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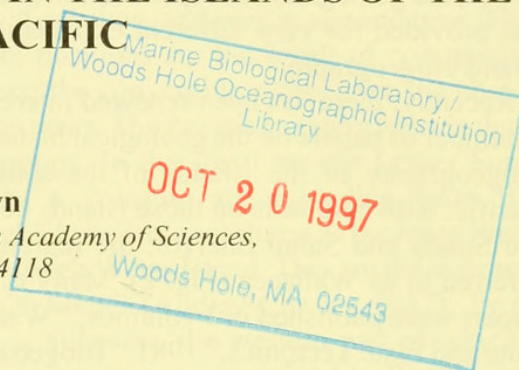
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BIOGEOGRAPHY OF AMPHIBIANS IN THE ISLANDS OF THE
SOUTHWEST PACIFIC

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Present patterns of distribution and endemism of frogs in the islands of the southwest Pacific are examined. These patterns are analyzed in terms of the generally accepted geological history and sea-level changes for the region.

The evidence indicates that the island anuran fauna includes three components. One is an Asian component. Representation of this component on the Sunda Shelf islands includes almost all the mainland genera and four on Borneo that are not known on the mainland. There is a great diversity and high endemism for species. The Philippine fauna includes less than half of the genera of the Sunda Shelf islands and a greatly reduced number of species. The islands of western Wallacea have about one-fourth of the Sundaland genera and about one-seventh as many species. Only two of the ranid genera (*Rana* and *Limnonectes*) of the Asiatic component occur in the islands east of western Wallacea; and there are only two or three species on any of these islands except for New Guinea. There the genus *Rana* has several endemic species.

The second component is one derived from the Australian anuran fauna. In New Guinea (the primary Sahul Shelf island), two of the three Australian genera of Hylidae (Pelodryadidae of some) occur, with a large number of species, most of them endemic. One of these (*Litoria*) dispersed to the Melanesian Arcs and the islands of eastern Wallacea, the second (*Nyctimystes*) only to the latter. Only 5 of 20 genera of the Myobatrachidae occur in New Guinea, and they have not dispersed beyond the Sahul Shelf.

The third component includes 16 genera in 2 endemic subfamilies of microhylids (centered in New Guinea) and 4 genera in an endemic subfamily of ranids. Three of these genera are centered in the Melanesian arcs, and one in Melanesia and the Philippines. Relationships of these subfamilies to other microhylid and ranid lineages are not clear at this time. Also one genus (*Batrachylodes*) in the subfamily Raninae is known only from the Solomons. It is not clearly related to any of the Asiatic ranid genera.

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The numerous islands of the southwestern and central regions of the Pacific Ocean, extending from the coast of southeast Asia and the northern coast of Australia to the Hawaiian, Line, and Tuamota islands in the Central Pacific (Fig. 1), provide isolated land areas of various ages. The

forms of life on these islands have been the basis for numerous biogeographic hypotheses.

From the time of Wallace's "Island Life" (1880) to Darlington's "Zoogeography: The Geographical Distribution of Animals" (1957), zoogeographers explained the presence of ani-

mals on islands in terms of the animals' use of known or imagined previous land bridges, their abilities to cross water barriers, or their possible transport by man. These explanations were based on the geological concept that the earth's crust was a surface covering of ocean and land areas occupying relatively fixed positions. Since the 1960s, the geological concept of continental drift has provided for very different explanations of island biogeography.

Recently, there has been renewed interest and a number of papers on the geological history and biogeography of the islands of the southwest Pacific, with emphasis on those islands between the Sunda and Sahul Shelves, the region often referred to as Wallacea (Fig. 2). Many of these papers were published in 3 volumes: "Wallace's Line and Plate Tectonics," 1981, "Biogeography of the Tropical Pacific," 1984, and "Biogeographical Evolution of the Malay Archipelago," 1987, Oxford Monogr. Biogeography, Clarendon Press, Oxford. As to organisms: angiosperms receive the most attention, with emphasis on palms in the plant kingdom; birds, mammals, and Lepidoptera receive most attention in the animal kingdom. Amphibians and other terrestrial, vertebrate fauna are dealt with in the paper by Cranbrook (1981). Shore-fish distribution is discussed in a separate paper (Springer 1982). Numerous other papers, limited to the geology of the region, have also been published in various geological journals or special publications during this same period. Other islands of the region including the Greater Sundas, Philippines, New Guinea and its satellites, Bismarcks, Solomons, and Fiji, are considered in many of these papers. Several papers have summarized the biogeography of the herpetofaunas on some major groups of islands (Allison 1996; Brown and Alcala 1970; Inger 1954, 1966). The present paper is limited to the amphibian fauna of these islands.

METHODS

In this study, distributional data for anuran species in the southwest Pacific islands is primarily based on island localities cited in Frost (1985), Duellman (1993), Allison (1996), Menzies (1982), Zweifel and Tyler (1982), Inger (pers. comm.), and Zweifel (pers. comm.). Determining accuracy of species' assignments in these sources, or by preceding authors, was not a part

of this study. These data are converted to distributional patterns of genera and species assigned to families or subfamilies native to southeast Asia and Australia, or subfamilies in Microhylidae or Ranidae that are centered in the islands.

These distributional patterns are evaluated in relation to: (1) the geological events that produced the islands and established their current spatial relationships, (2) past sea-level changes, (3) climatological history, (4) their dispersal abilities, routes, and opportunities, and (5) evolution and extinction events. Biogeographical hypotheses concerning these island anurans are reevaluated.

GEOLOGICAL HISTORY OF THE ISLANDS

The islands in the area under consideration can be assigned to one of five groups: (1) those on the shallow Sunda Shelf off the Asian coast, (2) those on the Sahul Shelf off northern Australia, (3) the clusters of islands between these two shelves, usually termed Wallacea (Fig. 2), (4) the Philippines, and (5) the Melanesian arcs: Admiralties, Bismarcks, Solomons, and Fiji.

