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**BIOGEOGRAPHY OF REPTILES ON SOME OF THE ISLANDS
AND CAYS OF EASTERN PAPUA—NEW GUINEA**

by **Harold Heatwole**

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BIOGEOGRAPHY OF REPTILES ON SOME OF THE ISLANDS AND CAYS OF EASTERN PAPUA—NEW GUINEA

by Harold Heatwole^{1/}

INTRODUCTION

During participation in part of the Fairbridge Expedition to New Guinea, February to May, 1969, I had opportunity to visit 17 islands and cays east of the New Guinea mainland for sufficient time to assemble reasonably complete collections of their terrestrial reptilian fauna. The purpose of this paper is to present the results of that survey. Fairbridge (1971) has previously published a brief report on the expedition and a more detailed one is in preparation.

The taxonomy of the New Guinea herpetofauna is not well known and much nomenclatural confusion exists. Consequently, placing species names on all insular specimens would have involved extensive taxonomic studies for which sufficient comparative material is not available. Rather than describe doubtfully new species, or use names which are of uncertain application to the insular populations, I have deferred judgment until proper taxonomic studies clarifying relationships can be made, and have referred to such taxa only by the generic name.

GENERAL DESCRIPTION OF THE ISLANDS

The eastern islands are in four groups, the northern most one being the Trobriands, consisting of the major islands of Kiriwina, Vakuta, Kuia, Kaileuna and Kitava (or Nowan) and a number of smaller ones to the west collectively known as the Lusancays (Figs. 1, 2). The larger islands and many of the smaller ones are raised coral; some of the small ones are sand cays.

The most southerly group is the Louisiade Archipelago. It is made up of 3 large rocky islands primarily of orogenic origin,

^{1/} Department of Zoology, University of New England, Armidale, N.S.W. 2351, Australia.

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Misima (or St. Aignan), Rossel and Tagula (or Sudest), their surrounding small islands and cays (Fig. 1), and a series of small raised-coral islands and atolls with sand cays, lying between the major islands and the New Guinea mainland (Figs. 3, 4).

Between the two major groups mentioned above are two central groups (Fig. 1). On the west are the D'Entrecasteaux Islands which consist of 3 large volcanic islands, Goodenough, Fergusson and Normanby with their associated smaller islands and cays. To the east is Woodlark Island (or Murua) and its nearby islands.

All these islands have a maritime tropical climate. Mean temperatures for the general area (at sea level) range from 24° to 30°C; average humidity is 80% (Tudor 1968). On Kiriwina during the hottest part of the year (December to March), the average maximum temperature ranges from 31.4° to 32°C and average minima are 22.8-23.3°C; in the coolest months (June to September) corresponding values are 28.5°-29.7°C and 22.7°-23.3°C (Brass 1959). Mean annual rainfall (coastal) is 356-391, 312-401, 419, 257, and 165 cm for Kiriwina, Misima, Woodlark, Fergusson and the Conflicts, respectively (Brass, 1959, Tudor, 1968). The year is divided into two seasons, the dry period of the southeast trade winds, May to November, and the wet period of the northwest monsoons, December to April (Tudor 1968). There are transition periods of doldrums between the two seasons (Brass 1959).

The principal islands and many of the smaller ones have long been inhabited, the population totalling approximately 57,300 in the mid-sixties for the area under consideration (Tudor 1968). Non-European influences include burning and clearing (Brass 1956); European ones have been the development of copra plantations on most of the islands suitable for raising coconuts, development of trade, establishment of missions, bringing of the native population under government control, extensive mining of gold on Woodlark, Tagula and Misima, and the use of a number of the islands for military purposes during World War II (Brass 1956, 1969; Tudor 1968).

The islands and cays visited by the author will be described in more detail. Areas of these and other islands to which reference is made, were obtained by planimetry of nautical charts and from Tudor (1968). Elevations were either estimated during visits or obtained from nautical charts or from Devery (1968). Some values from nautical charts seemed excessive and probably are elevations to tree-top level. These are followed by an asterisk in the text.

Kiriwina: This was the largest island surveyed. It has an area of 29,050 hectares and a maximum elevation of 46 m. Mangrove forests occur along part of the coastline; the interior is forested by second growth but is extensively cleared for the

raising of yams and taro. Copra is exported. The island is densely populated (about 9,000 in the mid-sixties; Tudor 1968), there being several large villages and missions with smaller ones scattered throughout. Losuia serves as a port for small vessels. Roads connect major villages. Livelihood is obtained from the sea, from gardening and fruit gathering, and from exporting wood-carvings, and selling these as well as shells, pearls and other items to tourists which come to the island's single hotel on a weekly commercial flight. The island served as a base for Allied fighter aircraft during World War II.

Sim Sim: This member of the Lusancays is a small island (64 hectares, elevation 68 m) consisting of a sandy, flat plain leading to a promontory of raised coral. A native village of about 60 inhabitants is located on the sandy portion. The vegetation of this part consists largely of coconuts and gardens; shrubs and trees occur on the rocky part. Livelihood seems to be predominantly from the sea.

Wagalasa: This island is close to Sim Sim and is very similar to it in topography. It has an area of 35 hectares and a maximum elevation of 62 m. It is not permanently inhabited although a number of huts are present and the inhabitants from Sim Sim make nearly daily excursions there. It is largely forested; coconuts are cultivated.

Kawa: This island has a steep, almost cliff-like perimeter. Maximum elevation is 52 m and the area is 47 hectares. A trail leads from a narrow beach up to a village and mission on top. The inhabitants subsist from gardening, fruit gathering and from the sea.

Gabwina: This is a low sand cay (elevation about 5 m). The area is 26 hectares. It is uninhabited though a few huts are present and people from other islands visit it to harvest coconuts. It is forested.

Panaete: This is the largest (3,010 hectares) of the Deboyne islands. It is mostly flat but a rocky area reaches an elevation of 223 m. Though mostly forested, there are a number of native gardens and plantations on the flat parts. A large village, complete with modern school, is present.

Panapompom: This member of the Deboyne group (Fig. 1) is rocky but bordered by a broad flat area containing a native village, gardens and plantations. It is mostly forested. The area is 871 hectares and maximum elevation is 158 m. It was used as a Japanese sea-plane base during World War II.

Wari (or Teste): This is a rocky island of the Louisiade Archipelago (Fig. 4). It has an area of 215 hectares and a maximum elevation of 119 m. It was influenced by humans more than most of the islands visited. The rocky peaks are grassy and are partly

eroded in places. The lower slopes and flat areas have gardens and coconut plantations; small forested areas with a heavy herbaceous undergrowth occur. One village is present.

Marai (or Stuers): This is a coral and sand island (area about 5 hectares, elevation 26m*). It is forested with Casuarina, coconuts and other trees. A shrub zone of Tournefortia, Scaevola and Suriana encircles the island at the level of the upper beach. It is uninhabited although apparently visited by copra collectors.

Quessant: This is a small sand cay of about 5 m elevation and an area of 64 hectares. It is largely forested. It is not permanently inhabited though coconut plantations are present and at the time of our visit, 6 natives were there collecting copra.

Unnamed Cay (Long Reef, Louisiade Archipelago) (Fig. 4), unofficially named Delores Cay by the Fairbridge expedition and referred to as such in the expedition report in preparation: This is a small (219 hectares), low (2 m) uninhabited sand cay covered by coconut palms, shrubs and small trees. There was an abundance of dead wood on the ground suggesting recent storm damage.

Panawan: This is a sand and coral cay (12 hectares, 31 m elevation*). It is uninhabited although copra plantations are present. It is mostly forested.

Irai: This island is low (about 3 m) and has an area of 97 hectares. It is forested in part but the majority of the vegetation consists of coconut plantations with an undergrowth of shrubs and herbs. The island is inhabited by the plantation owner and his wife and about 18 native laborers brought in from New Britain. Some plant-enriched, clay-like soils occur in small depressions.

Gabugabutau: This is a sand cay of 1.5 m elevation and an area of 3.2 hectares. It is long and narrow, in one place being no wider than several meters. Part is forested and contains coconuts; part has a shrub cover of Scaevola and Pandanus. Many trees were broken down and dead wood was abundant. This island showed the most severe storm damage of any I visited. It is uninhabited though the copra plantation is regularly worked by laborers from Irai.

Auriroa: This island is a sand cay similar in appearance and vegetation to Gabugabutau except it suffered less storm damage. It has an area of 61 hectares and an elevation of about 2 m. It is not permanently inhabited.

Tupit: An uninhabited sand cay containing a copra plantation with an open shrubby and herbaceous understory. A herd of 5 goats was present. It has an area of 1.6 hectares and an elevation of about 1 m.

Bare Sand Cay: This is a small cay near Gabugabutau with an area of 0.002 hectares and an elevation of about 0.5 m. It lacks vegetation and was the only island visited that did not have any terrestrial reptiles.

Several islands not adequately surveyed on the Fairbridge expedition are included in the biogeographic treatment. One of them, Kuia (area 174 hectares, elevation 3 m) was well collected by a party from the Australian Museum and I examined their specimens. The others were Kaileuna, Kitava, Fergusson, Goodenough, Normanby, Misima, Rossel, Tagula and Woodlark. Species lists for these islands and for the New Guinea mainland were assembled from my specimens (Misima, Goodenough), from the literature (de Vis 1892; Boulenger 1895a; de Rooj 1915, 1917; Burt and Burt 1932; Loveridge 1948; Brass 1959) and from an unpublished list of identified specimens in the American Museum of Natural History collected by the Archbold and Whitney expeditions (Zweifel, personal communication). As most of the specimens upon which these lists are based have not been examined by the author, only data on numbers of species are used in the present paper; with the exception of Kuia, faunal lists for these islands are not included in Appendices 1 and 2 nor in Table 1, nor are species present on them, but not on the islands I visited, discussed in the species account. Some literature (e.g., Boulenger 1895b, de Haas 1950) was not very useful as localities were often given as "Trobriand Islands" or "D'Entrecasteaux Islands" without specifying which particular island.

