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Introduction

Melanesia is important in any discussion concerned with the distribution of terrestrial Mollusca in the Pacific region, as a zone exhibiting an intermingling of faunas derived from different geographical areas. Along the chain of islands constituting Melanesia these faunal elements exhibit changing patterns consistent with island hopping across water gaps. Yet the numbers of species of Mollusca on these islands show a positive correlation with the size of the individual islands (figure 19) and not, as might be expected, with the distance of particular taxonomic groups from centres of dispersal. Variations in this pattern can be attributed to differences in the isolation of islands, ecological diversity and the paucity of collecting in many areas. It should be realized that the distributional patterns recorded for any particular taxon must reflect the frequency and density of collecting and the inadequacies of the systematics of the group, besides biological attributes of the taxon and the island. The limitations should not distract, however, from attempts to analyse the available information, instead they must serve as a guide to the difficulties involved.

This paper is concerned with an analysis of the distribution patterns in Melanesia, based on the preliminary results from the Royal Society Expedition to the Solomon Islands and published data. Important sources have been the papers and systematic revisions of Baker (1938, 1940, 1941); Clapp (1923); Clench (1941, 1949, 1955, 1959); Clench & Turner (1959, 1963, 1964, 1966); Cooke (1928); Cooke & Kondo (1960); Dell (1955*a–c*); Franc (1957); Germain (1932, 1934); van Benthem Jutting (1941, 1948, 1950, 1952, 1953, 1963*a*, *b*, 1964, 1965); Kondo (1968); I. Rensch (1934*a*, *b*, 1937); I. & B. Rensch (1935, 1936); Solem (1958*a*, *b*, 1959*a*, *b*, 1960, 1961); Wenz (1938–44); Zilch (1959–60).

A synthesis of recent systematic studies, at the family level, by Taylor & Sohl (1962) has been utilized in the faunal analysis; details at the generic level being derived from Wenz (1938–44) and Zilch (1959–60), with modifications suggested in the publications of Baker, Cooke & Kondo, and Solem.

It is necessary to define Melanesia as used in this paper; it includes New Guinea and the archipelagos of the Admiralty, Bismarck, Solomon, New Hebrides and Fiji Islands, but with New Caledonia excluded. The latter presents problems that are completely different from those of surrounding archipelagos and is therefore outside the scope of this paper.

Distribution of terrestrial molluscan families

Representatives of thirty-one families of terrestrial Mollusca are found on the islands between the mainland of Asia and the Central Pacific, of these, six belong to the Prosobranchia and the remaining twenty-six to the Pulmonata. On the basis of their geographical distribution and supposed centres of dispersal these families have been divided into four groups (Pilsbry 1900, 1916; Solem 1958*b*, 1959*b*), the Palaeo-Oriental, Southern, Pacific and Introduced faunal elements: the region dominated by any element being easily recognizable from the name applied to the group. The first three correspond in many respects to the Malaysian or Oriental, Australian and Polynesian categories devised for other taxa by various authors (e.g. Mayr 1941*a*). However, attempts to produce a biogeographic scheme equally applicable to all phyla may obscure the individual characteristics of a particular taxon. For example, in many aspects the distribution patterns of the terrestrial Mollusca in the Pacific region parallel those of the insects, but the Mollusca are unique in exhibiting, at the family level, a Pacific element that cannot be considered as an extension of the Palaeo-Oriental (Gressitt 1956).

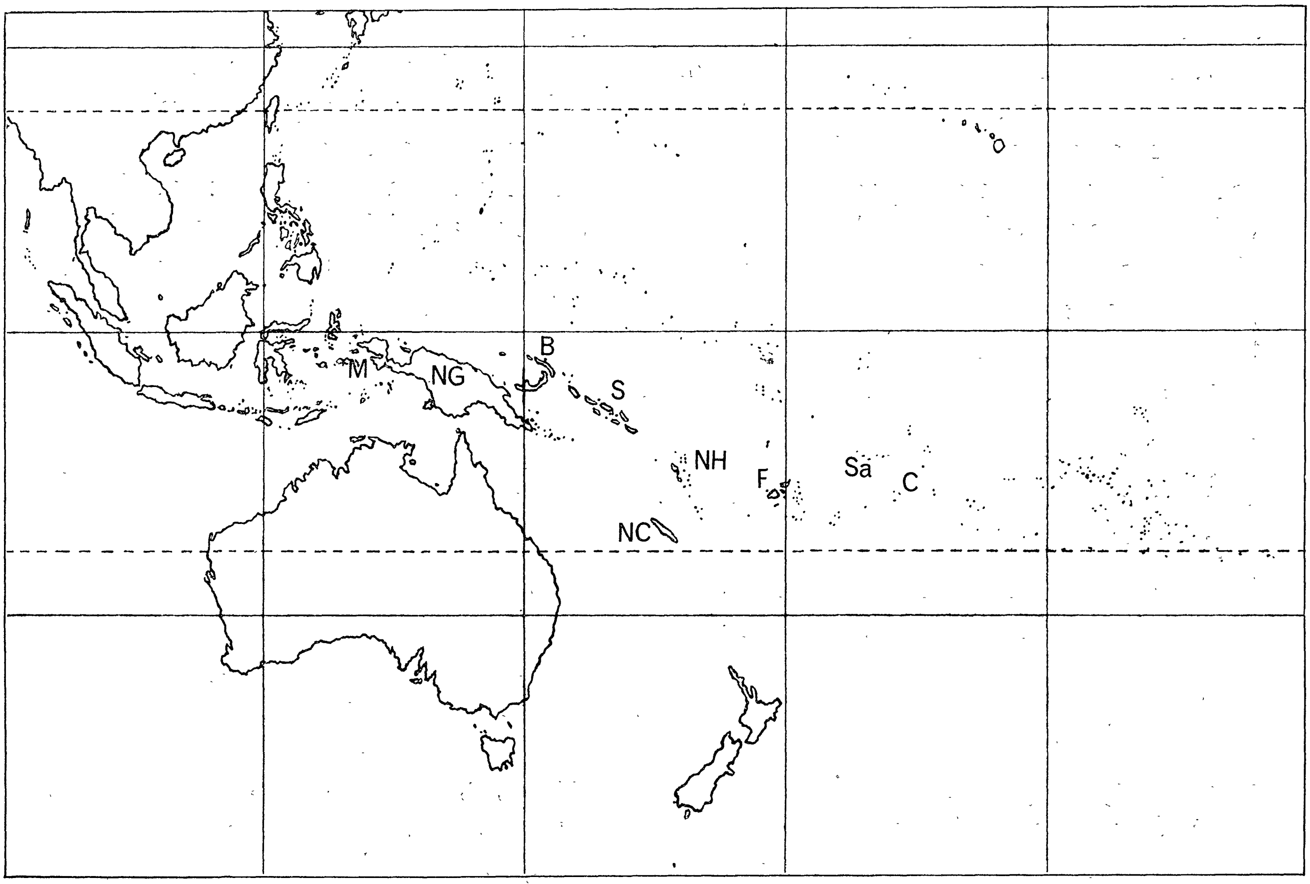


FIGURE 18. Pacific region: the major archipelagos considered in the text are indicated. M = Moluccas, NG = New Guinea, B = Bismarck Islands, S = Solomon Islands, NH = New Hebrides, NC = New Caledonia, F = Fiji Islands, Sa = Samoa, C = Cook Islands.