The geological history of this region is complex, and many uncertainties still exist. But recent studies have changed interpretations of the origins and history of southeast Asia and the islands as well as their probable ages. Geological processes are measured in terms of megayears; some of the important sea-level changes and climatological events in terms of thousands or hundreds of thousands of years.

All of southeast continental Asia from the Himalayan-Tibet region and southern China, as well as the Greater Sunda Islands, is believed to be the result of accretion of terranes over millions of years. The origins of these terranes and the times of their collisions are fairly well established for some but poorly understood for others, especially the older ones.

At least five such terranes have been identified in the Himalayan-Tibet region to the north of India. The origin of the oldest (most northerly) is thought not to be Gondwanan (Nishiwaki and Uyeda 1987), but at least the more recent of these terranes (south China and part of Indochina-Malay-Sundaland) are rift-blocks from eastern Gondwana along the north rim of the Australian region (Murphy 1987; Nishiwaki and Uyeda

1987; Audley-Charles 1987, 1988). This rift period may have extended from the late Carboniferous to the mid-Jurassic (150–300 MaBP) and was followed by long periods of northward drifting across the changing Tethys Ocean. The earliest terranes may have accreted to southern Asia before the end of the Jurassic (Audley-Charles 1987). Data indicate that India rifted from Gondwana about 140 MaBP and collided with Asia about 50+ MaBP (Butler 1995; Hallam 1981).

Greater Sunda Islands. — The Greater Sunda Islands include Sumatra, Java, Borneo, Palawan (western Philippines), and several (isolated or clustered) small islands, all situated on the Sunda Shelf off the coast of southeast Asia (Fig. 2). At times, these have been united as a subaerial extension of the Indochina-Malay region, most recently about 20,000 years BP, a result of lower sea levels during the last ice age. The origin of Sundaland has been open to several interpretations. Recent geological research indicates that it, like the Malay region, is the result of bringing together fragments of eastern Gondwana, Pacific arcs, and Seamounts. These are the most recent terranes to be added to the southeast margin of Asia, beginning about 50 MaBP (Audley-Charles 1987). However, the main geological processes which resulted in the present shape of Sundaland were completed about 15 MaBP (Ollier 1985).

Palawan, at the north end of the Sunda Shelf, is a composite island. The southern part is associated with Borneo and its development. The northern part and the Calamian Group are from a segment of a continental terrane that rifted from China, probably in the Cretaceous, and collided with the western edge of the Philippine plate and south Palawan in the mid- to late Miocene (McCabe and Cole 1987).

Sahul Shelf islands. — These islands, with the exception of the northern half of New Guinea, are part of the Australian continent that rifted from Antarctica and drifted northward between 45 MaBP and 15 MaBP. At that time the collision with the Pacific, Asian, and minor border plates occurred. The northern part of New Guinea and small satellites along the north coast and Vogelkop Peninsula are the result of the accretion of Tethys Ocean marginal arcs onto the New Guinea portion of the Gondwanan Australia-New Guinea Plate about mid-Miocene. There is evidence that the central region of New Guinea,

along the central mountain range, became subaerial in early Miocene (Hamilton 1979; Audley-Charles 1981). These islands, like those of the Sunda Shelf, have been connected to Australia by land bridges during periods of lowered sea levels.

Wallacea. — The islands of Wallacea, between the shelves (Fig. 2), are partly Asian and partly Australian, and vary in age and type. Their present positions are the result of compression between the converging plates over the past 40 million years. The Asiatic (western) part includes two groups. In the south are the Lesser Sunda Islands, a volcanic arc extending from Bali through Flores and continuing as the Inner Banda Arc through Wetar Island. This arc dates from at least 20 MaBP (Audley-Charles 1987). In the north is Sulawesi, the western part of which is Asian in origin and was joined to Borneo until the Eocene (Audley-Charles 1981, 1987; McCabe and Cole 1987). The northern and eastern parts, derived from the margin of the advancing Australia-New Guinea Plate, probably began to emerge as an island area about 5–10 MaBP at about the same time as it joined with western Sulawesi (McCabe and Cole 1987).

The remaining islands of Wallacea on the south and east originated from the advancing front of the Australia-New Guinea Plate. Those of the Outer Banda Arc from Sumba through Timor, Tanimbar, Kaie, and Ceram and Buru in the southern Moluccas (Fig. 2), are not volcanic, but the result of recent, probably Pliocene (1.5–5 MaBP), upthrust along the margin of the Australian Plate (Milsom and Audley-Charles 1986; McCabe and Cole 1987; Nunn 1994). The Banggai-Sula island group, according to one interpretation, became subaerial by late Miocene, 3 MaBP (Audley-Charles 1981, 1987). The northern Moluccan Islands, centered about the large island of Halmahera, are volcanic. Some of the volcanoes on Halmahera are Miocene, but most of the small islands are young, Quaternary volcanoes (Audley-Charles 1987; McCabe and Cole 1987). Areas of Wallacean islands are not currently as great as during Pleistocene periods of lower sea levels. At such times, some of them may have been united but not joined to the exposed areas of the Sunda or Sahul shelves.

