

THE ZOOGEOGRAPHY OF THE EAST INDIAN ARCHIPELAGO¹

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TRANSLATED FROM THE DUTCH BY

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TRANSLATOR'S NOTE

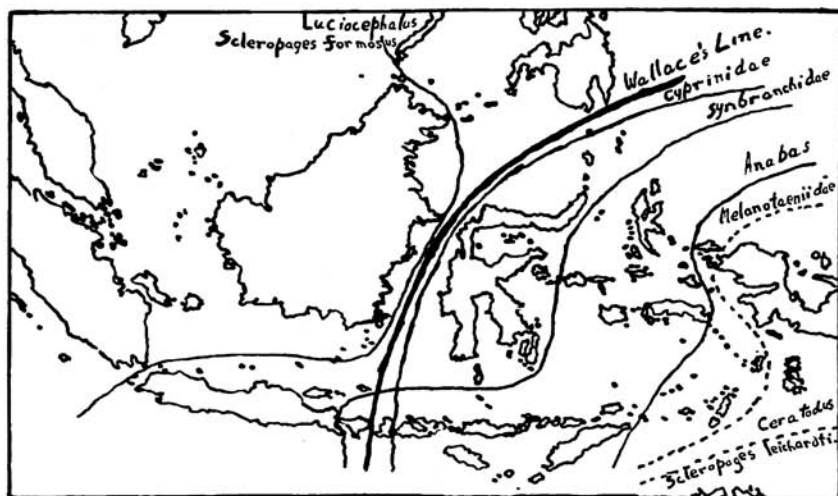
NEARLY a year ago I received from my friend Dr. van Kampen a paper which seemed at once of such present interest and general excellence that I believed it should be made available for English-speaking students of zoogeography. Its original publication in Java makes it inaccessible to many. The essay was written to be read before the Debating Club of the Batavian Royal Natural History Society; and I am under obligation to both Dr. van Kampen and the president of the Koninklijke Natuurkundig Vereeniging for permission to make and publish this translation.

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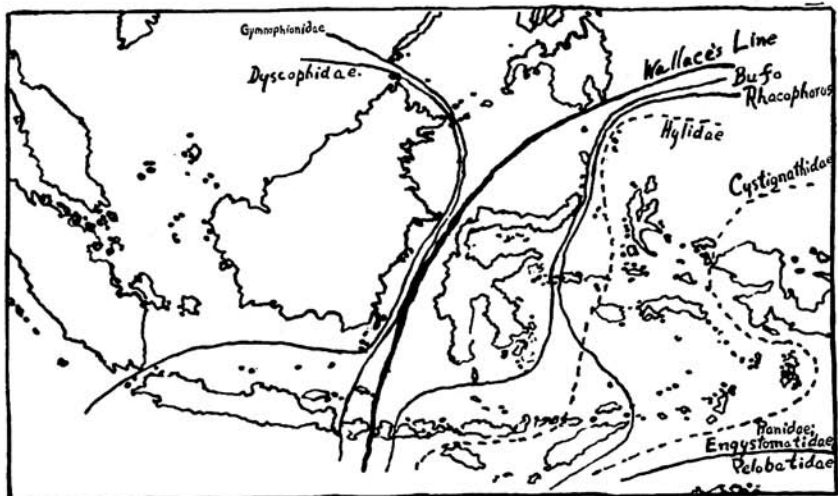
Even a superficial examination shows us that a very considerable faunistic differentiation exists between the western and eastern halves of the Indo-Australian archipelago. Perhaps this differentiation is most evident amongst the mammals. If one compares, for instance, Sumatra with New Guinea, one finds at once upon the first-named island a number of large mammals, such as the tiger and the leopard, the rhinoceros and the tapir, which are of course unknown upon New Guinea. Here, on the other hand, certain marsupials are found, as well as the strange egg-laying ant-eaters, of which there is no sign upon Sumatra. One finds similar phenomena upon

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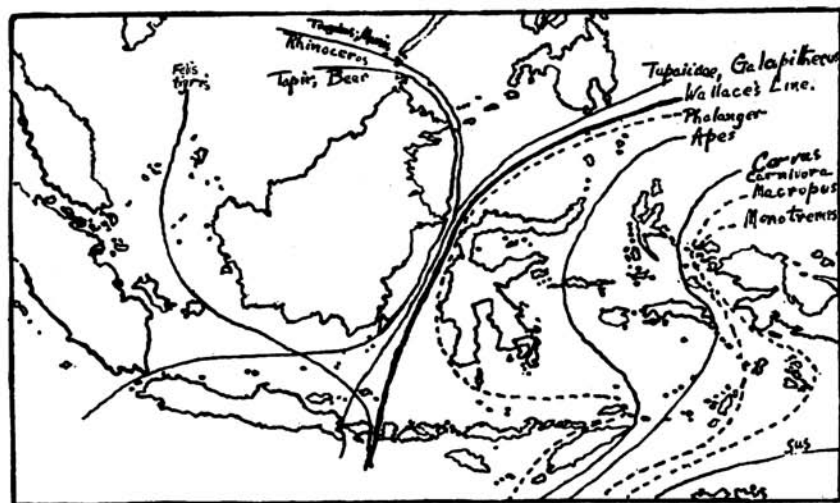
studying most of the other groups of animals. Faunistic differences comparable to these which we have here mentioned for the Indian archipelago are naturally found in other regions of the world. It is not long ago that zoologists gave little or no consideration to these phenomena of distribution, but simply busied themselves with describing hundreds of new species without caring whence these species came. It was only at the beginning of the nineteenth century that a change came about.