On the basis of small, incomplete collections made on Misima, Goodenough and Samarai, I can report as new records, the occurrence of Cryptoblepharus boutoni and the introduced toad, Bufo marinus on Samarai, and Lepidodactylus lugubris and Sphenomorphus sp. (perhaps undescribed) on Misima. I can confirm the presence of Emoia mivarti, Emoia caeruleocauda, Emoia atrocostata and Dendrelaphis sp. on Misima, and Emoia mivarti on Goodenough.

ACCOUNT OF THE TERRESTRIAL SPECIES

In the following account, the scientific name is followed by the common names, where known, in English, Pidgin and/or one of the native island languages. For the last, the spelling is phonetic.

It is felt that species lists for small islands are reasonably complete, especially for skinks. Geckos, snakes, and particularly Typhlops, tend to be more secretive and some species may have been overlooked on even the small cays. Faunal lists of islands the size of Kiriwina and larger, will almost certainly be added to in the future. In many cases I have only one specimen of a given species from an island. This gives a false impression, however, of the thoroughness of collecting.

For small islands, once a species was represented in the collection, further attempt to secure additional material was usually not made, though specimens proffered by helpful islanders were diplomatically accepted. Series were collected on the large islands (e.g., Kiriwina).

ORDER SQUAMATA

Suborder Sauria

Gekkonidae

Cyrtodactylus pelagicus: Records from museum specimens. No ecological data.

Gekko vittatus: Record from museum specimen. No ecological data.

Gehyra oceanica: This gray gecko of medium size, about 75 mm snout to vent (s-v), was found under loose bark or under logs in coconut groves and other, rather open beach-side areas. It is nocturnal.

Gehyra sp.: This species was found under dead bark in much the same type of habitat as G. oceanica. It is brown and reaches 45 mm s-v.

Lepidodactylus lugubris: This slender gecko (about 40 mm s-v) was found under loose bark in rather open situations and in houses. It is light brown with darker transverse markings on the back.

Lepidodactylus sp.: The single individual encountered was under a log. It was dark brown and 47 mm s-v.

Varanidae

Varanus indicus (Monitor Lizard, Goanna, Gawi): This species was found near water, either along rocky coasts or mangroves. It has been known to feed on marine organisms (Mertens 1934), and Hediger (1933-34) indicates it voluntarily enters the sea. On Kiriwina, it was most frequently seen basking on logs or mangrove roots along channels through swamps. In life it is black with yellow spots. It is the largest lizard on the islands; adults reach a total length of about 1 m.

Scincidae

Carlia fusca (Carpuyeta): This lizard was active from sun-up to dusk, and foraged over leaf litter and low herbs, usually in relatively open areas but with at least some canopy cover. Adults reach up to about 55 mm s-v and are rather heavy-bodied. Juveniles are dark with lines of white spots on the dorsum and side of the head; these are lost during growth and adults are nearly uniformly brown.

Cryptoblepharus boutoni: This extremely widespread species was one of the most abundant and common lizards on the islands.

It was usually found in sunny, rather open areas on tree trunks or piles of sticks, though it was sometimes seen on logs, large boulders containing crevices, and occasionally on the ground. It is a small (40 mm s-v), slender lizard, bluish gray below, darker above with pronounced dorsolateral white stripes and a middorsal band which varies in conspicuousness among individuals.

Emoia atrocostata: This is a medium-sized skink (about 75 mm s-v). It is found in sea-side habitats (Mertens 1934). Alcalá and Brown (1967) give its habitat as "rocky beaches and mangrove swamps". I found it in the former on Misima. On Gabugabutau it inhabited crevices in tree roots and logs near the high tide splash zone of a sandy beach. Hediger (1933-34) mentions that it is never found more than 100 m from the sea, and that individuals swim in tide pools. It is white beneath, becoming blue-gray to brown above, irregularly mottled with small whitish and dark spots. The sides have a series of large black spots nearly coalescing into a lateral band.

Emoia caeruleocauda: This is a small, blue-tailed skink. I obtained no ecological data.

Emoia cyanogaster: This lizard forages on shrubs and vines up to about 2 m above the ground, where there is a nearly closed canopy overhead. It is light green below becoming brown dorsally, with regularly scattered whitish scales. It has a white upper lip. Adult size is about 80 mm s-v. Hediger (1933-34) considers this species a branch occupant as compared to L. smaragdina which occurs more on tree trunks.

Emoia mivarti (Kulumamauva, Koyonikwá): This small (about 45 mm s-v), slender skink was extremely common. It is a ground form, foraging on the leaf litter, especially around palm fronds and other debris, in areas of partial canopy cover, though venturing into more open areas. It is brown above, lighter beneath. There is a middorsal lighter band of varying conspicuousness (or absent), a pair of white dorsolateral stripes, and a pair of white lateral stripes. A ventrolateral white line is frequently present on each side, though sometimes it merges with the ventral coloration.

Eugongylus rufescens: This short-legged, medium-sized (up to at least 115 mm s-v) skink is found in forested or partly open areas, in or under moist, decaying stumps and logs. It occasionally leaves these retreats to forage on the ground but returns to them at the slightest disturbance. It is white below and uniformly dark brown above.

Lamprolepis smaragdina (Tomwawanatobubusi): This is a medium-sized (about 100 mm s-v) bright green lizard (blue in alcohol). It is arboreal, occurring on tree trunks and branches and climbing hanging vines.

Lipinia noctua: Records based on museum specimens without ecological data. Hediger (1933-34) indicates it to be a good climber, though less arboreal than Dasia (= Lamprolepis smaragdina).

Lipinia virens (Kanavasía): This is a slender, medium-sized (about 55 mm s-v) skink found mostly on the herbaceous cover in forests or partly shaded areas. It is dull olive to bright green above and sulphur yellow to lemon yellow below (fades to pale brown or nearly white in alcohol).

Sphenomorphus jobiensis: Record based on specimen without ecological data. However, Hediger (1933-34) lists it as a strictly forest floor species.

Sphenomorphus sp.: A small, possibly undescribed skin. One specimen was collected without ecological data.

Suborder Serpentes

Boidae

Engyurus carinatus: Record based on museum specimen. No ecological data.

Colubridae

Dendrelaphis sp.: Record based on a museum specimen. No ecological data.

Stegonotus modestus (Tagegá): Specimen brought in by a native. No ecological data.

Typhlopidae

Typhlops depressiceps: The single specimen obtained was in a forest under loose bark of a tree, 1.5 m above the ground.

Typhlops braminus: Record based on museum specimen. No ecological data.

AQUATIC AND SEMI-AQUATIC SPECIES

ORDER CROCODILIA

Crocodylidae

Crocodylus porosus (Salt-water Crocodile, Puk-Puk, Urigova): This is one of the largest reptiles in the area, reaching an average length of about 4.5 m (Pope 1956). It is mainly associated with mangroves or estuaries and its insular distribution is probably restricted to those islands with rather extensive mangrove swamps. It occurs on Kiriwina and some of the other large Trobriand Islands.

ORDER CHELONIA

Cheloniidae

Chelonia mydas (Green Turtle, Wonu): This species probably occurs throughout the area. I found tracks where females had moved over the beach to lay their eggs and also a dead hatchling on Unnamed Cay. Adults were seen in the lagoon of Conflict Atoll.

Eretmochelys imbricata (Hawksbill): I encountered no live individuals but saw carapaces for sale on Kiriwina.

The other species of sea turtles which range widely in the Indo-Pacific region, i.e. the Loggerhead (Caretta caretta), the Pacific Ridley (Lepidochelys olivacea) and the Leatherback (Dermochelys coriacea, family Dermochelidae) all probably occur in the waters around most of the islands treated here. The Loggerhead is known from Kiriwina (Bustard and Limpus 1970).

ORDER SQUAMATA

Suborder Serpentes

Hydrophiidae

Laticauda colubrina (Banded Seasnake, Coral Snake): Fifteen species of seasnakes are present in New Guinea waters (Barme 1968), many of which probably occur around the islands studied. However, despite daily diving with Scuba or snorkel on the reefs by various expedition members, only 3 specimens were obtained, all Laticauda colubrina. Several other individuals of the same species were seen but escaped. A second (unidentified) species was seen at the surface on several occasions while the research vessel was moving between islands; a third (unidentified) species escaped just off Panaete Island.

L. colubrina is a small seasnake reaching a maximum snout-vent length of only about 1400 mm. Wide black bands alternate with pearl gray to bluish ones. The head and tail have bright yellow markings. It inhabits shallow water on coral reefs and can be found under blocks of dead coral on reefs exposed at low tide and occasionally on land. The deepest water my specimens came from was about 11 meters. The three locality records obtained were Wari Island, Misima Island, and the Conflict Atoll. Though this species (like the entire family) is venomous, the islanders were not afraid of it. It is gentle and seldom attempts to bite even when captured.

Colubridae

Subfamily Acrochordinae

Acrochordus granulatus (File snake, Tobwadi): This harmless species was found only at Kiriwina, where it was abundant in the mangrove swamps and adjacent mud flats. It was usually found lying on the mud in shallow water or under some debris on the mud. Some were observed actively swimming. This species is characteristic of mangroves and mud flats and its distribution in the area under consideration is probably restricted to islands with these habitats.