Philippine Islands. — The Philippine Archipelago is a region with a very complex geological history. The main islands of Luzon and Min-

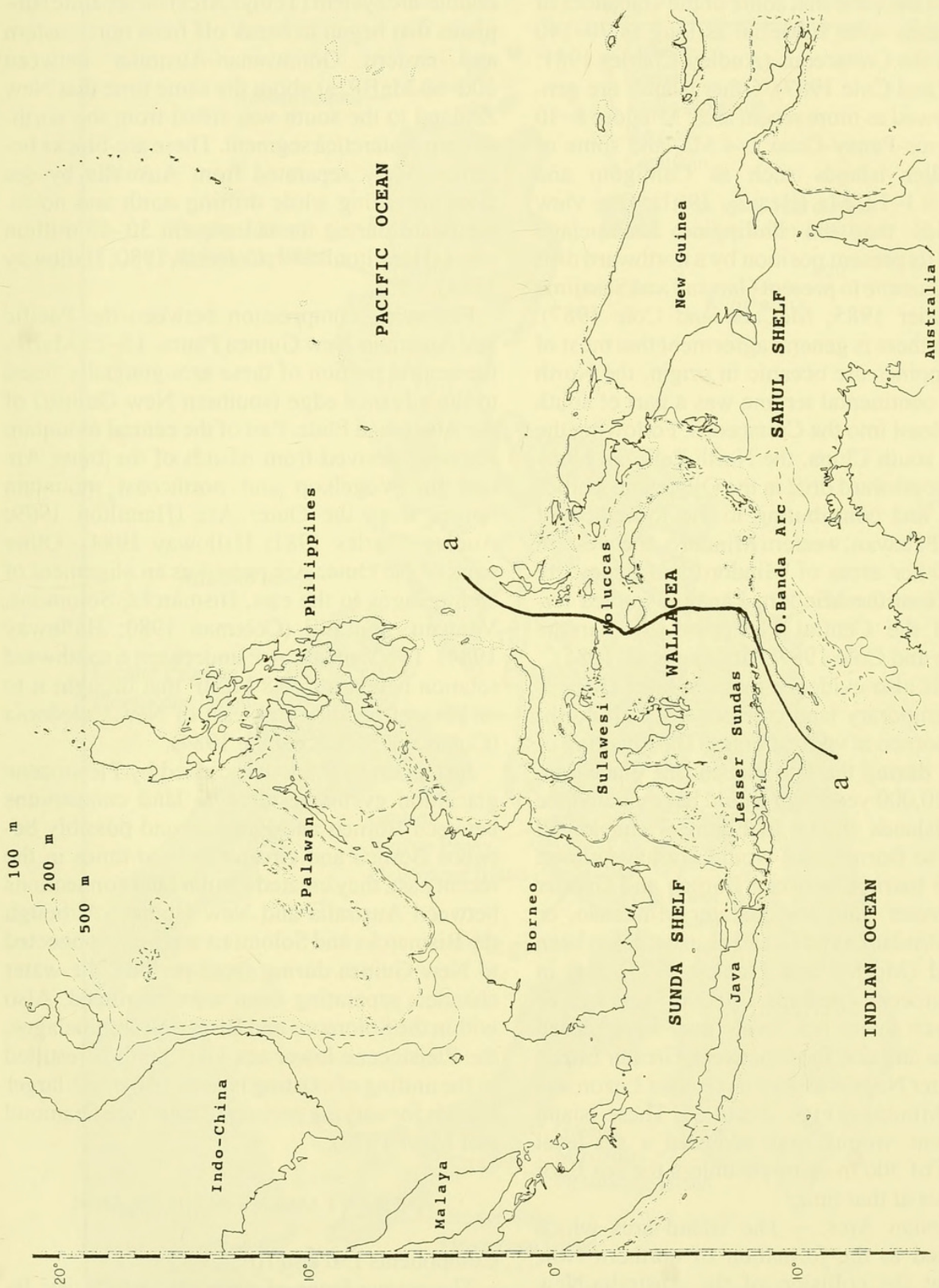


FIGURE 2. Islands of the southwest Pacific from the Asian coast to the eastern edge of New Guinea/Australia. The extent of the Sunda Shelf and Sahul Shelf land areas that would be exposed and joined with the adjacent continents and to which other islands would be increased is shown for lower sea levels: solid line—100 m, broken line—200 m, and dotted line—500 m. The line "a—a" marks the boundary between western Wallacea where Asian species dominate and eastern Wallacea where Papuan species dominate.

danao have large pre-Miocene areas (McCabe and Cole 1987; Heaney 1991). There is evidence to support the view that some of the volcanoes of these islands were subaerial as long as 70–140 MaBP in the Cretaceous (Audley-Charles 1981; McCabe and Cole 1987). Other islands are generally viewed as more recent arcs: Mindoro 8–10 Ma, Negros-Panay-Cebu 1–4 Ma, and some of the smaller islands such as Camiguin and Sibuyan 0.1–1.0 Ma (Heaney 1991). One view also holds that the Philippine Archipelago achieved its present position by a northward drift from the Eocene to present (Jarrard and Sasajima 1980; Ollier 1985; McCabe and Cole 1987). Although there is general agreement that most of the Philippines are oceanic in origin, the North Palawan continental terrane was a part of south China at least into the Cretaceous. Following the rift from south China, the North Palawan block began a southward drift in the Oligocene, colliding with and contributing to the formation of northern Palawan, western Mindoro, and western Panay. Other areas of Mindoro and Panay are derived from the Mindoro-Panay disrupted terrane and the Central Philippine Arc terrane (McCabe and Cole 1987; McCabe et al. 1985).

There is also evidence that sea-level changes caused temporary land connections with northeastern Borneo at various times. The lowering of sea level during the late Pleistocene glaciation, 18,000–20,000 years ago would have created the Greater Islands shown in Figure 3 and joined Palawan to Borneo, but would not have closed the water barriers between Borneo and Greater Sulu, Greater Sulu and Greater Mindanao, or Greater Mindanao and Greater Luzon. It has been suggested (Morley and Flenley 1987) that in mid-Pleistocene (perhaps 100,000 years ago or more) even lower sea levels may have closed these gaps and also those between Greater Luzon and Greater Negros as well as Greater Luzon and Greater Mindoro (Figs. 2 and 3). These island connections would have required a sea-level lowering of 300 m or more, unless the sea floor was higher at that time.

Melanesian Arcs. — The island arcs which contributed to the formation of northern New Guinea at the collision of the Australia-New Guinea and Pacific Plates, as well as the more eastern Admiralty, Bismarck, Solomon, Fiji Arcs, and the Palau Arc are also outside of Wallacea. Based on recent geological evidence, one

hypothesis concerning the history of the Melanesian Arcs is that they had their origin from a double-arc system (Tethys Arcs) on separate subplates that began to break off from northeastern and eastern Gondwanan-Australia between 100–60 MaBP, at about the same time that New Zealand to the south was rifted from the northeastern Antarctica segment. These arc-blocks became widely separated from Australia by sea floor spreading while drifting north and north-westward during the subsequent 30–40 million years (Hamilton 1979; Coleman 1980; Hallaway 1984).