Freshwater Fishes.



Amphibians.



Mammals.

EXPLANATION OF THE MAP

On the map are given the easterly boundaries of a number of Indian groups of animals, shown by continuous line; and the westerly boundaries of some Australian forms, shown by broken lines. Map No. 1 is based on fresh-water fishes; No. 2, upon amphibians; No. 3, upon mammals. On all three maps, Wallace's line is shown as an extra heavy one; and it will be seen by comparing this with the lines bounding the ranges of other classes that it has no value as a zoogeographic boundary. The Indian animals in very many cases reach to the eastward of it, while the Australian forms do not reach out to it, so naturally do not cross it. One sees at once that the Indian and Australian components of the fish fauna are widely differentiated; and that among amphibians and mammals it is necessary to take nearly the entire eastern half of the archipelago as the transition region which we have mentioned before.

They then began to divide up the earth into a larger number of "kingdoms," by separating one fauna from another according to its similarities or differences.

These divisions differed not alone according to their originators, but also greatly in accordance with the group of animals upon which they happened to be based. Finally, it became generally agreed that Wallace, the founder of the zoogeography of the present day, had found a division which held for all land animals. That this opinion was in reality incorrect will be shown later on.

The divisions proposed by Sclater date from about 1858. Founded on the distribution of birds, it has been held by almost everybody up to the present time as covering the distribution of birds and mammals. This division of the earth is, with a few minor changes, as follows:

1. *Palearctic Region*.—Europe; the greater part of Asia; Africa to the north of Atlas and Sahara.

2. *Ethiopian Region*.—Africa to the south of the Sahara; Madagascar and the neighboring islands; South Arabia.

3. *Indian or Oriental Region*.—India to the south of the Himalayas; south China; the western portion of the Indian archipelago.

4. *Australian Region*.—Eastern portion of the Indian archipelago; Australia; New Zealand; Polynesia.

5. *Nearctic Region*.—North America as far as northern Mexico.

6. *Neo-Tropical Region*.—Southern Mexico; the Antilles; South and Central America.

The subdivisions of these regions need not be taken up in more detail here. But it should be mentioned that Huxley in 1868 proposed the name of *Notogæa* for the Australian and Neo-tropical regions taken together as contrasted to the others, which he combined under the name of *Arctogæa*.

Zoogeography deals not alone with the question of how animals are spread over the face of the earth, but

rather attempts to explain the reasons for the peculiarities of their distribution. At first men sought the explanation especially in climatologic factors, or else they considered each zoogeographic region to be a particular center of special creation. Finally the theory of evolution in this, as in so many other subjects, spread a new light. Zoogeography has become, then, especially since it came under the leadership of Wallace, an essentially historical study.

Every type of animal has come into existence upon some specially circumscribed part of the earth, and has spread itself thence over a greater or lesser extent of surrounding territory. Only very seldom does it happen that one spreads itself over the whole earth or even a considerable part of it; the great majority are hindered by unsurmountable obstacles, and inhabit only a limited region. Zoogeography, then, on the one hand, must deal with the means of dispersal, and on the other hand with the hindrances which species may encounter.

These obstacles are, in general, spoken of as being of a climatic or orographic nature. The latter are not surprising; for if the surface of the earth were homogeneous in character, then the animals would naturally have distributed themselves in girdles or zones at even distances from the equator. Indeed, this is to a considerable extent the case with the marine fauna, against the spread of which such hindrances as we have mentioned play a minor rôle. Thus we can differentiate and recognize an arctic, a circumtropical, and an antarctic zone (Ortmann). The Indopacific Ocean, obviously belonging to the circumtropical belt, is faunistically a single entity, and to this our archipelago belongs.

While in earlier times climate and natural conditions were held as being most answerable for differences in land and fresh-water faunas, they far more slowly took the orographic factors at their true value; though naturally the first-named influences must not now remain unheeded.

Great deserts, high mountain ranges, and extensive

bodies of water are all impassable to most land animals. We can not then wonder that the fauna of North Africa is sharply differentiated from that which lies to the south of the Sahara; and so also that the Himalayas form a boundary between two zoogeographic kingdoms.