The faunal element consisting of introduced species is of recent origin in Melanesia, it tends to reflect the movements of traders and explorers and must therefore be excluded from an analysis of faunal relationships. In contrast, these forms must be included in the analysis of species numbers relative to island size. Further, it must be accepted that species in the remaining three groups are also occasionally spread by human agencies, but in these cases it is usually impossible to recognize particular examples with certainty. An extended and wide distribution is insufficient evidence for assuming human assistance in dispersal.

The three faunal elements, other than Introduced, may be characterized by a few specialized taxa (Solem 1959*b*), but for the purpose of this analysis it has been necessary to ascribe each of the twenty-two families to a particular element (table 9). While there are no apparent difficulties in assigning the majority of families, a few do pose special problems that will be discussed later, for example, the Helicinidae (see p. 288). The final decision regarding the position of these problematical families could be considered arbitrary, but in all cases they constitute, numerically, only a comparatively minor section of the fauna and therefore do not affect the major conclusions regarding distribution patterns. Two families do not fit this pattern, as the constituent subfamilies have radically divergent distribution patterns, indicative of major differences in the history of these taxa. These families are, therefore, included in more than a single faunal element; within the Euconulidae, one subfamily, the Microcystinae, is included in the Pacific element, but the distributions of the subfamilies in the other family, the Endodontidae, is more complex and follows the proposed divisions of Solem (1959*b*).

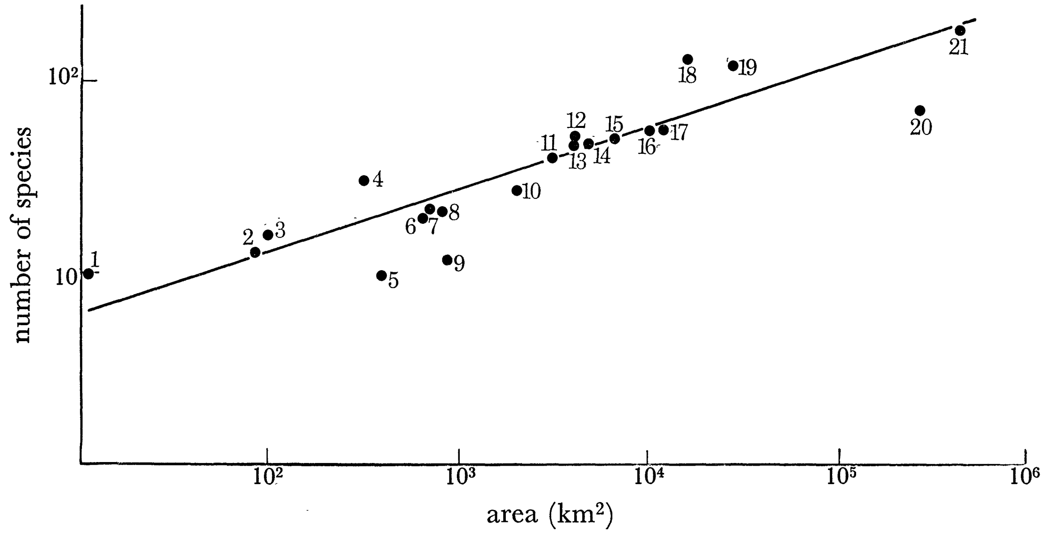


FIGURE 19. Relationship of area to numbers of molluscan species; the islands have been selected to illustrate a wide variety of sizes and geographical distributions in the region bounded by Sumatra in the west and Samoa in the east.

1	Krakatau	8	Vate	15	Guadalcanal
2	Nissan	9	Erromanga	16	Viti Levu
3	Treasury	10	Manus	17	New Ireland
4	Florida	11	Samoa	18	New Caledonia
5	Tanna	12	Malaita	19	New Britain
6	Rennell	13	Espirito Santo	20	Java
7	Tonga	14	San Cristobal	21	Sumatra

N.B. The data from Krakatau were not utilized in calculation of the regression line.

The Palaeo-Oriental fauna dominates the land masses from South–East Asia to the Solomon Islands and at the family level it is remarkably homogeneous on all the islands in this area. Only two, or possibly three, families do not have a contiguous distribution from Asia as far east as New Guinea and of the remainder only a single family is absent from the

Solomons. The eastern limit for the distribution of this element is variable; a few families occur in the Society Islands, but with the inclusion of the Helicinidae this boundary is extended to the Hawaiian Islands. There is a discontinuity between the Solomons and the New Hebrides, as three families fail to bridge this gap; two are represented by only a few species in the Solomons, but the third, the Camaenidae, is an important group containing numerous species that occur in a wide variety of ecological niches in the rain forests of the region (Peake 1968).

Table 9. Division of families of terrestrial Mollusca, occurring in the region between south–east Asia and the Central Pacific, into faunal elements

A. Palaeo-Oriental

Prosobranchia:
  Helicinidae
  Cyclophoridae
  Pupinidae
  Cochlostomatidae
  Assimineidae
Pulmonata:
  Vertiginidae
  Valloniidae
  Enidae
  Clausiliidae
  Corillidae
  Succineidae
  Streptaxidae
  Endodontidae
    (certain subfamilies)
  Philomycidae
  Trochomorphidae
  Euconulidae
    (excluding Microcystinae)
  Helicarionidae
  Ariophantidae
  Camaenidae
  Bradybaenidae
  Veronicellidae
  Rathouisiidae

B. Southern

Prosobranchia:
  Poteriidae
Pulmonata:
  Megaspiridae
  Athoracophoridae
  Acavidae
  Rhytididae
  Bulimulidae
  Endodontidae
    (certain subfamilies)
  ?Draparnaudinae

C. Pacific

Pulmonata:
  Achatinellidae
  Partulidae
  Amastridae
  Endodontidae
    (certain subfamilies)
  Euconulidae (single subfamily:
    Microcystinae)

The molluscan faunas of the archipelagos peripheral to the central Pacific basin, for example, Fiji, New Hebrides and the Solomon Islands, exhibit a high degree of endemicity at the generic level. These taxa are related to genera with a more western distribution and must therefore be included with these in the Palaeo-Oriental fauna; examples are *Dendrotrochus* and *Orpiella*, both in the family Ariophantidae. The Helicinidae provide an extension of this pattern, for this problematical family couples fragmentation at the generic level with a distribution that extends to the majority of Pacific Islands. *Orobophana* occurs on New Caledonia, Fiji, and the high islands of the central Pacific including Hawaii; *Sturanya* extends from the Solomons to the Cook islands and *Pleuropoma* occurs from Borneo to Hawaii including Rapa in the Austral Islands. In continental Asia, however, the Helicinidae are restricted to the peripheral regions of the land mass.

