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Processes of island colonization by terrestrial organisms

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SUMMARY

Colonization of islands by terrestrial organisms may have taken place through three main models of dispersal: a) vicariance, in case a part of a continent split off and became an island, with its endemic animals and plants; b) migration through land bridges, continuous or formed by discontinuous, temporarily emerged islands and «stepping stones»; c) migration by swimming, or by passive transport on natural rafts. It is argued that in the majority of cases colonizations took place through models a) and b). Contrary to a current opinion, model c) may have occurred only in restricted, favourable areas and in exceptional cases. Geological history and present conditions of several islands are analyzed in order to show how even far away oceanic islands may have been invaded through overland migrations, and cases are discussed in which migrations according to model c) are to be ruled out. Examples are brought forward from New Zealand, Madagascar, the Canary and Azores islands, the Western Mediterranean islands, the Antilles, the Galapagos and Indonesian islands. If correctly understood, island biogeography may become a highly useful tool for reconstruction of palaeogeography, crustal movements and geological processes of our planet.

Colonization of islands by terrestrial organisms is a problem of primary interest not only for its biological implications on evolution of endemic animals and plants but also for the highly valuable information it may provide in the field of palaeogeography and geological processes in general. The problem is not always easy to solve. In fact, the dilemma of colonization by active, or passive overseas transport versus migration through temporarily emerged land bridges may not always be decided on the basis of physical evidence: in most cases argument turns necessarily on speculations about the possibility, or impossibility of an assumed way of migration.

There is geological evidence that land bridges were formed between Northern Africa, Southern Europe and several islands during the Messinian dessiccation of the Mediterranean, but there is no positive evidence that such bridges were actually used by organisms to migrate between continents and islands: this will necessarily remain a reasonable assumption and no more. On the other hand, it is impossible to demonstrate, at least at the present state of knowledge, that no land connections were formed between, say, Corsica or Crete and the mainland during the Pleistocene, so that there was no possible way of migration except overseas transport.

Most islands are characterized by endemic faunas and floras, in some case survivors of lineages which had become extinct long ago. The Tuatara (*Sphenodon*) of New Zealand is a survivor of Rhynchocephalian reptiles which had a practically worldwide distribution during the Mesozoic but became extinct on the continents before the end of this period. But the Tuatara is no isolated case: the flightless Kivis and the recently extinct Moas (Dinornithids) are also descendants of a stock which still has relicts in living continental faunas.

The case of New Zealand is clear. Rhynchocephalians and ratites colonized the islands when they still were part of the Gondwana continent; they survived after the islands split off, presumably in the late Mesozoic, and evolved in their own ways. This is generally called the «vicariance» model. No other way of colonization may reasonably be assumed in this case.

A similar process of colonization, though not necessarily at the same time, may be assumed for the ratites, represented by fossil eggshells, in Lanzarote, one of the Eastern Canary Islands (Rothe and Schmincke, 1968, Sauer and Rothe, 1972). In the case of this island the occurrence of endemic (fossil) murids dates the separation of the island from the continent to the late Tertiary (Hutterer et al., 1988). No one would ever venture the idea that ratites swam across the 100 km. wide channel that divides Lanzarote from West Africa. The assumption that Lanzarote was once part of Africa is supported by geological evidence. Fuerteventura, the other Eastern Canary island, is largely made of Tertiary and Quaternary volcanics but rocks of the continental basement are exposed on its western coast, and the geologically similar Lanzarote is also believed to be underlain by continental crust (Rothe and Schmincke, 1868). But some of the Western Canaries, Gran Canaria and Tenerife, were also colonized by endemic, recently extinct rodents (reported by Hutterer et al., 1988), and Gran Canaria and Hierro were populated by endemic, large-sized lizards, most of which are now extinct. The problem of the colonization of these islands, volcanic structures without underlying continental crust, is still open. Rothe and Schmincke advanced the often repeated hypothesis of a passive transport by natural rafts, but this idea does not satisfy the problem raised by Stock (1990) on the stygofauna, the small invertebrates – mostly amphipod and isopod crustaceans – inhabiting continental ground waters and capable to disperse only along freshwater nappes or very shallow – no more than 2 m. deep – interstitial marine waters. According to Stock, the Eastern Canaries were colonized by stygobionts long ago, presumably in the Tertiary, but the Western Canaries were colonised in relatively recent times (not better specified).

The ages of volcanic activity in the Western Canaries range from early Miocene to late Pleistocene. The oldest lava dated by K/Ar was identified at La Gomera, which is one of the oldest islands (age range of lavas 19.3-4.96 Ma, according to Abd el Monem et al., 1971; ages may perhaps be older, according to newly calculated constants: see Ancochea et al., 1990). Miocene to Pleistocene lavas occur in Tenerife and Gran Canaria; in Hierro only Pliocene and Pleistocene lavas have been dated, and lavas of La Palma gave only

Pleistocene ages (Abd el Monem et al., 1971, 1972). Now these islands are separated by seas over 1000 m. deep, which make migrations of stygobionts impossible. A solution of the impasse, concludes Stock, is to be sought in geology.

Geology may also provide an explanation for the even more entangled problem posed by Madeira and the Azores (Balletto et al., 1990). These are entirely volcanic islands. Madeira, the oldest, dates from the Oligocene (30 Ma); the ages of the Azores range from 7 to 1 Ma. Several aspects of the endemic fauna were examined, with particular attention to the Lepidopteran *Hipparchia* and the Anuran *Rana*. The conclusion is that the fauna of these islands «may have been derived from elements original of the European continent, which reached the islands by a stepping-stone process. The possibility that animals and plants could only reach the Azores in recent times is to be ruled out, as most of their endemic species are certainly old, being highly differentiated from the more or less close relatives extant (or extinct) in the European mainland. The overall pattern is suggestive of the possibility that Madeira may have played a central role in the biogeography of Macaronesia, and that for instance in the late Tertiary the colonization of the Azores may have taken place through the senior island of Madeira». But the authors also recognized the existence, among animals and plants, of «pre-Atlantic elements», with affinities with elements from South Africa, Northern and Southern America etc. If correct, this implies a complicated history of crustal displacements dating from the opening of the Atlantic, of land bridges and stepping stones, possibly, but not necessarily all of volcanic origin.

