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HYPOTHESIS:

A GEOLOGICAL BASIS FOR SOME HERPETOFAUNAL DISJUNCTIONS IN THE SOUTHWEST PACIFIC, WITH SPECIAL REFERENCE TO VANUATU

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INTRODUCTION

Vanuatu is generally considered to form part of the Outer Melanesian Arc, which runs from New Guinea through the Solomons and eventually to Fiji and Tonga (Holloway, 1979). Within the arc, however, Vanuatu is relatively isolated by the surrounding Johnson Trough, Vitiav Trench and Vanuatu Trench (Coleman, 1970). A spreading ridge is present to the east of the group. Recent work (Chase, 1971) indicates that until 6-8 mybp Vanuatu lay north of Fiji and Tonga, along the border of a wider arc, adjacent to the Vitiav Arc (Carney and MacFarlane, 1982). Until the Miocene Vanuatu maintained its position relative to Fiji. At that time it began to drift. Subsequent arc bending and counterclockwise rotation has resulted in its present position (Gibbons, 1985). This theory is consistent with the current thought that many orogenic belts are actually composites of smaller blocks (terrane) of varied origins (Craw, 1982). In general, support for the terrane accretion origin of

composite regions comes from magnetic anomalies, heat flow studies, bathymetry and stratigraphy. Terranes of the North American Cordillera (Irving, 1979; Coney *et al.*, 1980) and the central Philippines (McCabe *et al.*, 1982, 1985) have been particularly well documented. Terranes of the former have been used in an attempt to explain the biogeography of bolitoglossine salamanders (Hendrickson, 1986) and it is possible that some of the peculiarities of animal distribution in Vanuatu may also be explained by its past fragmentation and movement.

THE VANUATUAN FAUNA AND ITS AFFINITIES

The herpetofauna of Vanuatu has traditionally been regarded as depauperate Paupuan (Baker, 1928, 1929; Darlington, 1948), having suffered attrition through filter effects that have reduced diversity away from the New Guinea source area. This 'impoverished' fauna has, however, been supplemented by species of

presumed New Caledonian origin (*Leiolopisma atropunctatum*) as well as by endemics, chiefly associated with a localised radiation of the scincid genus *Emoia* (Medway and Marshall, 1975). Although this evaluation of the Vanuatuan reptile fauna can explain the origin of most native species, it is limited in that it accounts for the taxa present by invoking equilibrium theory (McArthur and Wilson, 1963, 1967), an approach more nearly appropriate for biogeographical problem over ecological time than for those over geological time. Recent advances in the geology and paleogeography of the southwest Pacific (e.g. Chase, 1971) suggest explanations for the distribution of certain 'problem' groups of amphibians and reptiles in Pacific biogeography (e.g. *Platymantis* and *Perochirus*) while maintaining the applicability of existing hypothesis for the origin of more recently arrived and vagile groups. Gibbons (1985) first suggested the application of knowledge of the changing paleoposition of Vanuatu to herpetological problems. This paper expands on his views and suggests that initial reference to historical biogeographical implications for distribution may provide fruitful results in the analysis of the faunal origins and relations of older island groups.