The Pacific fauna is represented by four families that are either endemic to or exhibit the greatest development of genera and species on the high islands of the central Pacific that lie east of the Andesite line, with a further endemic family in the Hawaiian Islands. Pilsbry (1900) noted that the fauna of this region is remarkably homogeneous at the family level, a relationship that is further emphasized by the limitation of four of these families to a single suborder, the Orthurethra. The uniformity of the Pacific fauna and the possible 'primitive nature' of the Orthurethra led to the conclusion that the terrestrial Mollusca of this area represented a remarkably ancient element that evolved in the Pacific on a large, possibly continental, land mass (for example, see Pilsbry 1900, 1916). Constant selection by dispersal over extensive water gaps and the colonization of small islands could, however, produce a degree of homogeneity, but not necessarily a unique fauna almost exclusively limited to this region. Certainly the small size of the snails colonizing these isolated islands could be attributed to the selective processes of dispersal over long distances. Only a few species of the Pacific fauna possess a distribution extending to the larger islands and archipelagos of Melanesia and Indonesia. Whether these examples can be considered as sufficient evidence for human assistance in dispersal is doubtful, but the interesting feature exhibited by these taxa is their ability to become established in habitats dominated by the Palaeo-Oriental fauna. Further, these widespread forms tend to colonize marginal coastal habitats and low islands, that is coral atolls and raised reefs (Pilsbry 1916; Cooke 1928). These are, therefore, the taxa that would be expected to have the widest distribution. The endemic fauna is confined to the interior and typically more mountainous regions of the high islands (Cooke 1928).

The Southern fauna includes five families that have a disjunctive distribution, occurring only in Melanesia and areas to the south, New Zealand and Australia, but with extra-Pacific representatives in South America, West Indies, South Africa, Madagascar and Ceylon. The evidence for the past distribution of at least some of these families is consistent with the replacement of included taxa over large areas of their range by more successful species emanating from northern land masses. Also associated with this faunal element are two families having a similar distribution, limited to the south-western region of the Pacific, but with no extra-Pacific representatives.

At present it is impossible to estimate the antiquity of the families of terrestrial Mollusca found in Melanesia, as palaeontological evidence from the Pacific region is almost non-existent. Fossil shells congeneric with living forms, belonging to the family Endodontidae, have been recorded from the Miocene to Pleistocene deposits in the Marshall and Ellice Islands (Ladd 1957, 1958). Yet the extensive fossiliferous Tertiary deposits in Java have not produced any terrestrial molluscs older than Upper Pliocene (Jutting 1937).

If there has been little radiation of genera since the Miocene this could suggest that the origin of at least certain families should extend back into the Mesozoic (Solem 1959*b*). Such a conclusion must involve making predictions regarding the rate and consistency of evolution in these groups that are probably unjustified. The first appearance in the fossil record of extant families of terrestrial molluscs was during the Carboniferous (Rensch 1959) but the majority of pulmonate families appeared during the Lower Tertiary (Rensch 1959). Although these data stress the antiquity of the various taxa, they provide little information to aid an understanding of the distributional patterns.

The Pacific basin, as at present constituted, has existed since the Cretaceous, although information regarding the exact age distribution and extent of the land masses in and around the basin is minimal (Menard & Hamilton 1963; Durham 1963). Continental drift would not appear to have been of major importance in determining distributional patterns of the fauna since that period (Durham 1963; Darlington 1965). In Melanesia the geological evidence for at least one archipelago, the Solomons, indicates there is no need to postulate an origin for these islands earlier than the late Mesozoic (Coleman 1966) and it is claimed by Thompson & Hackman (1969) that the first land appeared above sea level during the Oligocene. New Guinea provides a marked contrast, for it has been suggested that certain areas have never been submerged since the pre-Cambrian period (Cheesman 1951), although the present form of the island is of comparatively recent origin. Within Melanesia extensive tectonic and volcanic activity from the Miocene to the Pleistocene must have profoundly changed the form and area of the land masses, for example, the extensive mountain blocks in the Solomon Islands originated during this period. Therefore the present distribution patterns were probably determined subsequent to the last period of extensive geological activity in the Pliocene-Pleistocene, although the taxa involved may have had a much earlier origin in the region or on adjacent land masses. The evidence suggests that only limited changes in the geographical arrangement of the islands have occurred since the Pliocene and therefore any preliminary attempts to explain the distribution of the fauna in Melanesia should be based on the present pattern of land masses. Only when this fails should recourse to speculation on geological features be envisaged.

During the maximum depression of the sea level in the Pleistocene certain of the larger islands within each major archipelago would have been united, but there is no conclusive evidence that these land bridges extended between archipelagos. A probable consequence of the lower sea levels would have been the presence of more suitable stepping stones between the large islands. Therefore while local distributions could have been influenced by this factor, it is doubtful if the general pattern along the chain of archipelagos would have been substantially modified by dispersal over land. Greenslade (1968) has discussed the influence of the lower sea levels on the distribution of the insect fauna in the Solomon Islands and concluded that the similarities between the islands of Bougainville, Choiseul and Santa Isabel, could possibly be attributed to this factor, although it should be noted that the sea gaps between these islands are comparatively small. Attention has also been also been drawn to the resemblances in the molluscan faunas of these same islands (Rensch 1936).

At the specific and generic levels the non-marine Mollusca of the Palaeo-Oriental, Pacific and Southern faunas exhibit a remarkable degree of island endemism that can easily obscure the over-all relationships. It is therefore impossible to recognize patterns at the specific level for molluscs similar to those described for other taxa, for example, the distribution of ants in Melanesia (Wilson 1961). Many species of ants show a continuous distribution from New Guinea, or even Asia, eastwards to the Solomons and beyond, very few molluscan species exhibit such a wide distribution. Contrasts between these taxa can probably be attributed to differences in dispersal rates of the two groups and by variations in the age or time factors involved in establishing the patterns.

MELANESIA AS A REGION OF FAUNAL INTERCHANGE

The islands of Melanesia occupy an intermediate position between two regions dominated by comparatively homogeneous faunas at the family level, these being the Palaeo-Oriental and Pacific elements. The intermingling of these two elements and the Southern fauna in Melanesia and the Polynesian archipelagos of Samoa and Cook Islands is illustrated in figure 20; the representation of each faunal element is based on the number of genera included in the families listed in table 9. This datum emphasizes the regular pattern in the distribution of the three elements in both westerly and easterly directions and is consistent with a process of island hopping across water gaps. The change from west to east is associated with increasing water gaps and decreasing area of islands, except for the large islands of Espirito Santo, Viti Levu and Vanua Levu (table 10). Tabulating the number of species representing each faunal element tends to reflect variations in the area of islands and certainly a more informative comparison would be between numbers of propagules or species colonizing an island or archipelago, but at present this is impossible. Comparisons of the numbers of genera therefore probably reflect the most informative measurement of faunal affinity available.

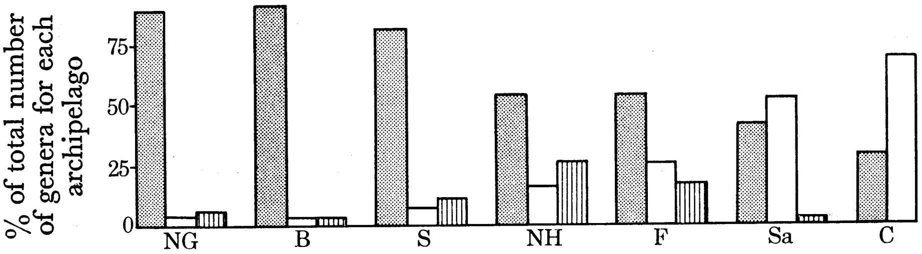


FIGURE 20. Representation of three faunal elements in seven archipelagos from New Guinea to the Cook Islands, expressed as the percentage of genera included in each group. NG = New Guinea, B = Bismarck Islands, S = Solomon Islands, NH = New Hebrides, F = Fiji Islands, Sa = Samoa Islands, C = Cook Islands. Palaeo-Oriental faunal element = stippling; Pacific faunal element = unshaded; Southern faunal element = vertical hatching.