How, now, are we to explain the cases where two similar faunas are separated from each other by what seems to be a similarly impassable barrier? How is it possible, to draw an example from our own archipelago, to make comprehensible the fundamental similarity of the fauna of Sumatra and of the Malay Peninsula? In this case only two possibilities are thinkable: either by some means or other the animals have been able to get across the sea, by flying or swimming, by the aid of wind or drift-wood, or through transport by human agency; or else there has been an earlier land connection which has now completely disappeared.

Above all others this last mentioned explanation is the most fruitful for further investigation, as in general it involves calling to aid geologic factors to elucidate the reason for zoogeographic evidences of differentiation. To Wallace belongs the credit of having brought to light the true import of these factors. Zoogeography, then, may now be considered as a science auxiliary to geology.

It is evident after stating the foregoing premises that it is quite impossible to divide up the earth into sharply defined areas of distribution which hold alike for all groups of animals. Different groups owe their spread over the earth to different reasons. Some may pass easily over mountains; others (notably birds) may as easily cross the sea; some are far more dependent upon climate and the condition of the ground on which they exist than others; the oldest groups of animals, speaking geologically, have had far more time to distribute themselves than have the younger; etc. We must, however, confess that, following in the footprints of Wallace, perverted conceptions have long held sway regarding the Indian archipelago.

As to the worth of zoogeographic data in explanation of these phenomena of dispersal, we must consider the frequent impossibility of gathering all the evidence bearing on the subject. This is not the place to do more than set forth in merest generality the justification for the assertions made in the following outline. These drawbacks, moreover, surely should not hinder us from continuing, with careful circumspection, to compare most inquisitively all the available facts, being certain that many important conclusions will be reached in the end. In this manner I purpose to give here a review of that which has already been learned regarding the Indian Archipelago.

The Indo-Australian Archipelago is, from a zoogeographic point of view, a region of the highest importance. It owes this special prominence to its lying upon the boundary of two great kingdoms, the Indian and the Australian, which show a greater faunistic differentiation between one another than the rest of the old world.

Sal. Müller first noticed this difference which exists between the western and the eastern portions of the Archipelago; and, following the teachings of his time, he laid this distinction to the influence of climate and natural conditions; so that while the western half has a purely Indian character, the eastern portion—the islands of which, generally speaking, are smaller—form an area of transition to the conditions which obtain in Australia. Müller in his conclusions came in reality nearer to the present opinion than did Wallace; but the real, underlying causes of the differences remained, of course, hidden from him. The boundary between both regions he drew through the Straits of Macassar, and in the south between the islands of Sumbawa and Flores; while with some doubts he placed the island of Mindanao in the eastern, and the remaining Philippine islands in the western, section of the group.

The first to bring geologic explanations to aid in explaining the faunistic differences between the eastern and the western parts of the archipelago was Earl. But

Wallace was the foremost really to back up his opinions with valid evidence in setting forth the theory which has proved so pregnant with suggestion.

Wallace, who made long journeys among the islands, was the discoverer of the famous "Wallace's Line," as it was named by Huxley, which still, to the present day, is carefully explained in many text-books; though in reality it is disproved, and Wallace himself is not so sure of its existence during the later years of his life.

According to Wallace's original opinion, based especially upon the distribution of mammals, birds and insects, he saw a sharp faunal boundary that could be drawn through the archipelago, which ran to the eastward of the Philippines, continued between Borneo and Celebes, and on between Bali and Lombok. The fauna to the west of this line was said to be Indian; to the east, Australian. Wallace's dictum is well known, that the faunas of Bali and Lombok are more sharply differentiated from one another than those of England and Japan.

Wallace sought the explanation of these phenomena in the fact that the western half of the archipelago had in earlier times been connected with the Indian mainland, the eastern islands with Australia; and that they remained joined together until they were divided by narrow arms of the sea. The exceptions which existed Wallace explained in part through transport across water, part as their being remains of the earliest fauna which had lived upon the old land connection between Asia and Australia.

According to the researches of more recent times, among which should be mentioned especially those of Von Martens, Max Weber, and the Sarasins, it becomes evident that such a sharp boundary as Wallace drew does not exist. Not only is there none where he drew it, but no such line exists anywhere in the archipelago. Of course it is possible to draw a line which apparently bounds the distribution of some single group; and Pelsener, upon the ground of the dispersal of molluscs, has constructed a new line which runs eastward of Celebes

and Timor, and which has been named by its author "Weber's Line." But taking the fauna as a whole it is quite certain that no line may be drawn; but, rather, we may lay out a transition zone in which the fauna of India and that of Australia are mingled, and wherein from the west to the east the Australian components increase more and more in number; and on the other hand, the Indian tend to die out. All of this region belongs to the eastern half of the archipelago from Celebes to New Guinea, and included in it we find a part of the Polynesian² Islands; but it is necessary to keep in mind that even the boundaries of this transition region are not sharply defined.