Following compression between the Pacific and Australia-New Guinea Plates, 15–20 MaBP, the central portion of these arcs gradually fused to the advance edge (southern New Guinea) of the Australian Plate. Part of the central mountain region is derived from islands of the Inner Arc and the Vogelkop and northcoast mountain ranges from the Outer Arc (Hamilton 1979; Audley-Charles 1981; Hallaway 1984). Other parts of the Outer Arc persist as an alignment of archipelagos to the east, Bismarcks, Solomons, Vanuatu, and Fiji (Coleman 1980; Hallaway 1984). The Vanuatu Arc underwent a southward rotation beginning 6–8 MaBP that brought it to its present position just east of New Caledonia (Coleman 1980; Kroenke 1984).

Just as lower sea levels caused by Pleistocene glaciation events resulted in land connections between Borneo and Palawan and possibly between Borneo and Greater Sulu at times in the recent past, they created similar land connections between Australia and New Guinea. Although the Bismarcks and Solomons were not connected to New Guinea during these periods, the water channels separating them were narrowed. Also within the Solomons and Bismarck archipelagos, the Pleistocene lower sea-level periods resulted in the uniting of existing islands into much larger islands for varying periods of time (see Diamond and Mayr 1976).

ANURAN FAMILIES IN THE ISLANDS

Components I, II and III

The anuran fauna of the southwest Pacific Islands can be assigned to one of three components: (1) Component I, those resulting from colonization by present-day Asian stocks, (2) Component II, those resulting from colonization



FIGURE 3. Philippines: present islands (pale stippled areas) and late Pleistocene, about 20,000 years BP (dark stippled areas) based on presumed lower sea levels of about 120 m (after Brown and Alcala 1994).

by present-day Australian stocks, and (3) Component III, those genera in distinct subfamilies that are centered in the islands. Adler, Austin and Dudley (1995) divided the island skinks that they were studying into comparable categories for their analysis of distribution patterns.

The first two components are easy to identify based on the genus and family (sometimes subfamily) to which the species are assigned. Six of the eight families represented in the island fauna are Asian (Component I) and nearly all of the genera are mainland genera (Table 1, Appendix A). The other two families are Australian (Component II), and the genera are mainland genera (Table 1, Appendix A). Component III includes two distinct subfamilies (Asterophryinae and Genyophryinae) of the family Microhylidae, with most of the genera restricted to New Guinea, and a distinct subfamily (Platymantinae) of the family Ranidae with most of the genera restricted to the Solomons and Bismarcks but with one genus (*Platymantis*) also centered in the Philippines (Table 2, Appendix C).

History of the Data Base

Data on the species of anurans in the islands of the southwest Pacific have been acquired over the past century and a half. Only a few species had been recorded prior to publication of "Island Life" (Wallace 1880), most notably the several species described from New Guinea (Peters and Doria 1878) and several from the Philippines (Boulenger 1882).

During the last couple of decades of the 19th century and the first couple of the 20th, collecting in the Solomons, New Guinea, and the Philippines greatly increased. Of particular interest was the discovery of the genera that we now classify as the platymantine ranids in the Solomons (Boulenger 1886). One of the genera (*Platymantis*) was also known from the Philippines. Two monographs (Kampen van 1923 and Taylor 1920) summarized the data on the frogs of the Indo-Australian Archipelago and the Philippines respectively.

A renewed interest in the herpetofauna of these islands began during World War II, and continues to intensify even today. The resulting literature includes numerous short papers describing species. Major publications during this period that summarize data on systematics and distribution of anurans worldwide include: Frost 1985;

Ford and Cantella 1993; and Duellman 1993. Several other major papers are limited to the southwest Pacific Islands (Brown 1953; Inger 1954, 1966; Brown and Tyler 1968; Zweifel and Tyler 1982; Allison 1996).

RESULTS

Because this paper is concerned with the biogeography of the anurans of the southwest Pacific Islands, but not those of mainland Asia and Australia, only the number of genera and species in Australia and southeast Asia are indicated in the tables. For the island areas, not only the total number but the number that are endemic is also given. The number of genera and species of the Asian and Australian anurans (Components I and II) and their distribution patterns are summarized in Table 1 and are listed by name in Appendix B.

Component I. — For the families Bufonidae, Megophryidae, and Rhacophoridae and the Asian lineages of the Microhylidae and Ranidae, 27 of 34 (82%) of the genera occur in the Greater Sundas (Appendix B). This, along with 67 of southeast Asian species on the larger Sunda Islands, suggests good dispersal opportunities in the relatively recent past.

This is consistent with the evidence that the Sunda Shelf islands have been connected to each other and to mainland southeast Asia at various times in the Pleistocene as a result of lower sea levels, most recently about 18,000–20,000 years ago. The presence of one endemic genus for both the Megophryidae and the Ranidae in Borneo and another *Staurois* in both Borneo and the Philippines may be the result of an extinction of those generic lineages on the mainland, their evolution in situ, or a sampling weakness for some areas of southeast Asia. I treat *Barbourula* in the Bombinatoridae (Ford and Cantella 1993) known from one species in Borneo and one in Palawan, as a relict genus of that Asian family represented by the genus *Bombina* in China but not in southeast Asia. The Eurasian lineage of the family Hylidae, with one species of the genus *Hyla* recorded from Indochina and Thailand, is not known from the Pacific Islands.