Madagascar is another highly informative case. This island was once part of the Gondwana continent and became detached from the African coast during the Jurassic. Opinions as to its former position diverge. According to some authors it was once joined to Mozambique and drifted eastwards, others assume that it was contiguous to the coasts of Southern Somaliland and Kenya and drifted southwards (see for opposing views Boccaletti and Flores, 1990).

This however has no bearing on the present argument, which centers on the Tertiary and Quaternary history of the island. After having been colonized by Palaeozoic and early Mesozoic amphibians and reptiles, Madagascar was invaded during the Tertiary by a peculiar fauna of rather primitive mammals: tenrecid insectivores, cricetid rodents, viverrid carnivores, lemurid primates, all belonging to early differentiated families of their orders and all of which gave origin to a radiation, evolving into specialized endemic taxa. The fauna is known only from living representatives and some late Quaternary fossils. The lack of representatives of more derived taxa, Such as canids, felids, simians, ungulates, all of which were present in the Miocene of East Africa (Leakey, 1957), dates the colonization to early times, the Oligocene or at most the earliest Miocene.

The Malgasy fauna differs from present continental faunas but cannot really be said to be unbalanced: it is a fairly good model of a rather differentiated early Tertiary fauna.

How could terrestrial, non swimming animals reach the island? An explanation may be found in geology. The marine Tertiary sequence of the Mozambique channel is interrupted during «at least the Oligocene» by a gap (Sigal, 1974, reported by Boccaletti and Flores, 1990). Although geologists left open the dilemma, whether the hiatus was due to emersion or to submarine erosion, the possibility remains open that during the early Tertiary a land connection was established between the island and the continent.

These views are supported by observations by Paulian (1990) on endemic insects. Within these, a group may be distinguished which immigrated before the splitting of the Gondwana continent, in the Mesozoic; a second group immigrated during the Tertiary, the Miocene according to Paulian, but the dating is approximate. Geology may thus provide an explanation for the immigration of entirely terrestrial mammals, as well as of insects and possibly also of the ratite *Aepyornis*, in the Tertiary, either the Oligocene or the early Miocene.

There remains however a more nasty problem. The fossil Malgasy fauna is also characterized by the occurrence of two species of pigmy hippopotami, *Hippopotamus lemerlei* and *H. madagascariensis* (Stuenes, 1989). Hippopotamids first appeared in continental Africa in the late Miocene with the primitive genus *Hexaprotodon* (which some authors consider a subgenus within *Hippopotamus*) and soon dispersed into India and the Mediterranean area (Savage and Russell, 1983). But at that time Madagascar had already reached its present position and the 400 km. wide Mozambique channel divided it from Africa. Stuenes discards the idea that the volcanic ridge, partly emerged in the Comoro islands and partly submerged, may have offered in the past a sort of bridge, or a series of stepping stones for a migration of hippos, mainly on the ground that volcanic activity along the ridge moved from East to West, in the opposite way of a presumable migration of hippos, and assumed a passage by swimming, possibly during a recent sea level lowering of about 100 m. This however would have reduced the width of the channel to no less than 300 km. Even if no strictly cogent argument can be raised against the hypothesis of a migration by swimming, the idea of herbivorous mammals venturing for such a distance into a sea where nothing could attract them is, to say the least, extremely improbable; it also presumes for hippos a power of endurance which is still to be demonstrated.

But hippos were not the only Pliocene-Pleistocene immigrants. In the insect fauna, besides older immigrants referred to above, Paulian (1990) recognized some endemic beetles which display close affinities with their mainland relatives and are considered to have immigrated in recent times, and have not yet had the time to develop an evolutionary radiation, as most older immigrants did once they settled in their new homeland.

As in the case of the Canaries, a solution is to be sought in geology.

The idea that islands were colonized by large mammals by swimming has had, and still has many supporters, mainly, but not only for colonizations which date from the Quaternary. It has also been observed that island faunas are generally unbalanced and large mammals are mostly represented by good

swimmers: elephants, hippos, cervids. This however is not always true: Mindoro in the Philippines and Sulawesi are inhabited by endemic pigmy buffaloes, and buffaloes are water-loving animals but not particularly good swimmers; and the small island of Pianosa in the Tuscan Archipelago was inhabited by an endemic pigmy ox (Azzaroli, 1978). And, since large mammals are often accompanied by small rodents and insectivores, which obviously could not swim across long distances, or could not swim at all, the idea of a passive transport over natural rafts of vegetation carried to the sea by streams has been proposed, and has met with wide acceptance. It has been applied even to the Galapagos islands, to explain the occurrence of endemic murid rodents, now mostly extinct, in spite of the enormous distance of this archipelago from the coast of Ecuador (Steadmann and Ray, 1982).

Other authors held different views. If terrestrial organisms, incapable of flying and not subject to possible passive transport by wind, water currents etc. invaded an island, in the majority of cases they moved over temporary land connections, or along girdles of temporary islands, crossing only minor stretches of sea by swimming or other means. In principle, the problem is shifted from its purely biological aspect into a historical setting based fundamentally on geological evolution.