The justice of the position taken here will presently be sustained by some examples gleaned from among vertebrate animals, especially from fresh-water fishes, amphibians and mammals. All three groups, on account of the small likelihood of their being spread abroad over the sea, are of much importance to us.

First of all, however, the origin of the fauna of Australia merits a word. It is now commonly agreed that in past times this island formed an essential part of Asia, connected by a previously existing land-bridge which included the archipelago as it exists to-day. Formerly this connection was considered to have occurred during the Jurassic period (Neumayer's "Jura-Continent"). The finding, however, of deep sea deposits laid down in Jurassic times in different parts of the archipelago (*e. g.*, on Borneo, Celebes and Buru) has made it seem more probable that the mooted connection was delayed until the Cretaceous period; and along this connection, then, the marsupials and lung-fishes spread to Australia; as well as also the teleost, *Scleropages leichardti*, of which a near relative, *Scleropages* (= *Osteoglossum*) *formosus*, is now found upon Borneo and Sumatra, but upon no other

² Van Kampen uses the word *Polynesian* in a sense which is to us fundamentally wrong. He means to include the Melanesian Islands of the Bismarck and Solomon groups.

islands in the region lying between. It is not at all impossible that also a considerable portion of the present fauna of the Australian part of the Archipelago exists as a *Relict-fauna* coming down from the earliest times, although the geologic data warn us that Celebes and a considerable portion of the remaining archipelago was also covered by the sea during the Cretaceous period (Sarasin, 1901). So that, according to the latest geological evidence, it becomes apparent that in the Cretaceous period the archipelago could not all have been above water. Australia may well have received its ancient fauna from South America (Sarasin), or may equally well have had a connection with nearer India lying to the southward of the existing Archipelago (see Verbeek's *Molukkenverslag*).

However that may have been, in any case the Indo-Australian continuity may well have been broken in Tertiary times, and thus the penetration of the Indian fauna into Australia have been brought to an end. Animals which up to that time had reached out into the archipelago would be unable any longer to reach Australia.

To such a class belong, for example, among the fresh-water fishes, the family Cyprinidæ; among the amphibians, the Ranidæ; both of which are present in the Indian region by numerous representatives, while they are wanting in Australia. It is thus of importance for us to search out what may be the easterly boundary of such groups in the archipelago. Following Wallace's theory, the line which he constructed should answer this purpose. As a matter of fact the Cyprinidæ have served as one of the most important arguments for his opinion, since they did really stop at the supposed boundary line; since then, however, upon Bali we find a single pair of species of this family (*Barbus maculatus* and *Raspora argyrotænea*). During the expedition of the Siboga, Professor Weber, happened by chance to collect *Raspora* upon Lombok (Weber, 1902, A); and I myself lately found the Gurami fish-ponds of the old pleasure-palace of Narmada filled with another

species of *Raspora*,³ so that the boundary of the Cyprinidæ is thus moved to the eastward of Lombok.

Absolutely different is the real condition of the Ranidæ. This family has penetrated throughout all of New Guinea and western Polynesia; one single species, indeed (*Rana papua*), having reached the Cape York Peninsula of Queensland. Other Indian families of amphibians (Engystomatidæ, Pelobatidæ) have also reached to New Guinea. We see here then the boundaries of this transition region well defined, the westerly by the Cyprinidæ, the easterly by the Ranidæ.

Among the families of the strictly fresh-water fishes conditions are similar; and some have even reached

	Sumatra	Borneo	Java	Wallace's Line		Timor	Celebes	Amboin	Halmahera	New Guinea	Australia
				Ball	Lombok						
FISHES											
Notopteridæ	+	+	+	-	-	-	+	-	-	-	-
Osteoglossidæ	+	+	+	-	-	-	-	-	-	-	+
Cyprinidæ	+	+	+	+	+	-	-	-	-	-	-
Siluridæ	+	+	+	+	-	-	-	-	-	+	+
Symbranchidæ	+	+	+	-	-	-	+	-	-	-	-
Cyprinodontidæ	+	+	+	-	+	-	+	-	-	-	-
Melanoteniidæ	-	-	-	-	-	-	-	-	-	+	+
Ophiocephalidæ	+	+	+	-	-	-	+	+	+	-	-
Anabantidæ	+	+	+	+	+	+	+	+	+	-	-
Nandidæ	+	+	+	-	-	-	-	-	-	-	-
Mastacembelidæ	+	+	+	-	-	-	-	-	-	-	-
Osphronomenidæ	+	+	+	+	-	-	-	-	-	-	-
AMPHIBIANS											
Gymnophionians	+	+	+	-	-	-	-	-	-	-	-
Pelobatidæ	+	+	+	-	-	-	-	-	+	-	-
Hylidæ ⁴	-	-	-	-	-	+	-	+	+	+	+
Bufoyidæ	+	+	+	+	+	-	+	-	-	-	-
Engystomatidæ	+	+	+	-	+	-	+	+	+	+	-
Dyscophidæ	+	+	-	-	-	-	-	-	-	-	-
Ranidæ	+	+	+	+	+	+	+	+	+	+	+

² It is entirely possible that these may have been brought in as eggs, along with the Gurami *Osphromenus olfax*, from Java.

