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The land invertebrates of the New Hebrides and their relationships

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Of the 30000 and more specimens of land invertebrates collected by the expedition, studies on five groups, the Oligochaeta, Isoptera, Dermaptera, Hemiptera-Heteroptera and Rhopalocera, are sufficiently advanced to use them as indications of what may be learnt from the collection as a whole.

We increased the number of known species there by from 30 % to over 100 % according to group, this increase being composed of approximately equal numbers of new species and new records. Our recovery of already recorded species was about 50 %.

Endemic species make about a third of the total. There are few genera. The rest of the species usually occur in more than one other nearby area. This is very similar to the Samoan and Tongan picture. There is little 'explosive speciation' and few unique relationships with Australia and New Caledonia.

A series of tables are provided to illustrate these conclusions.

1. Introduction

The 1971 Royal Society/Percy Sladen Expedition to the New Hebrides had as one of its outstanding results the collection of large numbers of land invertebrates. The soil and litter extracts, supplemented by hand collecting, yielded many thousands of specimens of nematodes, oligochaetes, mites, collembolans and insects. The sweeping of foliage and hand collections from the lower vegetation produced more than 15000 specimens of insects and the collections at mercury vapour lights at night a further 2000 insects.

All the animals extracted from soil and litter have been sorted to at least order and many to categories lower than this. The tubes in which each subdivided sample is kept are fully labelled. The insects collected by hand and at light have all been individually set and labelled and are available for distribution to specialists. A number of groups have already been dispatched and of these some have been returned and a paper, or in smaller groups a report, on them is already to hand. Some of the groups cannot be placed until interested specialists can be found.

In this summary account of our findings on this Expedition I make no attempt to go into details of all groups, for such a project is manifestly impossible at this stage. Instead I have selected several groups for which our studies and knowledge are presently quite advanced, and have used these as 'index groups' to indicate what may be expected from the entire collection when its analysis is further advanced.

The groups selected are the Oligochaeta (earthworms), Isoptera (white ants or termites), Dermaptera (earwigs), the suborder Heteroptera of the order Hemiptera (bugs) and the Rhopalocera (butterflies) of the order Lepidoptera.

In round figures the achievements of the Expedition for the groups selected may be tabulated as follows:

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TABLE 1. SUMMARY RESULTS OF THE COLLECTIONS MADE BY THE EXPEDITION FOR SIX GROUPS OF INVERTEBRATES

group	prior number of recorded species	number of these recollected	number of these not collected	new species	new records	present number of species
Oligochaeta	6	3	3	8	8	22
Isoptera	8	5	3	2	2	12
Dermaptera	10	9	1	3	3	16
Heteroptera	58	34	24	33	33	124
Rhopalocera	55	41	14	1	8	64
						237

TABLE 2. STRUCTURE OF THE FAUNA OF SIX GROUPS OF INVERTEBRATES IN THE NEW HEBRIDES

group	number of endemic species	% of endemic species	number of genera represented	number of endemic genera	% of endemic genera	mean number of species per genus
Oligochaeta	11	50	6	0	0	3.6
Isoptera	5	42	7	0	0	1.7
Dermaptera	5	31	10	0	0	1.6
Heteroptera	44	35	98	10	10	1.3
Rhopalocera	2	3	38	0	0	1.7

A comparison of the figures in the first and last columns of table 1 shows how substantially the available material has been increased as a result of our efforts in the field. Even in such a well collected group as the butterflies there was an increase in the number known from the New Hebrides of 15 %; in termites, which are a widely studied group in the Pacific area due to their economic importance, there was a 50 % increase. The numbers of the other selected groups were increased by much more. Also we accumulated a considerable number of new records of species on islands within the New Hebrides archipelago. The figures for new records in table 1 refer only to those described species recorded for the first time in the New Hebrides archipelago and not to individual new records in islands within the archipelago.

The derivation of the summary data presented in tables 1 and 2 is shown in table 9, which gives details of the distribution and relationships of the taxa of the index groups.

2. IS THE FAUNA OF THE NEW HEBRIDES DEPAUPERATE?

Gressitt (1961, 1964, 1974) saw the insect fauna of the New Hebrides as depauperate. In his opinion there may be several times more genera and species in the Solomon Islands than in the New Hebrides.

Tables 3 and 4 present comparable figures for the land area, number of species and genera (both total and endemic), the percentages of specific and generic endemism, and the mean number of species per genus for the Heteroptera and Rhopalocera respectively in the New Hebrides and in a series of other areas in the vicinity. I regret that more groups could not be tabulated in this way, but for most other groups species lists do not exist or are unpublished, as is my own catalogue of the Heteroptera of the region.

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Table 3. Comparison of the Heteropteran faunae of certain selected areas of the region

area	land area 10^3 km²	number of species	number of endemic species	% species endemic	number of genera	number of endemic genera	% genera endemic	mean no. of species per genus
Buru	9.5	84	18	21	61	1	2	1.4
Seran†	18	131	27	21	85	1	1	1.5
Timor	34	107	15	14	70	1	1	1.5
Australia	7704	1516	1294	85	613	293	48	2.5
New Guinea‡	795	1215	934	77	418	130	31	2.9
Solomon Is.	42	152	73	48	90	6	7	1.7
New Hebrides	15	124	44	35	98	10	10	1.3
New Caledonia§	20	208	119	57	139	35	25	1.5
Fijian Is.	18	157	77	49	119	14	11	1.3
Samoan Is.	3.1	117	49	42	85	6	7	1.4
Society Is.	1.6	42	15	36	33	2	6	1.3
Marquesas Is.	1.2	41	35	85	19	1	5	2.2
Hawaiian Is.	17	223	180	80	68	22	32	3.3

† Includes Amboina and the Uliaser Islands.
‡ Includes Bismark and Louisiade Archipelagoes and islands immediately west such as Misool and Waigeu but not the Aru or Ke Islands.
§ Includes Loyalty Islands.

Table 4. Comparison of the Rhopaloceran faunae of selected areas of the region

area	land area 10^3 km²	number of species	number of endemic species	% species endemic	number of genera	number of endemic genera	% genera endemic	mean no. of species per genus
Ceylon	66	238	10	4.2	110	0	0	2.2
Burma	578	1014	0	0	186	0	0	5.5
Malaya	131	839	11	1.3	220	0	0	3.8
Buru	9.5	147	13	8.8	78	0	0	1.9
Seran†	18	203	24	12	95	0	0	2.1
Timor	34	104	6	6	56	0	0	1.9
Australia	7704	364	175	48	121	28	23	3.0
New Guinea‡	795	738	456	61	151	26	17	4.9
Solomon Is.	42	134	42	31	32	1	3	4.2
New Hebrides	15	63	4	6.3	38	1	3	1.7
New Caledonia§	20	67	11	16	30	2	7	2.2
Fijian Is.	18	21	3	14	17	1	6	1.2
Samoa Is.	3.1	24	4	16+	21	0	0	1.1
Society Is.	1.6	10	1	10	10	1	10	1.0
Marquesas Is.	1.2	4	1	25	4	0	0	1.0
Hawaiian Is.	17	10	2	20	6	1	16	1.6

† Includes Amboina and the Uliaser Islands.
‡ Includes Bismark and Louisiade Archipelagoes and islands immediately west such as Misool and Waigeu but not the Aru or Ke Islands.
§ Includes Loyalty Islands.

The figures for the numbers of species in tables 3 and 4 suggest that Gressitt's opinion does not hold for either the Heteroptera or the Lepidoptera.

However, paucity or richness of a fauna must be related to some relevant yardstick of comparison. It is obvious that a small island will have a much smaller fauna than a continent, so this sort of comparison is not very illuminating. A relevant yardstick would be to establish some

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estimate of the number of species one would expect in the area under consideration, taking into account its size and geographic zone (tropical, arid, temperate etc.), and then to compare this with numbers of species actually found in collections.

McArthur & Wilson (1967) in discussing island biogeography devote a chapter to the thesis that the size of the fauna of islands is proportional to island size. The size of the fauna to be expected on an island in a certain region can be estimated by plotting the sizes of the faunae where known of other islands in the region against the areas of these other islands. The sizes o their faunas are claimed to be related to their respective areas by the expression $S = CA^Z$ where S is the number of species found or to be expected, and A is the land area of the island. If the sizes of the faunae of a series of increasing areas within the one island or land mass are plotted against these areas the same relationship is alleged to hold but with different values of C and Z.

C has a fixed value for each sequence of islands, or increasing series of areas in the one island or land mass, and the taxonomic group considered. As 1 raised to any power is still 1 when an area of unit size 1 is considered then $S = C$. C therefore is the intersect on the species axis when the area is 1 unit and is the number of species to be expected in an averaged first unit of area. If the unit of area chosen is large then more species can be expected in the first unit considered than if the area is smaller and C is correspondingly larger, similarly if the taxonomic group considered is more diverse and has more species than another then more species of the former can be expected in the first unit of area and the value of C is again correspondingly elevated. The zoogeographical and climatic regions are also relevant as more species can be expected per unit area of certain groups in the tropics than in temperate, arid, or arctic regions.

The factor Z also has a fixed value for each sequence of islands or increasing series of areas on the one island or land mass and the taxonomic group considered. If an island were to be divided up into a series of fenced areas of equal unit size, the fauna of each of which was artificially maintained as an exact replicate in number and identity of species represented of each other such area, then all the species to be encountered would be encountered in the first area studied and increasing the area would not increase S. The relationship would then be $S = CA^0$ as any number raised to the zero power is always 1. If on the other hand in each fenced area a number of species were artificially maintained equal to that of each other fenced area, but the species in each such fenced area were completely different from those in any other such fenced area, i.e. any single species occurred in only one such area, then the relationship would be $S = CA^1$ as any number raised to the unitary power is always itself. The factor Z therefore cannot be less than zero or exceed one. As in nature a situation intermediate between these two extremes is to be expected, Z has a fractional value between 0 and 1. If the distribution of the species is log–normal then as discussed in MacArthur & Wilson and earlier by Preston (1962) and Williams (1964) the value of Z should be about 0.27. In their discussions of values of Z differing from 0.27 the above authors have not allowed for one important perturbation, namely that Z is related to the mean range, in geographical or habitat terms, of the species concerned. For example if the species of a group are numerous and wide ranging then a great number of them should be present when the number of units of area considered is still low, and increasing the number of unit areas will not greatly add to the total, i.e. C will be high and Z low. But if the species have narrow ranges, e.g. those in certain habitats on the eastern side of an island or land mass are different from those on these same habitats on the western side, then though the taxonomic group over the whole area may be as large, in the first units of area

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considered relatively few will be present, but by increasing the number of units of area a high percentage of the forms encountered will be novel at each stage. In this case, for a group of equal taxonomic size to the first (over the whole area), C will be lower and Z elevated. A number of recent plots for insects, a group of great diversity and with many species with quite narrow ranges, give Z values much above the range $Z = 0.20$–0.35, which MacArthur & Wilson quote as most usual. This can be seen for the Z values in table 5.

Considering the sizes of the faunae of a series of islands each progressively further from the source of the immigrant fauna which each will ultimately acquire, there are many reasons why a species/area relationship such as $S = CA^Z$ should *not* apply. Briefly these are:

(1) An island may be geologically recent and still be acquiring a fauna, which consequently has not reached the final size.

(2) Though perhaps not so geologically recent the island may be so remote from a source of fauna and any intermediate 'stepping stones' that propagules arrive only infrequently and the fauna has not reached its final size.

(3) The island is ecologically more diverse, or less diverse, than others in the sequence being considered and the final size of its fauna can be expected to be greater or less than that estimated.

(4) In mountainous islands the true land surface is underestimated in gazetteers. Whereas low flat islands have a land area close to the gazetteer figure the effective areas of mountainous islands are greatly underestimated.

Despite these reasons it is remarkable how frequently the relation $S = CA^Z$ does hold for series of islands and land masses in close relationship to each other, provided that the sequence considered is in the same zoogeographical area and climatic zone, and provided that a sufficiently large taxonomic group is considered to mask any minor disharmonies in the species spectra. The implication of this is that propagules arrive at a much faster rate on newly formed or remote islands than we have been willing to concede in the past and that even relatively uniform looking islands may be more diverse ecologically than we suspect.

That this relationship does or does not hold in any particular sequence of islands or areas is easily determined by plotting the logarithm of the number of species (usually on the left ordinate) against the logarithm of the area when, according to the transform $\lg S = \lg C + Z \lg A$, a straight line should result. This transform is of the same form of the regression line formula $y = a + bx$. If this line is resolved with $\lg S = y$ and $\lg A = x$ then $Z = b$ and $C = \text{antilog } a$ if the latter is positive, or $C = \text{reciprocal antilog } a$ ($C = 1/\text{antilog } a$) if a is negative, as in the Rhopalocera plot whose values are illustrated in figure 2.

Figure 1 shows such a plot for the Heteroptera of the islands, island groups and areas listed in table 3, and figure 2 shows the plot for the Rhopalocera of the islands, island groups and areas listed in table 4. The plots for the British Islands on both these figures are for comparison only, to illustrate certain points I shall raise later, and were not used in the determination of C, Z or the degree of linearity.