During the Miocene and Pliocene the Gargano promontory in the southern Adriatic, the «spur» of the boot which is the Italian peninsula, was an island and was colonized by an endemic, typically insular fauna which rapidly evolved in situ. This fauna had no relationships with other Miocene or Pliocene faunas of continental Italy, but De Giuli et al. (1990) found evidence, in the geology of the southern Adriatic sea floor, of a possible land bridge which may have provided a passageway from the Balkans. Azzaroli and Guazzone (1980) discussed the possible ways of dispersal of terrestrial mammals of European and African provenance in the Mediterranean during the Oligocene and Miocene, until the Messinian crisis.

Sardinia and Corsica will be discussed in some detail as informative examples. Their pre-Quaternary history was already discussed by Azzaroli and Guazzone (1980) and Azzaroli (1983). There seems to be now a general consensus that Tertiary colonizations took place by overland routes but opinions diverge on interpretation of Pleistocene events. Reptiles, and even more amphibians are of high interest in this context, because most of them could only disperse through dry land. Most amphibians, in particular, are intolerant of salinity and could not even stand a ride on a raft floating over sea water. Unfortunately their remains are poorly represented in the record and are not always easy to interpret; moreover, they are difficult to date because of the low evolutionary rate. Lanza (1988) admitted possible pleistocene immigrations into Corsica of *Bufo*, *Emys*, *Testudo*, *Natrix*, *Tarentola*, *Hemidactylus*, *Podarcis*. The toad *Bufo* and the tortoise *Testudo*, in particular, could only have migrated through a land bridge. Baccetti (1964) proposed a possible Quaternary age for the immigration into Sardinia of the isopod *Armadillium nasutum* and for the endemic snake *Natrix natrix cetti*. Among plants, Mariotti (1990) distingui-

shed: a) old established species; b) species immigrated during the Messinian salinity crisis; c) species immigrated during the Quaternary through possible land connections through the Tuscan archipelago, followed by differentiation into endemic subspecies: *Cerastium arvense soleirolii*, *Viola corsica* and *Santolina corsica* in Corsica, *Viola corsica limbarae*, *Santolina corsica* and *Santolina insularis* in Sardinia.

Mammals are highly informative. They are richly represented in the fossil record and their rapid evolutionary rate provides a basis for datings with good resolution. Attention will be drawn here on a vole, *Tyrrhenicola henseli* and a cervid, *Megaceroides*.

Tyrrhenicola is closely related with the continental subgenus *Microtus* (*Allophaiomys*) (Van der Meulen, 1973, Mezzabotta, 1991), which is represented in continental Italy by four species with a narrow stratigraphic range: it has been identified in the late Villafranchian lignite mine of Pietrafitta near Perugia (Farneta faunal unit of Azzaroli, 1977a) and in faunal assemblages with late Villafranchian and early Galerian elements: Monte Peglia, Pirro, Colle Curti.

Cervids were also widespread and were described under several names in the literature, which extends now over nearly a century. In a recent review Caloi and Malatesta (1974) united them all in the genus *Nesoleipoceros* Radulesco and Samson, 1967, and in a single species, *N. cazioti* (Depéret, 1897). As a matter of fact, there are considerable differences between fossils from various sites (Comaschi Caria, 1955, 1956; Sigogneau, 1960; Azzaroli, 1961; Cordy and Ozer, 1972), although all cervids appear to have been derived from a common stem. Evolution on islands was presumably rapid, morphological differences may reflect differences in geological age, possibly also periods of separation and connection between the two islands. The use of a single species name obscures this reality.

Analysis of relationships of these cervids with their continental relatives is illuminating, not only for interpretation of their phyletic position but also to fix with reasonable approximation the date of their immigration.

In several papers the present writer (1952, 1961, 1979, 1982) stressed the affinities of Corsican and Sardinian deer with a stock represented in the early middle Pleistocene (Galerian) of continental Europe by a species originally called *Cervus verticornis* by Dawkins, in 1872, then *Cervus* (*Praemegaceros*) *verticornis* by Portis in 1920, *Megaceros* (*Megaceroides*) *verticornis* by the present writer in 1979 and eventually *Megaceroides verticornis* by Azzaroli and Mazza (1993). Changes in nomenclature were introduced because the subgenus name *Megaceroides* Joleaud 1914 has priority over *Praemegaceros* Portis 1920, and because *Megaceroides* is believed to have had an independent origin from *Megaceros* (now amended into *Megaloceros*) and should therefore have full genus rank.

Megaceroides verticornis is present in continental Europe, including the Italian peninsula, in the early middle Pleistocene (Galerian). It, or a closely related cervid is also represented by rather fragmentary remains in some transitional faunas with Galerian elements associated with late Villafranchian hold-

overs: Imola, Colle Curti, Pirro. However, the earliest occurrence of *Megaceroides* dates from the latest Villafranchian, Farneta faunal unit, with *Megaceroides boldrinii* Azzaroli and Mazza (1993), from the Pietrafitta lignite pit, where also *Allophaiomys* is recorded. So, *Megaceroides* overlaps the range of *Allophaiomys* and extends farther up into the Galerian.

This opens a query: were Corsican and Sardinian deer derived from *M. boldrinii*, from *M. verticornis*, or from some intermediate form? Analysis of the nearly complete skull from Macinaggio, Cape Corse (Sigogneau, 1960), of a braincase of Maritza, Northern Sardinian coast (Cordy and Ozer, 1972) and of the rich collection from Dragonara cave, also on the Northern coast of Sardinia, which includes skulls, jaws and most postcranial bones, reveals that island deer were more derived than *M. boldrinii*, but occasionally kept some primitive features in their dentitions and jaws. They were probably derived from giant deer living in the continent during the Villafranchian-Galerian transitional interval, in accordance with evidence provided by voles. The Cassian sea level low (Azzaroli, 1991) falls in this time interval.