⁴ *Anabas*, sp. found by me at Ampenan.

³ *Betta pugnax*, occurring upon Ternate according to Steindachner (1901).

⁴ *Hyla dolichopsis*, recorded from Java by me (1907 A), undoubtedly introduced with plants brought into botanical gardens.

⁷ Confined to the Cape York Peninsula.

farther than the Cyprinidæ. In these families one should include only those whereof all, or by far the greater majority, of the species are exclusively confined to fresh water. It is naturally evident that in other cases the possibility of their fortuitous transportation across the sea is not to be excluded. The appended table gives in outline the distribution of fresh-water fishes in the archipelago. It is gleaned, for the most part, from Weber (1894, 1897A), who has done more than any one else to add to our knowledge of the dispersal of the fresh-water fishes throughout the islands. For comparison a table is added giving the distribution also of the families of amphibians.

The eastern portion of the archipelago, including Celebes, possesses a very small fresh-water fish fauna. Those which are found most commonly in the rivers and lakes are, as Weber has pointed out, for the greater part "marine immigrants," that is to say, sea-fishes which have passed over to a fresh-water life. Of the true Indian fresh-water fishes which occur to the eastward of Wallace's line and Lombok are the Siluridæ; the New Guinea species, however, related to those of Australia and hence being in reality outside of our present range of discussion. The remaining ones are almost exclusively those which are able to withstand a drying-up—if this is not too long continued. These are, in truth, only a few species. *Haplochilus celebensis* among the Cyprinidontidæ does not get further than Celebes, nor does *Notopterus kapingat*; and two species of Symbranchidæ—*Symbranchus bengalensis* and *Monopterus javanensis*—*Ophiocephalus striatus*, *Anabas scandens* and *Anabas microcephalus* and possibly *Betta pugnax* are spread further to the eastward. The last-mentioned species have all a peculiar structure of the gill cavity which makes it possible for them to remain for a considerable time without water; and it has been shown by Volz for *Monopterus* that it may even live over through the dry monsoon without water.

The distribution of mammals in the eastern half of the Indian Archipelago is evidently not yet completely known. Even for New Guinea itself, with the exception of bats,

only a few species of mice and two of pigs (*Sus niger* and *S. papuensis*) have been discovered. Both of these last mentioned forms may perhaps have arisen from tame individuals which ran wild. Upon the Moluccas the only Indian mammals that occur are bats and mice, a single species of deer, perhaps also introduced; a few shrews, Viverridæ (*Viverra tangalunga* and *Paradoxurus hermaphroditus*), and wild pigs. Among the swine the well-known Babirusa is especially noteworthy, which is found only upon Celebes and Buru. The Moluccas (Batjan) have a single ape (*Cynopithecus niger*) in common with Celebes. But even here again it has frequently been suggested that this form was probably also introduced. In comparison with the richness in mammals of the Greater Sunda Islands, Celebes falls in with the Moluccas as showing their paucity.

The eastern half of the archipelago, in accordance with its character as a transition region, is not alone habited by immigrants which have come in from the west, but has received its fauna in part from Australia. If we take the three classes of animals which we have mentioned before, we then find here also a strong element which has spread itself even further from its origin, in this case Australia. Upon New Guinea the Melanotæniidæ among the fishes, the Hylidæ among the amphibians, and the marsupials and Monotremes among the mammals are well represented. These fishes have not dispersed themselves very far (the Melanotæniidæ not being known to have reached beyond the Aru Islands). The amphibians themselves are also almost as narrowly confined to the nearby islands, and have not even got as far westward as Celebes. The marsupials have got as far as Celebes and Timor. Although fifty-one species have been made known from New Guinea itself, so that only a small portion of these have gone farther westward; of these two have got to Celebes, both of the species belonging to the genus *Phalanger*. The fauna of New Guinea has, when one considers the Indian elements in it, about as much derived from the fauna of

Australia as that of Sumatra, Borneo and Java has derived from the mainland of Asia.

A general survey of all conditions leads to the conclusion that in post-Cretaceous times there was a broad connection between the three Greater Sunda Islands and Asia on the one hand, and between New Guinea and Australia upon the other; that further also between the Sunda Islands and New Guinea a connection must have existed which was really less easy to pass over. The configuration of the bottom of the ocean supports this opinion. The western half of the archipelago is united with Asia, standing on a plateau of not more than fifty fathoms depth; New Guinea is separated from Australia by a similarly shallow sea. An elevation of the sea bottom of 45 meters would connect the Greater Sunda Islands with the mainland of Asia; while on the other hand a rise of 20 meters is all that is necessary to bring about the joining of New Guinea with Australia. The seas intervening between these two regions have, on the contrary, for the most part a great depth.