Like that of other Outer Arc elements, the fauna of Vanuatu shows Papuan affinities with limited local endemism. Mega- and microchiroptera are the only native mammals, and fully half of the land birds are shared with New Guinea (Medway and Marshall, 1975). Further, the number of bird species in Vanuatu is in accord with the predictions of the McArthur-Wilson model. The herpetofauna is particularly poor in comparison with neighbouring New Caledonia or even with Fiji, further to the east. The Earl of Cranbrook (Medway and Marshall, 1975; Cranbrook and Pickering, 1981; Cranbrook, 1985) recognised a Vanuatuan terrestrial reptilian fauna of 20 species. In addition, there is one introduced species of hyliid frog, *Litorea aurea* (Meday and Marshall, 1975; Fischthal and Kunzt, 1967; Tyler, 1979). To this list may be added several additional endemic *Emoia* (W. C. Brown, in press) and perhaps *Crocodylus porosus*, identified from the trackways on Espiritu Santo (Baker, 1928, 1929). Further, *Gehyra vorax*, now generally recognised as specifically distinct from *G. oceanica* (contra Burt and Burt, 1932), has also been recorded from Vanuatu (Baker, 1928, 1929; Boulenger, 1885). The Fijian iguana, *Brachylophus fasciatus* has been introduced to the fauna recently by man (pers. comm., W. C. Brown). Of Vanuatuan reptiles *Gekko vittatus* (not included by Medway and Marshall, 1975) and *Gehyra mutilata* are known from single specimens collected by Baker (1928, 1929) and probably do not constitute native species. Similarly, the snake *Ramphotyphlops braminus* is likewise a recent addition, probably transported by man (Meday and Marshall, 1975). I accept the remaining taxa (approximately 21 species) as constituting the native herpetofauna of Vanuatu.

A distinct break between the faunas of New Caledonia and Vanuatu, especially in regard to the herpetofauna of these areas, was noted by Roux (1913), Baker (1928) and Sternfield (1920). Sub-

sequently, differences in the snail fauna (Solem, 1958) have also been indicated. In all cases the richer fauna occurs in New Caledonia and shows distinct affinities with New Zealand and especially Australia, in contrast to the poorer, Papuan fauna of Vanuatu. Cheesman (1957) noted breaks within the flora of Vanuatu and suggested that the southern islands, Aneityum, Erromanga and Tanna had probably been connected with New Caledonia during the Cretaceous, when both split off from Queensland. She believed that subsequent division occurred in the Late Miocene or Early Pliocene. Solem (1958) presented conflicting evidence from land snail distributions and pointed out the existence of the 6400m Vanuatu Trench separating the two regions. Among animal groups, only highly vagile forms and some parasitic groups such as the Diptera pupipara (Maa and Marshall, 1981) show a strong affinity across the Vanuatu Trench. Current views of plate tectonics clearly indicate that Vanuatu and New Caledonia have never been in contact and generally account for the differences in the faunal, and to some extent, floral affinities of the two areas.

As noted by Roux (1913) and Gibbons (1985), the Loyalty Islands, located approximately 100km off the east coast of New Caledonia and 150km from the southern islands of Vanuatu, possess an intermediate herpetofauna best characterised as a depauperate New Caledonian fauna with some typical Papuan elements and very low endemism. Brown (1956) considered the Loyaltys as the link between New Caledonia and the rest of Southern Melanesia. Berlioz (1962) also noted the Vanuatuan influence in the Loyaltys' avifauna. The age of the emergent Loyalty Islands is unknown, but appears to be very recent, perhaps Pleistocene. Thus the herpetofauna is probably only of recent origin, being derived via overwater dispersal, although parts of Maré may have been emergent for a much longer time and may, at one time, have been much closer to the New Caledonian source area.

The relationship of Vanuatu to other elements of the Outer Melanesian Arc, notably the Solomon Islands and Fiji, is more problematic. As mentioned, the herpetofauna of Vanuatu is slightly poorer than that of Fiji, which is more distant from the Papuan source area (elements of the Outer Arc have never been broadly connected by land, thus overwater dispersal is likely to have been responsible for the introduction of the fauna of the eastern elements of the arc). The Fijian herpetofauna, as reviewed by Pernetta and Watling (1979) consisted of 22 species of reptile and three amphibians (excluding the semi-marine *Crocodylus porosus*, Derrick, 1965). The addition of newly described species of *Emoia* (Brown and Gibbons, 1986), *Brachylophus* (Gibbons, 1981) and *Leiolopisma* (Zug, 1985), as well as the inclusion of *Ramphotyphlops flaviventer* and the removal of introduced forms (*Bufo marinus*, *Hemidactylus frenatus*, *H. garnotii* and *Hemiphyllodactylus typus*) yields a native fauna of about 27 species, including the two ranid frogs, *Platymantis vitianus* and *P. vitiensis*. The existence of the iguanine, *Brachylophus*, present in Fiji, Tonga and Wallis Island, is generally explained by overwater dispersal from the Americas (Cogger, 1974; Gibbons, 1981, 1985). If this is the case, its absence in Vanuatu

(where it has subsequently been introduced) would not be surprising.