Fifteen (48%) of the Bornean genera, exclusive of the relict *Barbourula*, are known from the Philippines. Eighteen species of these genera are shared with Borneo and 30 species are endemic. Six of the seven families in southeastern Asia and

TABLE 1. Distribution patterns for Components I and II (families and subfamilies of Asiatic and Australian anurans) in Southeast Asia (Thailand, Cambodia, Laos, Vietnam, and Malaysia), southwestern Pacific Islands, and Australia. The number of genera (G) and species (S) is followed by the number (in parentheses) that are non-mainland. (Bombinatoridae and Asian Hyliidae are not included.)

	Asian families					Australian families			Totals
	Megophryidae	Bufonidae	Microhylidae	Ranidae	Rhacophoridae	Hylidae	Myobatrachidae		
Southeast Asia	G 4 S 21	G 6 S 20	G 8 S 20	G 10 S 49	G 6 S 31			G 34 S 141	
Sunda Shelf Is.	G 4 (1) S 18 (13)	G 6 S 36 (24)	G 8 S 28 (15)	G 8 (1) S 48 (26)	G 5 S 43 (28)			G 32 (2) S 173 (106)	
Philippines	G 2 S 2 (2)	G 3 S 5 (3)	G 3 S 7 (4)	G 3 S 19 (11)	G 4 S 15 (10)			G 15 S 48 (30)	
Western Wallacea									
Sulawesi		G 1 S 1 (1)	G 1 S 2	G 4 S 13 (6)	G 2 S 4 (3)			G 8 S 20 (10)	
Lesser Sundas		G 1 S 1	G 1 S 2	G 4 S 8 (2)	G 1 S 1			G 7 S 12 (2)	
Eastern Wallacea									
Outer Banda Arc				G 2 S 5 (1)	G 1 S 1	G 1 S 5 (2)		G 4 S 11 (3)	
N. Moluccas				G 2 S 2 (1)		G 2 S 2 (1)		G 4 S 4 (2)	
Sahul Shelf									
New Guinea and satellite islands				G 2 S 10 (8)		G 2 S 80 (71)	G 5 S 7 (4)	G 9 S 97 (83)	
Melanesian Arcs									
Bismarcks				G 1 S 2		G 1 S 2		G 2 S 4	
Solomons				G 1 S 1				G 1 S 1	
Australia				G 1 S 1		G 3 S 69	G 20 (15) S 106	G 24 (15) S 176	

southern China are represented. This data is consistent with the concept that very narrow water channels or direct land connections may have existed between northwestern Borneo and Palawan and northeastern Borneo and Mindanao as recently as the lower sea-level event (18,000–20,000 years ago), and during earlier periods when sea levels were even lower (Fig. 3), mid-Pleistocene (100,000–500,000 years ago) and at other times back to the late Tertiary (Morley and Flenley 1987). The effect of sea-level changes on the distribution patterns of rhacophorid frogs within the Philippine Archipelago is discussed by Brown and Alcala (1994). There is no direct evidence as to how the composition of the current faunas have been affected by extinction or dispersal from the Philippines to Borneo.

Western Wallacea. — The sharp reduction in the number of Asiatic genera and species in Sulawesi and the Lesser Sundas (Table 1, Appendix B) indicates much more limited dispersal opportunities between eastern Sundaland and the islands of western Wallacea than existed between Sundaland and the mainland or the Philippines and Borneo. Eight (30%) of the Asia-Sundaland genera occur in Sulawesi and seven (26%) in the lesser Sundas. But at the species level, the number recorded from Sulawesi is almost twice that of the Lesser Sundas and endemism is five times greater. This is consistent with the lack of evidence of land connections between Borneo and Sulawesi or between Java and the Lesser Sundas at low sea-level times during the Pleistocene. The narrow, but deep Makassar Strait separates Sulawesi from Borneo and the Lesser Sundas from Java. Also, Sulawesi is geologically much more complex than the Lesser Sundas, with western Sulawesi older than the eastern part or the Lesser Sundas (Audley-Charles 1987; McCabe and Cole 1987).

Only three (10%) of the genera of the Greater Sundas (Table 1, Appendix B) are recorded from eastern Wallacea. Of the five species of ranids, one species *Limnonectes verruculosa* is treated as endemic, and *L. modesta* is otherwise known only from Sulawesi. These should be validated. Two species are conspecific or closely related to a group of species of *Rana* that evolved in New Guinea.

Only two (6%) Sundaic genera have successfully colonized the Sahul Shelf island of New Guinea. *Limnonectes* has only one species, the

widespread *L. grunniens*. *Rana* has a group of nine species, seven closely related and restricted to New Guinea, and two less clearly related. The seven species are very similar morphologically and cytologically (Menzies 1987). None of these species are conspecific with species in the Greater Sundas or western Wallacea.

Only one genus (3%) of the Sundaland genera is known from the Melanesian Arcs, with two species (one endemic) in the Bismarcks and one endemic species in the Solomons. These are the result of secondary colonization from the New Guinea radiation. One of the widespread species in New Guinea, *Rana daemeli*, is also known from a population on Cape York, Australia.

Component II. — For the two families (Hylidae and Myobatrachidae) of Australia, representation in the Sahul Shelf islands of New Guinea and its satellites differs in several respects from that of the representation of the southeast Asian fauna in the Greater Sunda Islands. Of the 23 genera in Australia, only seven (30%) are presently known from New Guinea (Table 1, Appendix A). However, the two families are very different. Two (67%) of the three genera of the Hylidae are in New Guinea, whereas only five (25%) of the 20 genera of the Myobatrachidae are in New Guinea.

At the species level they also differ greatly. For the Myobatrachidae there are only 7 species in the 5 genera, and none are endemic. For the Hylidae there are 80 species, 71 (89%) endemic. The number of species is actually greater than the 69 recorded from Australia (Table 1). For one of the genera, *Nyctimystes*, there is only one species known from Australia but 22 in New Guinea. These differences in colonization and radiation success of the two families suggest an earlier colonization for Hylidae than for Myobatrachidae.