There still remains much to do in substantiation of the proof of these conclusions; and the islands and island groups of the archipelago are still a fruitful field of inquiry for those who may be interested.

As already remarked above, Sumatra, Java and Borneo lie upon a shallow submarine plateau which binds them to further India. Upon this same plateau lie also a host of lesser islands such as Banca and Billeton, Madura and Bali. All of these islands, as well as those which lie along the west coast of Sumatra, and which are surrounded by a sea of considerably greater depth, possess a fauna which in all its principal characteristics is essentially that of the Malay Peninsula. Here alone one finds the great Indian mammals, such as the Orang Utan, the tiger, the leopard, the Malayan bear, elephant, tapir, rhinoceros and bantang. Even still more evident is the relationship of the mainland when one takes into account the finds among the fossils. Dubois has uncovered a Tertiary fauna upon Java that bears the most marked resemblance to the Pliocene Siwalik

fauna of Hindustan. Here he found, for instance, remains of Hippopotamus, Stegodon, a species of antelope, Hyæna, Gavialis, etc.

Taking the present condition alone into account, Sumatra and Borneo more than the others have a fauna that is almost identical with the fauna of the Malay Peninsula. Java shows a greater difference; whereupon one may draw the conclusion that it broke off earlier than the other islands from the mainland, since between Java and Sumatra there was more migration than between Java and Borneo, so that it was separated earlier from the last mentioned island than from Sumatra. The Javan Sea, as the Sarasins have determined from a study of the land snails, is of very ancient date.

On the other hand, Java has some mammals, *Rhinoceros sundaicus*, *Trajulus stanleyanus*, *Viverricula malaccensis*, *Helictus orientalis*, in common with the mainland, which up to the present have not been found upon either Sumatra or Borneo. So far, for this state of affairs absolutely no satisfactory explanation has been found.

We might also say of Borneo that it has received a small portion of its fauna evidently by way of Palawan and the Sulu Archipelago from the Philippines, and so directly from south China, and indeed from the Himalayan region itself.

Celebes has always been the great bone of contention from a zoogeographic point of view. We have already seen that Sal. Müller and originally Wallace considered it as belonging to the Australian half of the archipelago. Now, especially through the labors of Max Weber and the Sarasins, it has been made evident that its fauna is essentially Indian, even though it may be mixed with a few Australian types.

But even so, the fauna of Celebes is as yet only partly elucidated. We find here an astonishing number of peculiar types which no one has been able to find upon the other larger islands of the archipelago; and so there must always be a question as to the origin of its fauna.

The first peculiarity is the occurrence of a number of

animals which find their nearest relatives not in the further Indian Archipelago, nor yet even upon the continent of Asia, but in Africa itself. Taking the number of these species of animals together, we must conclude that they are of very ancient origin indeed. Among the birds which must be grouped in this way are such species as *Coracias temmincki* and *Cittura*, the most primitive kingfisher; among the mammals two species of monkey, namely *Macacus maurus*, and its next of kin, *M. arctoides*, which belongs in Hindustan, and *Cynopithecus niger*, most closely related to the African baboons;⁸ in addition, the strange *Babirusa*, a pig that is more like the African wart-hogs than any other variety of swine. The dwarf-buffalo, or Anoa (*Bos depressicornis*) may also be considered as a relic-species, of which its only near living relative, *Bos mindorensis*, inhabits the Philippines.

The explanation of this relic-fauna the Sarasins take to be an old invasion evidently spread out from Java, which most likely happened in the Miocene period. It can not have taken place earlier, since the same investigators were astonished at the geologic evidences that Celebes in Eocene times was wholly covered by the sea. The more recent fauna (that which shows itself among mammals in the abundance of species of squirrels) arrived later, and in all probability entered Celebes along the same land connection. This explanation is not entirely satisfying, since it does not make evident why these animals that we have mentioned exist on Celebes, but have died out everywhere else. On the other hand, that such things really can occur is proved by the abundance of the finds of fossil remains of animals in places where they no longer exist. The epoch-making discoveries of Dubois are of weighty import in this connection.

A further peculiarity of the fauna of Celebes is its great difference from that of Borneo. The Sarasins

⁸Matschie brings the monkeys of Celebes together into one genus (*Papio*), while he differentiates a number of new local races upon the same island. Trouessart, in the supplementary part of his "Catalogus mammalium," has united all these forms as varieties of one single species.

have announced that both islands have not one single species of animal common to them which is not also found upon Java, Sumatra or the Philippine Islands. There is not the slightest possibility of there having been a direct land bridge between Celebes and Borneo across the Straits of Macassar since the very earliest geologic times. This difference between Celebes and Borneo is beyond doubt one of the real reasons for the unjustifiable opinion of Wallace and for the placing, as he did, of his boundary line.