IMPORTANCE OF REPTILES TO THE HUMAN POPULATION

In addition to the indirect benefit of many lizards as insectivores and of some snakes in rodent control, there are a number of direct uses made of reptiles by the islanders.

The skin of the Monitor Lizard (Varanus indicus) is tough and durable and on Kawa (and presumably other islands as well) is used for drum heads (Fig. 5). The drum is played by tapping with the fingers and is used to set the rhythm for dances.

The flesh of the Monitor is not consumed in the Trobriands which is in marked contrast to the natives on some parts of the mainland of New Guinea and New Britain and to the aborigines of Australia who prize lizards of this genus for food. File snakes are not eaten in the Trobriands though they are hunted for food by Australian aborigines (Worrell 1963).

The only reptiles which I found to be eaten were sea turtles.

The carapaces of Eretmochelys imbricata are sold by natives to tourists visiting Kiriwina.

The salt-water crocodile (Crocodylus porosus) influences the daily life of the local inhabitants in several ways. Some of the Europeans hunt them and employ native skinners to prepare the hides for sale. C. porosus serves as a model for carvings which the people of the Trobriands make and sell to tourists. A wide variety of realistic, semi-stylized, and abstract crocodiles are carved from ebony as well as from less durable local woods. Price ranges from 25 cents to \$3.00 (Aust.) depending on size, type of wood, quality of workmanship, and bargaining skill of the buyer.

The most direct effect of the Salt-water Crocodile is its occasional predation upon the human population. The most recent case in the area under consideration occurred in May 1967 at Boli Point, Kiriwina (Fr. K. B. Murphy, personal communication). Three native girls, aged 15-16 were fishing at dusk in the backwaters of a mangrove swamp. A crocodile swam to them from the seaward side, grabbed the middle of the three and dragged her under the water and away into the swamp. A large hook on a chain was baited with meat and placed in the vicinity. A crocodile was subsequently caught and shot by local European residents, Tim Ward, Joe Stuart and Fr. Murphy. The animal was a female, 4.57 m long (Figs. 6, 7); its stomach contained the girl's grass skirt and earrings, and several human bones. The local inhabitants believe this individual to have been responsible for 8 human deaths.

This species is probably on the decline in the islands. I did not find any specimens on Kiriwina despite spending several days and part of one night searching the mangroves and diving with snorkel and mask in the channels running through the swamps.

Throughout the Territory as a whole, the total export value of skins has been dropping precipitously since 1965, due to over-exploitation (Downes 1969 a). In 1966, Ordinance No. 14, Crocodile Trade (Protection) Ordinance, was assented to by the House of the Territory of Papua and New Guinea. This ordinance restricted the hunting and commercial use of crocodiles; its regulations came into force in 1969. Funds have been provided for research into ways of protecting the crocodiles and the skin trade; studies are now in progress (Downes 1969 b).

ECOLOGY

The herpetofauna of the small islands is not a random assemblage of mainland species though some are related to New Guinea forms. Some are species which are widespread throughout many of the South Pacific island groups, e.g., Typhlops braminus, Gehyra oceanica, Lepidodactylus lugubris, and Lipinia noctua (Burt and Burt 1932, Bryan 1959, Whitaker 1970, Clapp and Sibley 1971) and a few are widespread southeast Asian-East Indian forms, e.g., Emoia atrocostata and Varanus indicus (Dammerman 1948, Bustard 1970). Cryptoblepharus boutoni (including a number of subspecies) ranges from islands off the west coast of Ecuador and Peru throughout those of the Pacific and Indian oceans to coastal Asia, Australia and Africa (Burt and Burt 1932, Mertens 1934, Bryan 1959, Bustard 1970) and perhaps has the most extensive geographic distribution of any living species of terrestrial reptile.

Certain species were found on specific types of islands and not on others. The most obvious category of difference was between rocky or raised coral islands and sand cays. More than substrate type was involved, however, in that rocky islands tended to be more heavily forested and hence probably cooler and moister than cays, and also had greater elevation.

Of the 24 species of terrestrial reptiles treated, 12 were found only on rocky islands, 2 only on coral cays, and 10 occurred on both types. However, 14 species occurred on only one or two islands and hence their requirements are difficult to evaluate. The remainder of the discussion is restricted to those species found on 3 or more islands. Of the 10 such species, 2 (Carlia fusca and Lipinia virens) were restricted to rocky islands, none to sand cays.

The two most abundant species, Cryptoblepharus boutoni and Emoia mivarti were found on both types. Their distributional pattern, however, requires more detailed examination. They were each found on 9 islands and had almost mutually exclusive distributions (Table 1). Every island had one or the other of these two species; only one had both together (Kuia). Cryptoblepharus boutoni was found on all sand cays except one (Gabwina) but occurred on only one rocky island (Kuia). By contrast, Emoia mivarti occurred on every rocky island examined. It was absent from all sand cays except Gabwina (the one lacking C. boutoni).

Two hypotheses suggest themselves.

One is that these species have rather narrow ecological amplitudes and that E. mivarti can normally survive only on rocky islands and C. boutoni only on sand cays. If so, fortuitously dispersed animals would usually be able to survive and establish themselves only on islands of the appropriate type. However, C. boutoni does frequently occur on small rocky islands in areas where E. mivarti is absent (e.g., some islands on the Queensland coast of Australia, Heatwole, unpublished data; Madagascar, Fricke 1970). Indeed, Loveridge (1946) indicates rock or cliffs of coral rag as the preferred habitat of this species, but states that where rocks are not available "this adaptable skink will adjust its life to local conditions and prosper among sandhills or similar situations near the shore." Hediger (1933-34) points out that differences in habitat occur among the various subspecies of C. boutoni. Hence the above hypothesis could be true if the form from the Eastern New Guinea islands is more restricted to a sandy habitat than those from other areas.

The second hypothesis is that on very small islands these two species competitively displace each other, with C. boutoni having the advantage on sand cays and E. mivarti the advantage on rocky islands. On large land masses, such as the New Guinea mainland and large rocky islands, where both species occur together, there is a greater ecological diversity than on small islands. This would permit coexistence by providing large areas of both types of optimal habitat, from which the species with the competitive advantage would be able to exclude its opposite number.

The likelihood of the second hypothesis being true is enhanced by the similarity in ecology of the two species. Both are small and insectivorous. E. mivarti forages on the ground whereas C. boutoni usually is found low on shrubs, rocks, tree trunks or other objects, hanging head-down. It uses such vantage points for scanning for prey and does feed on the ground at times. I have observed this myself and Fricke (1970) reports this species foraging in the intertidal zone. Thus, both species obtain at least some of their food from the ground and probably overlap in utilization of food resources when coexistent. However, a quantitative and comparative study is needed to decide between these two hypotheses. It is unfortunate that the only small island on which the two species are known to coexist (Kuia) was the only small one treated in this study with which I did not have first-hand field experience.

In contrast to what appears to be broad niche overlap and competitive exclusion in the above mentioned species-pair, most species showed ecological segregation and niche partitioning. One conspicuous separation was between the nocturnal geckos and the diurnal skinks and varanid. However, lack of overlap in activity period does not necessarily imply non-sharing of food

resources. Different species may feed on the same prey populations but at different parts of the diel cycle. Careful studies are needed before an assessment of overlap can be made. Similarly, insufficient data are available to evaluate how, or if, the various species of geckos interact among themselves.

Among the diurnal lizards on rocky islands, however, niche partitioning was evident and largely took the form of spatial separation. Vertical stratification involved an arboreal species (Lamprolepis), a low-shrub one (Emoia cyanogaster), a herb form (Lipinia virens), and two ground species (Carlia fusca and Emoia mivarti). The last two are different in size and therefore probably eat different sizes of prey. It is possible that there is niche overlap between juvenile Carlia and adult E. mivarti.

Eugongylus is a semi-fossorial species, burrowing in and under decaying wood. Even during surficial foraging, however, its much larger size would probably separate it from either of the other two ground forms (Carlia, E. mivarti).

Varanus indicus and Emoia atrocostata are water-side species and thus horizontally separated from the other forms. They are separated from each other by immense differences in body size. The smaller size of C. boutoni would separate it from both of the above even when it feeds in the intertidal zone.

Thus, on rocky islands, a combination of (1) spatial (vertical and horizontal) separation in habitat selected, and (2) body-size differences achieve effective ecological segregation of the diurnal lizards whose general habitat is known. Only four diurnal lizards, collected on only one island each, could not be included in this analysis. One of these, Sphenomorphus jobiensis is stated by Hediger (1933-34) to be an occupant of the inner forest in contrast to the more open situation preferred by Carlia fusca. He found these did not overlap.

The interactions of the various species where they occurred together on sand cays was the same as on rocky islands except that C. boutoni usually substituted for Emoia mivarti.