While continental Asia and the associated large islands to the west of New Guinea have probably been an important source area for the Palaeo-Oriental fauna at the family level, New Guinea would appear to have been a secondary centre for the origin of many elements that have spread east into the other Melanesian islands and west at least as far as the Moluccas. The importance of New Guinea as a source area for other phyla represented in the Melanesian fauna has been stressed by Mayr (1941 *b*) for birds, Gressitt (1967) for many groups of insects and by Wilson (1961) for families of ants. The data for molluscs are summarized in figures 21 and 22, where the eastern and western distribution limits for all subgenera occurring in Melanesia and neighbouring archipelagos are plotted; the records for prosobranch and pulmonate taxa have been maintained in separate tables. These figures suggest that although New Guinea is probably an important source for pulmonate taxa, the origin for prosobranchs is possibly farther west. It is impossible to decide if these differences reflect biological attributes or simply inadequacies in the data and systematics of the taxa. Information presented in the final vertical column on the right-hand side of figures 21 *a* and *b* can be misleading, for they include many taxa having affinities farther east with the Pacific fauna. The distribution of subgenera in the region of Fiji, Samoa and Tonga is confusing, as the fauna of these islands exhibits a combination of secondary radiation of a few taxa with a probably relict distribution for others. Systematic revisions at both the generic and subgeneric levels will undoubtedly produce modifications that will have to be incorporated into figures 21 *a* and *b*, but probably the generalized pattern as known at present will not be radically altered.

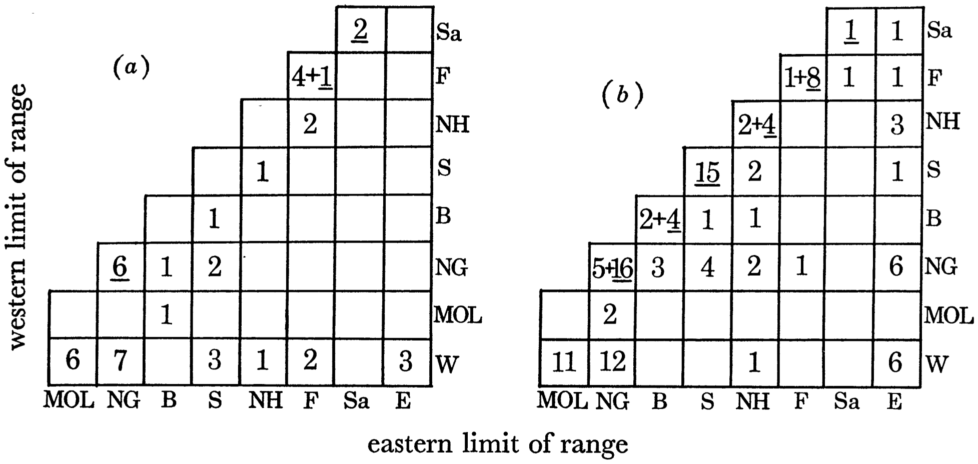
TABLE 10. AREA OF THE SIX LARGEST ISLANDS IN EACH ARCHIPELAGO; EXPRESSED IN SQUARE KILOMETRES

New Guinea	886 000
Bismarck Islands	36 800 8 500 1 370 1 300 520 470
Solomon Islands	10 100 6 500 4 700 4 700 3 900 3 400
New Hebrides	3 900 1 200 850 780 410 390
Fiji Islands	10 600 5 400 410 400 52 31
Samoa Islands	1820 1110 197 109 44 28
Tonga Islands	700 280 117 93 39 16
Cook Islands	67 52 26 21 18 18

Approximate distances separating each major archipelago; measured in kilometres between the larger islands in each archipelago:

New Guinea–Bismarck Islands	90
Bismarck Islands–Solomon Islands	170
Solomon Islands–New Hebrides	650
New Hebrides–Fiji Islands	950
Fiji Islands–Samoa Islands	850
Samoa Islands–Cook Islands	Archipelago too diffuse to make any measurement reflecting degree of isolation

The importance of New Guinea as a potential source of propagules is not confined to an east–west axis, for related taxa are recorded from Australia, particularly the rain forest region of Queensland and from the Caroline Islands to the north (McMichael & Iredale 1959; Solem 1959 *b*).



(a)

western limit of range	MOL	NG	B	S	NH	F	Sa	E
Sa							$\underline{2}$	
F						$4+\underline{1}$		
NH						2		
S					1			
B				1				
NG		$\underline{6}$	1	2				
MOL			1					
W	6	7		3	1	2		3

(b)

western limit of range	MOL	NG	B	S	NH	F	Sa	E
Sa							$\underline{1}$	1
F						$1+\underline{8}$	1	1
NH					$2+\underline{4}$			3
S				$\underline{15}$	2			1
B			$2+\underline{4}$	1	1			
NG		$5+\underline{16}$	3	4	2	1		6
MOL		2						
W	11	12			1			6

Figure 21. Western and eastern distributional limits for subgenera in (*a*) Prosobranchia and (*b*) Pulmonate. Numbers of endemic genera underlined. W = West; MOL = Moluccas; NG = New Guinea; B = Bismarck Islands; S = Solomon Islands; NH = New Hebrides; F = Fiji Islands; Sa = Samoa Islands; E = East.

Island size and isolation

The correlation between island size and the number of species of terrestrial molluscs occurring on the islands of Melanesia is illustrated in figure 19: in this context the parameter of island size is both a measure of ecological diversity and absolute area. On the basis of this relationship it is possible to consider the molluscan faunas of these islands as saturated, with all available niches for terrestrial snails occupied. Another interpretation, however, must be considered: the number of species on each island being dependent on the equilibrium point between processes of extinction and colonization of species (Preston 1962; MacArthur & Wilson 1963, 1967; Greenslade 1969). From this hypotheses various predictions have been made regarding the behaviour of island faunas in relation to

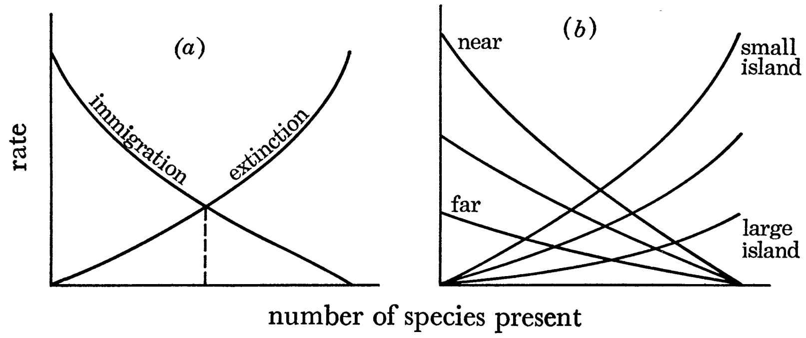


Figure 22. (*a*) Diagrammatic representation of equilibrium model for faunal size on a single island. The point of intersection between the two lines, representing rate of immigration of new species and extinction of existing species, indicates the equilibrium between two processes on the particular island (after MacArthur & Wilson 1963, 1967). (*b*) Equilibrium model expanded to cover a number of parameters; immigration rate being influenced by varying distances from source area, that is near to far, and different sizes of islands, small to large. Variations in these factors will alter the predicted equilibrium point, for example, both reduction in the size of the island and increase in isolation will reduce the predicted faunal size (after MacArthur & Wilson 1963, 1967).