That the Java sea is, according to the Sarasins, of great age is shown by the fact that a curved line may be drawn through this sea and continued into the Straits of Macassar, which terminating blindly, so to speak, at both ends, cuts the archipelago into two portions, or, we might better say, bounds one part where the islands of younger geologic age have apparently had no connection with the mainland. It has thus an entirely different significance from the boundary line as it was formerly drawn.

A third peculiarity of Celebes upon which Weber has laid particular stress is the paucity of certain groups of animals in comparison with the three Greater Sunda Islands. Weber has considered the fauna of Celebes as being essentially an impoverished Indian one. This poverty appears best brought out by the appended table,⁹ wherein the comparison as regards the approximate extent of the islands is given.

	Sumatra	Borneo	Java	Celebes
Surface in sq. km	431,000	733,000	126,000	179,000
True fresh-water fishes ¹⁰	212	292	131	4
Amphibians.....	50	78	37	25
Reptiles.....	175	191	129	87
Mammals (exclusive of bats).....	115	133	68	39

⁹ These data in this table are drawn for the most part from Weber (1894), Popta (1905-6), and Volz (1907), for the fishes; Van Kampen (1907 B), for the amphibians; Sarasin (1901) for the reptiles; Tjeenk Willink (1906) and Schneider (1905), for the mammals.

¹⁰ These are drawn from the same families that were mentioned in the table upon page 547.

This difference is noticeable among the fishes above all others. On the other hand, the difference is less among the birds, and the opposite holds for land and fresh-water molluscs whose number is reckoned by the Sarasins for Sumatra as 129 species; Borneo, 311; Java, 233, and Celebes, 238.

Weber explains the poverty of fauna in this manner: that Celebes, as we understand it to-day, has not long been in its present condition, but rather that it was formed by the uniting of a number of small islands which, as is always the rule in such cases (especially among the fresh-water fishes) possess a sparse or poor fauna. In this same wise is it made evident why the fresh-water mussels (Unionidæ) which occur upon the continent of Asia and Australia, and upon the Greater Sunda Islands, are lacking on Celebes. Von Martens comes to this same conclusion, that they (along with other generally distributed families of fresh-water molluscs) do not occur upon small islands. They are wanting thus upon the Moluccas and on Celebes, where the entire fauna has been made up by the merging together of those of several smaller islands to form a single one.

The opinion of the Sarasins is somewhat different from the explanation of Weber. They are of the opinion, brought forward as especially important, that between the different parts of the island ancient faunistic differences are demonstrable, a peculiarity of the fauna of Celebes which has been thoroughly investigated by them. The Sarasins have taken this up especially from the point of view of distribution of land and fresh-water molluscs. Von Martens had already noticed that north and south Celebes possessed hardly a single species of mollusc in common; and the Sarasins made evident that there existed an easterly mollusc fauna, besides a well-differentiated fauna in the great lakes of central Celebes. Other animals exist, divided from each other in this same manner. So among the mammals, the Babirusa and the crested baboon, *Cynopithecus*, are found in the northern

portion of Celebes only; as is also that remarkable bird *Megapodius cumingi*, as well as some others.

Another point emphasized is the fact that the molluscs of the different peninsulas of Celebes show closest relationship with the island lying near them. The Sarasins found among the groups of animals which they studied that the species which have survived and which have become peculiar now to Celebes, as well as those which have a wider spread at the present time through the archipelago, show in part a relationship to species from Java, in part to those from the Philippines, or from the Moluccas, or again from the Lesser Sunda Islands, especially Flores. The proportion of these four components of the fauna of Celebes is about the relationship of 4:3:2:1. Here again is emphasized the overwhelmingly Indian characters of Celebes, since alone among these last two mentioned smaller groups no Australian species have been found. A close relationship with Borneo is, as we have mentioned previously, entirely non-existent.

The explanation of the Sarasins is this. Celebes rose from the sea in Eocene times, and in Pliocene times especially received its fauna along four land bridges, each of which connected the island with one of the previously mentioned islands or island groups. The position of these bridges is still traceable through submarine shallows, or else by groups or chains of islets. The Java bridge ran from the southern peninsula out through what are now Postillon, Paternoster and Kangean Islands, to eastern Java. The Philippine bridge bound the northern peninsula with Mindanao, and included the present Sangi and Talaut groups. The Moluccan bridge went off from the eastern peninsula; and united together the Peling and Sula Islands, and apparently then split up into two bridges, one of which ran off to the Obi and Halmahera groups, the other to Buru. This last connection is postulated by the geographic distribution of the Babirusa, and also by the birds. The latter, from the mountains of Buru, show a close relationship with Celebes. However, during the expedition of the Siboga,

the strait between Buru and the Sula Archipelago was found to be of considerable depth (about 4,100 meters), an argument against any such land connection.