Because land bridges between Australia and New Guinea would have been created by the same lower sea-level events as were the Sundaland bridges, the dispersal opportunities for anurans during the Pleistocene were probably similar between Australia and New Guinea to those proposed between southeast Asia and the Sunda Shelf islands. Two factors are most important: the large land mass of Australia compared to that of southeast Asia adjacent to the Sunda Shelf and variation in climate for different regions of Australia. A comparison limiting the

TABLE 2. Distribution patterns for anurans of Component III (subfamilies Platymantinae in Ranidae and Asteroophryinae and Genyophryinae in Microhylidae) in the southwestern Pacific Islands and Australia. The number of genera (G) and species (S) is followed by the number (in parentheses) that are endemic.

	Microhylidae	Ranidae
Philippines	G 1 S 2 (2)	G 1 S 15 (15)
Western Wallacea		
Sulawesi	G 1 S 3 (3)	
Lesser Sundas	G 1 S 2 (2)	
Eastern Wallacea		
Outer Banda Arc	G 1 S 1	
Northern Moluccas	G 3 S 5 (5)	
Sahul Shelf		
New Guinea and satellite islands	G 16 (13) S 101 (99)	G 1 S 4 (3)
Melanesian Arcs	G 2 S 2 (1)	G 4 S 23 (23)
Fiji Islands		G 1 S 2 (2)
Palau Islands		G 1 S 1 (1)
Australia	G 2 S 15 (14)	

source fauna of Australia to that of the northern subtropical and tropical regions might well reveal colonization success similar to that found between southeast Asia and the Greater Sunda Islands. The radiation of the hylid genera in New Guinea is independent of dispersal opportunities. It is doubtless related to the availability, at the time, of unoccupied anuran niches in the diverse communities of the large, mountainous, tropical island of New Guinea.

Both genera of Hylidae (*Litoria* and *Nyctomystes*) have colonized islands of eastern Wallacea, but Myobatrachidae is limited to New Guinea. *Litoria* has two species (one endemic) in the outer Banda Arc and four (two endemic) in the northern Moluccas along with an endemic species of *Nyctomystes* (Table 1, Appendix B). *Litoria* also occurs in the Bismarcks and the Solomons with two non-endemic species (Table 1, Appendix B).

Component III. — For the subfamilies Asteroophryinae and Genyophryinae (Microhylidae), centered in New Guinea and its satellite islands, all 16 recognized genera occur there, with 13 (81%) endemic. There are 101 species, 99 (98%) endemic. One to three genera (6 to 19%), and from two to five species in each genus are known from several islands of Wallacea as well as the Philippines and Melanesian Arcs. Two genera with 15 species are recorded from northern Australia (Table 2, Appendix C).

For the subfamily Platymantinae (Ranidae), the four recognized genera are in the Solomons, two (50%) are known from the Bismarcks, and one (25%) is known from New Guinea, Fiji, Palau, and the Philippines. The number of species of *Platymantis* is 23 in the Melanesian Arcs (all endemic), one endemic in the Palaus, two endemic in Fiji, and 15 endemic in the Philippines (Table 2, Appendix C). In addition, there is

one genus (*Batrachylodes*) in the subfamily Raninae (Ranidae) with eight endemic species in the Solomons. Its relationship to other ranine genera is unknown.

In summary, the Asiatic families (Component I) have all been highly successful in colonizing the Greater Sunda Islands, moderately so for the Philippines, but in western Wallacea only a few genera and species have succeeded. These differences correlate well with the geological histories of the three areas. The successful colonization of New Guinea and a few islands in eastern Wallacea may be better explained as probably assisted by man at one or more points in time since his migrations began, perhaps as early as 50,000 years ago as well as recently. There is no evidence that these two genera are more successful in dispersal across marine barriers by means other than human assistance.

The two Australian families (Component II) are very uneven in their colonization of the Sahul Shelf island of New Guinea. The Hylidae have been highly successful and have undergone an extensive radiation in the diverse habitats provided by this large, mountainous island. The Myobatrachidae are represented by only a few genera and species.

The boundary between the predominantly Asian fauna and predominantly Australian fauna (Components I and II), as originally proposed by Wallace (1863) for amphibians, was along the western edge of Wallacea (the Makassar Strait) and extended north between Borneo and the Philippines. He later modified this to include the Philippines on the Asian side. A distribution pattern of predominantly Australian or Asian components holds for all classes of land vertebrates, based on the large data bases available today (Cranbrook 1981). The line for the anuran fauna, based on the data currently available, is close to the midpoint of Wallacea, between the Outer Banda Arc and the Lesser Sundas in the south and between Sulawesi and northern Moluccas (Fig. 2).

The Problem of the Island-Centered Microhylids and Ranids (Component III)

Although some genera of the microhylids have been recognized as unique to New Guinea for a century (Méhely 1898) and some of the ranid genera unique to the Solomons (Boulenger 1886), both families were known to be in Asia,

which was thought to be the immediate source area. The geological concept of stable land and ocean areas also supported this view until the late 1960–early 1970 period (e.g. Boulenger 1920; Noble 1931; Darlington 1957). However, the systematic treatment of these (Component III) subfamilies has differed since the time of their discovery. I, therefore, summarize separately the treatments accorded them.

The New Guinea subfamilies (Asterophryinae and Genyophryinae) of microhylids have been regarded as restricted to the southwest Pacific Islands and secondarily, Australia by nearly all systematists and biogeographers (e.g. Kampen van 1923; Parker 1934; Tyler 1979; Zweifel and Tyler 1982; Allison 1996). Savage (1973) differed in including the Asian genus *Calluella* in the Papuan subfamily Asterophryinae.