On figure 1, and if the five low plots for Australia and the British, Fijian, Hawaiian and Marquesas Islands, are omitted on figure 2, a high degree of linearity of the other plots, which cover a range of islands, island groups and areas along an axis stretching from Indonesia (in figure 2, Ceylon) deep into the Pacific, is evident. However, in order to illustrate a finer structure within the plots in both figures 1 and 2 the abscissa has been 'stretched' by plotting the logarithm to the base 2 of the units of area (1000 km^2) whereas the logarithm to the base 10 of

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the number of species on the left ordinate is plotted. This method of plotting actually conceals the real degree of linearity. How near a straight line *all* the plots (except the British Islands) on figure 1 and the plots (excluding the previously mentioned 5 low ones) of figure 2 actually do

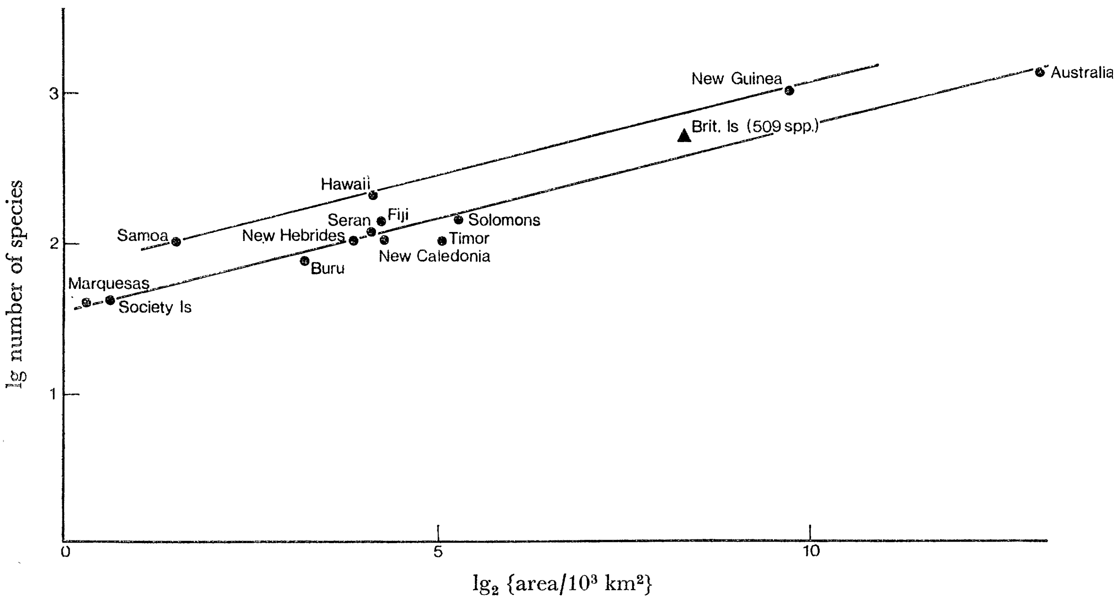

FIGURE 1. Logarithmic plots of the number of species of Heteroptera against the areas of the New Hebrides and surrounding areas.

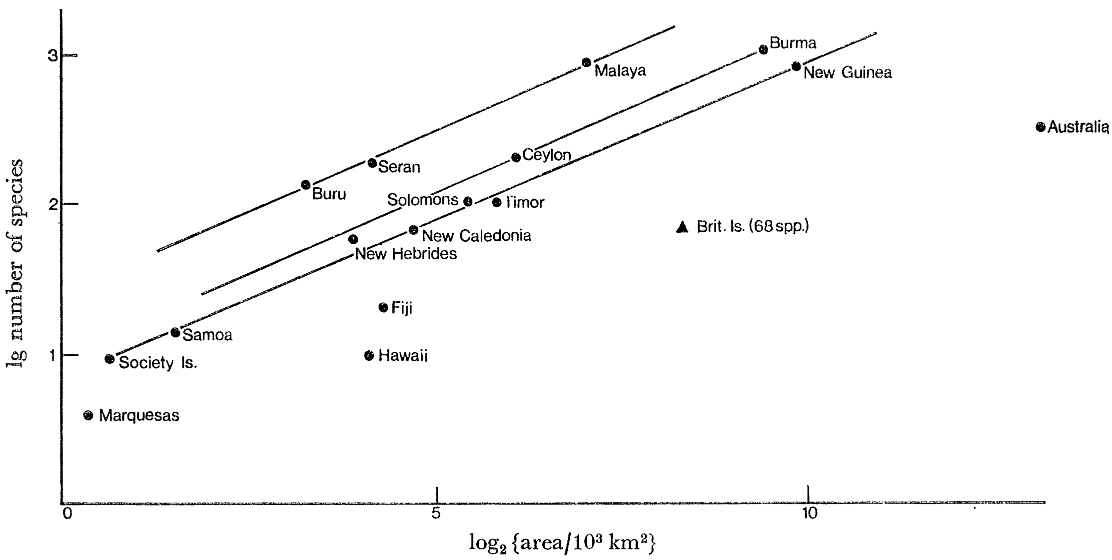

FIGURE 2. Logarithmic plots of the number of species of Rhopalocera against the areas of the New Hebrides and surrounding areas.

lie is illustrated in table 5 below, where the number of species has been plotted as if on the left ordinate to a logarithmic base 10 and the units of area (now 1 km^2) on the abscissa also to the logarithmic base 10, and the values for C, Z and linearity (r) determined.

The parallel lines of finer relationships on figures 1 and 2 were drawn by eye and not by determining the values of C and Z for the parameters used in those two plots.

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Table 5. Values of C and Z in the relation $S = CA^Z$ for the series of areas, island groups and islands on tables 3 and 4 where S and A (in units of 1 km²) are represented by their logarithms to the base 10 and r is the product moment correlation coefficient for each determination

plot	C	Z	r
Heteroptera (table 5 and cf. figure 1)			
all points except Brit. Is.	2.2	0.43	0.94
Marquesas – Society – Buru – New Hebrides – Seran – New Caledonia – Fiji – Timor – Solomons – Australia	2.2	0.41	0.97
Samoa – Hawaii – New Guinea	3.7	0.43	1.0 (0.9996)
Lepidoptera (table 4 and cf. figure 2)			
all points except Marquesas, Hawaii, Fiji, British Is. and Australia.	0.06	0.75	0.92
Society – Samoa – New Hebrides – New Caledonia – Solomons – Timor – New Guinea	0.06	0.73	1.0 (0.9899)
Ceylon – Burma	0.15	0.65	1.0
Buru – Seran – Malaya	0.28	0.68	1.0 (0.9976)

To return to Gressitt's original contention that the fauna of the New Hebrides is unusually depauperate in relation to the Solomon Islands, we see from figures 1 and 2 that this contention is not born out, at least in the Heteroptera and the Rhopalocera, if the different areas of the two are taken into account. The New Hebrides has a fauna of the expected and calculated size.

The position of the New Hebrides on or near the lower of the parallel lines drawn on figures 1 and 2 and the meaning of these lines is a fruitful field for conjecture.

MacArthur & Wilson discuss the concept of the optimum sized fauna an island may accumulate, with often the hint that this is the maximum. I believe that the 'stable' figure ultimately reached is not necessarily the maximum figure that may from time to time be found there and that the word 'optimum' should perhaps be equated with 'stable' or 'final' rather than with 'maximum'. Therefore on both figure 1 and figure 2 I regard the lowest of the lines drawn there as representing the stable condition for the region as a whole.

Where animals and plants are dispersing over the sea from a large source area to an island the proportion of the number of genera relative to the number of species on the island may rise in relation to the ratio in the source area. This follows laws of randomness but tempered because species of some genera, or groupings of genera, are more vagile than the species of other genera available in the source area (figure 3*a*–*c*).

If dispersal is slow it would be some time before certain habitats and niches receive from the source area those species best able to exploit them. This deficiency may be overcome by some of the species that arrive expanding their abilities to exploit the situation. Probably they are intrinsically able to do this in the source area but cannot due to competition. Additionally there may be some formation of new species either by change of an immigrant species into a new species which replaces its parent in its niche, or by fission of an immigrant species into two or more new species each able to exploit an additional niche (figure 3*d*). The fauna by immigration and formation of some new species duly reaches the optimum number of species though there are relatively fewer species per genus than in the source area. This effect is apparent in the last columns of tables 3 and 4 as one goes eastwards from New Guinea or Australia into the western parts of the Pacific Basin.

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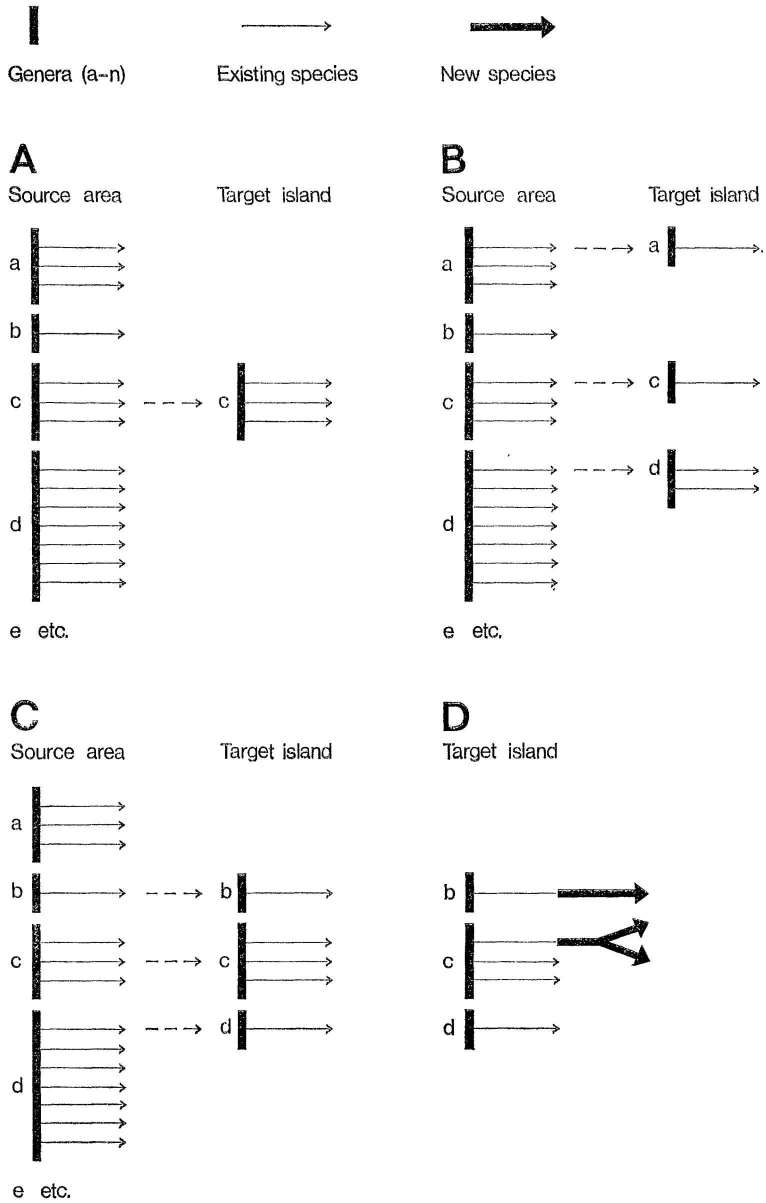

FIGURE 3. Changes in ratio number of species: number of genera in a fauna dispersing to an island. A, this situation is statistically unlikely. Ratio number of species: number of genera similar to source area. B, this situation is statistically more likely and assumes completely random dispersal. Ratio number of species: number of genera lower than in source area. C, this situation is most likely as it assumes that dispersal is not completely random but that some species of some genera are more vagile than others. Ratio number of species: number of genera still lower than in source area. D, after a period some speciation occurs in the target island to fill some unoccupied niches. The speciation occurs by some immigrant species changing gradually into a new one (genus b) and some immigrant species splitting into two or more species (one species of genus c).

If such an island then becomes a source area for dispersal of fauna to an island much further on (from the first source) then the rate of arrival of fauna to this second island may be much slower, and even after a long period relatively few lines only may have arrived, representing only a fraction of the fauna of the intermediate island (figure 4*a*). This may leave a number of habitats unexploited because they are beyond the adaptability of those species which have

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arrived. They may be filled, however, by new species arising (often by sequential fission) out of some of the migrants (figure 4*b*). Hence the number of species per genus may rise again. This effect is also evident on table 3 for the Marquesas and Hawaii.

In some genera there may be an 'explosive evolution' of species. The classic example is that of Darwin's finches in the Galapagos Islands but there are many examples in insects and in other groups. For example, of the 223 species of Heteroptera belonging to 68 genera in Hawaii 116

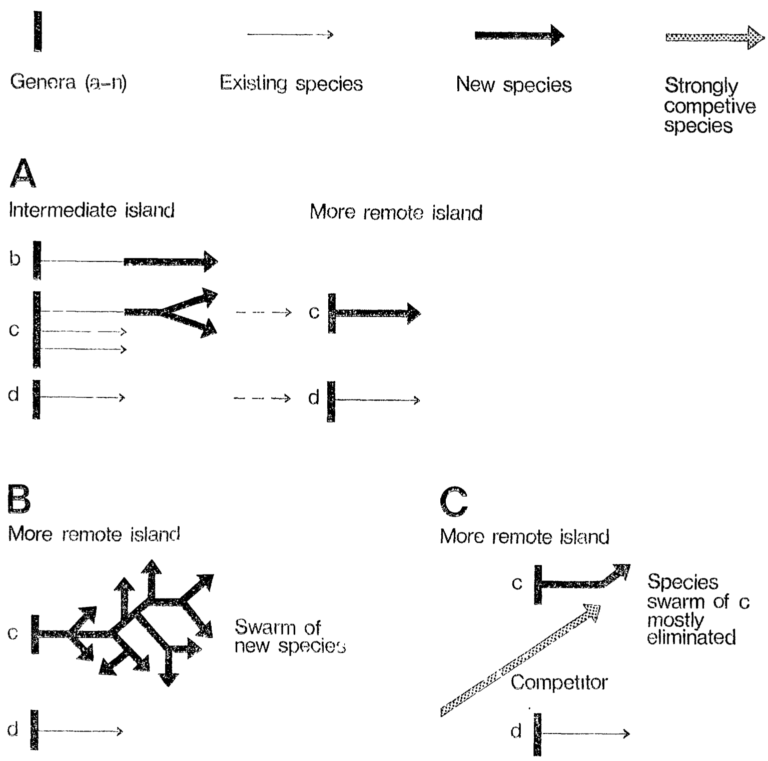

FIGURE 4. Explosive evolution and extinction of species on a remote island. A, very few lines disperse to the remote island and their rate of arrival is very slow. B, an 'explosive' evolution of a 'swarm' of new species from some of the immigrant species occurs. Ratio of number of species: number of genera now higher than on the intermediate island and sometimes higher than in the primary source area. C, a species highly competive to the species of one of the new swarms of species appears, either from elsewhere or the further evolution of one member of the swarm. The majority of the species of the swarm are eliminated and the ratio of the number of species: number of genera drops.

belong to only six genera. In the widespread genus *Nysius* Dallas (Lygaeidae) about half of the world's species occur in Hawaii, where most of them are endemic. In the Marquesas Islands the 41 species of Heteroptera belong to 19 genera. Eleven of these species belong to the genus *Campylomma* Reuter (Miridae) and seven to *Germalus* Stål, and all 18 are endemic.