isolation and area. For example, faunal size will decrease with isolation from potential sources of colonizing propagules. However, any discussion of faunal size in relation to the factors of immigration and extinction must consider the autochthonous radiation and evolution that has occurred in the molluscan faunas of Melanesia, for example, in the genus *Placostylus*. Variations in the data presented in figure 19 do not correspond with the predictions, suggested by the hypothesis given above, regarding the influence of isolation and although this could be attributed to inadequacies in the original data or theories, a more logical explanation is available. The islands of Melanesia have been

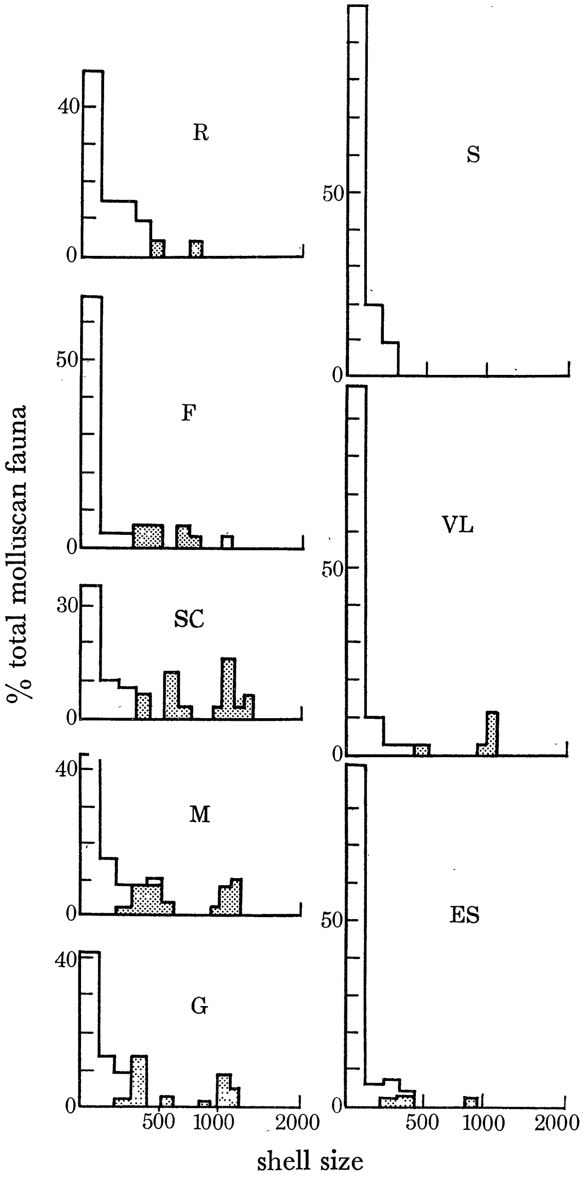


Figure 23. Size distributions of the molluscan species occurring on eight islands; large species belonging to the two families Bulimulidae and Camaenidae are indicated by stippling. See text for details of index utilized as a measurement of shell size. For convenience the axis for shell size is expressed on a logarithmic scale. *Solomon Islands*: R = Rennell Island, F = Florida Island, SC = San Cristobal, M = Malaita, G = Guadalcanal; *New Hebrides*: ES = Espirito Santo. *Fiji Islands*: VL = Viti Levu. *Samoa Islands*: S = total for all islands.

colonized by at least two faunal elements possessing extremely wide ranges of dispersal potential and from two apposing centres of distribution. In such a complex situation any influence of isolation would tend to be obscured. If, however, only large species are considered then certain predictions are fulfilled.

The size distribution of the molluscan faunas of eight islands, selected to illustrate a wide range of geographical conditions, are given in figure 23. A suitable index of shell size was provided by multiplying shell breadth by altitude and this is utilized throughout this paper. The islands chosen for this comparison consist of five in the Solomons, representing three large islands (Guadalcanal, Malaita and San Cristobal), a single smaller island from the central archipelago (Florida) and an isolated island (Rennell). The others being Espirito Santo in the New Hebrides, Viti Levu in the Fiji group and a combined total for all of the Samoan Islands. This series illustrates both variables of decreasing size and increasing isolation, but these factors do not operate independently and at present the data are insufficient to warrant undertaking a more detailed analysis. An examination of figure 23 suggests that species with a size index greater than 300 can be considered as presenting a comparatively homogeneous group of large forms and in the Solomons these constitute a unified ecological unit. The majority of species in this group belong to two families, the Camaenidae and the Bulimulidae; the former represented by two taxa, the genus *Chloritis* (s.l.) and the subfamily Papuininae, and the latter by the genus *Placostylus* (s.l.). In figure 23, the numbers of species belonging to these two families is indicated by stippling. Representatives of other taxa constitute only a small percentage of the group of large species and a number of these are included in genera with predominantly small species. These large forms can therefore probably be considered as autochthonous, having evolved from smaller species possessing greater potential for dispersal.

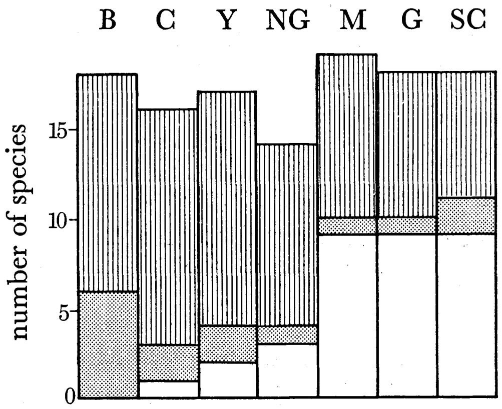


FIGURE 24. Numbers of species representing two families, Bulimulidae (unshaded area) and Camaenidae (shaded area) on seven islands of comparable size in the Solomon Islands. The numbers of species belonging to the subfamily Papuininae in the Camaenidae is indicated by vertical hatching; the remaining species in this family by stippling. B = Bougainville, C = Choiseul; Y = Santa Isabel, NG = New Georgia, M = Malaita, G = Guadalcanal, SC = San Cristobal.

In the Solomon Islands the ecological niches occupied by the species belonging to the two families, Camaenidae and Bulimulidae, overlap to a considerable degree, for there would appear to be no sharp distinction between arboreal and ground living forms and no clear vertical stratification of these taxa (Peake 1967, 1968). In this analysis these large forms can therefore be considered as a single ecological unit. Further evidence for this conclusion is provided by comparing the proportion of these snails that occur on the seven large and comparable islands in the Solomons (figure 24). Although the total number of large forms in these two families is similar on each island the proportion they contribute to the fauna varies considerably. In this situation, the number of species representing a particular element must reflect the opportunities for that taxon to radiate and secondly the exclusion or replacement of species in a saturated fauna.

