analysis the divergence time of Araucaria feeding bark beetles (Scolytidae) between those in Australia and in South America, and estimated it to be late Cretaceous to Palaeocene. In view of contiguity of Australia-Antarctica-South America at this time vicariance of the beetles may be inferred.

Poole & Gottswald (2001) have pointed out that the Upper Cretaceous and Early Cenozoic sediments in the Antarctica have yielded a rich assemblage of well preserved fossil dicotyledonous angiosperm wood, and they have noted that “Palaeobotanical evidence provides evidence for strong floristic similarities, local floristic differentiation, Antarctic endemism and latitudinal floristic gradients between Antarctica, South America and Australasia…”.

The primitive Eumolpinae (Tribe Spilopyrini) show a disjunct distribution among lands of Gondwanan origin. They are represented by Spilopyra (Australia and New Guinea), Macrolema (Australia and New Guinea), Richmondia (Australia), Cheiloxena (Australia), Stenomela (Chile), Hornius (Chile and Argentina), and Bohumiljania (New Caledonia) (Jolivet 2004; Verma & Jolivet 2004). Verma & Jolivet (2006) compared the spilopyrins from the standpoint of their food plants, anatomical features, and developmental stages. Keeping in view the palaeogeological history of the Southern Hemisphere they inferred that the New Caledonian and the South American spilopyrins are particularly close. Gomez-Zurita et al. (2007) recalibrated the phylogenetic tree of spilopyrins and estimated that the “ancestral” lineage, leading to the present genera of spilopyrins separated from the lineage, leading to the extant European Eupales ulema, about 45 Mya. The earliest separation of South America and Antarctica occurred 35–30 Mya, and that of Antarctica and Australia 35.5 Mya (McLoughlin 2001). Hence it was quite likely that the ancestral spilopyrins reached the Gondwanan lands, on which the tribe is represented, by vicariance.

Trewick and Morgan-Richards (2005) have studied New Zealand wetas (Orthoptera) using sequences of mitochondrial DNA (cytochrome oxidase 1) and nuclear DNA (12S DNA) to determine extent of diversity and timing of speciation. On basis of their observations they have hypothesized “that at least three distinct groups of wetas survived the Oligocene marine transgression and radiated subsequently”. Thus presence of wetas in New Zealand seems to be due to vicariance.
Other rare cases of vicariance in New Caledonia can be found among other insects and among other families of Coleoptera, as Tenebrionidae, Scarabeidae, etc. (Jolivet 2007; Jolivet & Verma 2008). Among the Chrysomelidae, *Zira nitens* Reid, 2004 exclusively localized over high mountains and living on “archaic” Araliaceae (Myodocarpaceae) and, shows affinities with the South American *Lioplaciis elliptica* Stal, 1860, according to Daccordi (1994) (also pers. comm.). Their external features are really very similar, even if *Lioplaciis* has more complex genitalia. However, *Lioplaciis* feeds on *Baccharis* (Asteraceae). It is more difficult to see the impact of the Australian affinities of several Cryptochelininae, Zeugophorinae, Criocerinae, and Hispinae. Passive dispersal of many species of Chrysomelidae is also evident, some during the Neogene, others more recently (e.g. *Chaetocnema confinis* Crotch, 1873). Common occurrence of certain genera, as *Dematochroma*, in New Caledonia, Lord Howe Island and Norfolk could be due to dispersal, but may have resulted also through old ephemeral land connections with New Zealand (Jolivet et al. 2007). Mountains of New Caledonia seem to constitute a high center of endemism (Jolivet et al. 2003, 2005), and often the affinities are with an old pre-Oligocene biota distribution. *Dematochroma* has been recently discovered in Vanuatu (Jolivet et al., 2009) and that could be result of dispersal as also its presence in Timor, in the North, but New Caledonia seems to be a real center of differentiation for the genus.

Upchurch (2008) discussed at length the problem of vicariance versus dispersion. He has pointed out that a number of authors have tried to infer the sequence of Gondwanan break-up on basis of phylogenetic closeness or distance of related species in the lands of the Gondwanan origin. But in such attempts confusion may arise because of three factors, viz. (a) geodispersal (i.e. expansion of species into areas when geographical barriers disappear), (b) extinction of forms, and (c) missing data or sampling errors. The confusion, created by these factors, has been referred to by the author as “distributional noise”. The perspective, created by the distributional noise, makes it “more difficult to detect vicariance than trans-oceanic dispersal”. As an example of this he has cited Sampson et al. (1998), who, noted that the fossils of abelisaurid theropods were known from South America, India and Madagascar, but not from Africa, and who held this situation as a support for the Africa-first hypothesis, according to which Africa separated from the Gondwanan before other landmasses. But later abilosaur fossils were discovered in Africa (Sereno et al. 2004). Thus this transient support for the Africa-first model, resulted from a distributional noise caused by missing data.