FAUNAL SIMILARITY

Heatwole and MacKenzie (1967) have shown that for various Caribbean islands, faunal similarity as measured by Preston's (1962) index, 1-z, depends on inter-island distance and time of isolation. In the present study, the relation of inter-island distance to faunal similarity differed, depending on whether the two members of the island pair were of the same or different substrate types. When both members were of the same type, faunal similarity did not change greatly over a wide range of inter-island distances (at least between 15 and 350 km for rocky islands and between 6 and 95 km for sand cays) (Table 2, Fig. 8). This can be called the range of neutral distances. Somewhere below these

observed ranges, distance becomes important and at very small values, faunal similarity is great ($1-z = 1.0$; the faunas are identical). Similarly, when the upper range is exceeded, distance again becomes important and faunal similarity drops with increasing distance, reaching 0 (no species shared by the members of the island-pair). For the sand cays of this study, this occurred at values between 95 and 300 kms (Fig. 8). The upper range for rocky islands is not known as the most widely separated islands had high faunal similarity indices. It is evident, however, that the rocky islands maintain approximately the same faunal similarity over greater separation distances than do sand cays. It is suggested that this may reflect the fact that sand cays are usually small and therefore subject to high extinction rates, but on the other hand are also easily recolonized by strand species. Thus a high species-turnover would be expected with faunal composition constantly shifting. Most exchange would occur among near islands and at any one time their faunas should be more similar than for island-pairs with greater separation. Rocky islands usually being larger and more stable, would be expected to have lower extinction rates and lower species-turnover. Once a species became established on such an island it would be apt to remain for long periods. Given enough time, each species would occupy most of the nearby islands with suitable habitat, and faunal similarity would show a smaller distance-effect.

If this theory is correct, it would explain not only why rocky islands maintain faunal similarity over greater separations, but also why similarity indices are generally higher for rocky islands in the range of natural distances. The mean faunal index in the range of neutral distances was significantly higher for rocky islands than for sandy ones (Dice-Leraas graphic test, 5% rejection level, fig. 8). However, the values for sand cays fall into two groups, one of which has a mean almost identical to rocky islands, the other considerably lower (Fig. 8). If this grouping is not coincidental or due to chance factors arising from the small species-numbers characteristic of sand cays, its cause remains a mystery. There were no obvious differences between these two groups of island-pairs which would explain why one should behave like rocky islands and the other not.

The pattern is less distinct for island-pairs in which the members are of different substrate types (Fig. 8). Though very near islands have identical faunas, there is no clear range of neutral distances and $1-z$ values of zero occur throughout a wide range of island separations; there is wide overlap of low and high faunal similarity indices.

The similarity index for most island-pairs was well below the value of 0.73 (dashed line in fig. 8), which Preston (1962) has indicated as the level at which the two faunas are at complete equilibrium. Below this value some degree of genuine isolation exists. It is clear from fig. 8 that all of the New Guinea island-pairs separated by more than 5 km show some degree of isolation of their reptilian faunas. Those closer together show no isolation.

SPECIES-NUMBERS

The number of species on an island has been postulated to result from an equilibrium between immigration and extinction rates (MacArthur and Wilson 1963, 1967). These in turn undoubtedly depend on a variety of factors, and insular species-numbers have been correlated with island area, elevation, and ecological diversity, and with distance from mainland or other islands (e.g., Levins and Heatwole 1963, Hamilton *et al.* 1963, Hamilton and Rubinoff 1963, 1964, 1967, Harrison 1965, Thornton 1967; see also review by MacArthur and Wilson 1967). Latitude would almost certainly be an important factor for reptiles.

The present study involves islands from a small range in latitude and all with the same probable faunal sources. An opportunity is thus provided for assessing the relative roles of various other determinants of species-numbers of reptiles. Vegetation diversity and climatic diversity vary greatly among the islands treated. Unfortunately, quantitative data on neither topic are sufficient for use in relating to species-number. However, the former is often correlated with island size and both with elevation. Consequently log area in hectares (A), log maximum height in meters (E) of the islands, the reciprocal of the distance (in kms) to the New Guinea mainland (M) and the reciprocal of the distance to the nearest island larger than itself (L), were chosen as parameters to be used in multiple regression analyses of log species-number carried out by a computer.

The model used was thus:

$$\log S = \log a + b \log A + c \log E + d (1/M) + e (1/L) + \text{error}$$

where all lower case letters represent constants. The significance of the regression coefficients was tested using a t-test. Rocky islands and sand cays were treated separately and gave quite different results. For sand cays none of the regression coefficients (except a) was significant ($P > 0.50$ in all cases). Thus none of these parameters was important in influencing species-numbers. The lack of an effect of area can also be appreciated from figure 9.

For rocky islands, neither distance measure had a significant effect on log species-number (P ranged from 0.08 to 0.80). However, both area and elevation when treated separately, had a significant effect. The slope of the regression coefficient of each was significant ($P < 0.001$ in both cases). However, in a multiple regression, reduction in sum of squares due to fitting elevation after area was not significant ($P = 0.71$). Thus, the apparent effect of elevation may be attributable to the correlation of elevation and area, elevation not exerting a significant independent effect.

The regression was repeated for both types of island using species-numbers rather than log species-numbers. The results were similar to the above. For rocky islands, area accounted for 68% of the variation in species-number whereas it accounted for 74% of the variation in log species-number. Thus the latter

measure is preferable. Transformation to natural logarithms gave similar results as base ten logs and also accounted for 74% of the variation. Thus there is little to choose between the two types of logs in the present study. Only base ten logs are referred to below.

As only area had a significant effect on species-numbers, the expression relating these two variables is adequate for descriptive or predictive purposes. The calculated line (Fig. 9) for rocky islands, including the mainland of New Guinea is: $S = 0.51 A^{0.335}$. New Guinea was, however, excluded from the multiple regression analysis as one of its distance measures was zero and consequently not subject to treatment.

MacArthur and Wilson (1967) reviewed the exponents obtained by various authors for the species-area formula. The expected value is 0.27 and most observed values were between 0.20 and 0.35. Those higher than 0.27 were attributed to the breaking up of biotas on large islands into semi-isolated communities due to increase in topographic barriers and environmental variation. This seems to be the case in the present study as a value (0.335) near the upper limit of previously observed ones was obtained. Preston (1962) gives an exponent of 0.318 for West Indian lizards and snakes.

On the basis of the above analyses, it can be concluded that in eastern New Guinea, a sand cay large enough to have any terrestrial reptilian species at all, is large enough to have the maximum number for cays; areal effects if present are small enough to be ignored. In contrast, species-number increases markedly with island area on rocky islands. Species-number of neither group seems to be independently influenced by elevation or distance, at least within the range of values occurring in the present study.

The lack of an effect of area on species-numbers of sand cays requires further discussion. It is possible that very small islands may not be subject to the same areal effect as large ones and thus, in the present study, if rocky islands as small as the smaller sand cays could have been examined, their values might have resembled those of sand cays, i.e., the observed differences in areal effect may not have been due to substrate differences at all, but to discrepancies in average size of sand cays and rocky islands.

The "small island effect" is not restricted to the present study. On Kapingamarangi Atoll, species-number of higher plants did not increase with area on islands in the lower end of the size range (below about 3.5 acres), whereas it did on larger islands (Niering 1963). Carlquist (1967), and Whitehead and Jones (1969) suggest that the small-island effect is due to the fact that on small islands, establishment is restricted to the flotsam-transported segment of immigrants (hardy, salt-tolerant forms), and all such species can colonize a wide range of small island sizes. A similar argument could be advanced for the

present data; "strand" reptiles (the widespread Pacific element) adapted to high temperatures and salinities, would be able to survive well on small islands and would be tolerant of environmental conditions during flotsam transport. Hence their immigration rates would be high, and even small cays (with presumed high extinction rates) could maintain high species-numbers by frequent re-invasion. Most of such hardy, mobile species would be present on many islands, regardless of size or substrate, and hence there would be little or no areal effect on species-number (note that in the present study there were no common species restricted to sand cays). However, once a certain island size is reached (perhaps about the upper size limit for sand cays), habitats suitable for non-strand reptiles would become available and those arriving by means other than flotsam could become established.

Strand species would, of course, still be present in beach habitats. Thus, an inflected species-area curve could result from a linear base-line for strand species (line for sand cays and its dotted extrapolation in figure 9) upon which the linear species-area curve of non-strand species is superimposed.

An inflection is also suggested by species-area data on reptiles from Californian and Caribbean islands (Fig. 10); none of these islands were sand cays. However, analysis of more archipelagoes, particularly those with very small islands, is needed before the extent of inflections in species-area curves for reptiles can be elucidated.

A second feature of possible importance to the observed difference in species-area curves for rocky and sandy islands is that the relationship between ecologic diversity and area may differ between the two substrate types. For rocky islands, larger area often means greater diversity in vegetation and climate, with a corresponding influence on species-number. However, all sand cays within the size-range studied show little change in environmental diversity; increase in area results merely in more habitat of the same type rather than a greater number of habitats, and consequently in relatively few additional species.

MacArthur and Wilson (1967) postulate a different explanation. They feel that islands below a certain size are highly unstable and that all the biota (regardless of ecological and adaptation) would consequently be periodically extirpated independently of island size within a certain range of small values. An example might be the effect of hurricanes on small cays. Storm-induced extinction would be independent of island size until a sufficient size were reached that (1) parts of the island might lit outside of the main path of the storm or (2) that topographic diversity would be adequate to provide shelter permitting survival.

In summary, the differences in effect of area on reptile species-numbers between sand cays and rocky islands may reflect a difference in relationship of ecological diversity to area on the two types of island. On the other hand, it may not be due to substrate differences at all, but to differences in average size of islands of the two substrate types. The "small island effect" has been postulated by other investigators to result from (1) area-independent extinction on small, unstable islands or (2) from selective establishment of flotsam-transported, strand species on very small islands.^{2/} Assessment of the relative merits of these theories requires further study.