Again, we are facing the problem: migrations through a land bridge, or by swimming and by passive transport on natural rafts across the 30 km. wide channel between Corsica and Capraia, the westernmost island of the Tuscan archipelago?. Apart from the singularity that such improbable events may have taken place at the same time, there are other difficulties. The Corsican channel is swept by a current of 1m/sec. flowing North, which would divert swimmers and rafters towards the Ligurian Sea. The islands of the Tuscan archipelago are scattered on a platform less than 200 m. deep but the channel between Capraia and Corsica exceeds 400 m. depth. A sea level fall may have made migrations possible from the mainland as far as Capraia and reduced the width of the channel to some 20 km., but the current would presumably have been stronger. Moreover, natural rafts of vegetation may form in large rivers draining luxuriant tropical forests. There are no such rivers, nor forests, in the Mediterranean basin. The relatively small rivers draining western Italy may occasionally carry logs and bunches of vegetation during heavy floods, but small mammals would hardly venture on such rafts or, if trapped in them, would likely be drowned in the turbulent stream.

Conchon (1979) analyzed the geology of the northern Tyrrhenian and found evidence of active Quaternary tectonics in the coasts of North Eastern Corsica, with vertical displacements of the order of 6 cm. per century. Such a rate may account for a displacement of 600 m. in 1 Myr, more than the amount needed to admit a foundering of less than 400 m. in the Corsican channel. It may reasonably be assumed that the sea floor was shallower for some time interval in the Pleistocene and that a dry land corridor was formed during the Cassian low stand, providing a passage for deer, voles, toads, tortoises, isopods and plants. Of course, it may still be objected: this is a possibility which still lacks demonstration. It has also been contended that the argument turns on an axiom: there are terrestrial continental organisms on the islands, *therefore* there must have been a land bridge. This may be true, but it is easy to object that:

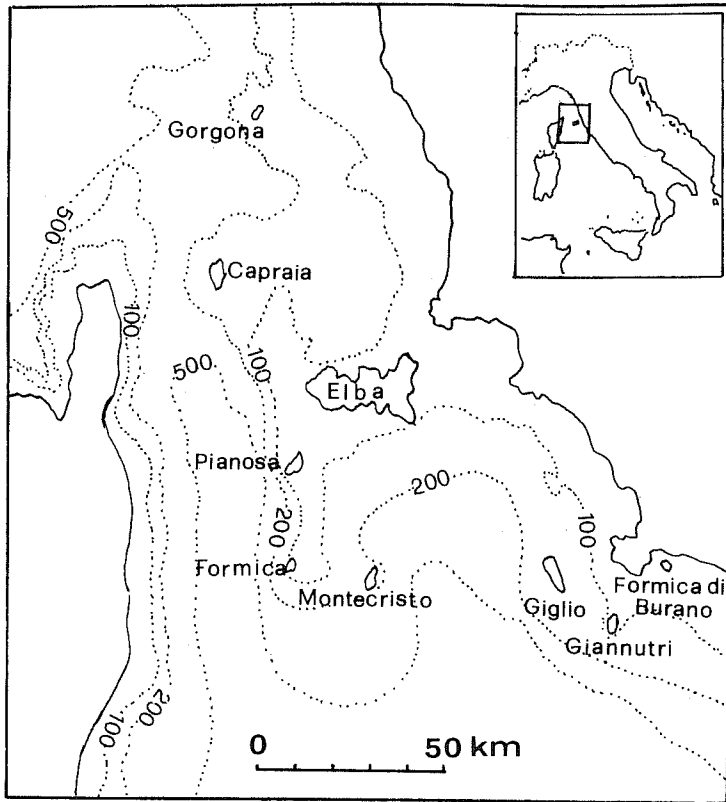


Fig. 1 - Sketch map of the Northern Tyrrhenian Sea between Tuscany and Corsica.

1) migration by swimming or rafting is unlikely for some organisms, impossible for others; 2) the objection to the land bridge hypothesis rests on another axiom: that the crust of the Earth did not move during the Quaternary, and this is contradicted by experimental evidence.

The Northern Channel Islands off the California coast were populated by pigmy elephants during the Pleistocene. It has been assumed that they reached the islands by swimming, but the area is tectonically highly active and connections with the mainland were possible in a more or less recent past. On the other hand, the occurrence on the islands of endemic terrestrial rodents of the genus *Peromyscus* is not easily explained without recourse to former land connections (Azzaroli, 1981). It may be pointed out that endemic mammals occur in all the northern islands but are conspicuously lacking in the Southern Channel Islands.

The Galapagos archipelago was briefly mentioned above but deserves more attention for the problems it raises. These are geologically young, entirely oceanic islands of volcanic origin. They are generally believed to have been formed