Evidence for the exclusion or replacement of species is frequently difficult to produce, but a particular distribution pattern in the Solomon Islands can be interpreted in such a manner. Living examples of *Placostylus* species have never been recorded from Bougainville, although a single species exists on Choiseul. Propagules have reached Bougainville for dead specimens of *Placostylus founaki* (Homb. & Jacq.) are recorded by Clench (1949) and further individuals from this island exist in other museums, for example, the Dominion Museum, Wellington, New Zealand. While there is no evidence that this species is established on Bougainville, these records indicate that it has been successfully dispersed to the island. This absence can be attributed to the presence of potential competitors of *Placostylus* on Bougainville and the islands farther west; possible candidates are the two species of the genus *Quirosena* in the Camaenidae.

A correlation between the number of species and island size exists for large forms (figure 25) comparable to that demonstrated for the total molluscan fauna. Further, it is possible to investigate the influence of island isolation on species number by plotting the difference in the observed faunal size from the calculated, expressed as a percentage of the calculated, against the distance of the particular island from the nearest large island (figure 26). The first parameter is obtained from the regression line in figure 25, and the latter is utilized as a measure of isolation, although admittedly it excludes the influence of smaller islands as potential stepping stones. Figures 25 and 26 confirm a correlation for large forms between faunal size, island area and degree of isolation; an important feature being the relationship between faunal size and degree of isolation. The islands represented in the upper left section of figure 26 are all members of close knit archipelagos with several large islands. Complex methods of estimating isolation of islands have been devised and, if utilized in this study, these would have probably eliminated this tendency for grouping, but a more simple method is sufficient for the present analysis. Shell size must therefore influence the dispersal potential of species and this is reflected in the distribution patterns of the molluscan fauna. Dispersal may be considered as exhibiting a negative correlation between animal size and distance dispersed across water gaps.

The wide distribution of small species is illustrated by species of the Diplommatinidae, Achatinellidae and Microcystinae, that extend over large areas of the Pacific region and surrounding land masses. The restricted range of the two families with predominantly large forms is given in figure 27 and there contrasted with a genus, *Trochomorpha* (s.l.), having a more widespread dispersion, and an intermediate size range. The total size distributions for all Melanesian species of the taxa included in figure 27 are given in the histograms of figure 28; these emphasize the difference in size between *Trochomorpha* and other taxa. The data for species of Camaenidae (figure 28) demonstrate the presence of a few

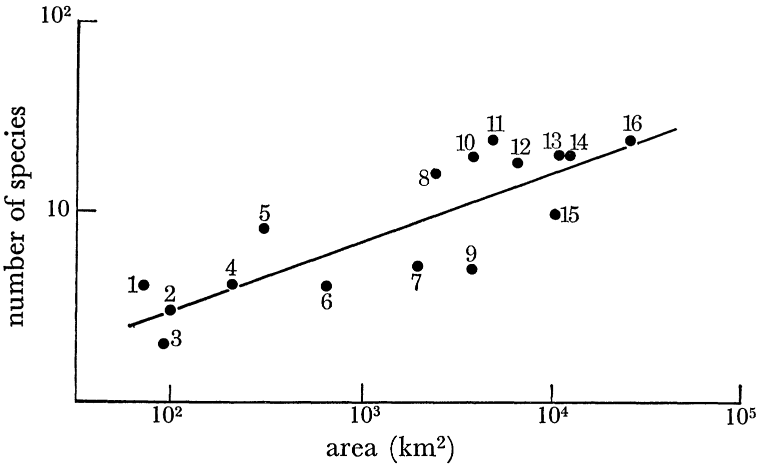


Figure 25. Relationship of numbers of large species of Mollusca on individual islands; see text for definition of large species:

1	Agi	7	Manus	12	Guadalcanal
2	Treasury	8	Choiseul	13	Bougainville
3	Nissan	9	Espirito Santo	14	New Ireland
4	Ulawa	10	Malaita	15	Viti Levu
5	Florida	11	San Cristobal	16	New Britain
6	Rennell				

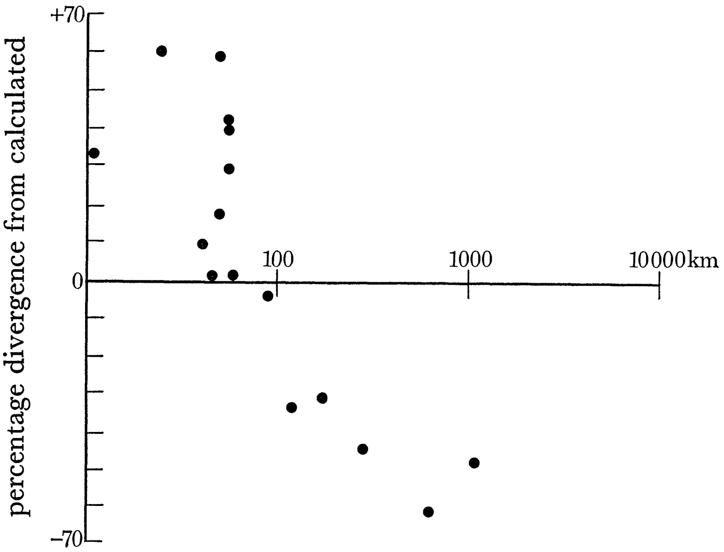


Figure 26. Relationship between observed faunal size, expressed as a percentage of the calculated (derived from figure 8), and degree of isolation from nearest large source island.

forms of smaller intermediate size in this family, which are restricted to New Guinea. In the Solomon Islands, only large forms exist and the resultant lower probability for dispersal of these species could contribute to the absence of this family on the islands to the east.

The modes of dispersal of land molluscs across sea gaps are largely unknown or rather unobserved, but this is not unexpected if the probability for the occurrence is small. Several compilations have been made of information available on different methods (Kew on an island indicates whether they have dispersed across wide ocean gaps by natural means or have been carried by man. If they have dispersed naturally it is reasonable to assume that they have been arriving for as long as suitable conditions for their dispersal and establishment have existed, i.e. in the case of the Solomons probably since mid-Tertiary times, and there should be a high level of endemism on the islands, as in the megascolecid earthworms of New Caledonia and New Zealand. If they have been carried by man they can have been on remote islands for at most only a few thousand years, and the level of endemism should be low, as in the megascolecid earthworms of the Solomon Islands. Gates (1959) concluded that six species of *Pheretima* that he identified from Rennell Island have probably been introduced by man from the large land masses to the west, while *Dichogaster bolaui*, the only other earthworm known from Rennell, has probably been similarly introduced and must have originated from America or Africa. Of the 15 Solomons species it seems likely that most, if not all, the species of *Pheretima* have been introduced from the west and spread within the Solomons archipelago by Melanesian and Polynesian man, that *Dichogaster bolaui*, *Ocnerodrilus occidentalis* and *Pontoscolex corethrurus* have been introduced in the same way, or possibly by European man as they apparently have been in many tropical countries, and that only the intertidal earthworm *Pontodrilus matsushimensis* has reached the Solomons by natural means, dispersed by ocean currents.