Using morphological features and molecular data from five nuclear and mitochondrial genes, Boyer and Giribet (2009) have studied three endemic genera of opiliones from New Zealand belonging to the family Petralidae (Suborder Cyphophthalmi) and also six other members of the family from Chile, South America and Australia. The family has a typical Gondwanan distribution. The authors point out “Despite the lack of precise dating, the history of Cyphophthalmi in New Zealand has clearly been influenced by ancient Gondwanan vicariance…”.

Sharma & Giribet (2009) have studied phylogenetic relations among Troglosironidae (Opiliones) of New Caledonia through DNA sequence data for two nuclear ribosomal genes and two mitochondrial genes. It has been inferred from these studies that the group in New Caledonia have had a monophyletic origin, and that the origin has been quite ancient (200 Mya), and later in Eocene there has been diversification of the group in isolation. The authors have further inferred “relictual nature of the taxa among New Caledonian biota…”.

They find the notion of total submersion of New Caledonia in Palaeocene a hypothesis difficult to test, as “New Caledonia is known to have undergone extensive volcanism in the Cenozoic… and metapopulations of relictual taxa may have persisted on small, ephemeral volcanic islands…”.

Other examples are also bringing out the role of distributional noise. The living South American ratite *Rhea* is more closely related to the Australian *Emu* than to the African Ostrich. On the other hand the African and South American lungfishes are more closely related than they are to the Australian lungfish. Geodispersal consideration may solve this riddle. Upchurch (2008) said, “…Samafrican pattern (i.e. the future South America and Africa separated from the rest of the Gondwanan mass 170-140 Mya, i.e. in Jurassic, with opening of the Weddell Sea, and later Africa and South America started separating with opening up of the South Atlantic) could have been generated during Early Cretaceous, and then overwritten by the Africa-first pattern during the late Cretaceous. This raises the question, what happened during the mid-Cretaceous to cause the switch from one vicariance pattern to another? The simplest explanation requires South America to form a connection with East Gondwana (probably through a Patagonia-Antarctica contact …) during mid-Cretaceous, enabling geodispersal of terrestrial and freshwater organisms between these regions.” Such distributional noises, as this author said, may create “a bias against the discovery of well supported vicariance patterns and a false impression that trans-oceanic dispersal is the correct explanation for distributions of
organisms”. (For sequence of separation of land masses from the supercontinent Gondwana see Figs. 1–3.)

3. Vicariance as well as dispersal

A number of authors have opined involvement of both vicariance as well as dispersal in development of the southern biota. For example, Waters & Craw (2006), in context of Nothofagus distribution, have clearly stated that vicariance and dispersal have not been mutually exclusive.

Trewick et al. (2007), in case of the Chatham Island, which became emergent only 1 to 3 Mya, pointed out that most of the island biota reached by dispersal, crossing a water gap of >800 kms., while survival of some vicariant forms cannot be denied.

Gibbs (2006) has said that “All that we can truthfully say is that the New Zealand biota still seems to contain a mix of relictual Gondwana descendants and groups that have dispersed across oceans ...” This author too has regarded vicariance and dispersal in the southern context not mutually exclusive.

McDaniel & Shaw (2003), who have studied a trans-Antarctic moss, have inferred presence of the moss in South America and Australia due to vicariance, and between Australia and New Zealand there would have been dispersals.

Michaux & Leschen (2005) have found the biota of New Zealand, and Subantarctic Islands of a mixed nature, part of it derived from West Gondwana and is relictual, and part from East Gondwana with many species identical with those in the main land. The former part is vicariant and the latter appear to have arrived through dispersals.

Noonan & Chippindale (2006), discussing history of distribution of boid snakes, have said that “Diverge time estimates suggest that this strong congruence between geography and phylogeny is the result of several vicariant and dispersal events in the late Palaeocene associated with the fragmentation of the Gondwanan supercontinent.”

Cook & Crisp (2004), discussing the origin of extant distribution of Nothofagus, have opined that “Both vicariance and dispersal have clearly played a role in the current distributional patterns of Nothofagus.”

Daccordi (1996), dealing with distribution of Chrysomelinae (Fam. Chrysomelidae), including Chrysolina genera, with Gondwanan distribution, has also suggested the role of both vicariance and dispersal.