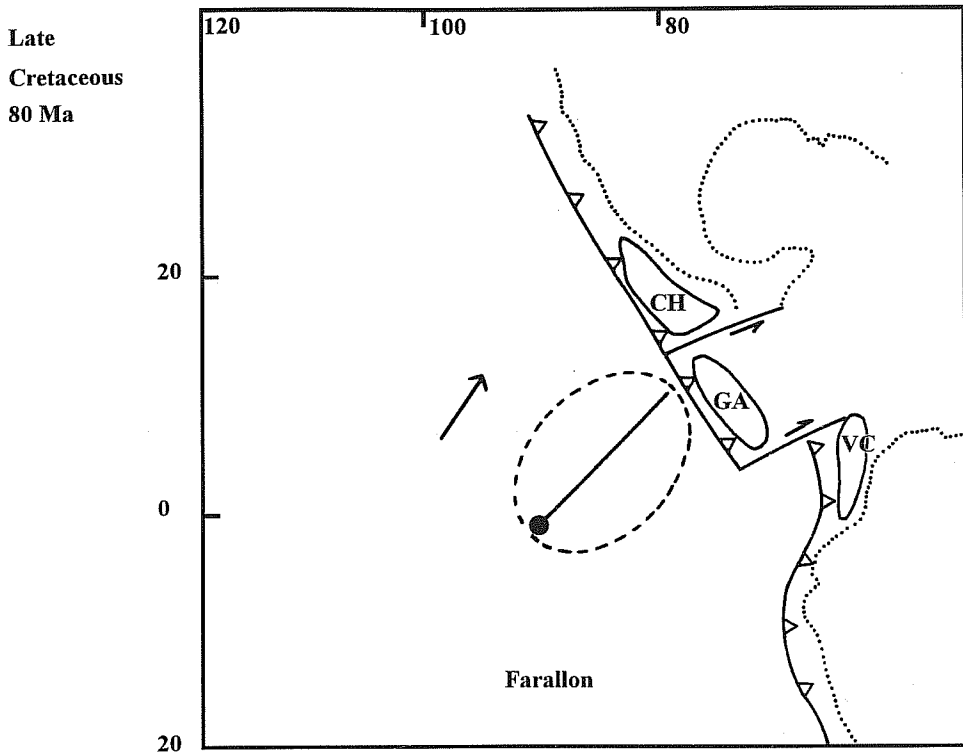


Fig. 2 - Late Cretaceous eastern Equatorial Pacific Ocean. Heavy dot: Galapagos hotspot; heavy line: hotspot track; arrow: direction of movement of the Farallon plate relative to the hotspot; CH: Chortis Block; GA: Greater Antilles; VC: Villa de Cura Complex; broken line: contour of the rigid basalt plate. Adapted from Duncan and Hargraves (1984).

in the Pliocene and Pleistocene and never to have had connections with continents. Their terrestrial fauna is therefore believed to have reached the islands by some form of active or passive transport. As a consequence, the endemic characters of the islands have been viewed as recent developments. However, Wiles and Sarich (reported by Christie et al., 1992) concluded from molecular analysis of proteins that the endemic iguanas differentiated from a common stock some 15-20 Myr ago. Christie et al. found a possible explanation in geology. The islands are the product of a hotspot over which the Nazca plate is moving eastwards. As a result, volcanic activity in the western islands is younger than in the eastern ones. The Carnegie ridge, which extends eastwards from the archipelago, is the «track» left by the hotspot as the plate moved past. Christie et al. found that at least some of the seamounts on the ridge, to the east of the extant islands, were emerged in the Miocene, at various ages between 5 and 9 Myr; and, of course, other islands may have existed which have not yet been, and may perhaps never be identified. This settles the problem of the time span needed for the evolution of iguanas, but not of the colo-

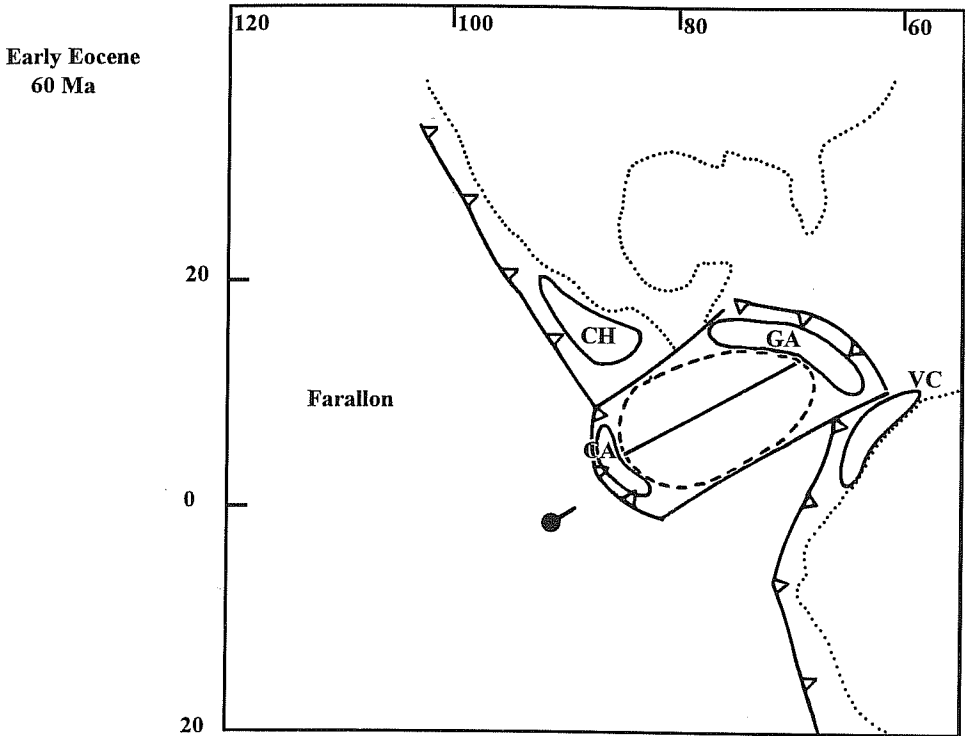


Fig. 3 - Early Eocene eastern Equatorial Pacific. A Central American block (CA) has formed at the trailing end of the basaltic plate. Adapted from Duncan and Hargraves (1984).

nization of the islands. Iguanas, or at least some of them, are good swimmers and the Galapagos finches are fairly good fliers, so the problem seems to be settled. But it is not. Christie et al. looked farther: «we consider it likely that islands have existed through the entire 80-90 Myr history of the hotspot activity». This may be true, but according to Duncan and Hargraves (1984) 80 Myr ago the Farallon plate, which occupied a large part of the eastern Pacific, was moving north-eastwards over the Galapagos hotspot, and a 2000 km. long «hotspot track» extended in the same direction to join the Greater Antilles, which lay well to the West of their present position. Lavas erupted from the hotspot had formed a large, rigid oceanic plateau which extended from the hotspot, on either side of the track, until the Greater Antillean arc. The present Cocos Ridge seems to be what remains of the track. In the Paleocene the basaltic plateau had moved farther NE, following the movement of the Farallon plate, and a newly formed Central American Arc at its trailing end divided it from the track. In the early Miocene the large Farallon plate had broken into the smaller Cocos plate to the N and the larger Nazca plate to the S. The Carnegie ridge began to form at this time.