The ranid subfamily Platymantinae (Cornuferinae of Noble) is diagnosed by early authors as including various southeast Asian genera (Boulenger 1920; Noble 1931; Savage 1973). To the best of my knowledge the first diagnosis, limiting the genera to those restricted to the islands, was that of Tyler (1979) and Zweifel and Tyler (1982). In this conclusion they were followed by Duellman and Trueb (1985). The latter were presumably unaware of descriptions of three species (*Cornufer* [= *Platymantis*] *xizangensis* Hu, *Platymantis liui* Yang, and *Platymantis reticulatus* Zhao and Li) found in western China and Tibet between 1977 and 1984. Dubois (1987) further confused the issue by erecting the genus *Ingerana* to include these three species and several Asian *Rana* and *Micrixalus*. He included *Ingerana* in the same subfamily as the island platymantine frogs. Zhao and Adler (1993) adopted a conservative view and referred all species of *Ingerana* to *Micrixalus*. I follow the last classification.

DISCUSSION

Whether we are considering hypotheses proposed during the period advocating fixed land areas or continental drift, some elements of the island fauna are unquestionably relatively recent colonizers. These are genera common to the islands and mainland faunas (Components I and II). The island-centered genera and subfamilies of the Microhylidae and Ranidae (Component III) are the source of many differences in bio-

geographic hypotheses. My starting point is the close of the fixed-land area period and the views of Darlington (1957).

Darlington regarded the old-world tropics (Africa and Asia) as the source area for amphibians. Successive waves dispersed from that center as the more recent families evolved and older ones became extinct except in peripheral areas (e.g., New Zealand). He thought the southwest Pacific Island anurans to be the result of relatively recent dispersal through southeast Asia and the fauna of Australia to be somewhat older but by way of the same conduit (Darlington 1957).

Most biogeographic papers since 1957 that have included the New Guinea-centered microhylids have continued to cite southeast Asia as the immediate source area (Duellman and Trueb 1985; Zweifel and Tyler 1982; Allison 1996). The most radical dissent from this view is that of Savage (1973). He would derive the New Guinea microhylids from an Australian stock that became extinct in that continent during the Cenozoic. Because he included the southeast Asian genus *Calluella* in the Asterophryinae, he viewed that family as dispersing from New Guinea to southeast Asia. He viewed other southern Asian genera as derived from a stock that reached Asia by way of the Indian subcontinent.

Recent biogeographic papers that included the platymantine frogs have also treated southeast Asia as the source area, although presumably at an early date. As previously noted, many of these authors included south Asian genera in the Platymantinae (Savage 1973; Dubois 1987, 1992). Other papers (Tyler 1979; Zweifel and Tyler 1982; Duellman and Trueb 1985; Allison 1996) limit the platymantine frogs to the island genera, but as having evolved from Asian stocks that colonized the islands very early. A satisfactory explanation of how they were able to disperse through the islands as far as Fiji has not yet been proposed. Inger (pers. comm.) refers to the Philippine *Platymantis* as Papuan elements and suggests they may have colonized the Philippines in the pre-Oligocene period when the Philippines had a more southern position.

One answer to the question of how and when the ancestral platymantine and microhylid stocks arrived in Melanesia is more attainable today than it was in 1982. If the hypothesis that the Inner and Outer Tethys Arcs were derived from terranes rifted as ridges from eastern Australia

prior to the separation of that continent from the rest of Gondwana (p. 26) is correct, the ancestors to the endemic platymantines and microhylids could presumably have been transported on those rift blocks such as the Solomon Ridge. This assumes that parts of the ridge were subaerial throughout the time, and either prior to or subsequently, these stocks became extinct in Australia. The presence of leiopelmatid anurans in New Zealand and their probable presence in Australia is analogous, although there is no fossil evidence to support this.

Patterns of endemism and distribution within islands beyond the Sunda Shelf for the genera *Metroxylon* and *Pigafetta* in the palm family (Arecaceae, subfamily Calamoideae) are similar to the patterns of the platymantines and microhylids; and a Gondwanan origin is also hypothesized (Dransfield 1987).

Similarly, the carphodactyline geckos and some of the skinks of New Caledonia are believed to be the result of vicariant events of stocks isolated following rifting from the eastern part of Gondwanan Australia in the Mesozoic (Bauer 1988, 1990; Bauer and Vindum 1990). New Caledonia is east of Australia at the southern tip of islands that were part of the Inner and Outer Arcs.

In this study I have isolated recent and very old anuran colonizers of the Pacific Islands and analyzed their distribution patterns independently. Phylogenetic studies at the levels of species, genera, and subfamilies are much needed for both the ranids and microhylids. Such studies should help either to confirm, modify, or deny the interpretation presented here. Also a better, future understanding of the geological history, especially of the Inner and Outer Tethys Arcs, may provide a more adequate explanation of the current island distributions of these endemic ranid and microhylid frogs.

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APPENDIX A

Southeast Asian Anuran Genera, (B) means also in Borneo.

Megophryidae

Leptobrachium (B)

Leptolalax (B)

Megophrys (B)

Hylidae

Hyla

Bufonidae

Ansonia (B)

Bufo (B)

Leptophryne (B)

Pedostibes (B)

Pelophryne (B)

Pseudobufo (B)

Microhylidae

Calluella (B)

Chaperina (B)

Glyphoglossus

Kalophrynus (B)

Kaloula (B)

Metaphrynella (B)

Microhyla (B)*Phrynella* (B)

Ranidae

*Amalops**Elachyglossa**Hoplobatrachus* (B)*Huia* (B)*Limnonectes* (B)*Micrixalus**Occidozyga* (B)*Paa**Phrynoglossus* (B)*Rana* (B)

Rhacophoridae

*Chirixalus**Nyctixalus* (B)*Philautus* (B)*Polypedates* (B)*Rhacophorus* (B)*Theloderma* (B)

Australian Anuran Genera, (NG) means also in New Guinea.

Hylidae

Litoria (NG)*Nyctimystes* (NG)*Cyclorana*

Myobatrachidae

*Adelotus**Arenophryne**Assa**Crinia* (NG)*Geocrinia**Heleioporus**Lechriodus* (NG)*Limnodynastes* (NG)*Megistolotus**Metacrinia**Mixophyhyes* (NG)*Myobatrachus**Neobatrachus**Notaden**Paracrinia**Phyloria**Pseudophryne**Rheobatrachus**Taudactylus**Uperoleia* (NG)

APPENDIX B

Asiatic and Australian Families and Genera of Anurans in the Islands of Wallacea, New Guinea, and the Melanesian Arcs.