Such species are usually closely allied to each other and tend to exploit niches not very different from those of their congeners, which implies that during this stage the fauna may be able to exceed the calculated optimum size. It is at this stage I see the heteropterous fauna of New Guinea, Hawaii and Samoa, all points on the upper line of figure 1, to be. The speciation (and subspeciation) in New Guinea is most evident to any student of that fauna. In Heteroptera the genera *Pristhesancus* and *Paloptus* show this feature to an especially marked degree. Samoa is presumably an unstable group of islands lying on the edge of the great subduction zone of the Tonga-Kermadec trench, and the Hawaiian islands form a chain of islands migrating towards

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the southeast by the raising of new islands ahead of the archipelago and the foundering of islands in its wake, with a pattern therefore of continuous migration to the new islands as they appear, without an opportunity for the fauna to stabilize.

The fate of a fauna which is greater than the calculated optimum size may be as illustrated on figure 4*d* where in due course a species more adaptable than any of the species of the local species swarm may develop from amongst them, or arrive from elsewhere, and compete successfully within them, eliminating most of them. The number of species would then fall to the optimum size. I profess to see the faunae of those areas falling along the lower lines of figures 1 and 2 to be either at this stage (figure 4*c*) or at the stage of figure 3*d*.

In figure 2, especially for New Guinea, this effect is masked by the fact that the Rhopalocera are a more recent group than the Heteroptera, and a situation such as illustrated in figure 4*b* for species tends to be at the earlier stage of the formation of a swarm of precursor species (subspecies). The plot on the left ordinate of figure 2 is of species as in figure 1, whereas if subspecies had been the parameter plotted the point for New Guinea would have been much higher while most of the other points would have been shifted but little.

The parallel plots on figure 2 therefore seem to require a different explanation from those on figure 1.

On figure 2 we might profitably begin with the very low points. On figure 1 we see a remarkable linearity (table 5) of all points from Buru to the Marquesas and Hawaiian Islands. The fact that Australia is on the lower stable line indicates that the number of Heteroptera to be expected in an area of given size is not affected by aridity (Australia is one third desert and another third quite arid), or by temperate conditions (half of Australia lies below the tropic), a point which is supported by the point for the temperate British Islands. The numbers of Rhopalocera to be expected is affected by temperature, and also by aridity, as only 16% of the Australian Rhopalocera occur in the arid to desert two thirds of the continent (R. Fisher, personal communication), and if this whole region were to be inundated by the sea only one of the 364 Australian species of Rhopalocera would vanish. We have than a logical explanation of the low plots on figure 2 for Australia (and the British Islands). The other three low points (Fiji, Hawaii and the Marquesas) may be due to the effect of 'drop off' over large distances of ocean. If this is so then the phenomenon occurs far further east along the axis Ceylon to the Marquesas than the traditional theories of dispersion out of southeast Asia suppose, in fact east of the New Hebrides and New Caledonia. However two other remote groups of islands, the Samoan and Society groups, do have the calculated stable final population and this effect does not seem to be the whole answer.

The upper lines on figure 2 are difficult to explain. It may be that Malaya, Seran and Buru are relatively recently uplifted lands and are each drawing their fauna from both eastern and western sources, resulting in another sort of temporary richness than suggested by figure 4*b*. In this case species with very similar ecological preferences arrive simultaneously from two directions and will coexist until by further evolution one or other gains the ascendancy and the number of species drops back to the stable level.

This would imply that there are local centres of evolution in the Indian–Burma area, the area around Borneo and the Celebes, and in New Guinea.

Returning to figures 1–4 the New Hebrides fauna, like the other points along the lowest and allegedly 'stable numbers' line of figures 1 and 2, appears to be either the stage of figure 4*c* or figure 3*d*, probably the latter.

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In any event the fauna has reached its stable or optimum size, at least for Heteroptera and Rhopalocera. In the six index groups only three of the 259 genera listed have more than one or two species (table 9). The oligochaete genus *Metapheretima* Michaelson has 9 species of which 7 are endemic, in the heteropterous genus *Creontiades* Distant (Miridae) there are 8 of which 5 are endemic. The rhopaloceran genus *Euploea* Fabricius (Danaidae) has 6 species, but in this case all are clearly migrants. There are then only incipient signs, or relict traces, of explosive evolution there.

3. Disharmony of the New Hebrides fauna

It follows from the above outline of the features of dispersion to islands that the fauna of islands will be strongly disharmonic, i.e. the proportions of species and higher taxa may be different from those seen on larger land masses, and some groups may be entirely absent. This is a consequence of varying vagility between the members of higher taxa and even within these taxa.

In Heteroptera the families Tessaratomidae, Coreidae, Nepidae and Belostomatidae are absent or poorly represented on islands in the Pacific Basin, whereas the Cydnidae, Lygaeidae, Rhopalidae and Alydidae are proportionately better represented than in either Australia or New Guinea. In Rhopalocera the Papilionidae and Satyridae are proportionately poorly represented in comparison with either southeast Asia, Australia or New Guinea.

Detailed comparisons of the New Hebrides fauna as shown in table 9 with lists of species from the larger lands to the west will show this very clearly.

4. The origins of the invertebrate fauna of the New Hebrides

The origins of the land invertebrates of the New Hebrides are but one facet of the problem of the origin and dispersal of the tropical flora and fauna which extend from India in the west across the Malaysian, Philippine, Indonesian and New Guinea–Solomons areas out into the Pacific as far as Hawaii and Easter Island.

Until global tectonics brought a new perspective to geological history the most popular views tended to see the continents and larger islands fixed, at least since the Cretaceous period, in much their present positions. The tropical fauna and flora of the old world were visualized as originating along the southern and eastern edge of the Eurasian land mass, where much can still be found. Many authorities saw the same region as the source of most of the world's modern taxa, and visualized it as a sort of Pandora's Box from which sprang an endless array of new forms and lines.

No convincing argument was ever advanced to explain the extraordinary fecundity of this tropical source area and why in contrast the rest of the earth was relatively passive; its fecundity was associated with its tropical climate, but then, as now, several other parts of the globe had a tropical climate.

From this source area it seemed a long line of ever improved forms dispersed out to the far ends of the earth. Many crossed into North America via a Behring land bridge and across the Isthmus of Panama region into South America. Marsupials and other earlier forms were deemed to have entered Australia by a convenient land bridge between southeast Asia and Australia which disappeared before the advent of the Eutheria, or by Simpson's 'sweepstakes' route along the Indonesian islands. To the tip of Africa it was but a long overland trek.

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Cases of unexpectedly close relationships between some elements of the faunae and florae of the southernmost regions of the three southern land masses were explained as indicating that these distant areas had as yet only received the earlier forms to disperse, and since nearly all such came from the same source area they would be closely related.

The colonization of Pacific islands by recent plants and animals after the sinking of the supposedly continuous former land bridge between southeast Asia and Australia was viewed in the same light as a diffusion eastwards and southwards of this Indo-Malayan source element where and when it could.

As this diffusion eastwards in later times involved the crossing of a series of water gaps, and past the Philippines and New Guinea these gaps are and were wide, the number of orders, families, genera and species represented should progressively decrease. In the larger land masses like Australia, and perhaps also in New Guinea and New Caledonia, each with a longer history above water than other nearby, some lines would have arrived quite early and undergone some local diversification before the arrival of later, superior lines.

Among the latest authoritative works which expound rather along these lines and which also summarize the earlier views on the topic are those of Darlington (1957) and Gressitt (1961, 1964).

The figures in tables 3 and 4 are only partly consistent with this sort of picture. In the Pacific Basin proper the expected steady drop in numbers of genera and species, if the different land areas are taken into account, is indicated only in the Lepidoptera, and then only eastward of the New Hebrides or New Caledonia.

Since genera are much more ancient than many of their included species, the number of genera in the New Guinea fauna relative to the two areas from which they are supposed to have come is something of a puzzle, even after the obviously Australian genera in the New Guinea fauna are subtracted. Similarly, the depauperate nature of the heteropteran fauna of Timor and islands close by is difficult to explain, for unlike New Guinea, there is a continuous string of quite large islands to their west (all within sight of each other) right to the Malayan Peninsula. The Timor area is subject to a very dry monsoon in the middle months of the year and there is no rain forest there, but there is monsoon forest and it is in this formation that most of the Heteroptera in such a tropical area live.

New evidence from plate tectonics, continental drift and sea floor spreading makes it necessary to reconsider the biogeographic relationships of southeast Asian, Indonesian, Philippine, New Guinea–Solomon Islands and Pacific Islands florae and faunae.

Recent studies of the break-up of the old Gondwanaland supercontinent seem to agree that Africa, South America, Australia, Madagascar, India, New Zealand, New Caledonia, and Antarctica were at one time part of it. Papers by Hurley (1968), Smith & Hallam (1970), Dietz & Holden (1970*a*, *b*), Jones (1971), Tarling (1971), Tarling & Tarling (1971), Veevers (1971), Veevers, Jones & Talbut (1971), and Dewey (1972) summarize modern thinking on the former shape and then break-up of Gondwanaland and give references to other important works. However they do not agree on the relative positions of the component parts of the old Gondwanaland or on the timing of the events which mark their separations. The new interpretations of palaeogeography have caused authors who had regarded southeastern Asia as the one major source area to reconsider their ideas on the biogeography of the Pacific, e.g. Darlington (1965) and Gressitt (1974). Recent investigations of Ridd (1971), Audley-Charles, Carter & Milsom (1972) and Crawford (1974) indicate that some of the eastern portions of

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the present Eurasian land mass, together with one or more of the three large Sunda Islands (Sumatra, Java and Borneo), may also have been originally part of Gondwanaland. If this supposition gains further support concepts of the palaeobiogeography of the whole area from India out into the Pacific may have to be revised.

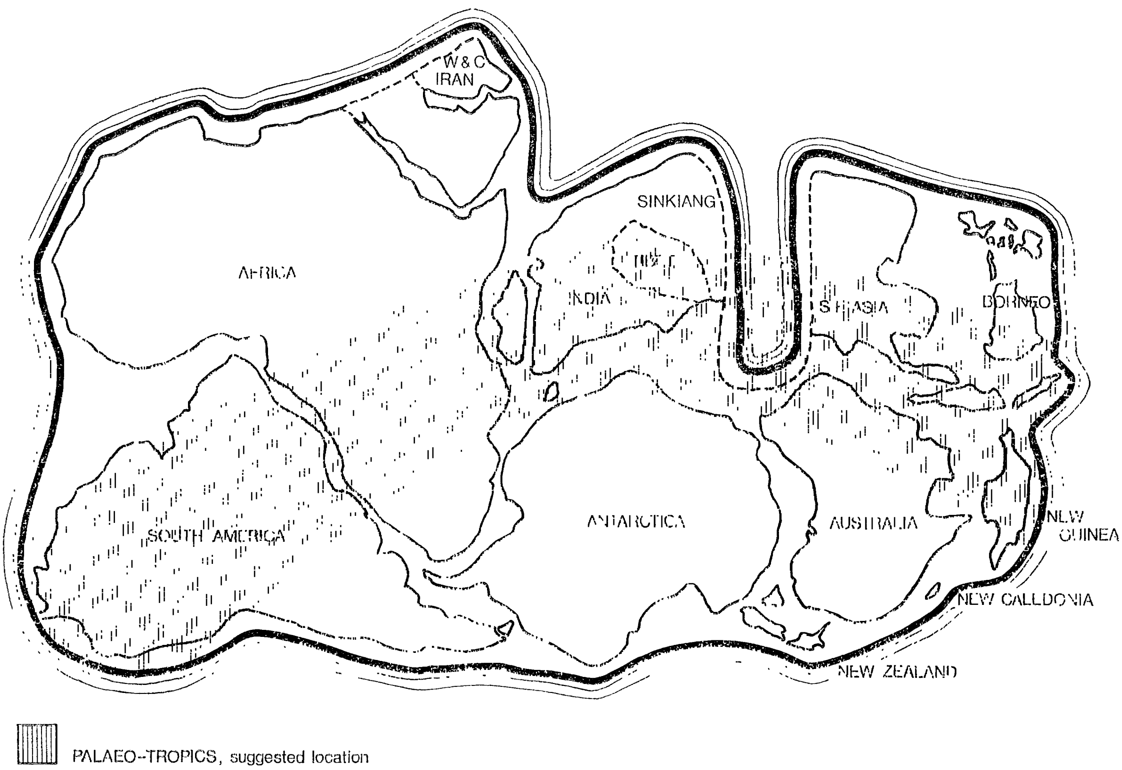

FIGURE 5. Suggested reconstruction of the Gondwanaland plate in Early to Middle Cretaceous times showing the possible location of the beginnings of the tropical biota of today. The coastlines of the present land masses are shown for orientation. No attempt is made to depict what portions of these areas were above the sea nor their coastlines at that time. There was, for example, a marine transgression deep into central Australia which subsequently receded towards the Gulf of Carpentaria, but whose western margin is uncertain. Most of New Guinea was submerged until the Late Pliocene.

Figure 5 is a suggested reconstruction of Gondwanaland as it might have looked in the middle Cretaceous or a little before, in which the lower portion of the reconstruction of Dewey (1972, p. 66) is augmented by the portions of Iran, Tibet and the Tarim which Crawford (1974) shows on his reconstruction, together with the Sinkiang region of China and the southeast Asian region.