Early Miocene
21 Ma

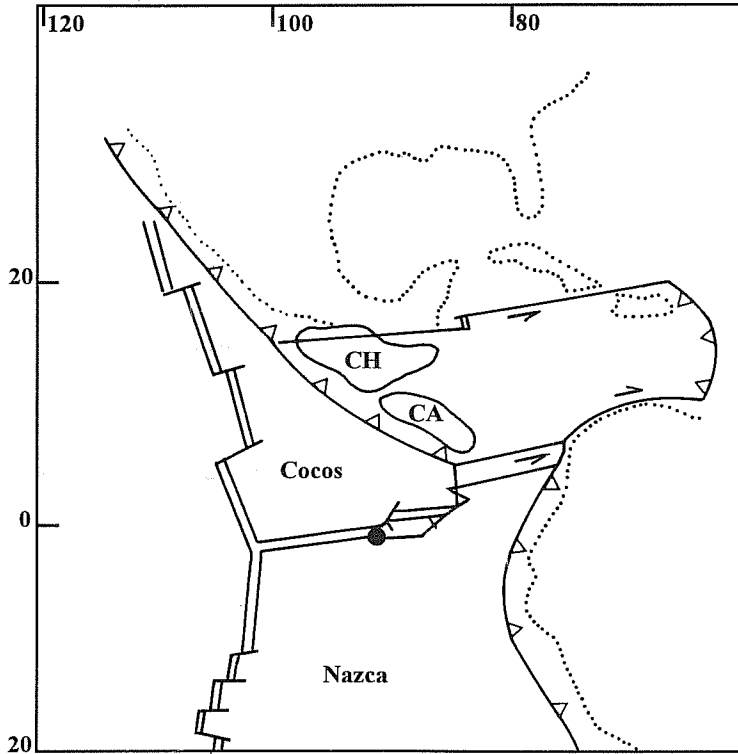


Fig. 4 - Early Miocene Equatorial Pacific. The Farallon plate has broken onto the Cocos plate to the N and Nazca plate to the S. Adapted from Duncan and Hargraves (1984).

Volcanoes emerging from the hotspot tracks of the Cocos and the Carnegie ridges may thus have provided a stepping-stone route for migrations of iguanas and finches. But what about tortoises and rodents? Land tortoises do certainly not swim very far, their migrations may perhaps have been possible only on dry land, over successively emerging and foundering islands; there does not seem to be other acceptable explanation for their migration. Geology may indicate the way for a plausible solution of the problem, but with the transformations that our mobile Earth is steadily undergoing, it would be unreasonable to expect clear and univocal evidence that such a route of migration did actually exist in the past. It may only be said that some problems of biogeography leave little room for alternative interpretations.

But if the Carnegie ridge may possibly have offered a passageway for tortoises, this does not seem to be the case for rodents. Steadman and Ray (1982) discussed at some length the possibility that rodents reached the archipelago by passive transport on natural rafts. Strictly speaking, this is not impossible; but it is highly unlikely that small animals could survive not for days, but for weeks, the time necessary to cross the 1000 km. from Ecuador to the islands,

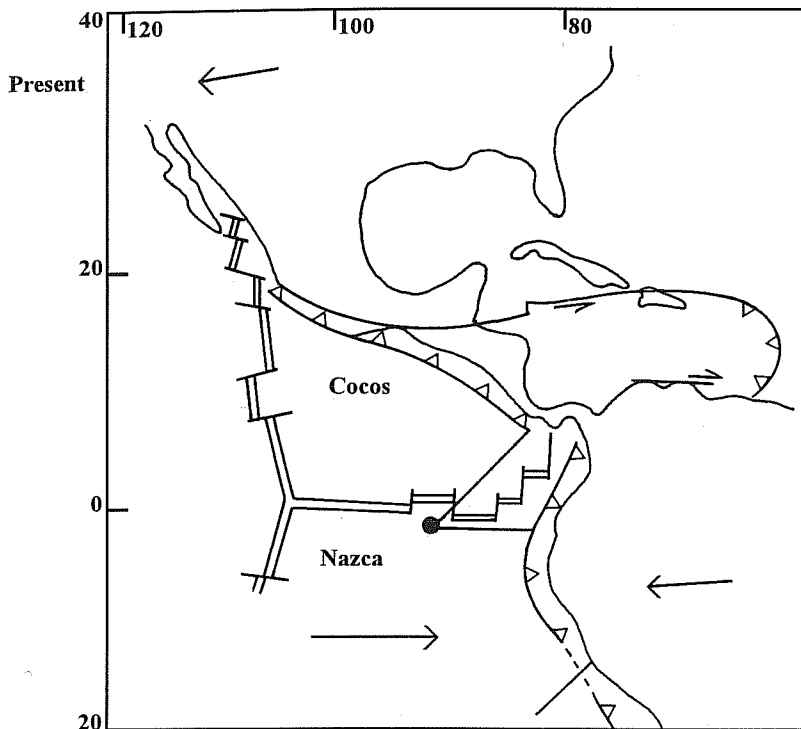


Fig. 5 - Present situation of the equatorial Eastern Pacific and Antillean region. Adapted from Duncan and Hargraves (1984).

on precarious mats of withering vegetation without dehydrating, if not starving to death. The Carnegie ridge, as discussed above, may possibly have offered a passageway for tortoises, but would hardly have been practicable for murids: they are not recorded in South America before the late Pliocene (Marshall, 1985). Still, palaeogeographic reconstructions may possibly offer a clue. The Central American Arc was connected with the North American continent in the Oligocene and Miocene (Burke et al., 1984) and, as noted above, a hotspot track, a possible forerunner of the present Cocos ridge, linked it to the Galapagos hotspot.