The equilibrium hypothesis of MacArthur & Wilson is not affected by the mode of migration of species that reach an island. It is sufficient that the species arrive, by whatever means. However, the modes of migration available to any particular group of animals do affect the chances of arrival in any given time, and so affect the rate of immigration in MacArthur & Wilson's equilibrium model. For a group of animals such as earthworms, greatly restricted in their ability to cross ocean gaps, the time required for equilibration on isolated islands must be very long, long enough that though there has apparently been land in the Solomons area since mid-Tertiary times, earthworms are still in a preliminary stage of establishment and spread and these considerations apparently outweigh all others in determining the present distribution pattern. By contrast, for animals such as birds and flying insects, with well-developed powers of dispersal across ocean gaps, the time required to attain equilibrium would be expected to be relatively short. That such groups do fit MacArthur & Wilson's hypotheses reasonably well is shown in some of the examples chosen to illustrate their thesis. Lee (1968) discusses the distribution of megascolecid earthworms on sub-antarctic islands. The islands (apart from Auckland Islands, which have some species related to New Zealand megascolecids) were apparently depopulated during the Pleistocene glaciations. A small group of euryhaline species of *Microscolex* has apparently spread, carried by the West Wind Drift, in an easterly direction from South America. On individual islands there are only one or two species of *Microscolex*, and in the absence of competition they have spread through various habitats from the intertidal zone to upland soils. They are analogous to *Pontodrilus matsushimensis* in the Solomon Islands. Subsequently, two species of Lumbricidae have been introduced, apparently by man. These species are analogous to the widely distributed species that make up the remainder of the Solomons fauna.

MacArthur & Wilson's equilibrium model takes no account of the order in which events occur. Nemertine worms are found living in terrestrial habitats on some isolated islands

Von Martens (1867) recorded five species from the island in 1867 and Dammermann (1948) summarizes the information from 1883 onwards as follows:

	1889	1908	1921	1933
number of species	0	2	6	9 or 10

The larger and more conspicuous species failed to recolonize the island from either Java or Sumatra, although a single species from Java related to a previous member of the fauna was found to be abundant in 1908.

The size of this species (*Amphidromus porcellanus*, Mouss.) is comparable to many species of the Camaenidae and confirms the ability of a large snail to disperse across water. Further it provides an indication of the parameters necessary for a study of the colonization of islands by such forms. The basic data are that a large species colonized a small island, with an area of about 11 km², in a period of less than 20 years across a water gap of about 40 km from Java. An examination of figure 19 demonstrates that 44 years after the eruption, the number of species found on the island corresponds with that predicted by the species–area relationship. The extension and development of this datum from a restricted condition to a

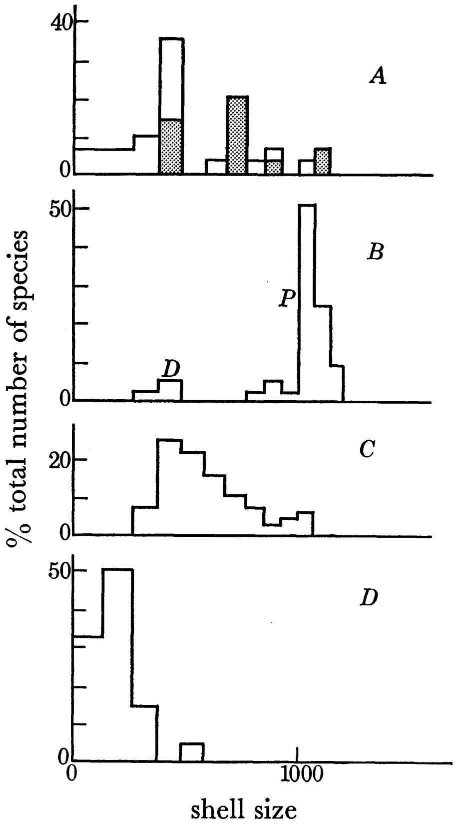


Figure 28. Size distribution of species occurring in molluscan taxa represented in figure 27; for convenience the axis for shell size is expressed on a logarithmic scale. (*A*) Camaenidae, excluding species in the subfamily Papuininae; the stippled areas indicate species occurring in the Solomon Islands. (*B*) Bulimulidae: *P* = *Placostylus* species and *D* = species of the genus *Diplomorpha*, endemic to the New Hebrides. (*C*) Camaenidae, only species in the subfamily Papuininae. (*D*) *Trochomorpha*.

more generalized form presents many problems, for it is impossible to estimate the effect of variations in local conditions. An exponential form of dispersal will result when the mean dispersal is comparatively small and dispersal is in a uniform and determined direction, for example, when it is achieved by means of wind or air currents and, even in a few circumstances, by water currents. The other important type to be considered is the 'normal' form of dispersal that occurs when direction of movement is random and continually changing, as might occur with a drifting log in the sea (MacArthur & Wilson 1967); this will exhibit a decrease at the rate of e^{-x^2}, whose x equals the distance between the two areas. No single form of dispersal will, however, reflect the complete picture and neither can any be mutually exclusive. The extrapolation of the data from Krakatau, by the two methods given above, suggests the conclusion that dispersal across water gaps at least 75 km and probably 150 km is feasible in the period since the Oligocene (or even less) for islands the size of Krakatau and a dispersal centre the size of the south–west coast of Java. That is the distance between New Guinea and each of the successive islands progressing eastwards until the last large island of the Solomons, San Cristabal. Variations in size of both the recipient island and the dispersal centre do not appear to be of sufficient magnitude to invalidate the application of the results from Krakatau to the situation in Melanesia, but differences in many other local factors cannot be estimated. An inference from these data could be that the probability of dispersal of large forms over long distances, in the order of 200 to 600 km, must be very low in the period available since the Oligocene. In these situation stepping stones, such as the Santa Cruz and Banks Islands, might be extremely important in aiding dispersal between isolated islands or archipelagos (MacArthur & Wilson 1967). Unfortunately information on the molluscan faunas of these islands is meagre; on Santa Cruz there is a single species of *Placostylus*, related to other members of the genus occurring in the New Hebrides, and a dubious record of a '*Papuina*' (Camaenidae) (Solem 1959*a*), but there are not records of large species from the Banks Islands.

A possible explanation for the differences in the distribution of some groups of large species found in the Solomon Islands and the New Hebrides can be found in the history of the taxa, expressed as variations in the time available for colonization. Species belonging to the Camaenidae are confined to a region where there are comparatively narrow water gaps between the major islands and thus contrasts sharply with the pattern for the Bulimulidae where species occur on scattered islands with large intervening water gaps. The geological evidence is insufficient to determine the permanence of these gaps. The two families belong to two different faunal elements, the Camaenidae to the Palaeo-Oriental and the Bulimulidae to the Southern. A suggested interpretation of the history of these two elements in Melanesia indicates that the Bulimulidae belong to an element which has existed for a longer period in the area, when compared to the Camaenidae. It is these differences in age that could have resulted in the wider distribution of the Bulimulidae.