The overriding influence of area on species-numbers and the negligible effect of elevation and distance found in the present study is not applicable to all groups of organisms nor to all archipelagoes. For example, Hamilton *et al.* (1963) found no correlation between species-number of Galápagos plants with island area, whereas elevation, area of adjacent island, distance to nearest island, and distance to center of the archipelago had significant effects. Similarly, distance measures accounted for the majority of variation in species-numbers of finches on the Galápagos, with plant diversity and elevation being less important; island area was not a determinant (Hamilton and Rubinoff 1963, 1964). Lack (1969) has subsequently challenged this conclusion on the basis that isolation is ecological rather than imposed directly by distance. In any event, the Galápagos finches are probably exceptional because island area is the major predictor of species-numbers in most multiple regression analyses carried out on insular avifaunas (Hamilton and Rubinoff 1967). An understanding of the physical factors acting as determinants of species-numbers clearly demands study of the proximate factors in dispersal, establishment and extinction of various taxa on many archipelagoes, as well as additional multiple correlation analyses.

Species-numbers are almost certainly influenced by the ecological interactions within the fauna. For example, Wilson and Taylor (1967) found that species-numbers of native ants in the Pacific were higher than those of tramp species on islands of comparable sizes even though the available pool of the latter was much higher than the number present on any one island. They attributed this to the fact that among native ants there has been opportunity for niche partitioning to occur within the assemblage, whereas most tramp species are recently introduced and evolutionary adjustment among them has not taken place. In the present study only two species had a nearly mutually exclusive mosaic distribution. All others for which there were adequate data showed niche partitioning, and the equilibrium species-number for the eastern New Guinea archipelago has probably undergone evolutionary adjustment.

^{2/}Heatwole and Levins (in prep.) have added still another alternative, i.e., that species-numbers may be influenced by type of trophic structure which can be maintained on specific types of very small islands.

In comparison to two other archipelagoes (Caribbean and Californian islands) the equilibrium species-numbers of the larger islands are high in the New Guinea area, though those for the smaller islands are about the same (Fig. 10).

MINIMUM INSULAR AREA

The Minimum Insular Area (MIA) for a given taxon is here defined as the minimum island area necessary for supporting at least one species of that taxon.

The smallest cay on which reptiles were found was Tupit (area 1.62 hectares). Bare Sand Cay (0.002 hectares) was the only one examined on which they were absent. Thus the Minimum Insular Area for reptiles on sand cays in eastern New Guinea is estimated to lie between 0.002 and 1.62 hectares. The corresponding value for rocky islands is not known as none smaller than 30 hectares was examined. However, extrapolation of the species-area curve indicates that, on the average, species-number becomes less than 1.0 on islands smaller than 7.6 hectares (Fig. 9). If such an extrapolation is valid, this method provides an objective way of calculating the MIA for comparative purposes, i.e., the point where the species-area curve intersects the line $Y=1$, in this case 7.6 hectares. However, extrapolation of the species curve would not be valid when inflections in the curve are present (see above). MIA may have to be separately calculated for "strand" and "non-strand" species. MIA probably differs greatly among different taxa, and even for a given one (e.g. reptiles) there may be regional differences dependent upon physiological tolerances of species in the source area. Comparative studies are badly needed.

CONCLUSIONS AND SUMMARY

An analysis of the insular reptile fauna of eastern Papua-New Guinea has suggested that niche partitioning has occurred among most species but that members of one of the species-pairs may competitively exclude each other, one being favored on sand cays, the other on rocky islands. Faunal similarity is greatest between members of island-pairs which are very close together, lowest when inter-island distances are very great. However, over an intermediate range of distances, there is no effect of distance on faunal similarity. This range extends further upward for rocky island-pairs than for those whose members are sand cays. Where members of island-pairs are of different substrates, relation of distance to faunal similarity is much more variable.

Species-number on rocky islands is strongly area-dependent. On sand cays, species-number is area-independent. Two hypotheses are suggested to explain this. One is that there is less change in ecological diversity with island size on sand cays than there is on rocky islands. The second is that there is no real differences between the two types, the apparent differences arising from

the fact that the smaller islands were all sand cays and the larger ones rocky islands, with the species-area curve being non-linear, the inflection coincidentally occurring at about the upper size limit of sand cays.

Several hypotheses as to the nature of the "small island effect" are discussed. Species-numbers were not significantly influenced by island elevation, distance from New Guinea, or distance to nearest larger island.

A new ecological term, Minimum Insular Area (MIA) is defined.

More questions are raised than are answered by this study. It is hoped that the hypotheses suggested will have heuristic value and will stimulate further investigation in this field. Data are now being collected from a large number of islands by myself and my colleagues in order to elucidate some of the problems arising from the data presented here.

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APPENDIX 1

Terrestrial herpetofauna of some islands and cays of eastern Papua and New Guinea examined by the author, and of Kuia (museum specimens)

Trobriand Islands

Kiriwina

Cyrtodactylus pelagicus

Gehyra sp.

Varanus indicus

Carlia fusca

Emoia cyanogaster

Emoia mivarti

Lamprolepis smaragdina

Lipinia noctua

Lipinia virens

Sphenomorphus jobiensis

Engyrus carinatus

Dendrelaphis sp.

Stegonotus modestus

Typhlops braminus

Kuia

Cyrtodactylus pelagicus

Gecko vittatus

Gehyra oceanica

Lepidodactylus lugubris

Varanus indicus

Carlia fusca

Cryptoblepharis boutoni

Emoia caeruleocauda

Emoia mivarti

Eugongylus rufescens

Lipinia virens

Lusancays

Sim Sim

Emoia mivarti

Wagalasa

Emoia mivarti

Kawa

Varanus indicusEmoia mivartiEugongylus rufescens

Gabwina

Emoia mivarti

Deboyne Islands

Panaete

Gehyra oceanicaCarlia fuscaEmoia atrocostataEmoia cyanogasterEmoia mivartiLamprolepis smaragdinaTyphlops depressiceps

Panapompom

Emoia cyanogasterEmoia mivartiLipinia virens

Louisiade Archipelago

Wari

Carlia fuscaEmoia cyanogasterEmoia mivartiEugongylus rufescensLipinia virens

Marai

Cryptoblepharis boutoniEugongylus rufescens

Quessant

Cryptoblepharis boutoni

Eugongylus rufescens

Unnamed Cay (Long Reef)

Gehyra oceanica

Lepidodactylus sp.

Cryptoblepharis boutoni

Panawan

Gehyra sp.

Cryptoblepharis boutoni

Irai

Gehyra oceanica

Varanus indicus

Cryptoblepharis boutoni

Emoia cyanogaster

Lamprolepis smaragdina

Gabugabutau

Lepidodactylus lugubris

Cryptoblepharis boutoni

Emoia atrocostata

Auriroa

Cryptoblepharis boutoni

Sphenomorphus sp.

Tupit

Lepidodactylus lugubris

Cryptoblepharis boutoni

Bare Sand Cay

No herpetofauna

APPENDIX 2

Distribution of reptiles on the islands examined by the author,
and on Kuia (museum specimens)

Gekkonidae

Cyrtodactylus pelagicus

Kiriwina; Kuia

Gecko vittatus

Kuia

Gehyra oceanica

Kuia; Panaete; Unnamed Cay (Long Reef); Irai

Gehyra sp.

Kiriwina; Panawan

Lepidodactylus lugubris

Kuia; Gabugabutau; Tupit

Lepidodactylus sp.

Unnamed Cay (Long Reef)

Varanidae

Varanus indicus

Kiriwina; Kuia; Kawa; Irai

Scincidae

Carlia fusca

Kiriwina; Kuia; Panaete; Wari

Cryptoblepharis boutoni

Kuia; Marai; Quessant; Unnamed Cay (Long Reef);
Panawan; Irai; Gabugabutau; Auriora; Tupit

Emoia atrocostata

Panaete; Gabugabutau

Emoia caeruleocauda

Kuia

Emoia cyanogaster

Kiriwina; Panaete; Panapompom; Wari; Irai

Emoia mivartiKiriwina; Kuia; Sim Sim; Wagalasa; Kawa; Gabwina;
Panaete; Panapompom; WariEugongylus rufescens

Kuia; Kawa; Wari; Marai; Quessant

Lamprolepis smaragdina

Kiriwina; Panaete; Irai

Lipinia noctua

Kiriwina

Lipinia virens

Kiriwina; Kuia; Panapompom; Wari

Sphenomorphus jobiensis

Kiriwina

Sphenomorphus sp.

Auroiroa

Boidae

Engyrus carinatus

Kiriwina

Colubridae

Dendrelaphis sp.