The Antilles had also a complicated history. Endemic solenodontid insectivores are restricted to Cuba, Hispaniola, Puerto Rico and the Cayman Islands. They are believed to have descended from North American Apternotid insectivores in the early Tertiary, to have entered the islands when they still were part of the North American landmass and to have been separated when the islands split off: the classical «vicariance model» (MacFadden, 1980). But platyrrhine primates, edentates and hystrocognath rodents were derived from ancestors endemic of South America. Woods (1990) admits a possible migration through stepping stones, possibly the Lesser Antilles, or now drowned islands on the

Beata or Aru ridges (see Holcombe and Edgar, 1990 for marine geology). Woods also pointed out, in this context, that in the Oligocene and early Miocene sea level was lower than now, and that his migration model does not necessarily imply continuous land bridges, and admits that islands may have formed stepping stones along which terrestrial mammals may have moved, crossing short stretches of sea by swimming or on natural rafts.

Indeed, this is an area in which natural rafts are a plausible hypothesis. The Gulf of Mexico is, and was earlier surrounded by continents with luxuriant forests and large rivers; it is also subject to hurricanes, which may have played a role in driving rafts around. There is however something odd in the picture. Edentates, platyrrhines and hystrocognath rodents are confined to the Greater Antilles; in the Lesser Antilles fossils are scanty, but are represented only by sigmodontine rodents (Woods, 1990), which are of North American origin and reached South America in the late Pliocene (Marshall, 1985). Also, the lack of late Tertiary immigrants from North America in the Greater Antilles looks somewhat odd in face of the rich representation of the South American fauna.

Another intriguing problem is offered by the islands between South-Eastern Asia, Australia and New Guinea. Audley Charles and Hooijer (1973) found in the geological evolution of western Indonesia an explanation for a possible overland migration of the endemic proboscideans of Timor. Because, they argued, «an elephant (and presumably a stegodont) could not swim across the Sunda Sea and Ombai Strait, the existence of a land connection between Flores and Timor during the Pleistocene must be postulated».

Over a century ago Wallace recognized in this area a territorial demarcation between the fauna of Asian origin and the Australian fauna. The situation is actually more complicated than Wallace had imagined and modifications of «Wallace's line» were proposed (Warren Carey, 1976: 430 ff.). As a matter of fact, between Talau and Aru islands there is an area, limited by sinuous contours, in which Asian and Australian mammals occur associated. This area comprises Sulawesi, Halmahera, Ceram, Timor and some smaller islands (Simpson, 1980, fig. 6.14). This is a tectonically highly active area where Asian and Australian continental plates (the latter including New Guinea) collided, giving rise to a complicated network of emerged ridges and deep troughs (Warren Carey, 1976, fig. 180-184). The strange shape of Sulawesi results from the coalescence of two arcs, the outer one of which is part of a ridge that, running through Flores, Java and Sumatra joins the Malay Peninsula and the Asian continent, with a sharp loop East of Flores, which was due to the westward push of New Guinea: and the inner arc, according to the reconstructions of Warren Carey, is part of a ridge that ran eastwards to join New Guinea and the Australian plate.

Considering now the distribution of mammals in Indonesia and in the Antilles, it will be realized that the model is not random, as would be expected in the hypothesis of migrations by swimming or passive transport, but seems to be controlled by definite geological constraints. Evidence, admittedly, is far from conclusive, but provides an indication that should not be overlooked.