Gondwanaland seems to have been largely separated from any more northern masses during the Permian and Lower Triassic, as during those epochs there was a characteristic Gondwanaland assemblage of early plants, reptiles and amphibians. The most significant elements of this biota are summarized by Colbert (1973, figure 31). During the Upper Triassic, the Jurassic, and the Lower Cretaceous there was more interchange between the then northern land mass and Gondwanaland as many groups of dinosaurs which evolved during those epochs are common to both areas. Such Lower Cretaceous angiosperm fossils as are known and identified tend to belong to genera which occur, or have occurred, in both the northern and southern lands

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and include such genera as *Cinnamomum*, *Artocarpus* (Breadfruits), *Magnolia*, *Eucalyptus*, *Casuarina*, *Quercus*, etc.

The development of the prototropical flora and fauna of angiosperms and modern animals can reasonably be argued to have started in the middle Cretaceous. On figure 5 it is interesting to note that all of the present major areas which bear a tropical flora and fauna lie in a band across the presumed Gondwanaland.

The flora of the Upper Cretaceous is well documented only for the northern hemisphere, where it includes a whole series of genera not to be seen in the southern hemisphere until white men introduced them as garden plants (*Platanus*, *Liquidambar*, *Sassafras* etc.), and this evidence along with the fact that placental mammals of that era did not reach Australia suggests that the old division between the northern and southern groups of continents had re-opened. It also suggests that the early tropical biota did not exist in the northern continents.

Students of continental drift disagree a little on the timing of the events which occurred during the break-up of Gondwanaland, though the sequence seems to be fairly well agreed. South America began first to separate from Africa but was to retain a tenuous connexion with Antarctica to the present day. Dewey (1972) sees this beginning as late as the Early Cretaceous (135×10^6 years B.P.) and well established towards the end of the Cretaceous (65×10^6 years B.P.). This moved the South American tropics away from the rest of the then Gondwanaland tropics. The former may then have been further isolated from the southern portion of South America by inundation of the Amazon region, which cut the continent in two (Kurtén 1969). The continued association of southern South America with Antarctica helped save some of the Gondwanaland temperate biota.

Dewey puts the movement north of India, and we may imply also Africa and the southeast Asian block, at about the beginning of the Palaeocene (65×10^6 years B.P.) and these various fragments had made their contact with the Eurasian land mass by the middle of the Eocene (45×10^6 years B.P.). At this time a tropical flora had appeared in western Europe and Britain and may have come from the Gondwanaland fragments, as it had close relationships with the present African and Indo-Malaysian floras.

Simultaneously a tropical flora appeared in North America, with stronger relationships with the present Neotropical flora. This may have migrated north along the isthmus of Panama which was established in the Palaeocene or late Cretaceous, when the Condylarthra, Litopterna, Notoungulata and other early placental mammals entered South America from the North (Pearson, 1964).

As India, along with the other parts of Asia and Africa, came into contact with Eurasia Dewey (1972), Jones (1971) and Veevers (1971) see Australia breaking from Antarctica (65×10^6 years B.P.). At this time also New Zealand and New Caledonia may have separated from Australia, coming to lie on a smaller but parallel plate separated from the Australian plate by a mega-shear (Jones 1971). The southern portions of Africa and Australia, together with New Zealand and New Caledonia, each retained a component of the Gondwanaland temperate biota.

The old Gondwanaland tropics after the separation of South America could have then been subdivided into up to four major lobes, the African, Indian–Ceylonese, southeast Asian–Sundaland and the New Guinea–Australian areas, and the plates would thus not have parted company until many of the modern genera had been established (at the beginning of the Tertiary), though today the species of these same genera are sometimes quite different between the eastern and western 'lobes'.

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The figures in tables 3 and 4 are consistent with this view. For example, if the Australian–New Guinea plate came north without a tropical biota then it is only towards the very end of the Tertiary and into the Recent that New Guinea could have been emergent and in any position to acquire a sizeable flora or fauna, except a few wide ranging waif species and the genera to which they belong, from areas which now lie to its west. It this were so, then the present fauna and flora of New Guinea after subtraction of an element shared with Australia should bear much the same sort of relationship in relative number of genera to the biota of the Moluccas or the Celebes as the Solomons now bear to New Guinea. New Guinea simply would not have had time to develop the considerable number of tropical genera it now has. As the situation is contrary to this it is suggested that New Guinea or some emergent land in that vicinity did bring up the eastern lobe of the later Gondwanaland tropical biota and is at present a source for immigration of this biota to the west as well as to the east. The Celebes and Moluccan areas are richer generically than the Solomons because they are simultaneously picking up a biota diffusing eastwards from the western, or if one exists middle, 'lobe'.

There are still problems to be explained, notably (1) the depauperate nature of the biota of the Lesser Sunda and Banda Arcs, (2) the depauperate nature of the tropical elements in the biota of northern Australia in contrast to New Guinea, and (3) the separation of the fauna of Australia into a northern tropical element and a southern and strongly endemic element, though there is in fact a great deal of mixing of these two elements.

The deserts of Africa, India and Australia seem also to date from the beginning of the Tertiary when these fragments lay close to each other, as there are a number of strong relationships in both plants and invertebrates between them which are not shared with the arid portions of South America. The Australian desert has played a major part in separating the tropical from the temperate elements, as has the African desert. In New Caledonia and New Zealand, where there are no deserts, there is a mixing of tropical and southern temperate genera. The uplift of the eastern mountain ranges of Australia in the late Tertiary has allowed some recent mixing of these two elements to occur in Australia, at least in the east.

There is little agreement on the origins of the islands of the eastern section of the Lesser Sunda Arc and the Banda Arcs. Veevers (1971) sees Timor as having a long connexion with Australia and Audley-Charles *et al.* (1972) see the easternmost islands of the Lesser Sunda Arc, which are colinear with those of the outer Banda Arc, as perhaps fringing islands of the Australian plate throughout the whole period of the drift of the latter northward. In the tables which follow for simplicity I call them the 'Sahul Fragments', though this is not meant to be read as indicating I am sure they are detachments from the margin of the Sahul Shelf in contrast to a fringing arc.

As other developments Cleary & Simpson (1971) see a split developing in the Australian plate and passing through the continent. Audley-Charles *et al.* (1972) believe New Guinea has moved from a position just east of Queensland, where its southern tip was in contact with New Caledonia, to its present position during the drift north of the Australian plate. If this were so then parts of its present northern coast may well have been in contact with Fiji and those portions of the New Hebrides represented now by ultrabasic cores.

Pleistocene climates were much less severe in the continents of the present south than in those of the present north. In Australia, for example, there are signs of Pleistocene glaciation only in the Australian Alps and in Tasmania and in New Guinea only in the highest mountains. This would have been enough though to push the present desert belt of Australia north to about

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the Darwin region and to have led to considerable extinction of tropical elements in the north of Australia and on the Sahul Shelf and the Sahul Shelf Fragments. In the mountains (or islands) of the then New Guinea many survived, as did a few on the higher Sahul Shelf Fragments, In both cases the altitude would have resulted in increased rainfall, as all were bordered by the sea.

Raven & Axelrod (1972) come to conclusions which in some respects are similar and in others different to those suggested above. Their chronology is very much the same as adopted here but they do not take any account of the possibility of the Malaysian and Indo-China block being also of Gondwanaland origin nor, in my opinion, enough account of Antarctica having been either nearer the equator than it now is, or the Southern Hemisphere more equable, as the fossil record shows it to have been.

We have then the possibility that there may be an early trilobed structure, and certainly at least a bilobed one, of the biota of that portion of the tropics extending from India to the islands of the Pacific Basin, but confused by subsequent migration, in *both* ways, between those lobes.

We should no longer be so adamant that the origin and source of dispersal of groups which are found well represented in each of the lobes is invariably in the southeast portion of modern Asia. Therefore the term Indo-Malayan to describe this tropical biota and its presumed origin would now seem to be inappropriate. The terms Oriental or Indo-Pacific, each widely used, are better and less restrictive in meaning.

Whatever the history of the area from New Guinea westwards and southwards and the special problems associated with the florae and faunae of New Caledonia, New Zealand, and the Lesser Sunda and associated southwest Pacific Islands, the original populating of the outer islands of the Pacific Basin has been in the main by eastward dispersal over the sea.

5. The immediate origins of the New Hebrides invertebrate fauna

The New Hebrides fauna has a quite high degree of endemism. For six sample groups which comprised the groups listed on table 1 and the Macroheterocera the average endemism at specific level is 35 %, but as the groups are not of equal size the average is weighted towards those of the Heteroptera and Macroheterocera. Those species and genera which are endemic seem in the main to be most closely related to other species in this general area. Those genera and species which are not endemic (see table 9) generally have a wide distribution outside the New Hebrides on other neighbouring island groups and in many cases over the whole Indo-Pacific region. In the case of the latter we should, I suggest, no longer claim that they are all migrants from as far west as the Indo-Malayan tropics, as the source of a number of them may be not so distant, perhaps in the New Guinea area, from where they could have migrated both east and west (and perhaps north and south also).

The endemics tell us little; from their appearance their ancestors came from various directions. The widespread species also give no indication of their immediate source; any neighbouring island group or large land mass may have provided them. Some indication of origins might be derived from the present distribution of these species which the New Hebrides share with one, or two, island groups or land masses. Data for the index groups are summarized in tables 5 and 6.

There is no clear predominance of any immediate source area over any other in the populating

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of these islands. It may be more meaningful to examine the possible pathways through which the total non-endemic fauna could have arrived. This is attempted in table 8. Table 8 does not take into account the possibility that some of the species may have evolved in the New Hebrides and spread from there, rather than migrating to this archipelago.

Table 6. Numbers of species shared between the New Hebrides and only one other island group or land mass (numbers approximate only)

other area	no. of species in common
Solomon Is.	6
New Guinea	5
Australia	3
New Caledonia	6
Fiji	4
Sahul Fragments	0

Table 7. Numbers of species shared between the New Hebrides and only two other island groups or land masses (numbers approximate only)

other area	no. of species in common
New Guinea area and Solomon Is.	3
New Guinea and Australia	3
New Guinea and Fiji	1
New Guinea and New Caledonia	1
Solomon Is. and Australia	0
Solomon Is. and Fiji	2
Solomon Is. and New Caledonia	0
Australia and New Caledonia	3
New Caledonia and Fiji	1
Sahul Fragments and Australia	2
other Pacific island groups	5

Table 8. Number of species which must have, could have, or could not have arrived in the New Hebrides via the areas listed (total non-endemic species considered 171 and numbers approximate only).

via	only source possible	50 % possible	possible, but more than one other source also possible	unlikely as not recorded there
Solomon Is.	6	4	49	107
New Guinea	5	9	64	69
Australia	3	6	63	95
New Caledonia	6	4	45	107
Fiji	4	4	44	115
other Pacific Is.	3	5	41	111
Sahul fragments	0	3	37	138
extralimital	5	1	39	111

Tables 6–8 show that the Solomon Islands and New Caledonia as possible sole sources are only marginally preferable to New Guinea, Fiji or the other Pacific Islands, and each of these is only marginally preferable to Australia.

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In addition, except in the case of New Guinea, no one of the other areas listed on table 8 could have provided even half of the fauna, as the number of species which very likely or possibly came from each is exceeded by the number of species which most likely did not.

Nearly two thirds of the New Hebrides species are *not* known outside an area stretching from the Sahul Shelf Fragments and the islands immediately west of New Guinea out into the tropical portion of the Pacific Basin. Of those that are known outside this area, several occur only in New Zealand and/or Norfolk Island, which I have treated as extralimital though they are also in the Pacific Basin (but not tropical). Therefore less than a third of the species could have come from the Indo-Malayan region (unless widespread extinction there is assumed).

This last point is consistent with the concept of a bilobed or trilobed structure of the Indo-Pacific tropical fauna.

On the other hand, a number of genera may have come originally from the Indo-Malayan area, but equally they may have been present in the tropical portion of Gondwanaland before the breaking away of the fragments. Such genera would have to have been distinct by the beginning of the Palaeocene.

Presuming that most of the immigrant forms to the New Hebrides did come originally from places generally to the west of these islands, inspection of the data of tables 5 and 6 for possible and most used routes of entry shows that, of the few species which are shared between the New Hebrides and only one or two other areas, about 11 may have come via the Solomon Islands whereas about 18 others are likely to have entered the New Hebrides along a west–east line lying south of the Solomon Islands, say somewhere in the vicinity of Torres Strait. Another eight entered by a route and sometimes a direction other than these two. Whether the New Hebrides may have belonged to an eastward detachment of sections of the old Australian continent or were portions of a small mass on a small plate lying east of the Australian plate, which likewise moved north from Gondwanaland, cannot be decided on the evidence of the collections made by the Expedition.

New Zealand, Norfolk Island, New Caledonia, the Loyalty Islands, and the New Hebrides all have endemic species of Araucariaceae, indicating Gondwanaland affinities either by connection directly to the antarctic portion or to the New Guinea and/or Australian portions. A group of archaic genera of flightless Aradidae (fungus bugs), which occurs in Australia, New Zealand, New Caledonia, the New Hebrides, Fiji, Samoa and New Guinea, suggests also that these land masses may formerly have been connected. However, work on members of this family from the New Hebrides has only just begun. Specimens collected by the expedition are being studied by Mr G. Monteith of the University of Queensland and he has recently visited the New Hebrides to collect more. Results that shed further light on this problem may well come from the study of these insects.

6. Summary of conclusions based on Expedition collections on the origins of the New Hebrides invertebrates

(1) The fauna is not depauperate for a group of islands of this size in this region but is about the expected size.

(2) The composition of the fauna is as one would expect for islands in this region and its main geographic origin was probably from the larger masses of the eastern lobe of the Indo-Pacific. However, the immediate source of most groups is not obvious.

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(3) There are few relationships at species level with the fauna of the supposed western lobe of the Indo-Pacific and regions beyond, but there are more at generic level. The genera concerned are mostly widely spread over the eastern lobe also and there is little evidence to suggest in which lobe they originally developed or whether they were present in the Gondwanaland tropics before the separation of the lobes.

(4) There are few relationships with the temperate faunas of New Zealand and Australia, or the Australian deserts, and not many relationships with New Caledonia.

(5) Sufficient lines arrived in the New Hebrides in time to prevent any but incipient explosive evolution of swarms of new species belonging to relatively few genera. The quite large proportion of endemic (including new) species have probably developed as the result of simple modification of early immigrant species rather than the splitting of older species into two or more new species.