Sulawesi and Sula-Banggai

Bufonidae.—*Bufo celebensis*Microhylinae (Microhylidae).—*Kaloula baleata*, *K. pulchra*Ranidae.—*Limnonectes cancrivorus*, *L. grunniens*, *L. heinrichi*, *L. kuhli*, *L. modesta*, *Phrynoglossus celebensis*, *P. laevis*, *P. semipalmata*, *Rana arathooni*, *R. celebensis*, *R. chalconta*, *R. erythraea*, *R. macrops*Rhacophoridae.—*Rhacophorus edentulus*, *R. georgi*, *R. monticola*, and *Polypedates leucomystax*

Lesser Sundas (Lomboc, Sumbawa, Flores, Wetar)

Bufonidae.—*Bufo biporcatus*Microhylinae (Microhylidae).—*Kaloula baleata*Ranidae.—*Limnonectes cancrivorus*, *L. limnocharis*, *L. macrodon*, *L. verruculosa*, *Phrynoglossus florensis*, *P. laevis*, *Occidozyga lima*, *Rana florensis*, *R. elberti*, *R. daemeli*Rhacophoridae.—*Polypedates leucomystax*

Outer Banda Arc (Sumba, Timor, Tanimbar, Seram, Ambon, Buru)

Hylidae.—*Litoria amboinensis*, *L. capitula*, *L. everetti*, *L. infrafronata*, *L. vagabunda*Ranidae.—*Limnonectes grunniens*, *L. modesta*, *L. verruculosa*, *Rana elberti*, *R. grisea*Rhacophoridae.—*Polypedates leucomystax*

Northern Moluccas (Halmahera, Morotai, Obi, Bacan, Ternate)

Hylidae.—*Litoria infrafronata*, *Nyctimystes rueppelli*Ranidae.—*Limnonectes modesta*, *Rana moluccana*

New Guinea

Ranidae.—*Limnonectes grunniens*, *Rana arfaki*, *R. daemeli*, *R. garritor*, *R. grisea*, *R. jimiensis*, *R. novaeguinae*, *R. papua*, *R. semevella*, *R. supragrisea*

Melanesian Arcs

Bismarcks (New Britain, New Ireland)

Ranidae.—*Rana krefftii*, *R. daemeli*Hylidae.—*Litoria infrafronata*, *L. thesaurensis*

Solomon Islands

Ranidae.—*Rana krefftii*Hylidae.—*Litoria infrafronata*, *L. thesaurensis*

Australia

Ranidae.—*Rana daemeli*

APPENDIX C

Non-Asiatic and Non-Australian Subfamilies
of Anurans in the Islands of Wallacea, Philip-
pines, New Guinea, and Melanesian Arcs.

Western Wallacea

Sulawesi and Sula-Banggai

Genyophryinae (Microhylidae).—*Oreo-
phryne celebensis*, *O. variabilis*, *O. zim-
meri*

Lesser Sundas

Genyophryinae (Microhylidae).—*Oreo-
phryne jeffersoniana*, *O. monticola*

Eastern Wallacea

Outer Banda Arc

Asterophryinae (Microhylidae).—*Callu-
lops fuscus*

Northern Moluccas (Halmahera)

Asterophryinae (Microhylidae).—*Callu-
lops boettgeri*, *C. dubia*Genyophryinae (Microhylidae).—*Cophix-
alus montanus*, *Oreophryne frontifas-
ciata*, *O. moluccensis*

Philippines

Platymantinae (Ranidae).—*Platymantis
corrugatus*, *dorsalis*, *insulatus*, *guen-
theri*, *hazela*, *ingeri*, *lawtoni*, *levigatus*,
mimulus, *montanus*, *polilloensis*, *pan-
ayensis*, *reticulatus*, *spaeleus*, *subterres-
tris*Genyophryinae (Microhylidae).—*Oreo-
phryne annulata*, *O. nana*

Sahul Shelf

New Guinea and satellite islands

Platymantinae (Ranidae).—*Platymantis
cheesmanae*, *P. batantae*, *P. punctata*, *P.
papuensis*Asterophryinae and Genyophryinae (Mi-
crohylidae).—The 16 genera and 101 spe-
cies (99 endemic) are not listed here but
may be found in Frost (1985) and Duell-
man (1993).

Melanesian Arcs

Bismarcks (New Britain, New Ireland, New
Hanover)Platymantinae (Ranidae).—*Platymantis
akarithymus*, *P. boulengeri*, *P. gilliardi*,
P. macroceles, *P. magnus*, *P. mimicus*, *P.
nexipus*, *P. schmidtii*, *Discodeles guppyi*Geneophryne (Microhylidae).—*Oreo-
phryne brachypus*, *Sphenophryne me-
helyi*

Admiralty Islands

Platymantinae (Ranidae).—*Discodeles ven-
tricosus*, *Platymantis gilliardi*, *P. species*

Solomon Islands

Platymantinae (Ranidae).—*Platymantis
acrochordus*, *P. aculeodactylus*, *P. gup-
pyi*, *P. myersi*, *P. neckeri*, *P. parkeri*, *P.
solomonis*, *P. weberi*, *Discodeles bufoni-
formis*, *D. guppyi*, *D. malukuna*, *D. opis-
thodon*, *Ceratobatrachus guentheri*,
*Palmatorappia solomonis*Raninae (Ranidae).—*Batrachylodes ele-
gans*, *B. gigas*, *B. mediodiscus*, *B. minu-
tus*, *B. montanus*, *B. trossulus*, *B.
vertebralis*, *B. wolffi*

Fiji

Platymantinae (Ranidae).—*Platymantis vi-
tianus*, *P. vitiensis*

Palau Islands

Platymantinae (Ranidae).—*Platymantis pe-
lewensis*



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