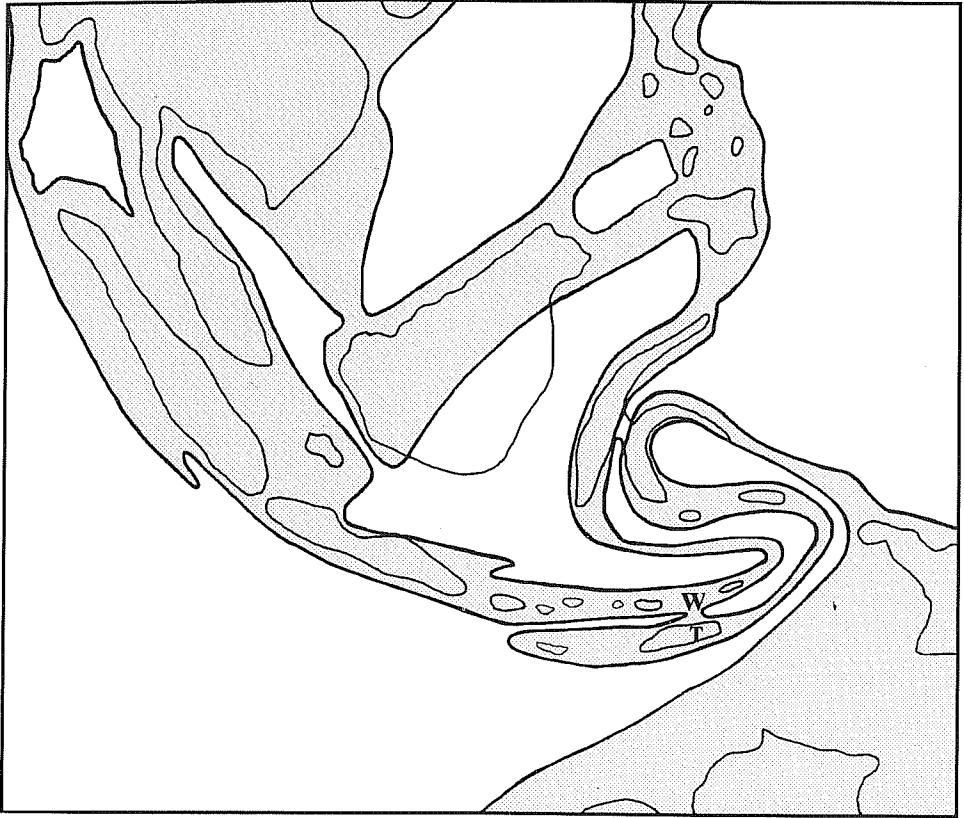


Fig. 6 - Sketch map of the Indonesian area in the Pliocene to early Pleistocene. T: Timor; W: isthmus postulated by Audley Charles and Hooijer between Watar and Timor. A similar isthmus joins now the outer and inner arcs in Sulawesi. Adapted from sketch maps by Warren Carey, (1976).

Still, the model of overland migrations raises questions which have not yet found a proper explanation. Why are island faunas so oligotypic and unbalanced?

This is not always the case. What survives of the Tertiary fauna of Madagascar shows that it was not oligotypic; it may possibly even have been more diversified at the beginning. The picture offered by the late Pleistocene invasion of Sicily is also significant. Sicily was colonized several times, the last time in the late Pleistocene, with the arrival of man, besides *Equus caballus*, *Equus hydruntinus*, *Sus scrofa*, *Cervus elaphus*, *Bos primigenius*, *Lepus europaeus*, *Erinaceus europaeus*, *Vulpes vulpes*, *Crocota spelaea*, *Ursus arctos*, *Panthera leo* (reported by Kotsakis, 1979). There is also a record of a dwarfed form of *Bos primigenius*, (Brugal, 1987). Clearly, immigration took place during the late Pleistocene sea level low, which culminated about 20 ka ago, and the dwarfed ox may testify of a rapid dwarfing process following isolation. The

small deer of Capri island also immigrated during the last sea level low and became dwarfed before the Bronze Age (Azzaroli, 1977b), another example of rapid evolution in the insular environment.

On the other hand the oligotypic, unbalanced character of older Sicilian faunas is no isolated case: suffice it to mention here the Balearics, Cyprus, Crete, the Galapagos. Sardinia and Corsica had a moderately diversified fauna in the early Pleistocene, presumably a remnant of a more varied fauna immigrated during the Messinian sea dessiccation. Deer, vole and possibly a dog immigrated at the end of the early Pleistocene, but at that time the mammalian fauna was reduced to no more than six species: of the older fauna only the ochotonid *Prolagus*, the large murid *Rhagamys* and the soricid *Episoriculus* survived. The dog, incidentally, seems to have been adapted more to fishing than to preying on land (personal observation, unpublished).

More to the point, most Pleistocene immigrations were selective: elephants, hippos, cervids, rodents. Bovids are poorly represented. Characteristically, caprines were restricted to islands which were colonized in the Miocene or early Pliocene: Sardinia, the Balearics. In other words, they only migrated before the evolutionary radiation of cervids, which made them masters of the field in Europe; immigration of bovids may have been thwarted by their competition. Still, the fact remains that the majority, if not all the larger endemic mammals are represented by good swimmers. This is easily understandable. If a connection between island and continent was established by some geological event, the process was necessarily gradual: at a certain time of this process, the width of the sea channel dividing island and continent was reduced to a minimum, say few km., a distance that good swimmers could easily negotiate. In some case the junction between island and continent may not have been completed; of the larger mammals, only hippos and elephants could migrate, the distance from the continent was perhaps too great for cervids. And, conceivably, once an island had been saturated by the first immigrants, their competition may have prevented the immigration of other species.

These, however, are no more than speculations. As a matter of fact, very little is known of the history of faunal evolution within islands during their periods of isolation. The last invasion of Sicily might have been an informative case, in spite of its short duration, had human activity not interfered too heavily on the local fauna. It should be pointed out however that during earlier periods of the Pleistocene, in spite of the narrow distance separating the island from the mainland, there were no faunal exchanges across the strait of Messina. And the last, late Pleistocene invasion of Sicily remains, so far, an isolated case. In previous invasions of this island, as well as in other islands, immigrations were controlled by some filtering effect, which was not necessarily the same for all islands; and what we know of their endemic fauna does not necessarily represent all the original immigrants, some of which may have been wiped out in the fossil record.

Moreover, the filtering effect of land bridges and of the expansion of immigrants into new lands is not restricted to islands. To quote only a recent exam-

ple, the Bering bridge opened a migration way between Eurasia and Northern America, but only few taxa of bovids took advantage of it; and with few exceptions, these bovids remained confined to areas of present day Canada and the United States. There is a strange contrast between their fate and the extraordinary power of expansion of *Equus* from Northern America into Eurasia, Africa and Southern America. Mastodons migrated through the Panama bridge, but elephants did not. We have to accept the idea that much still remains to be learned about factors controlling the geographical dispersal of organisms, a problem which was already raised and discussed by Simpson (1980).

To sum up, all models of island colonization are possible: vicariance; migration through temporary, continuous or discontinuous land bridges; active or passive transport. It is argued here that vicariance and migration through land bridges were the most common models of colonization. The third model is seen as possible only in few, exceptionally favourable cases. The first two models imply geological processes which may be clear in some case but are not always easy to solve. Still, attention should be concentrated along these lines. Undiscriminated acceptance of the model of active, or passive transport skirts the geological problem and may lead to detrimental neglect of valuable lines of investigation on the geological processes which were, and are still active on our mobile Earth.

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