(6) From the proportion of endemic species, which is comparable to smaller island groups in that general area, I do not see the New Hebrides as being wholly a young archipelago, geologically speaking.

7. Distribution patterns within the Archipelago

Table 9, which gives the full distribution of the species as we know them of the index groups both within the New Hebrides and in those areas I have used for comparison, shows that there is some tendency for the three southern islands, Erromanga, Tanna, and Aneityum, to share species which do not occur in the northern islands of Espiritu Santo, Malekula, and Efate, and for these northern islands to share species which are not known in the south. I have not enumerated examples, but the data will be found in table 9.

8. Other groups of invertebrates

For groups other than the five index groups there is not yet much information available.

Yeates (1972, 1973) has examined the nematodes extracted from 14 of our soil samples. There were present 71 species in 59 genera (mean number of species per genus = 1.2). Forty-one of these species (52 %) were endemic. Among the 30 species which are also known elsewhere Yeates recognized 11 cosmopolitan species, 7 pantropical species, 3 southern hemisphere species and 2 with New Zealand affinities. His results are in general accord with conclusions based on the index groups.

Mrs Penelope Greenslade has so far examined Collembola from about a third of the 38 sets of soil samples and has found about 30 species. Isotomidae are the most numerous family followed by Entomobryidae. The seven most common species are also found in the Solomons and three of them in Australia. The 37 litter samples showed signs that condensation of water had occurred in the funnels during extraction, with consequent decay of the specimens, but another 20 species can be recognized; in this case there is a higher proportion of Symphypleona. No Collembola have been recorded previously from the New Hebrides and this collection is important as it confirms previous ideas about the main characteristics of the Pacific Island Collembola and extends the range of some species to the southwest of their previously known distributions.

The conclusions of Solem (1958) on the New Hebrides land and fresh water molluscs are of interest. Excluding West Indian and African 'tropical tramps' introduced by modern man,

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TABLE 9. DISTRIBUTION OF FIVE GROUPS OF INVERTEBRATES IN THE NEW HEBRIDES, IN AREAS ADJACENT, AND BEYOND

For locations of the islands in the New Hebrides archipelago see Lee (this volume, figure 1).

	New Hebrides area								other Pacific areas						extra limital
taxa	Banks/ Santa Cruz	Espiritu Santo	eastern arc	Malekula	Efate	Erromanga	Tanna	Aneityum	New Caledonia	Fiji	other Pacific	Solomons	New Guinea	Australia	
OLIGOCHAETA															
Megascolecidae															
Metapheretima Michaelsen	.	.	.	.	.	.	.	.	.	.	.	f	f	.	Oriental Papuan
agathis m.s.n.	.	.	.	.	.	*	.	.	.	.	.	.	.	.	
apunae m.s.n.	.	*	.	*	.	.	.	.	.	.	.	.	.	.	
buckerfieldi m.s.n.	.	.	.	.	.	.	.	*	.	.	.	.	.	.	
erromangae m.s.n.	.	.	.	.	.	*	.	*	.	.	.	.	.	.	
loriae (Rosa)	.	.	.	.	.	.	.	+	.	.	.	o	o	.	
pickfordi (Gates)	.	+	.	+	+	.	.	.	.	.	.	o	.	.	
speiseri (Mich.)	E	E	E	.	+	+	.	+	.	.	.	.	.	.	
voeltzkowi (Mich.)	.	.	.	+	.	.	.	.	.	.	.	.	.	.	Malagasy
sp.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	
Amynthas Kinberg	.	.	.	.	.	.	.	.	.	f	f	f	.	f	Oriental
esafatae (Bedd.)	R	.	.	+	S	.	.	.	.	.	.	.	.	.	
eltoni m.s.n.	.	.	.	.	*	.	.	.	.	.	.	.	.	.	
sladeni m.s.n.	.	.	.	*	*	.	.	.	.	.	.	.	.	.	
taitensis (Grube)	R	.	.	.	R	.	.	.	o	.	o	.	o	.	
upoluensis Bedd.	.	+	.	+	+	+	+	.	.	o	o	o	.	.	
Pheretima Kinberg	.	.	.	.	.	.	.	.	f	f	f	f	f	.	India to Pacific Is.
montana Kinb.	R	.	.	.	.	.	R	.	o	o	o	o	o	.	
malamaniensis (Benham)	.	.	.	.	R	.	.	.	o	.	.	.	o	.	
unicystis m.s.n.	.	.	.	*	.	*	.	.	.	.	.	.	.	.	
Pithemera Sims & Easton	.	.	.	.	.	.	.	.	.	f	f	f	f	.	
corneri m.s.n.	.	.	.	*	.	*	.	.	.	.	.	.	.	.	
s. sedgwicki (Mich.)	.	.	.	.	.	.	.	+	.	o	.	.	o	.	
s. quadritheca n. subsp.	.	.	.	*	.	*	.	.	.	.	.	.	.	.	
Dichogaster Beddard	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
bolaui (Michaelsen)	.	S	.	S	S	S	.	S	.	.	.	.	.	.	Tropicopolitan
sp.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	
Glossoscolecidae															
Pontoscolex Schmarda	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
corethrurus (Muller)	.	+	.	+	.	+	.	.	.	.	.	.	.	.	Tropicopolitan
ISOPTERA															
Kalotermitidae															
Cryptotermes Banks	.	.	.	.	.	.	.	.	f	f	f	f	f	f	cosmopolitan but absent from Palaearctic
albipes Holmgren	.	.	.	.	+	.	+	.	o	.	o	.	.	.	
Glyptotermes Froggatt	.	.	.	.	.	.	.	.	.	f	f	f	f	f	
schmidti Krishma	.	D	.	.	.	.	.	.	.	.	.	.	.	.	
xantholabrum Hill	.	.	.	S	.	+	.	.	.	.	o	o	o	.	
Neotermes Holmgren	.	.	.	.	.	.	.	.	f	f	f	f	f	f	cosmopolitan except Nearctic
sanctae-crucis Snyder	F	G	.	+	+	G	+	+	.	.	o	o	o	.	
sjostedti (Desneux)	.	D	.	E	D	.	.	.	.	.	.	.	.	.	
n.sp.	.	*	.	.	.	.	.	.	.	.	.	.	.	.	

*, new species.
+, new record from New Hebrides.
D, described from New Hebrides, not known elsewhere. Not rediscovered by expedition.
E, described from New Hebrides, not known elsewhere. Rediscovered by expedition.
F, described from New Hebrides, later reported elsewhere. Not rediscovered by expedition.
G, described from New Hebrides, later recorded elsewhere. Rediscovered by expedition.
R, described from elsewhere, subsequently recorded from New Hebrides. Not found by expedition.
S, described from elsewhere, subsequently recorded from New Hebrides. Found by expedition.
o, species occurs.
f, genus occurs.

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TABLE 9 (*cont.*)

taxa	New Hebrides area: Banks/ Santa Cruz	Espiritu Santo	eastern arc	Malekula	Efate	Erromanga	Tanna	Aneityum	other Pacific areas: New Caledonia	Fiji	other Pacific	Solomons	New Guinea	Australia	extra limital
ISOPTERA (*cont.*)															
Kalotermitidae (*cont.*)															
Procryptotermes Holmgren	.	.	.	.	.	.	.	.	f	f	f	.	.	.	Ethiopian, Malagasy, Neotropical
malekulae MS	.	.	.	*	*	.	.	.	.	.	.	.	.	.	
speiseri Holmgren	.	.	G	.	.	.	.	.	.	o	.	.	.	.	
Rhinotermitidae															
Prorhinotermes Silvestri	.	.	.	.	.	.	.	.	f	f	f	f	f	.	Oriental, Malaysian, Nearctic, Neotropical
inopinatus Silvestri	R	.	.	+	+	.	.	.	o	o	o	o	o	.	
Microcerotermes Silvestri	.	.	.	.	.	.	.	.	f	.	f	f	f	f	cosmopolitan
sp.	.	.	.	*	.	.	.	.	.	.	.	.	.	.	
Termitidae															
Nasutitermes Dudley	.	.	.	.	.	.	.	.	f	f	f	f	f	f	cosmopolitan
kaewiengensis (Hill)	.	S	.	+	+	.	.	.	.	.	o	.	o	.	
novarum-hebridarum (Holmgren)	F	G	F	+	G	.	.	.	o	.	o	o	o	.	Moluccas
DERMAPTERA															
Carcinophoridae															
Carcinophorinae															
Euborellia Burr	.	.	.	.	.	.	.	.	.	.	.	f	f	f	cosmopolitan
annulipes (Lucas)	.	.	.	.	.	R	.	.	.	.	.	.	.	.	cosmopolitan
verhoeffi Zacher	.	S	+	S	+	+	.	+	.	.	.	.	o	o	
Brachylabinae															
Brachylabis Dohrn	.	.	.	.	.	.	.	.	.	.	.	f	.	.	
cordata Brindle MS	.	*	.	.	.	.	.	.	.	.	.	.	.	.	
Labiidae															
Nesogastrinae															
Nesogaster Verhoeff	.	.	.	.	.	.	.	.	f	f	.	f	f	f	
apicalis Hincks	G	G	.	.	.	.	.	.	.	.	.	o	o	o	
bakeri Hinks	.	E	+	E	+	.	.	D	.	.	.	.	.	.	
Sparattinae															
Auchenomus Karsch	.	.	.	.	.	.	.	.	.	.	.	f	.	.	
insularis Brindle MS	.	*	.	.	.	.	.	.	.	.	.	.	.	.	
Labiinae															
Chaetolabia	.	.	.	.	.	.	.	.	f	f	f	f	.	.	
stoneri (Caudell)	.	.	.	.	.	+	.	.	.	o	.	o	.	.	
dentata Brindle	.	.	*	.	.	*	.	*	.	.	.	.	.	.	
Labia Leach	.	.	.	.	.	.	.	.	f	.	f	f	f	f	cosmopolitan
curvicauda (Motschulsky)	.	S	+	R	.	R	.	.	.	.	.	.	.	.	cosmopolitan
bituberculata Brindle	.	+	.	.	.	+	.	.	.	.	.	o	.	.	
Sphingolabis Bormans	.	.	.	.	.	.	.	.	.	.	.	f	.	f	S. Africa to lesser Sundas
hawaiiensis (Bormans)	S	S	+	+	.	+	+	.	.	.	o	.	.	.	Lesser Sundas
Spongiphorinae															
Marava Burr	.	.	.	.	.	.	.	.	.	.	f	f	f	f	cosmopolitan
arachnidis (Yersin)	.	+	.	S	.	R	.	.	.	.	.	.	.	.	cosmopolitan
feae (Dubrony)	.	S	.	.	.	.	.	.	.	.	o	.	o	o	
Chelisochidae															
Chelisoches Scudder	.	.	.	.	.	.	.	.	.	.	f	f	f	f	
morico (Fabricius)	S	S	S	S	S	S	S	S	.	.	.	.	o	.	cosmopolitan ex Neotropical
cheesmanae Hincks	D	.	.	.	.	.	.	.	.	.	.	.	.	.	
Hamaxas Burr	.	.	.	.	.	.	.	.	.	.	f	f	f	.	Burma to Celebes
nigrorufus (Burr)	.	+	.	.	+	+	.	.	.	.	o	o	o	.	Celebes to New Guinea

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TABLE 9 (*cont.*)

taxa	New Hebrides area								other Pacific areas						extra limital
	Banks/ Santa Cruz	Espiritu Santo	eastern arc	Malekula	Efate	Erromanga	Tanna	Aneityum	New Caledonia	Fiji	other Pacific	Solomons	New Guinea	Australia	
HEMIPTERA-HETEROPTERA															
Enicocephalidae															
Systelloderes Blanchard	.	.	.	.	.	.	.	.	.	.	.	.	.	.	N.Z., Crozet Is. and cosmopolitan except Palaearctic
n.sp.	.	*	.	*	.	.	.	.	.	.	.	.	.	.	
n.sp.	.	.	.	.	*	.	.	.	.	.	.	.	.	.	
Oncylcotis Stål	.	.	.	.	.	.	.	.	f	.	.	.	.	f	subantarctic islands and cosmopolitan except Palaearctic and Nearctic
villosulus (Jeannel)	.	+	D	D	.	.	.	.	.	.	.	.	.	.	
Dipsocoridae															
cf. *Ceratocombus*	.	.	.	.	.	.	.	.	.	.	.	.	.	f	Palaearctic. Indo-Pacific
n.sp.	.	.	.	*	*	.	.	*	.	.	.	.	.	.	
n.sp.	.	.	.	*	.	.	.	.	.	.	.	.	.	.	
Schizopteridae															
gen.nov.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
n.sp.	.	.	.	*	.	.	.	.	.	.	.	.	.	.	
Cimicidae															
Cimex Linne	.	.	.	.	.	.	.	.	.	.	f	.	f	f	cosmopolitan
hemipterus Fabr.	.	.	.	.	.	.	.	.	.	.	o	.	o	.	
Nabidae															
Gorpinae															
Gorpis Stål	.	.	.	.	.	.	.	.	.	.	.	f	.	.	
simillimus Harris	.	.	.	F	.	.	.	.	.	.	.	o	.	.	S.E. Asia
Arbela Stål	.	.	.	.	.	.	.	.	.	f	.	f	f	.	Philippines
costalis Stål	.	.	.	R	.	.	.	.	.	o	.	o	.	.	
immista Harris	.	.	.	F	.	.	.	.	.	.	.	.	o	.	
inerma Harris	.	.	.	.	.	.	.	.	.	.	.	.	o	.	
nitidula (Stål)	.	.	.	.	.	.	.	.	.	.	.	o	o	.	India and Philippines
Tropiconabis Kerzhner	.	.	.	.	.	.	.	.	f	.	f	f	f	f	Carolines Indonesia
nigrolineatus (Distant)	.	.	.	.	.	R	.	.	o	.	o	o	o	o	Lord Howe, Norfolk, New Zealand
Anthocoridae															
Gen. ?	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
sp.	.	.	.	.	.	*	.	.	.	.	.	.	.	.	
Miridae															
Cylapinae															
Vanniopsis Poppius	.	.	.	.	.	.	.	.	.	.	.	.	.	.	endemic genus
rufescens	.	D	.	+	.	.	.	.	.	.	.	.	.	.	
Deraeocorinae															
Cimicicapsus Poppius	.	.	.	.	.	.	.	.	.	.	.	.	.	f	New Zealand
n.sp.	.	*	.	*	.	*	.	*	.	.	.	.	.	.	
Bryocorinae															
Felisacus Distant	.	.	.	.	.	.	.	.	.	f	f	.	f	f	India, Indonesia, New Zealand
sp.	.	.	.	+	.	.	.	+	.	.	.	.	.	.	
Grossicoris Carvalho	.	.	.	.	.	.	.	.	f	.	.	.	.	.	
maculatus Carvalho	.	*	.	*	.	.	.	.	.	.	.	.	.	.	
Phylinae															
Campylomma Reuter	.	.	.	.	.	.	.	.	.	.	f	.	.	f	cosmopolitan
sp.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	
sp.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	
Psallus Fieber	.	.	.	.	.	.	.	.	.	.	f	.	.	f	cosmopolitan
sp.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	
sp.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	
Hyalopsallus Carvalho & Schaef.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
n.sp.	.	.	.	.	.	*	.	.	.	.	.	.	.	.	
Cyrtopeltis (*Engytatus*) Reuter	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
nicotianae (Koningsb)	.	.	.	+	.	.	.	.	o	o	.	.	.	o	Malaya, New Zealand