Gamble et al. (2007) have studied through phylogenetic analysis of molecular sequences data for the sphaerodactyl geckos (Reptilia: Squamata), covering both New World species as well as Old World ones. They have inferred that the ancestral area for these lizards was in North Africa, and that “the split between the sphaerodactyl geckos and their African relatives coincided with the Africa/South America split and the opening of the Atlantic Ocean”. This strongly suggests vicariance in the distribution of the extant geckos. But the authors have not denied the role of trans-oceanic dispersals in the distribution of the southern biota. They said that “The combination of robust, multi-gene phylogenies, relaxed dating techniques, and event based methods of biogeographical reconstruction should not be seen as favouring one paradigm over another (preferring dispersal over vicariance), but should instead be viewed as a major step forward in biogeographical research as a whole”.

McDowall (2007) has discussed biogeography of New Zealand. Though he is a strong supporter of trans-oceanic dispersion, he has not denied the possibility of some vicariance. He said “However, there are elements in the biota that seem to have broad distributions that date back to Gondwanan times, and also some that are thought unlikely to have been able to disperse to New Zealand across ocean gaps, especially freshwater organisms.”

Barker et al. (2007) have studied, through chloroplast DNA sequence data, the plant family Proteaceae having Gondwanan distribution. They have said that “The findings suggest that disjunct distributions in Proteaceae result from both Gondwanan vicariance and transoceanic dispersal.”

Ladiges & Cantrill (2007), on basis of geological history and estimated divergence dates of some taxa, including birds (kagu-sunbittern clade), Nothofagus, and Myrtaceae, have inferred that “the geological history of the region (New Caledonia-Australia) is complex, but there is evidence of land persisting into Cenozoic (Palaeocene/Eocene) that possibly allowed old biota to persist. Vicariance explanations of divergences cannot justifiably dismissed in favour of long-distance, over water dispersal for such taxa.”

Edgecombe & Giribet (2009) have constructed a cladogram for the scutigeromorph centipedes of the Australian and New Caledonian faunas on basis of morphological and molecular data, and have said “the cladogram... depicts a vicariant pattern across Australia as well as tropical Australian affinities for New Caledonian Scutigeromorpha. New Caledonian diversity may derive from a single colonization”. This opinion suggests that either vicariance or short distance dispersal from eastern Australia has led to the presence of scutigeromorphs in New Caledonia.

The above review of some recent relevant publications clearly convey that both vicariance and dispersal have been involved in shaping the southern biota. The role of vicariance, especially in relation to animal
distribution, cannot be undervalued, as demonstrated by Sanmartin & Ronquist (2004). McGlone (2005) has overemphasized the role of dispersal in this context to the extent of giving the title “Goodbye Gondwana” to his communication. He said that “The recent flood of evidence supporting trans-oceanic dispersal … has put it in the driving seat.” Obviously further studies on the disjunct and fascinating biodistribution in the south should be with the attitude of “vicariance and/or dispersal”, and not “vicariance versus dispersal”. In order to account for the disjunct distribution of Gondwanan forms, it may be kept in view that short range dispersals among lands of Gondwanan origin, when they had not drifted far, were more likely than long range successful trans-oceanic dispersals.

The last expressed notion in the preceding paragraph finds support in the work of Sanmartin et al. (2007). These authors have selected a data set of 23 published phylogenies of plant groups in New Zealand, Australia, and/or South America, and used parsimony based tree fitting to work out number and directions of dispersal in each group. They have inferred that “Observed differences in dispersal asymmetry may partly be explained by the relative connectedness of the areas. New Zealand and Australia are geographically much closer to one another than to South America.” This is one of the reasons for more frequent dispersals between Australia and New Zealand than to South America across the southern Pacific Ocean.

The problem of the so-called Early Tertiary submersion of New Zealand and New Caledonia

It is a general notion among geologists that, during Eocene-Oligocene, there was an expansion and thinning of earth’s crust in the region of the Australian plate, and this led to submersion of New Zealand and New Caledonia (Cooper et al. 1987; Campbell & Landis 2003). A debatable point among biogeographers, dealing with the south biota, is whether the submersion of NZ and NC was total or partial and incomplete.

It is being strongly felt that the submersion was not total, and that some parts of NZ and NC remained emergent during this period allowing survival of some terrestrial organisms. Sanmartin (in a personal communication, dated 29th May 2006, to the senior author) indicated that “There are groups in NZ such as tuataras and Podoaceae (Anacardiaceae) that are older than Oligocene submergence … if the Palaeogene submergence of NZ eliminated the old Gondwanan lineages, we would not expect the NZ taxa to occupy a basal position in the phylogeny as it is the case in many animal groups.”