If colonization of the Solomon Islands by species of *Placostylus*, that is members of the Bulimuliade, occurred from the New Hebrides in an east–west direction, then the analysis of the importance of stepping-stones by MacArthur & Wilson (1967) produces an alternative hypothesis to the one given above. There is, unfortunately, an absence of palaeontological evidence to supporting migration in either direction. The tentative phylogeny suggested by Solem (1959*a*, *b*) for Bulimulidae found in the Pacific region indicates that the species of *Placostylus* found in New Zealand and the New Hebrides belong to a more primitive group than those from New Caledonia, Fiji, and the Solomon Islands. Therefore it is suggested that subsequent to an original invasion of New Zealand, from a source in New Guinea, there must have been a secondary colonization of New Caledonia, Fiji, and the Solomons from New Zealand. The evidence for the development of present patterns in this sequence is tenuous and open to other interpretations. However, if an east to west dispersal for *Placostylus* is accepted the importance of small islands as stepping stones becomes extremely significant. In mathematical models simulating the effect of one or more stepping stones the following conclusions were reached by MacArthur & Wilson (1967). Where a single stepping stone exists it does not alter the proportions of species exchanged between two sources areas; however, if one or more extra stepping stones are introduced and colonized in sequence, then together they will increase the relative flow from the source island closest to them. The latter is the situation that occurs when a fringing archipelago or group of small islands surrounds a larger land mass. This model expresses the situation that occurs in the areas under consideration; the Santa Cruz and Banks Islands, that is the stepping stones, occur in closest proximity to the New Hebrides, thereby favouring faunal exchange from the New Hebrides to the Solomons, presuming other factors to be equal in both directions. This pronounced bias towards dispersal in an east–west direction would greatly favour the movement of *Placostylus* to the Solomon Islands rather than any contrary dispersal of the Camaenidae to the New Hebrides.

The relationship between island area and species numbers, even large species, has already been discussed, but a further factor emerges from an examination of these data. The regression lines for different size groups would intersect the base-lines at different points, indicating the ability of the smaller species to maintain viable populations on smaller islands than the larger forms. In Fiji the absence of any species of *Placostylus* from the small islands of the Lau Group contrasts sharply with their presence on the larger, more central islands, for example, Viti Levu and Vanua Levu. The largest island of the Lau Group has an area of about 50 km^2, but the majority are much smaller and large tracts of all these islands provide an unsuitable habitat for *Placostylus*. These islands are therefore near or even smaller than the minimum size necessary for maintenance of viable populations of species in this genus. Further the isolation of the Lau group from the larger islands of Fiji is in the order of at least 75 to 150 km and many are of comparatively recent geological age (Ladd & Hoffmeister 1945). Certainly their absence from these islands cannot be taken as evidence of the inability of *Placostylus* to cross water gaps and, therefore, evidence for the presence of former land bridges (Cooke 1928). The absence of species of this genus from the small islands of the Lau Group is consistent with the size and isolation of these islands.

Conclusions and summary

Fundamental to any discussion of the patterns considered in this paper is the positive correlation between island size and the number of species of terrestrial Mollusca occurring on each island. On the basis of this correlation it is feasible to consider the molluscan faunas of the islands in Melanesia as approximately saturated and possibly any change in species representation could involve processes of both colonization and extinction.

The molluscan fauna of this region can be divided into three elements on the basis of the geographical distribution of the constituent families. These elements exhibit a regular pattern of representation on the islands between New Guinea and the Cook Islands that is consistent with a process of island hopping across water gaps. There is a gradual change from a fauna dominated by a Palaeo-Oriental element on islands in the west of Melanesia to one dominated by a Pacific element on islands in the Central Pacific and eastern Melanesia. This variation is associated with decreasing island size and increasing gaps between the islands and archipelagos, when progressing in an easterly direction from New Guinea. Undoubtedly these two factors have had a profound effect on the distribution of the terrestrial Mollusca in Melanesia, but this does not obviate the effect of other features. For example, variations in the climatic conditions during the Tertiary. Unfortunately the available information on this aspect is inconclusive, but certainly tropical conditions were more extensive during the Tertiary (Axelrod 1952). During the Pleistocene the lowering of the sea level would have permitted faunal interchange across dry land between islands now separated by shallow seas and the number of stepping stones between archipelagos would have also increased during the same period (Durham 1963).

The gradual attenuation of the Palaeo-Oriental and Pacific faunal elements in, respectively, easterly and westerly directions raises many problems regarding the recent and present expansion or contraction of these elements. Unfortunately the high degree of island endemism at both the specific and generic levels makes any analysis extremely difficult. Ladd (1960) has argued for an east–west expansions for many taxa and this might appear to be true when applied to the Pacific element, but further discussion of this aspect is outside the scope of this paper.

Islands have been divided into two categories, continental and oceanic, on the basis of whether the terrestrial fauna was derived by migration across land connexions or dispersal across sea gaps, not all members of the fauna necessarily being derived by the same method (Mayr 1941 *b*). The islands of Melanesia are assigned to both types depending on which authors or animal groups are being considered. The evidence provided by the distribution of the molluscan fauna suggests that it is extremely difficult to apply such a classification and any attempt to divide the islands of Melanesia into such categories reflect the importance of certain geographical features and not the mode of origin of the fauna. The criticisms against the division of islands into two groups has been summarized by Darlington (1957); he suggests a more arbitrary classification. The geological data provide no conclusive evidence for any land bridges between the major archipelagos in Melanesia, at least during the Tertiary. Further, if land bridges did exist, the present distribution of the fauna does not appear to follow the paths suggested for such land connexions, that is, in a series of arcs running parallel to the east coast of Australia. In fact the patterns exhibited by many taxa, including Mollusca, are at right angles to these axes and bring into association islands that lie on different arcs (see Mayr 1941 *b*).

The positive information available on the dispersal of terrestrial molluscs is extremely limited, but it is possible to make certain deductions from the resulting distribution patterns. There is apparently a relationship between the size of the animal and the distance over which successful dispersal and colonization has occurred; the smallest species being transported the greater distance and vice versa. Variations in the distribution of taxa of similar size could reflect differences in the history of the species in the area and therefore time available for dispersal to have occurred. No doubt many other factors are of equal importance, these must include the geographical position of stepping stones, the ecological requirements of the mollusc, the number of propagules for dispersal and the methods of dispersal employed. The smaller species are probably more readily dispersed by air currents and the larger forms by floating islands of vegetation, although probably no single method is exclusive to any particular group of molluscs. The differences in the probability of successful dispersal by these two methods are extremely great; dispersal by air currents will tend to be directional and will follow the expression e^{-x}, that for floating logs non-directional following the expression e^{-x^2} (MacArthur & Wilson 1967).

The distribution patterns exhibited by the terrestrial molluscs in Melanesia are consistent with those for other elements of the biota, for example, birds (Mayr 1941 *a*; Greenslade 1969) and at least certain families of insects (Gressitt 1956, 1967; Greenslade 1968). Colonization of, at least, the Solomon Islands and islands farther east having occurred across sea gaps and *not* by migration along land bridges. The inference must be that dispersal is successful and therefore the important questions are not necessarily concerned with means or methods but also with why particular elements have become established and the consequences of this colonization. It is extremely interesting that the patterns exhibited by the Mollusca are in agreement with the models predicting the influence of particular geographical features, for this suggests future lines of research. It is to be hoped that collecting in such areas as the Santa Cruz Islands and further taxonomic studies will help to elucidate some of the interesting problems that can be studied in the Melanesian region.

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