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TABLE 9 (*cont.*)

taxa	New Hebrides area: Banks/ Santa Cruz	Espiritu Santo	eastern arc	Malekula	Efate	Erromanga	Tanna	Aneityum	other Pacific areas: New Caledonia	Fiji	other Pacific	Solomons	New Guinea	Australia	extra limital
HEMIPTERA-HETEROPTERA (*cont.*)															
Orthotylinae															
Halticus Hahn	.	.	.	.	.	.	.	.	.	.	.	.	.	.	widespread
tibialis Reuter	.	+	.	+	+	+	.	.		.	.	.	.	.	Indonesia, Micronesia, Asia, New Zealand
Pseudoloxops Kirkaldy	.	.	.	.	.	.	.	.	.	f	f	.	.	f	
sp.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	
sp.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	
Cyrtorhinus Fieber	.	.	.	.	.	.	.	.	.	f	f	.	f	f	New Zealand
fulvus Knight	.	+	.	.	.	.	.	.	.	o	o	.	o	.	Micronesia, Indonesia, Philippines
lividipennis Reuter	.	.	.	+	.	.	.	.	.	o	o	.	o	o	east Asia through Is. area
N.gen.	.	.	.	.	.	.	.	.	.	.	.	.	.	f	
n.sp.	.	.	.	.	*	.	.	.	.	.	.	.	.	.	
Mirinae															
Bertsa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	India
n.sp.	.	.	.	*	.	.	.	.	.	.	.	.	.	.	
Creontiades Distant	.	.	.	.	.	.	.	.	f	.	f	f	f	f	
pallidifer (Walker)	R	.	.	.	.	.	.	.	.	o	o	.	.	.	eastern Asia to Pacific
modestus (Distant)	.	+	.	+	.	+	.	.	.	.	.	.	.	o	
n.sp.	.	.	.	.	.	*	.	.	.	.	.	.	.	.	
n.sp.	.	.	.	.	.	.	.	*	.	.	.	.	.	.	
n.sp.	.	*	.	.	.	.	.	.	.	.	.	.	.	.	
n.sp.	.	*	.	.	.	.	.	.	.	.	.	.	.	.	
n.sp.	.	*	.	*	.	.	.	.	.	.	.	.	.	.	
biseratense (Dist.)	.	.	.	.	.	+	.	.	.	.	.	.	o	.	
Sidnia Reuter	.	.	.	.	.	.	.	.	.	.	f	.	.	f	
n.sp.	.	.	.	*	.	.	.	.	.	.	.	.	.	.	
Taylorilygus Leston	.	.	.	.	.	.	.	.	f	f	f	.	f	f	New Zealand
sp.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	
oceanicus (Reuter)	.	.	.	.	D	.	.	.	.	.	o	.	.	.	
pacificus Poppius	.	.	.	.	.	.	.	.	.	.	.	.	.	.	endemic sp.
Tinginotum Kirkaldy	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
n.sp.	.	.	.	*	.	.	*	*	.	.	.	.	.	.	
Dolichomiris Reuter	.	.	.	.	.	.	.	.	f	f	.	.	.	f	
c.f. *linearis* Reuter	.	.	.	.	+	+	.	.	o	o	.	.	.	o	
Hyalopeplus Stål	.	.	.	.	.	.	.	.	f	.	f	.	f	f	India eastwards
rama Kirby	.	+	.	.	.	.	.	+	.	.	.	.	.	.	
N.gen.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
n.sp.	.	.	.	.	.	.	.	*	.	.	.	.	.	.	
Tingidae															
Teleonemia Costa	.	.	.	.	.	.	.	.	f	f	f	.	.	f	} introduced widely to control Lantana
scrupulosa Stål	.	.	.	.	.	.	.	.	o	o	o	.	.	o	
Gen.?	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
sp.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	
Nesocypselas Kirkaldy	.	.	.	.	.	.	.	.	.	f	.	.	f	.	
inanna Drake	.	D	.	.	.	.	.	.	.	.	.	.	.	.	
Reduviidae															
Saicinae															
Polytoxus Spinola		.	.	.	.	.	.	.	f	f	f	.	f	f	Ethiopian, Palaeartic, Philippines
hebridanus Villiers	.	+	.	E	+	.	.	.	.	.	.	.	.	.	
c.f. *marianensis* Usinger		+	.	.	.	.	.	.	o	o	o	.	.	o	
Emesinae															
Tridemula Horváth	.	.	.	.	.	.	.	.	f	f	f	.	f	f	E. Asia, Moluccas
babayna (Distant)	.	.	.	.	.	R	.	R	o	.	.	.	o	.	
en.?	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
n.sp.	.	*	.	.	.	.	.	.	.	.	.	.	.	.	
en.?	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
n.sp.	.	*	.	.	.	.	.	.	.	.	.	.	.	.	

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TABLE 9 (*cont.*)

taxa	New Hebrides area								other Pacific areas						extra limital
	Banks/ Santa Cruz	Espiritu Santo	eastern arc	Malekula	Efate	Erromanga	Tanna	Aneityum	New Caledonia	Fiji	other Pacific	Solomons	New Guinea	Australia	
HEMIPTERA-HETEROPTERA (*cont.*)															
Harpactorinae															
Euagoras	.	.	.	.	.	.	.	.	.	.	.	f	f	.	Philippines to Moluccas
sp.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	
Saldidae															
Gen. ?	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
sp. ?	.	+	.	.	.	.	.	.	.	.	.	.	.	.	
Aradidae															
Chinamyersiinae															
Gnostocoris Kormilev	.	.	.	.	.	.	.	.	.	.	.	.	.	.	endemic genus
gressitti Kormilev	.	D	.	.	.	.	.	.	.	.	.	.	.	.	
Aneurinae															
Aneurus Curtis	.	.	.	.	.	.	.	.	.	.	f	f	f	f	cosmopolitan
cheesmani Kormilev	D	.	.	.	.	.	.	.	.	.	.	.	.	.	
Carventiinae															
Zimmermania Usinger	.	.	.	.	.	.	.	.	.	f	.	f	f	.	
usingeri Kormilev	.	.	.	D	.	.	.	.	.	.	.	.	.	.	
Mezirinae															
Ctenoneurus Bergroth	.	.	.	.	.	.	.	.	f	f	f	.	f	f	Ethiopian, New Zealand
minutus Kormilev	.	.	.	D	.	.	.	.	.	.	.	.	.	.	
Pictinellus Usinger & Matsuda	.	.	.	.	.	.	.	.	f	f	f	.	f	.	
moturikiensis Kormilev	.	.	.	R	.	.	.	.	.	o	.	.	.	.	
Mezira Amyot & Serville	.	.	.	.	.	.	.	.	f	f	f	f	f	f	cosmopolitan
micronesica Esaki & Matsuda	.	+	.	.	.	.	.	.	.	o	o	o	o	.	
Camerarius Distant	.	.	.	.	.	.	.	.	.	f	f	f	f	.	Aru Islands
sp. ?	.	.	.	.	.	+	.	.	.	.	.	.	.	.	
Acaraptera Usinger & Matsuda	.	.	.	.	.	.	.	.	f	f	f	f	f	.	New Zealand
sp. ?	.	*	.	.	.	.	.	.	.	.	.	.	.	.	
Coreidae															
Gen. ?	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
sp. ?	.	.	.	.	.	.	.	+	.	.	.	.	.	.	
Mictis Leach	.	.	.	.	.	.	.	.	f	f	f	.	f	f	Palaeartic, Ethiopian, Malagasy, India to Philippines
oceanensis Distant	.	+	.	.	.	.	.	.	.	.	.	.	.	.	endemic species
profana (Fabr.)	.	+	.	+	.	.	.	+	o	o	o	.	o	o	
Amblypelta Stål	.	.	.	.	.	.	.	.	f	.	.	f	f	f	
bilineata Stål	.	.	.	.	S	.	.	.	o	.	.	.	.	.	
Leptoglossus Guerin	.	.	.	.	.	.	.	.	f	f	f	f	f	f	Tropicopolitan
australis (Fabr.)	.	S	.	.	S	.	S	.	o	o	o	o	o	o	Tropicopolitan
Alydidae															
Leptocorisa Latreille	.	.	.	.	.	.	.	.	f	f	f	f	f	f	Oriental to Australian Regs.
acuta Thunb.	.	.	.	.	S	S	.	.	o	o	o	o	o	o	
discoidalis Walker	.	.	.	S	S	.	S	.	.	o	.	o	o	.	
Noliphus Stål	.	.	.	.	.	.	.	.	.	f	f	f	f	f	Philippines, Malaya, Indonesia
discopterus Stål	.	.	.	.	.	.	.	.	.	.	o	.	.	.	
insularis Stål	.	.	.	.	.	.	.	.	.	o	.	.	.	.	
Melanacanthus Stål	.	.	.	.	.	.	.	.	f	f	f	.	.	f	east Asia to Moluccas
sp. ?	.	.	.	.	+	.	.	.	.	.	.	.	.	.	
Riptortus Stål	.	.	.	.	.	.	.	.	f	f	f	+	f	f	Ethiopian, Malagasy, E. Asia, Philippines, etc.
sp. ?	.	.	.	+	.	.	.	.	.	.	.	.	.	.	
Rhopalidae															
Leptocoris	.	.	.	.	.	.	.	.	f	.	f	f	f	f	Ethiopia, Nearctic, India to Philippines
tagalica (Burm.)	.	.	.	.	.	.	S	.	o	.	o	.	.	o	
Lygaeidae															

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TABLE 9 (*cont.*)

	New Hebrides area								other Pacific areas						extra limital
taxa	Banks/ Santa Cruz	Espiritu Santo	eastern arc	Malekula	Efate	Erromanga	Tanna	Aneityum	New Caledonia	Fiji	other Pacific	Solomons	New Guinea	Australia	
HEMIPTERA-HETEROPTERA (*cont.*)															
Lygaeinae															
Graptostethus Stål	.	.	.	.	.	.	.	.	f	f	f	.	f	f	
manillensis (Stål)	.	.	.	.	.	.	.	.	.	o	o	.	o	o	Africa through S. Europe to Indonesia
nigriceps Stål	.	.	.	.	.	+	+	.	o	o	o	.	.	o	
sp.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	
Spilostethus Stål	.	.	.	.	.	.	.	.	f	.	f	f	f	f	Palaearctic, Ethiopian, Indopacific
hospes (Fabr.)	.	+	.	+	.	.	.	.	o	.	o	o	o	o	
Nesostethus	.	.	.	.	.	.	.	.	.	f	f	.	.	.	
n.sp.	.	.	.	.	.	.	*	.	.	.	.	.	.	.	
Orsillinae															
Nysius Dallas	.	.	.	.	.	.	.	.	f	f	f	f	f	f	cosmopolitan
c.f. *caledoniae* Distant	.	+	.	.	.	+	+	.	o	.	o	.	.	.	
Ischnorrhynchinae															
Neocrompus China	.	.	.	.	.	.	.	.	.	f	f	.	f	.	
kellersi China	.	.	.	.	.	.	.	.	.	.	o	.	.	.	
Cyminae															
Cymoninus Breddin	.	.	.	.	.	.	.	.	.	f	.	.	.	.	
sechellenis (Bergroth)	.	.	.	.	.	.	.	.	.	o	.	.	.	.	Africa to Fiji
Geocorinae															
Germalus Stål	.	.	.	.	.	.	.	.	f	f	f	.	f	f	African, Oriental, Philippines
unipunctatus (Montandon)	.	+	.	E	E	.	.	+	.	.	.	.	.	.	
Rhyparochrominae															
Botocudo Kirkaldy	.	.	.	.	.	.	.	.	.	.	f	f	.	f	American, African, Oriental, etc.
sp. ?	.	+	.	+	+	+	+	+	.	.	.	.	.	.	
Brentiscerus Scudder	.	.	.	.	.	.	.	.	f	.	f	f	f	f	
sp.	.	+	.	.	.	+	.	.	.	.	.	.	.	.	also New Zealand
Gen. nov.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
sp.nov.	.	*	.	.	.	.	.	.	.	.	.	.	.	.	
Gen. nov.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
sp. nov.	.	.	.	.	.	.	*	*	.	.	.	.	.	.	
Narbo	.	.	.	.	.	.	.	.	.	.	f	.	.	f	Oriental, Indonesian, Philippines
biplagiatus	.	.	.	.	.	+	.	.	.	.	o	.	.	o	
Pachybrachius	.	.	.	.	.	.	.	.	f	f	f	f	f	f	cosmopolitan
sp.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	
sp.	.	+	.	.	.	+	+	.	.	.	.	.	.	.	
Bedunia	.	.	.	.	.	.	.	.	.	f	f	f	.	f	Ceylon to Micronesia
c.f. *nesiotes*	.	.	.	.	.	.	+	+	.	o	o	.	.	.	
Colobathristidae															
Phaenacantha	.	.	.	.	.	.	.	.	.	f	.	.	f	f	
sp.	.	+	.	+	+	.	.	+	.	.	.	.	.	.	
Pyrrhocoridae															
Dysdercus	.	.	.	.	.	.	.	.	f	f	f	f	f	f	Tropicopolitan
sidae (Montrouzier)	.	R	.	S	.	S	S	S	o	o	o	o	o	o	
decussatus (Boisduval)	.	S	.	R	+	R	+	.	.	.	.	o	o	.	Indonesia
Pentatomidae															
Platynopus Amyot & Serville	.	.	.	.	.	.	.	.	f	f	f	f	f	f	Africa, Malaysia, Philippines, Indonesia
melacanthus (Boisduval)	.	S	.	S	.	.	.	.	o	o	o	o	o	.	
Caystrus Stål	.	.	.	.	.	.	.	.	.	.	.	.	f	f	African, Indonesia, Philippines
pallidolimbatus (Stål)	.	+	.	.	.	.	.	.	.	.	.	.	o	o	
Gen. nov.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
sp.nov.	.	.	.	.	.	.	.	*	.	.	.	.	?	?	
Axiagastus Dallas	.	.	.	.	.	.	.	.	.	.	.	f	f	f	Oriental and Indonesian
campbelli Distant	.	S	.	S	.	.	.	.	.	.	.	o	.	.	