Kiriwina

Stegonotus modestus

Kiriwina

Typhlopidae

Typhlops depressiceps

Panaete

Typhlops braminus

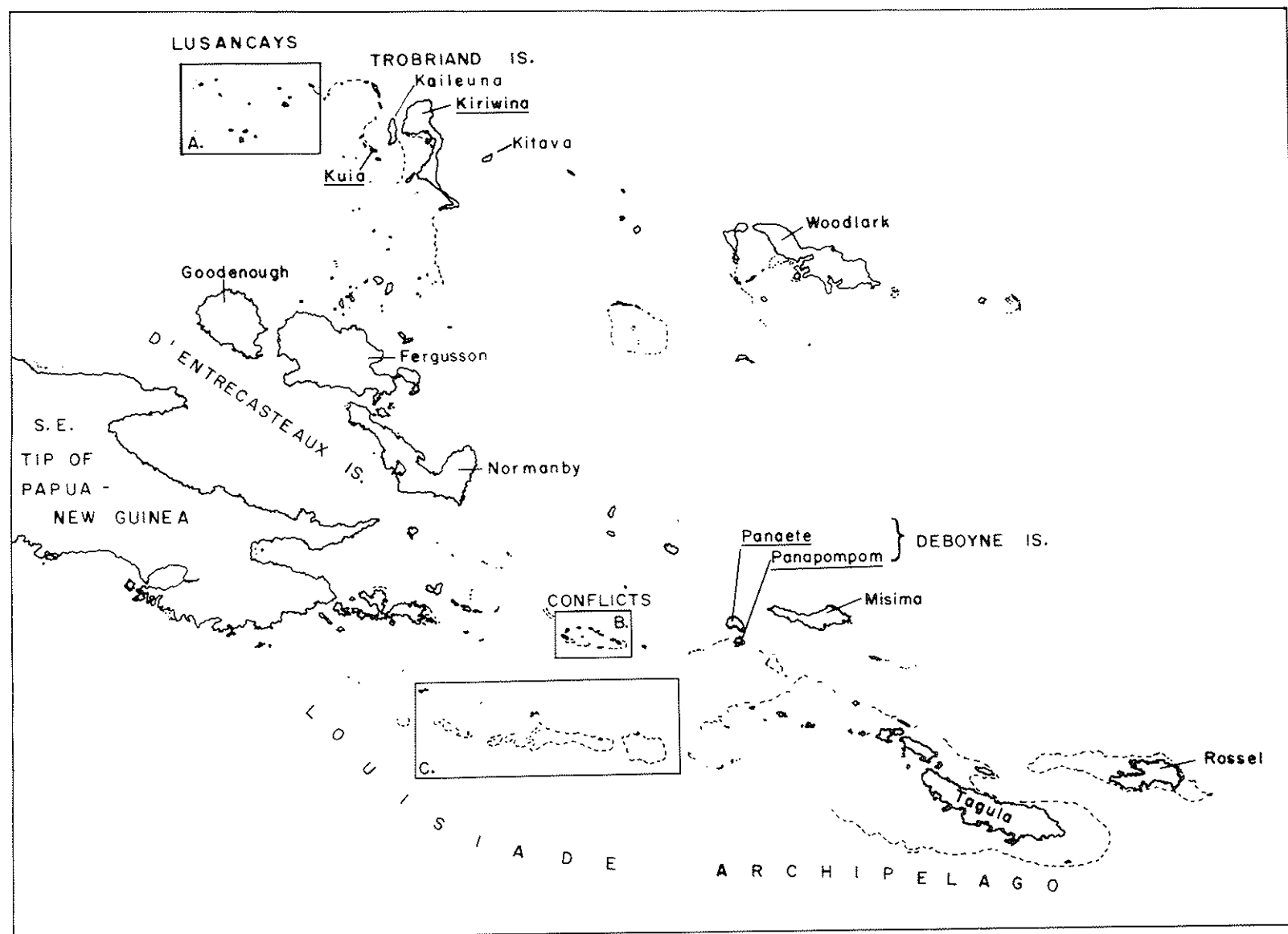
Kiriwina

TABLE 1. DISTRIBUTION OF TERRESTRIAL REPTILES ON SOME SMALL ISLANDS AND CAYS OF EASTERN PAPUA-NEW GUINEA. x = specimen examined, o = sight record by author

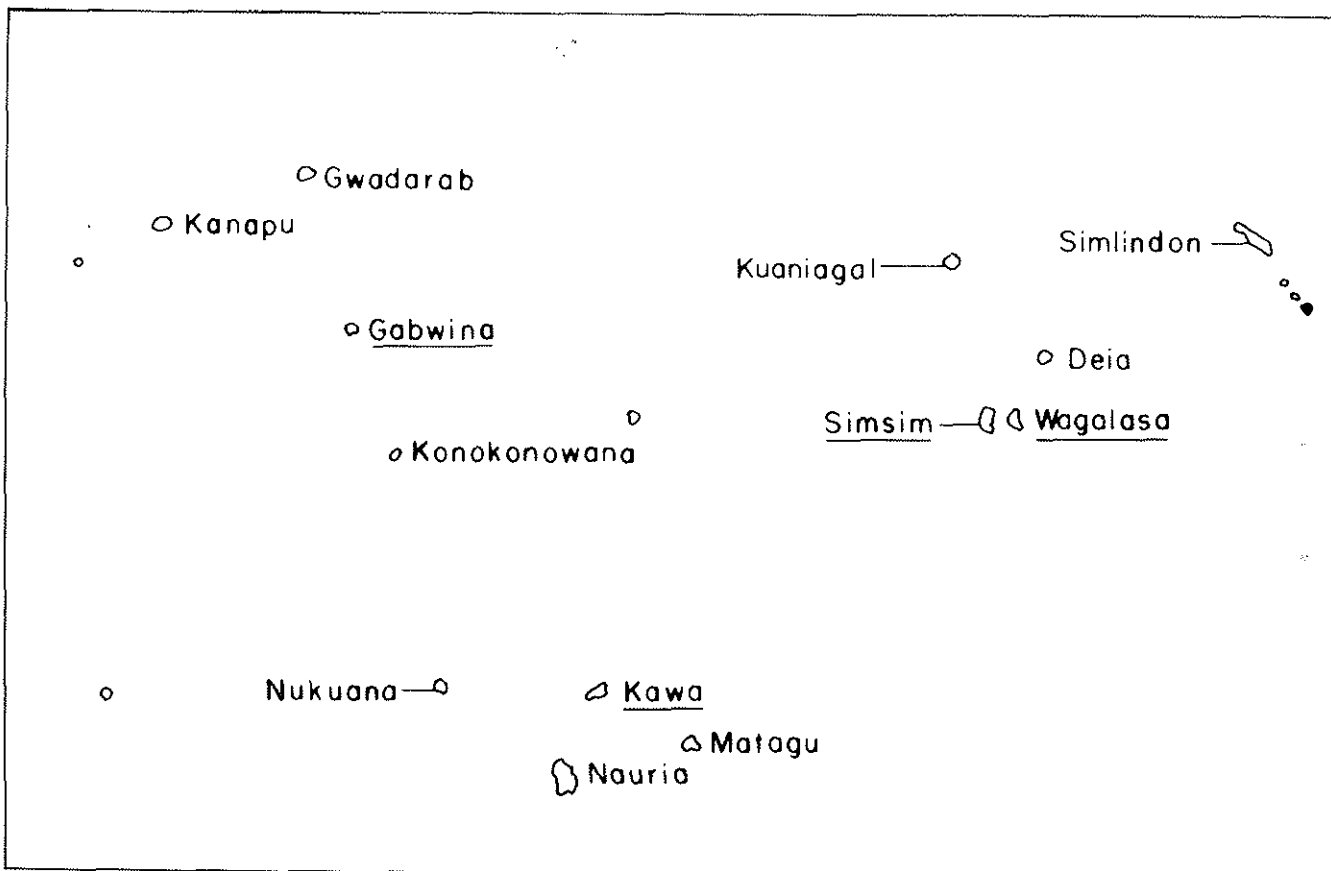
SPECIES	TROBRIANDS		LUSANCAYS			DEBOYNES		SOUTHWEST LOUISIADES				CONFLICTS					
	KIRIWINA	KUIA	SIM SIM	WAGALASA	KAWA	GABWINA	PANAETE	PANAPOMPOM	WARI	MARAI	QUESSANT	UNNAMED	PANAWAN	IRAI	GABUGABUTAU	AURIROA	TUPIIT
GEKKONIDAE																	
<i>Cyrtodactylus pelagicus</i>	x	x															
<i>Gecko vittatus</i>		x															
<i>Gehyra oceanica</i>		x					x				x			x			
<i>Gehyra sp.</i>	x												x				
<i>Lepidodactylus lugubris</i>		x													x		x
<i>Lepidodactylus sp.</i>											x						
VARANIDAE																	
<i>Varanus indicus</i>	x	x			x												o
SCINCIDAE																	
<i>Carlia fusca</i>	x	x					x		x								
<i>Cryptoblepharis boutoni</i>		x								x	x	o	x	x	x	x	x
<i>Emoia atrocostata</i>							x								x		
<i>Emoia caeruleocauda</i>		x															
<i>Emoia cyanogaster</i>	x						x	x	o								o
<i>Emoia mivarti</i>	x	x	x	o	x	x	x	x	x								
<i>Eugongylus rufescens</i>		x			x				x	x	x						
<i>Lamprolepis smaragdina</i>	x						x										o
<i>Lipinia noctua</i>	x																
<i>Lipinia virens</i>	x	x						x	x								
<i>Sphenomorphus jobiensis</i>	x																
<i>Sphenomorphus sp.</i>																	x

TABLE 2. INDICES OF FAUNAL SIMILARITY (1-z) AND INTER-ISLAND DISTANCES (km) OF ISLAND-PAIRS INEEASTERN PAPUA-NEW GUINEA. Only terrestrial species of reptiles are included; * indicates close faunal similarity though z-values cannot be calculated because all species on one island are included in the fauna of the other (see Preston 1962 b).