The absence in Vanuatu of frogs of the genus *Platymantis*, however, is perplexing. These ranids are speciose in the Solomon Islands and are represented by two endemic species in Fiji. Schmidt (1930) hypothesised differential extinction in Vanuatu in order to reconcile this gap with a continental, or Papuan, origin of the genus. If Brown's (1952) assertion that the ranids are an old group in the Solomons (and Fiji) is correct, the appearance of Vanuatu at its present position in the Neogene would seem to explain the absence of Vanuatuan *Platymantis*. However, Tyler (1972) considered the ranids as having Pleistocene entry into the Solomons, and thus into Fiji. It seems difficult to reconcile the latter view of platymantine origins with the terrane theory of Vanuatuan origin. The most recent discussion of the age of this group (Zweifel and Tyler, 1982) implies that the platymantines have inhabited the region since the Miocene.

As first suggested by Gibbons (1985) the presence of elapids (*Ogmodon*) in Fiji but not in Vanuatu is likewise accounted for by the relatively recent shift of Vanuatu into a southern position. The distributions of *Ramphotyphlops flaviventer* in Fiji and the Solomon Islands superficially suggests a similar explanation, but upon closer examination this seems unlikely given the difficulty in locating typhlopids, their ability to be transported in soil and the uncertain status of even alpha level systematics in *Ramphotyphlops*. The absence of Vanuatu would also have left Fiji closer to a New Zealand/New Caledonian source area for *Leiolopisma* and account for the absence of unique species of this genus in Vanuatu.

Another anomaly of the Vanuatuan fauna is the presence of *Perochirus guentheri*. This gekkonine is known from few specimens (Medway and Marshall, 1975; Brown, 1976) and its congeners occur only on Guam, Tinian, Ponape, Marcus Island, the Truk Islands and Kapingamarangi Atoll, all in Micronesia. While speculative, a former, northern position of Vanuatu might account for the presence of this species (Gibbons, 1986), as a position to the north of Fiji would have 'exposed' Vanuatu to dispersing migrants from the northwest. Prior to this suggestion the only existing hypothesis for the disjunct distribution of *Perochirus* had been the past existence of a continental mass connecting virtually all of the islands in the Pacific (Baur, 1897).

For the remainder of the herpetofauna of Vanuatu, a more traditional explanation (i.e. dispersal along a track from New Guinea through the Solomons) of origin seems on the basis of species diversity to apply. Thus, for both *Emoia* and the boïd genus *Candoia* species diversity is highest in the Solomon Islands and drops to the south and east. Although speciation has occurred in Vanuatu and elsewhere among *Emoia* populations, morphological differences are minor and are not inconsistent with recent expansion in the Pacific. The remainder of the Vanuatuan species are broadly distributed in the western Pacific (*Gehyra vorax*) or are pan-Pacific — (*Cryptoblepharus boutoni*,

Lepidodactylus lugubris, *Gehyra oceanica*, *Lipinia noctua*, *Nactus pelagicus*), implying recent dispersal across their present ranges. Finally, there are those species with broad distribution which have been transported by aboriginal or modern man.