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

TABLE 9 (*cont.*)

	New Hebrides area								other Pacific areas						extra limital
taxa	Banks/ Santa Cruz	Espiritu Santo	eastern arc	Malekula	Efate	Erromanga	Tanna	Aneityum	New Caledonia	Fiji	other Pacific	Solomons	New Guinea	Australia	
HEMIPTERA-HETEROPTERA (*cont.*)															
Pentatomidae (*cont.*)															
Catacanthus Spinola	.	.	.	.	.	.	.	.	f	f	f	.	f	f	Oriental through Philippines and Indonesia
n.sp.	.	.	.	.	.	.	.	*	.	.	.	.	.	.	
Nezara Amyot & Serville	.	.	.	.	.	.	.	.	f	.	.	.	f	f	cosmopolitan
viridula (Linn.)	.	.	.	.	.	.	.	S	o	.	.	.	o	o	cosmopolitan
Gastraulax Herr. Schaeff.	.	.	.	.	.	.	.	.	f	f	.	.	f	.	
simmondsi Izzard	.	.	.	F	+	.	+	.	.	o	.	.	.	.	
Plautia Stål	.	.	.	.	.	.	.	.	f	f	.	f	f	f	India through Indonesia
sp.	.	+	.	.	.	.	.	.	.	o	.	.	.	.	
Glaucias Kirkaldy	.	.	.	.	.	.	.	.	f	f	f	f	f	f	New Zealand
sulcata (Montrouzier)	.	.	.	.	.	.	.	+	o	.	o	.	o	o	
sp.	.	+	.	.	.	.	+	.	.	.	.	.	o	.	
Cuspicona Dallas	.	.	.	.	.	.	.	.	f	.	.	.	f	f	Indonesia, New Zealand, Philippines
privata Walker	.	.	.	+	.	.	+	G	o	.	.	.	.	o	
cheesmanae Gross	.	*	.	*	.	.	.	.	.	.	.	.	.	.	
Vitellus Stål	.	.	.	.	.	.	.	.	f	f	.	.	f	f	Moluccas
sp. c.f. *forficuloides*	.	+	.	.	.	.	.	.	.	.	.	.	.	o	
Pegala Stål	.	.	.	.	.	.	.	.	f	f	f	.	.	f	
c.f. *virens* Distant	.	+	.	.	+	.	.	.	o	.	.	.	.	.	
Scutelleridae															
Coleotichus White	.	.	.	.	.	.	.	.	f	f	f	f	f	f	Sumatra
sordidus Walker	.	S	.	.	.	S	S	S	o	o	o	.	.	o	
Tectocoris Hahn	.	.	.	.	.	.	.	.	f	f	f	.	f	f	S.E. Asia through Indonesia
diophthalmus (Thumb)	.	S	.	.	S	.	S	.	o	o	o	.	o	o	S.E. Asia through Indonesia
Lampromicra Kirkaldy	.	.	.	.	.	.	.	.	f	.	.	f	f	f	Malaysia through Indonesia
sp.	.	+	.	+	.	.	+	+	.	.	.	.	.	.	
Calliphara Germar	.	.	.	.	.	.	.	.	f	.	.	f	f	f	Orient to Moluccas
praslinia (Guérin-Méneville)	.	.	.	S	S	.	.	S	.	.	.	o	o	o	Indonesia
Eucorysses (Amyot & Serville)	.	.	.	.	.	.	.	.	f	.	.	.	.	.	Ceylon to Lesser Sunda Islands
sp.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	
Plataspidae															
Brachyplatys Boisduval	.	.	.	.	.	.	.	.	.	f	f	f	f	f	Africa to Indonesia
pacificus Dallas	.	S	.	S	S	S	S	S	.	.	o	o	.	.	
Cydnidae															
Adrisa Amyot & Serville	.	.	.	.	.	.	.	.	f	.	f	.	.	f	Orient to Moluccas
sp.	.	+	.	.	.	.	+	.	.	.	.	.	.	.	
Aethus Dallas	.	.	.	.	.	.	.	.	.	.	f	f	f	f	Oriental
indicus (Westw.)	.	.	.	.	.	.	.	.	.	.	.	o	o	o	Africa to New Guinea
Geotomus Mulsante & Rey	.	.	.	.	.	.	.	.	f	f	f	.	f	f	Africa to New Guinea
pygmaeus (Dallas)	.	S	.	S	.	.	S	S	o	o	o	.	o	.	
Gerridae															
Halobates Eschscholtz	.	.	.	.	.	.	.	.	f	f	f	f	f	f	circumtropical
flaviventris Eschscholtz	R	.	R	.	.	.	.	.	.	.	o	.	.	.	Africa to Micronesia
proavus White	.	R	.	.	.	.	.	.	.	.	.	o	.	.	
Linmogonus Stål	.	.	.	.	.	.	.	.	f	f	f	.	f	f	cosmopolitan
luctuosus (Montrouzier)	.	.	.	.	S	.	.	.	o	o	o	.	.	o	
Hydrometridae															
Hydrometra Lamark	.	.	.	.	.	.	.	.	f	.	.	f	f	f	cosmopolitan
c.f. *risbeci* Hungerford	.	+	.	.	.	.	.	.	o	.	.	.	.	o	New Zealand
Notonectidae															
Anisops Spinola	.	.	.	.	.	.	.	.	f	f	f	f	f	f	New Zealand
cheesmanae Lansbury	.	.	.	D	.	D	.	.	.	.	.	.	.	.	
nasuta Fieber	.	R	.	.	.	.	.	.	.	.	o	o	o	o	
tahitiensis	R	.	.	S	S	.	.	.	.	.	o	.	o	o	Tahiti to Andaman Island
Enithares Spinola	.	.	.	.	.	.	.	.	f	.	.	f	f	f	
bergrothi Montandon	R	S	.	.	R	R	R	R	o	.	.	.	.	.	

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TABLE 9 (*cont.*)

taxa	New Hebrides area								other Pacific areas						extra limital
	Banks/ Santa Cruz	Espiritu Santo	eastern arc	Malekula	Efate	Erromanga	Tanna	Aneityum	New Caledonia	Fiji	other Pacific	Solomons	New Guinea	Australia	
HEMIPTERA-HETEROPTERA (*cont.*)															
Ochteridae															
Ochterus Latreille	.	.	.	.	.	.	.	.	f	.	.	f	f	f	widespread
australicus Jaczewski	.	.	.	.	.	.	.	.	o	.	.	o	o	o	
RHOPALOCERA															
Hesperiidae															
Hasora Moore	.	.	.	.	.	.	.	.	f	f	.	f	f	f	India, China through Philippines
chromus bilunata Butler	.	.	.	.	.	.	.	.	.	o	.	.	o	o	Japan to New Guinea
kh. khoda Mabille	.	.	R	.	.	.	.	.	o	.	.	o	o	o	India to New Guinea
Badamia Moore	.	.	.	.	.	.	.	.	f	f	.	.	f	f	India to New Guinea
atrox flava Evans	.	.	.	.	+	.	.	.	o	o	o	.	.	.	
exclamationis (Fabr.)	.	.	.	.	+	.	.	+	.	o	o	o	o	o	
Borbo Evans	.	.	.	.	.	.	.	.	f	.	.	f	f	f	India, China to New Guinea
cinnara (Wallace)	.	+	R	+	R	+	.	+	o	.	.	o	o	o	
Pelopidas Walker	.	.	.	.	.	.	.	.	.	.	.	f	f	f	Turkey to Australia
agna agnata Evans	.	.	.	.	.	.	.	.	.	.	.	o	o	o	Ceylon to New Guinea
lyelli mathewi Evans	.	.	.	.	.	.	.	.	.	.	.	o	o	o	Moluccas
Papilionidae															
Graphium Scopoli	.	.	.	.	.	.	.	.	f	.	.	f	f	f	old world
c.f. *sarpedon* subsp.	.	+ (sight)	.	.	.	+ (sight)	.	.	.	.	.	o	o	o	
Papilio Linnaeus	.	.	.	.	.	.	.	.	f	f	.	f	f	f	widespread
canopus hypsicles Hew.	.	+	.	+	+	+	+	+	.	.	.	.	.	o	Lesser Sundas, Tenimbar
Pieridae															
Catopsilia Hübner	.	.	.	.	.	.	.	.	f	.	.	f	f	f	Oriental and Indonesian
pomona (Fabr.)	.	+	.	.	+	.	.	.	.	.	.	o	o	o	Madagascar through India, Malaysia, Indonesia and Philippines
pyranthe lactea Butler	.	+	.	+	R	R	+	.	.	.	.	o	.	o	
Eurema Hübner	.	.	.	.	.	.	.	.	f	.	.	f	f	f	
hecabe sulphurate Butl.	.	+	.	+	S	+	+	+	o	o	.	o	o	o	
Delias Hübner	.	.	.	.	.	.	.	.	f	.	.	.	f	f	Moluccas, Lesser Sundas
nysa santo Talbot	.	.	.	.	.	.	.	.	o	.	.	.	.	o	
Anapheis Hübner	.	.	.	.	.	.	.	.	f	f	f	.	f	f	Africa to Indonesia
java peristhene Boisd.	.	+	.	+	S	.	+	.	o	o	o	.	.	o	
Cepora Dallman	.	.	.	.	.	.	.	.	f	.	.	f	f	f	Oriental to Indonesia
perimale jeanneli Viette	.	.	.	+	+	.	+	.	o	.	.	o	o	o	Lesser Sundas, Moluccas
Appias Hübner	.	.	.	.	.	.	.	.	f	.	.	.	f	f	
albina wallacei Butler	.	.	.	.	.	.	.	+	o	.	.	.	o	.	
Nymphalidae															
Danaus Kluk	.	.	.	.	.	.	.	.	f	f	f	f	f	f	cosmopolitan
p. plexippus (Linn.)	.	S	.	S	S	S	S	S	o	o	o	o	o	o	cosmopolitan
chrysippus petilia (Stoll)	.	+	.	+	.	.	.	.	.	o	.	.	o	o	Lesser Sundas
affinis albistriga Talbot	.	.	.	.	+	+	+	.	o	.	.	o	o	o	
hamata moderata Butler	.	+	R	+	S	+	+	.	.	o	.	o	o	o	
pumila hebridesia Butler	.	+	.	+	+	+	+	+	o	.	.	.	.	.	
Euploea Fabricius	.	.	.	.	.	.	.	.	f	f	f	.	f	f	India to Indonesia
lewinii libybaea Fruhs.	.	S	R	R	S	S	S	S	o	o	o	.	.	.	
boisduvali bakeri Poult.	R	S	R	R	S	S	.	.	.	.	.	.	.	.	
boisduvali torvina Butler	.	.	.	.	.	.	S	S	.	.	.	.	.	.	Lesser Sundas, Moluccas
sylvester tristis Butler	R	.	R	R	R	.	.	R	.	.	.	.	.	o	Timor
treitschkei jessica Butler	R	R	R	R	S	+	.	.	o	.	.	.	o	o	
tulliolus incompta Herr. Schaef.	R	.	.	.	.	+	S	.	o	o	.	.	o	o	Lesser Sundas
nemertes subspp.	R	S	R	R	S	+	R	S	o	o	.	o	o	.	Moluccas
Melanitis Fabricius	.	.	.	.	.	.	.	.	f	f	f	f	f	f	India to Indonesia
leda solandra Fabr.	R	+	.	+	S	+	+	+	o	o	o	o	o	o	
Mycalesis Hübner	.	.	.	.	.	.	.	.	.	.	.	f	f	f	Moluccas and Lesser Sundas
perseus perseus Fabr.	.	.	.	R	.	.	.	.	.	.	.	.	o	o	Timor