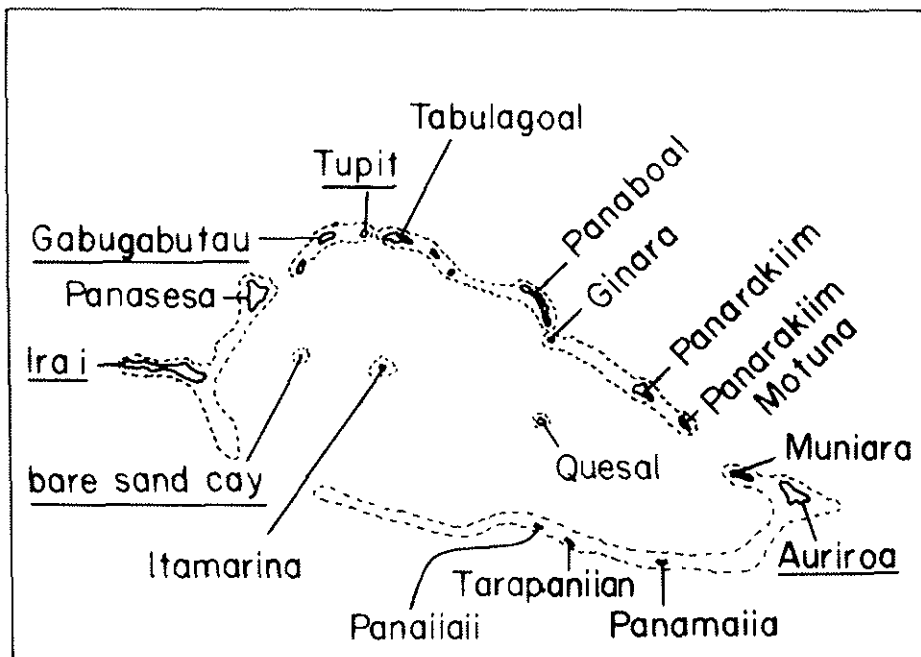
Distance 1-z	KIRIWINA	KUIA	SIM SIM	WAGALASA	KAWA	PANAETE	PANAPOMPOM	WARI	GABWINA	MARAI	QUESSANT	UNNAMED	PANAWAN	IRAI	GABUGABUTAU	AURIROA	TUPIT
KIRIWINA		15	57	56	74	248	260	240	87	266	263	263	284	222	220	233	220
KUIA	0.33		46	45	57	227	289	260	74	226	284	285	307	250	248	262	248
SIM SIM	*	*		1	20	322	335	289	30	306	313	320	350	285	285	300	285
WAGALASA	*	*	1.00		22	322	335	289	32	305	313	320	349	285	285	298	285
KAWA	0.33	0.35	*	*		325	335	284	20	298	310	317	349	285	285	284	285
PANAETE	0.45	0.47	*	*	0.39		4	146	347	144	136	96	65	59	65	50	64
PANAPOMPOM	*	0.35	*	*	0.59	0.40		146	357	143	132	100	61	71	78	54	76
WARI	0.46	0.52	*	*	0.45	0.43	*		302	17	28	54	102	65	72	93	74
GABWINA	*	*	1.00	1.00	*	*	*	*		318	327	339	366	305	305	322	305
MARAI	0	*	0	0	0.24	0	0	0.27	0		17	46	94	71	78	78	78
QUESSANT	0	*	0	0	0.24	0	0	0.27	0	1.00		35	84	64	69	84	69
UNNAMED	0	*	0	0	0	0.18	0	0	0	0.24	0.24		48	43	48	54	48
PANAWAN	0.21	0.22	0	0	0	0	0	0	0	0.43	0.43	0.24		57	61	45	61
IRAI	0.33	0.37	0	0	0.22	0.43	0.45	0.16	0	0.27	0.27	0.45	0.27		6	22	6
GABUGABUTAU	0	0.35	0	0	0	0.18	0	0	0	0.24	0.24	0.26	0.24	0.22		22	1
AURIROA	0	0.22	0	0	0	0	0	0	0	0.43	0.43	0.24	0.43	0.26	0.24		22
TUPIT	0	*	0	0	0	0	0	0	0	0.43	0.43	0.24	0.43	0.26	*	0.43	



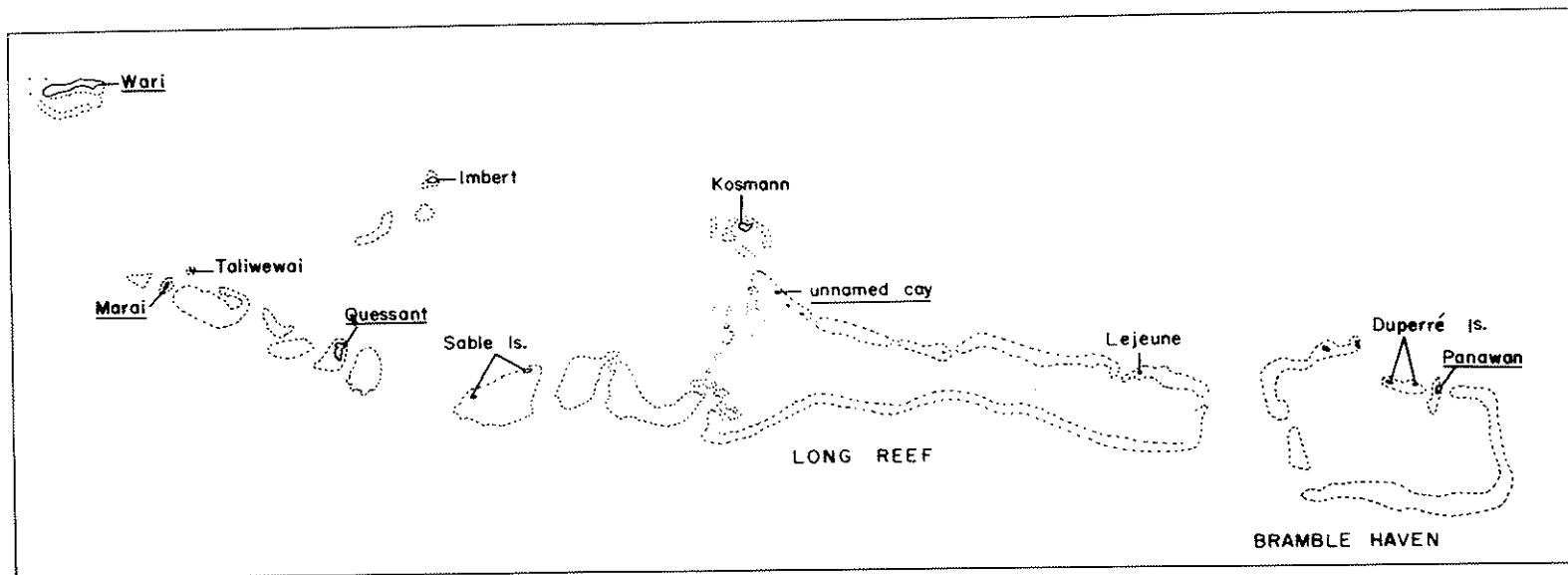
1 Islands of eastern Papua-New Guinea. Islands with names underlined are those treated in detail in the present study. Boxes A,B,C indicate location of Figs. 2,3,4.



2 The Lusancays. Islands with names underlined are treated in detail in the text. No collections made on other islands.



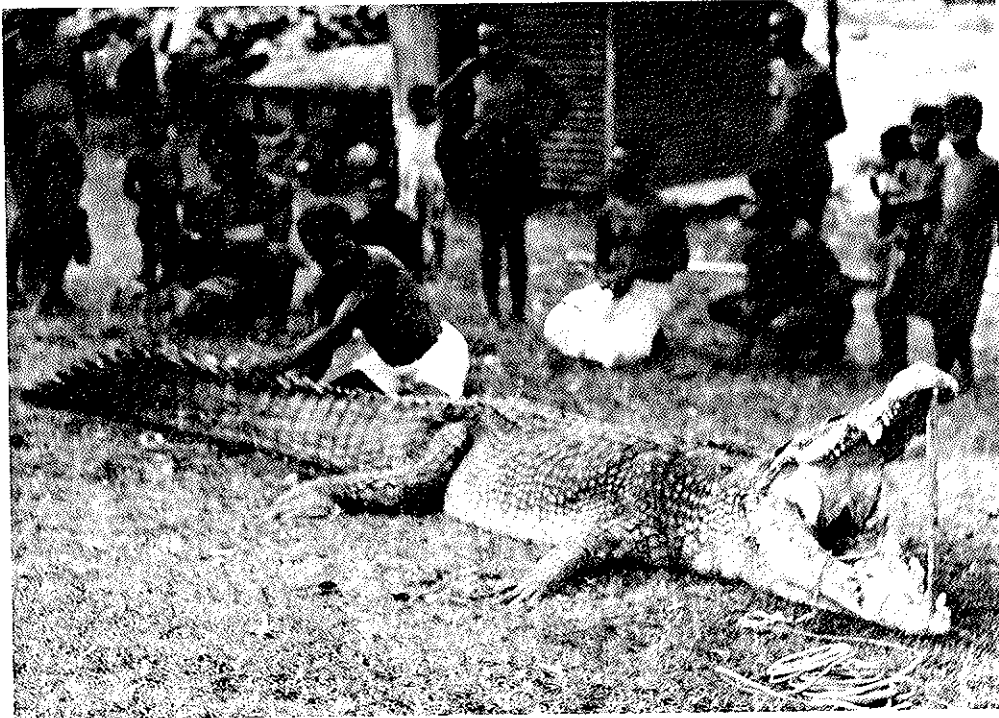
3 Conflict Atoll. Islands with names underlined are treated in the text; others not examined.



- 4 The southwestern Louisiade islands. Islands with names underlined are treated in the text; others not examined.