PATTERNS OF COLONISATION

The herpetofauna of Vanuatu exhibits a historical complexity that belies its modest diversity. At least four broad categories of colonisation by reptiles and amphibians have characterised the western Pacific. The first, and most complex of these, involves movement of taxa most parsimoniously explained by known changes in paleogeography of emergent land masses. Most of the western Pacific islands of Miocene or greater age obtained their faunas through prior contact with other land masses or through dispersal from adjacent regions (some now quite distant). The herpetofaunas of New Zealand and New Caledonia consist primarily of taxa ultimately derived from continental Gondwanaland (Bauer, 1986). In the case of Vanuatu, some faunal elements (e.g. *Perochirus*) may date from previously existing near-neighbour relationships with other island groups while other groups (*Platymantis*, elapid snakes) may have been excluded for the same reasons. This type of faunal origin, historical in the sense that there are geological clues to prior positions, allows for the prediction of distributed attributes of other animal and plant groups of suitable age.

A second category of colonisation by organisms is that based upon a probabalistic theory of dispersal with the framework of a static (or in other words, recent) geography. Predictions of the equilibrium models of island biogeography fit this mode and may be related to the distribution of *Candoia* and *Emoia* in Vanuatu.

Thirdly, wide ranging forms, which because of biological features such as reproductive characteristics (parthenogenesis, low egg-shell permeability, etc.) (Gibbons, 1985) may become distributed and established rapidly, without speciation (either because of maintenance of genetic contact or insufficient time or habitat differences). Examples in Vanuatu include *Lepidodactylus lugubris*, *Nactus pelagicus* and *Emoia cyanura*.

Finally, human assisted transport, either intentional or accidental, places a fourth level of complexity on distribution. The presence of species such as *Litoria aurea* and *Ramphotyphlops braminus* are known examples of this category of colonisation. Although the last two modes are primarily responsible for the distribution of reptiles in the eastern Pacific (Ineich, 1982; McKeown, 1978), Vanuatu, and the western Pacific are influenced by all four.

The view of Vanuatu as a recent entrant into the Outer Melanesian Arc seems the most reasonable explanation of apparent herpetofaunal anomalies of the region, both on geological and zoological grounds. In addition to the herpetofaunal examples cited above, it also appears to explain disjunctions in the

distribution of a wide variety of groups in the Outer Arc (e.g. the Cryptotympanini [Insecta: Cicadoidea] Duffels, 1986). The analysis of faunal and floral elements in light of this information may yield further evidence of Micronesian, or simply northern, affinities in the Vanuatuan fauna, particularly in groups of pre-Neogene origin or arrival in the western Pacific.

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The ideas presented in this paper were stimulated by work authored by the late J. R. H. Gibbons of the University of the South Pacific, Suva, Fiji. This paper represents an expansion and interpretation of concepts introduced by Dr. Gibbons (1985) and is dedicated to his memory.

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POPULATION ECOLOGY AND CONSERVATION OF TORTOISES: THE ESTIMATION OF DENSITY, AND DYNAMICS OF A SMALL POPULATION

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ABSTRACT

Part 1: Line transect methods were used in three areas with known densities of *Testudo hermanni*. This enabled calculation of the proportion of the population available for finding (PAF); that is, excluding tortoises in refuges or in thick cover. At times of peak daily activity PAF varied between about 0.1 and 0.3, and was greater in spring than in summer. Males had higher PAF than females on summer evenings, the main courtship period, and PAF of males was greater in a population with a male-biased sex ratio. Transect sampling is useful for estimating the density of tortoise populations, provided that the low PAF is taken into account. Values of effective transect width are given for a variety of habitat types.

Part 2: A small population of *T. graeca* at Alyki was studied between 1980-1986; its size was estimated at about 25 adults, with an even sex ratio. Immature animals were recruited into the adult population, which was stable or increasing during this period. Adult size and juvenile growth rate were similar to other coastal populations of *T. graeca* in the region. The implications for the conservation of endangered tortoises are discussed.

INTRODUCTION

The threat to Mediterranean tortoise populations from collection for the pet trade (Lambert, 1969, 1979, 1981a) has now ended. The problem of habitat loss is, however, still present (Lambert, 1984; Cheylan, 1984).

Basic information on tortoise populations is needed to evaluate this threat (Honegger, 1981; Groombridge, 1982). This paper considers two aspects of the population ecology of tortoises which have special relevance to conservation.