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TABLE 9 (*cont.*)

taxa	New Hebrides area: Banks/ Santa Cruz	Espiritu Santo	eastern arc	Malekula	Efate	Erromanga	Tanna	Aneityum	other Pacific areas: New Caledonia	Fiji	other Pacific	Solomons	New Guinea	Australia	extra limital
RHOPALOCERA (*cont.*)															
Nymphalidae (*cont.*)															
Orsotriaena Wallengen	.	.	.	.	.	.	.	.	.	.	.	.	f	f	S.E. Asia through to Indonesia
medus (Fabricius)	.	+	.	.	R	.	.	.	.	.	.	.	.	.	India to Indonesia
Doleschallia C. & R. Felder	.	.	.	.	.	.	.	.	f	f	.	f	f	f	India, Philippines, Indonesia
bisaltide montrouzieri Butl.	.	+	.	S	S	.	.	.	o	o	.	o	o	o	
bisaltide herrichi Butler	.	.	.	.	.	R	+	+	.	.	.	.	.	.	
Hypolimnas Hübner	.	.	.	.	.	.	.	.	f	f	f	f	f	f	cosmopolitan exc. Palaearctic
antilope n.subsp.	.	+	.	.	+	.	.	+	.	.	.	o	o	o	Moluccas, Timor area
bolina subspp.	.	+	R	.	S	S	+	+	o	o	o	o	o	o	New Zealand, India
missippus (Linn.)	.	+	.	.	.	.	.	.	.	.	.	o	o	o	Pantropical, believed introduced in the Americas
o. octocula Butler	R	+	.	+	+	+	+	.	o	.	.	.	.	.	
pithoeka Kirsch	.	.	.	.	+	+	.	.	.	.	.	o	o	.	
Precis Hübner	.	.	.	.	.	.	.	.	f	f	f	f	f	f	Old World, tropics
v. villida (Fabricius)	.	+	.	S	S	+	.	+	o	o	o	o	o	o	
Parthenos Hübner	.	.	.	.	.	.	.	.	.	.	.	f	f	.	India to Indonesia
sylvia n.subsp.	R	+	.	.	.	.	.	.	.	.	.	o	o	.	
Yoma Doherty	.	.	.	.	+	+	.	.	.	.	.	f	f	.	India to Moluccas
sabina Cramer	.	.	.	+	.	.	.	.	.	.	.	o	o	.	India to Moluccas
Vagrans Hemming	.	.	.	.	.	.	.	.	f	.	f	f	f	f	India to Pacific
egista bowdenis Butler	.	+	.	.	S	+	.	+	o	.	o	o	o	o	India, Indonesia, Marianas
Acraea Fabricius	.	.	.	.	.	.	.	.	f	f	f	f	f	f	Africa to Pacific
andromacha (Fabr.)	.	.	.	+	R	+	.	+	o	o	o	o	o	o	
Lycaenidae															
Arhopala Boisduval	.	.	.	.	.	.	.	.	.	.	.	f	f	f	S.E. Asia to Moluccas
araxes eurisus Druce	.	.	.	.	.	.	.	.	.	.	.	o	o	o	
Deudorix Hewitson	.	.	.	.	.	.	.	.	.	f	f	.	f	f	India to Indonesia
epijarbas Moore	.	.	.	.	+	.	.	.	.	o	o	.	o	o	India to Indonesia
Nacaduba Moore	.	.	.	.	.	.	.	.	f	f	f	f	f	f	India, Japan, S.E. Asia, etc.
nebulosa Druce	.	.	.	.	.	.	.	.	.	.	.	.	o	o	Moluccas
n. novahebridensis Druce	.	.	.	.	.	.	.	.	.	.	.	.	.	.	endemic species
m. mallicollo Druce	.	.	.	R	+	.	R	.	.	.	.	.	.	o	Lesser Sundas
biocellata armatilla Butler	.	.	.	.	+	.	+	.	o	.	.	.	.	.	
dyopa Herrich-Schaeffer	.	+	.	.	+	.	.	.	.	o	.	.	.	.	
Catapyrops Toxopeus	.	.	.	.	.	.	.	.	f	f	.	f	f	f	
florinda (Butler)	.	.	.	.	.	.	.	.	o	o	.	.	.	o	Timor area
keira nebulosa (Druce)	.	.	.	.	R	R	.	.	.	.	.	o	.	.	
Jamides Hübner	.	.	.	.	.	.	.	.	.	f	f	f	f	f	Ceylon to Formosa and Moluccas
bochus kava Druce	.	.	.	+	+	+	.	.	.	.	o	.	.	.	Timor area, Ceylon, Malaysia, etc.
bochus pulcherrima Butler	.	.	.	.	.	.	.	.	.	.	o	.	.	.	
morphoides Butler	.	.	.	.	.	.	.	.	.	.	.	.	.	.	endemic species
c. carissima Butler	.	.	.	.	.	.	.	.	o	.	.	.	o	.	
celeno Cramer	.	.	.	.	.	.	.	.	.	.	.	o	o	o	Islands west of New Guinea
Syntarucus Butler	.	.	.	.	.	.	.	.	.	.	.	f	f	f	India to Moluccas
plinius pseudocassius Murray	.	.	.	.	.	.	.	.	.	.	.	o	o	o	
Lampides Hübner	.	.	.	.	.	.	.	.	f	.	.	.	.	f	western Europe to Hawaii
boeticus (Linnaeus)	.	S	.	+	.	.	.	.	o	.	.	.	.	o	Europe, Africa, Asia
Catochrysops Boisduval	.	.	.	.	.	.	.	.	f	f	f	f	f	f	
panorumus caerulea Tite	.	.	.	.	.	.	.	.	o	.	.	o	o	o	Timor area. Island west of New Guinea
taitensis Boisduval	.	+	.	.	+	+	.	+	.	o	o	.	.	.	Africa through India and S.E. Asia
Euchrysops Butler	.	.	.	.	.	.	.	.	f	f	f	f	f	f	Africa through to Indonesia
cnejus subsp.	.	+	.	+	S	R	.	+	o	o	o	o	o	o	
Zizula Chapman	.	.	.	.	.	.	.	.	.	f	.	f	f	f	Tropicopolitan
hylax (Fabricius)	.	+	.	.	.	.	.	.	.	o	.	o	o	o	Oriental, Ethiopian and Neotropical

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TABLE 9 (*cont.*)

taxa	New Hebrides area: Banks/ Santa Cruz	Espiritu Santo	eastern arc	Malekula	Efate	Erromanga	Tanna	Aneityum	other Pacific areas: New Caledonia	Fiji	other Pacific	Solomons	New Guinea	Australia	extra limital
RHOPALOCERA (*cont.*)															
Lycaenidae (*cont.*)															
Zizina Fabricius	.	.	.	.	.	.	.	.	.	f	f	.	f	f	Africa to Japan and Indonesia
labradus Godardt	.	+	.	+	+	+	.	.	o	o	.	o	o	o	New Zealand, Norfolk Is.
Zizeeria Chapman	.	.	.	.	.	.	.	.	.	f	f	.	.	f	Europe, Africa, S.E. Asia
a. asulus (Herr. Schaeff.)	.	.	.	.	.	.	.	.	.	o	o	.	.	o	Africa to Indonesia
Luthrodes Druce	.	.	.	.	.	.	.	.	.	.	.	f	f	.	Molucca and Lesser Sunda Is.
cleotas excellens Butler	.	+	.	.	R	.	+	.	o	.	.	o	o	.	Lesser Sunda Is.
Ionolyce Toxopeus	.	.	.	.	.	.	.	.	.	.	.	f	f	.	Moluccas
sp.nov.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	

and perhaps a dozen species transported by earlier migrations of men, the land snails of each archipelago of the region show almost 100% endemism. Solem recognizes three types of distribution of the higher taxa which he calls Palaeo-Oriental, Southern Relict ('Australasian') and Pacific Ocean ('Polynesian'). In his explanation of these terms the Palaeo-Oriental equates fairly well with what I have called the Gondwanaland tropical element (as after the separation of India and South America), the Southern Relict would appear to be the temperate section of the Gondwanaland fauna brought north by southern Australia and New Zealand and the Polynesian seems to indicate again the former integrity of some of the islands lying to the east of Australia. Of the 73 New Hebridean land snail species 15 are probably distributed by man, 57 are endemic and one is shared with New Caledonia. The endemic species belong to 24 genera of which 14 occur also in Fiji and 8 in New Caledonia, 4 of these 8 are widely distributed over the Pacific. Solem's interpretation of the distribution of the families in the area was developed before the new theories of plate tectonics were proposed, and in terms of invasions of the whole area from the far northwest. No doubt different conclusions can be drawn now, but his listed distributions of the higher taxa do not seem to be significantly different from those described here for the other groups.

Cheesman (1957) believed the New Hebrides may have belonged to a southern land mass lying east of Australia and cites some evidence from plants and insects to support this.

Gressitt (1961, 1964) saw the New Hebrides fauna as quite impoverished in contrast to the Solomons, Fiji and New Caledonia and claimed the Solomons have many times more species and several times as many genera as the New Hebrides. This claim is not born out by our results. He saw the whole tropical area from the Indo-Malayan region eastwards into the Pacific Basin as one which he called the Oriental Region. To its south lay his (temperate) Australian region comprising southern Australia, New Zealand and the Chatham Islands, the two regions blending in northern Australia and southern New Guinea. Apart from differing from the opinion expressed here on the size of the New Hebrides fauna, and tending to see an origin for more of the Pacific Basin fauna in the Indo-Malayan area than I would concede, the remainder of his observations agree reasonably closely with the propositions advanced here. Gressitt (1974) takes much the same views on the fauna of the New Hebrides and the Pacific Basin as in his earlier works but modifies some of his concepts in the light of continental drift.

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Author's Note added in proof (July 1975). Since the manuscript of this paper was forwarded to the printer several additional species which ought to be added to table 9 were noticed in the literature or in our material. They are:

subfamily	taxon	new description (D) or new record (R)	New Hebrides localities	other localities
Kalotermitidae	*Incisitermes semilunaris* (Homlgren)	R	Aneityum	New Caledonia
Aradinae	*Aradus erraticus* Kormilev	R	Epi	Torres Straits Islands, Queensland.
Calisiinae	*Calisius hebridensis* Kormilev	D	Espiritu Santo, Malekula	—
Carventiinae	*Carventus hebridensis* Kormilev	D	Efate	—
	Carventus malekulensis Kormilev	D	Malekula	—
	Carventus minusculus Kormilev	R	Efate	Fiji
Mezirinae	*Mezira subtriangula* Kormilev	R	not stated	New Guinea, Solomon Is.
	Arbanatus subparallelus Kormilev	D	Efate	Bismark Archipelago

Also *Pictinellus moturikiensis* Kormilev has become *Arbanatus moturikiensis* (Kormilev). (The few consequent small alterations necessary in some of the tables and figures for complete accuracy have no significant effects on any of the authors conclusions.)

References (Gross)

Audley-Charles, M. G., Carter, D. J. & Milsom, J. S. 1972 Tectonic development of eastern Indonesia in relation to Gondwanaland dispersal. *Nature Phys. Sci.* **239**, 35–39.

Cheesman, L. M. 1957 Biogeographical significance of Aneityum Island, New Hebrides. *Nature, Lond.* **180**, 903–904.

Cleary, J. R. & Simpson, D. W. 1971 Seismotectonics of the Australian continent. *Nature, Lond.* **230**, 239–241.

Colbert, E. H. 1973 *Wandering lands and animals.* New York: Dutton.

Crawford, A. R. 1974 A greater Gondwanaland. *Science, N.Y.* **184**, 1179–1181.

Darlington, P. J. 1957 *Zoogeography: the geographical distribution of animals.* New York: Wiley.

Darlington, P. J. 1965 *Biogeography of the southern end of the world.* Cambridge: Harvard University Press.

Dewey, J. F. 1972 Plate tectonics. *Scient. Am.* **226**, 56–68.

Dietz, R. S. & Holden, J. C. 1970*a* Re-construction of Pangaea: breakup and dispersion of continents, Permian to Present. *J. geophys. Res.* **75**, 4939–4956.

Dietz, R. S. & Holden, J. C. 1970*b* The breakup of Pangaea. *Scient. Am.* **223**, 30–41.

Gressitt, J. L. 1961 Problems in the zoogeography of Pacific and Antarctic insects. *Pacif. Ins. Mongr.* **2**, 1–94.

Gressitt, J. L. 1964 *Pacific basin biogeography.* Honolulu: Bishop Museum.

Gressitt, L. J. 1974 Insect biogeography. *A. Rev. Ent.* **19**, 293–321.

Hurley, P. M. 1968 The confirmation of continental drift. *Scient. Am.* **218**, 52–64.

Jones, J. G. 1971 Australia's Caenozoic drift. *Nature, Lond.* **230**, 237–239.

Kurtén, B. 1969 Continental drift and evolution. *Scient. Am.* **220**, 54–64.

MacArthur, R. H. & Wilson, B. C. 1967 *The theory of island biogeography.* New Jersey: Princeton University Press.

Pearson, R. 1964 *Animals and plants of the Cenozoic era. Some aspects of the faunal and floral history of the past sixty million years.* London: Butterworths.

Preston, F. W. 1962 The canonical distribution of commonness and rarity. Part I. *Ecology* **43**, 185–215. Part II. **43**, 410–432.

Raven, P. H. & Axelrod, D. I. 1972 Plate tectonics and Australian paleobiogeography. *Science, N.Y.* **176**, 1379–1386.

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Ridd, M. F. 1971 South east Asia as part of Gondwanaland. *Nature, Lond.* **234**, 531–533.
Smith, A. G. & Hallam, A. 1970 The fit of the southern continents. *Nature, Lond.* **225**, 139–144.
Solem, A. 1958 Biogeography of the New Hebrides. *Nature, Lond.* **181**, 1253–1255.
Tarling, D. H. 1961 Gondwanaland, palaeomagnetism and continental drift. *Nature, Lond.* **229**, 17–21, 71.
Tarling, D. H. & Tarling, M. 1971 *Continental drift: a study of the Earth's moving surface*. New York: Doubleday.
Veevers, J. J. 1971 Phanerozoic history of Western Australia related to continental drift. *J. geol. Soc. Aust.* **18**, 87–96.
Veevers, J. J., Jones, J. G. & Talent, J. A. 1971 Indo-Australian stratigraphy and configuration and dispersal of Gondwanaland. *Nature, Lond.* **229**, 383–388.
Williams, C. B. 1964 *Patterns in the balance of nature and related problems in quantitative ecology*. London: Academic Press.
Yeates, G. W. 1972 Taxonomy of some soil nematodes from the New Hebrides. *N.Z. Jl Sci.* **15**, 673–697.
Yeates, G. W. 1973 Abundance and distribution of soil nematodes in samples from the New Hebrides. *N.Z. Jl Sci.* **16**, 727–736.

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