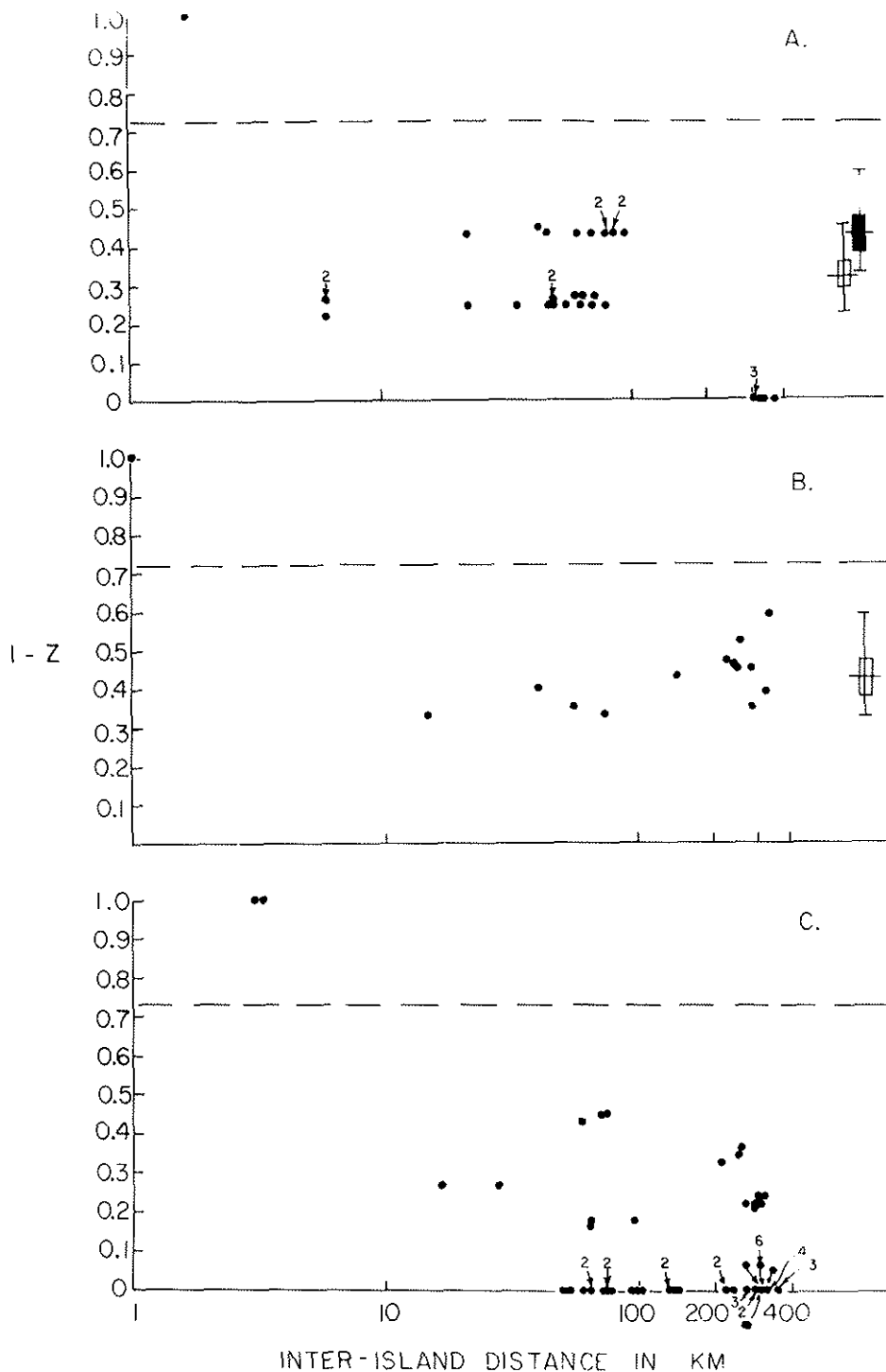
5 .Drum from Kawa Island showing use of *Varanus indicus* skin for the head (grass cord used to bind drum head to drum lost).



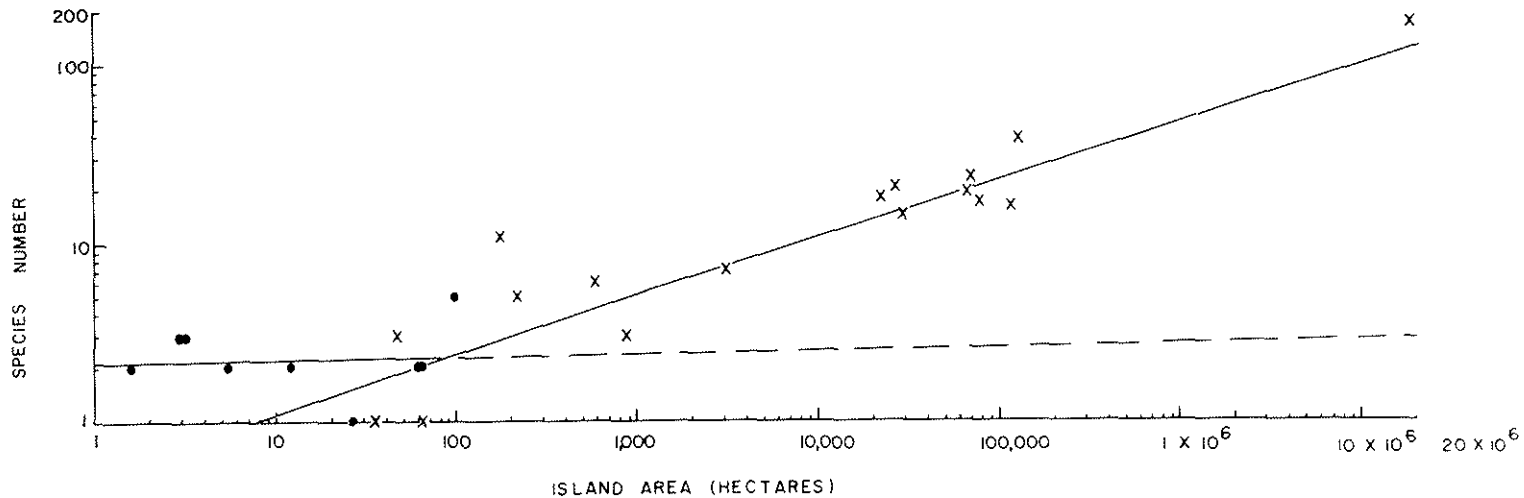
6 Natives of Kiriwina with a *Crocodylus porosus* which had eaten a 15-year-old girl.



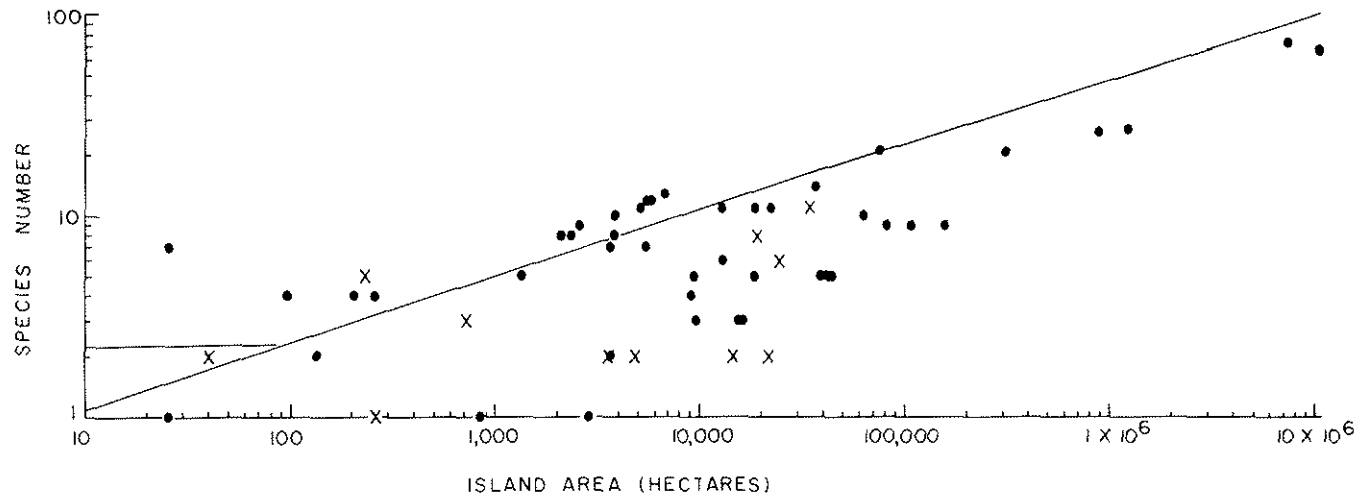
7 Head of same crocodile
(Photos by Rev. K.C. Murphy, M.C.S.).



8 Relation of Preston's (1962) index of faunal similarity ($1-z$) to inter-island distance for some small islands and cays of eastern Papua-New Guinea. A. Island-pairs in which both members were sand cays. B. Island-pairs in which both members were rocky islands. C. Island-pairs in which the members were of different substrate types. Symbol on the right summarizes values in the range of neutral distances (see text); vertical line represents the range, horizontal line the mean and the rectangle indicate 2 standard errors on either side of the mean. In part A, the black symbol represents values from part B shown for comparison. Dashed line is $1-z=0.73$, the value Preston (1962) gives as the limit below which genuine isolation is present.



9 Relationship between species-number and island area of the Papua-New Guinea islands. Dots represent data from sand cays, x's those from rocky or raised-coral islands. The dashed line is an extrapolation of the line for sand cays. Lines calculated by least squares method.



10 Relation of species-number of terrestrial reptiles and island area in 3 archipelagoes. Lines are those calculated from the Papua-New Guinea data on sand cays (horizontal line) and rocky islands (slanting line). Dots are values from Caribbean islands (data from Levins and Heatwole, 1963) and x's those from California islands (data from Savage, 1967, excluding those values resulting from combining data from several islands). Islands lacking reptiles are excluded.