Trevick et al. (2007) have pointed out that “At present, there is insufficient geological evidence to compellingly demonstrate permanent land or total submersion (of Zealandia).” (Zealandia was a part separating as an arc from the Gondwana at about 80 Ma, and it includes New Caledonia, Lord Howe Island, Norfolk ridge, and Chatham rise, in addition to NZ.)

Waters & Craw (2006), discussing biogeography and geology of New Zealand, have regarded complete Oligocene submergence of NZ not yet decisively proven. They have indicated that “Survival of the terrestrial descendants of this Gondwanan biota, however, requires that at least some of the NZ landmass remained above sea level since the rifting event (i.e. separation of NZ from the Australian part of Gondwana).”

McLoughlin (2001) has pointed out the possibility that New Caledonia was not fully submerged during Palaeocene-Eocene-Oligocene. As noted above, New Caledonia, along with the rest of Zealandia, separated from Gondwana about 80 Ma. Its gymnosperm flora includes the genus Acmopyle (Podocarpaceae), which is also in Fiji. Fossils of this genus are known from North Patagonia and Antarctica in Cenozoic geological formations (De Forges et al. 1998). This suggests survival of Acmopyle in NC through Tertiary, which could be possible if some of the island remained emergent during Early Tertiary.

Macphail (1997) has given a long list of plants in a table, showing the time of their first appearance in Australia and NZ. Several plants, enlisted, have been mentioned as first appearing in Australia in Eocene or Early Oligocene and then appearing in NZ in Middle or Late Oligocene. Such dispersal from Australia could have occurred only if at least some of the NZ was not submerged in Oligocene.

Flora of New Zealand includes six extant species of Nothofagus. Besides distribution of fossil pollen and macrofossils of Nothofagus have been shown in NZ in a map, depicting Nothofagus distribution in Late Cretaceous in the Southern Hemisphere (Hill 1992). This suggests continued presence of Nothofagus in NZ through Early Tertiary and denying total submersion of the island in that period.

As noted above, Swenson et al. (2001) have pointed to the possibility of a land link between NZ and NC. Meffre et al. (1996, 2002, 2006) have reported results of dredging between NZ and NC in the region of the Three Kings ridge. They discovered in the ridge continental rocks, including “Gondwana-derived zircons” and fossil leaves. They inferred that in Oligocene the ridge was emergent as an arc. Heads
(2006) has emphasized that NZ and NC resulted from amalgamation of emergent terranes, many of Gondwanan origin. It remains possible that some of the terranes were above sea level in Early Tertiary. Discovery of fossilized leaves in marine sediment may be taken as supporting evidence and not an absolute evidence that this region, where the fossil has been discovered, had an emergent past.

Heads (2008) has traced the geological history of NZ and NC, and of other South-west Pacific islands. He has pointed out that both NZ and NC have had a composite origin. NC has resulted from accretion of seven or eight geological terranes, and NZ of nine. It does not seem unlikely that some of the terranes, contributing to these land masses, were not fully submerged during the Paleocene-Oligocene floodings. Referring to the flooding controversy Heads (loc. cit.) has said that “Aspects of the New Caledonian flora … indicate that plant life cannot have been eliminated at this time. … With respect to New Zealand, a ‘mouse-like’ mammal discovered there in Miocene strata and identified as an endemic relic basal to monotreme-marsupial-placental lineage (Jones et al. 2006) … provides good evidence that the country was not totally submerged at any one time.” Occurrence of certain basal ancestral forms in NZ and NC also point to the possibility of some of the contributing terranes escaping submergence during Paleocene-Oligocene period. Heads (2009) indicated that “The New Zealand wrens (Acanthisitrinae) are basal in passerine birds and in New Caledonia, the closest country to New Zealand, Amborella is basal in angiosperms.”

Concluding remarks

From the previous sections two obvious conclusions may be drawn:
1. Vicariance and dispersals (mainly relatively short distance dispersals) both have been involved in development of the southern biota, and it would not be reasonable to take into imaginary long distance dispersals as main distributional events and to downplay the Gondwanan effect in southern biogeography;
2. Early Cenozoic total submersion of NZ and NC is not yet proven and seems improbable.

It is hoped that fresh studies on the interesting biota of lands of Gondwanan origin may be carried on without preformed notions and biases hereafter; hence “Good morning Gondwana”. Certainly geological observations can infer a total submersion of at least New Caledonia, but some botanical and zoological observations remain in favor of some higher altitudes surviving during the Oligocene submersion, since passive introductions for some biota remain highly improbable.

References