It occurs to me that the past events which have been reconstructed by the Sarasins are just as well explained by Weber's opinion, which is that the separated islands, which gave rise to Celebes, by consolidation, have received their fauna in the way which the Sarasins have suggested. The point of difference is indeed simply a question of interpreting the significance of the earlier history. In either case it is entirely plausible that Celebes has received its fauna from the south,¹¹ the north, and the east; not directly from Borneo, but rather by means of small islands or narrow land bridges; which fact has had a great influence on the impoverishment of the fauna. On the other hand, animals from Celebes have been enabled to spread out along these same land connections, so that occasionally we find evidences among the Philippines and the Lesser Sunda Islands of this having happened by their having certain common animal types.

It is peculiar that the truly Indian character of Celebes (the great westerly island of the transition region) remained unsuspected for so long; while on the other hand, no one doubted, but rather laid stress upon, the Australian relationship of that vast easterly island, New Guinea, the fauna of which is fully as Indian as that of Celebes is Australian. It simply happened that those groups of animals which at once were most evident, and which had been most frequently used in elucidating zoogeographical questions—especially birds and mammals—are preponderatingly Australian upon New Guinea, and happen to show upon Celebes also a considerable Australian admixture. Had earlier investiga-

¹¹ Weber brings into existence two different land bridges as an argument to explain the difference between the fauna of Java and Flores. He is inclined to the opinion that there was here a land mass of considerable extent which has given rise to the great depths of the Flores Sea by an extensive sinking.

tors laid more stress upon the amphibians, then an entirely different result would have been arrived at: New Guinea possesses here again 39 species which belong to Indian families as against 24 Australian.¹² Among other groups of animals New Guinea is more Indian than Australian. This is the case with the scorpions and the earthworms.

New Guinea, then, has a mixed fauna, whereof the Australian elements are explained by the existence of a now broken connection with Australia; and whereof the Indian elements evidently arrived from the Moluccas. The Sarasins have constructed, in explanation of this, two bridges, one of which connected New Guinea with Halmahera—the New Guinea bridge of Kuckenthal (1903); the other, with Ceram. The Aru and Ke islands range themselves along with New Guinea. Upon both, for instance, we find a true kangaroo, *Macropus brunii* [sic], an animal which does not occur further to the west of New Guinea. The Aru Islands possess a fresh-water fish of the family Melanotæniidæ, the remaining members of which are confined to Australia and New Guinea (Weber, 1907B). This same relationship is shown by birds such as crown-pigeons, birds of Paradise, and cassowaries, as well as among amphibians and other groups. One can, therefore, take it for granted that at the same time as New Guinea both of these two island groups were united with Australia, although the Ke Islands are cut off by a greater depth of sea.

From the already mentioned faunistic difference between Celebes and New Guinea, it follows that for many families and genera of animals both the westerly as well as the easterly boundaries must lie in the Moluccas. Here one would expect to be able to place a boundary line which would exactly fit each special case. But here we are hindered further by the fact that just these is-

¹² In this are included the species described by me in a memoir the preliminary of which will appear in *Nova Guinea*. See also Van Kampen (1906). [The paper in "Nova Guinea" has already been published.—Translator.]

lands are the ones which are still only incompletely known. With the exception perhaps of certain groups of animals—birds, butterflies, etc.—which on account of their value are specially sought for, there are great gaps in our knowledge. Only during the last few years have Halmahera, Ternate and Batjan been systematically studied by Kuckenthal. These islands then are the best known. Obi, Buru, Ceram, the Sula Archipelago and others are no more than zoologic blanks upon the map. It is a fact that upon the Sula Islands a short time ago 19 species of land snails were collected, while only a short time before only one single species was known (Schepman). These last-mentioned islands are of importance as having belonged to the Molucca bridge of the Sarasins.

Another question is whether the Moluccas have received their Indian fauna along this Molucca bridge from Celebes, as the Sarasins claim, or along still a different way, as perhaps through the Talaut Islands from the Philippines, as some cases tend to show.

These questions must wait for a definite answer until researches have brought more light to bear upon them. Before this we can only go so far as to say with certainty that the fauna of the Moluccas is a mixed one, as is that of New Guinea; and that in large part on account of the generally small size of the islands both the Indian and Australian components are found impoverished in comparison with the neighboring greater islands.

Hardly more complete is our knowledge of the Lesser Sunda Islands. Weber (1902) placed them among the very least known of any in the archipelago. Here remain a number of knotty questions still to be explained, although it has been definitely proved that the sharp line which Wallace drew between Bali and Lombok must be given up for good and all. The existence of one of the most fundamental supports of this boundary was disproved by the expedition of the Siboga; and that was regarding the great depth of the Lombok Straits. Indeed, this strait is somewhat deeper than that between the other

islands of the series from Bali to Ombai; and the Sarasins believe that it was in reality one of the oldest, although more recent than the Strait of Macassar, and thus well within the Secondary Epoch. This allows us to explain a certain faunistic differentiation between Bali and the other islands; for we know, for instance, that cockatoos do not occur further to the westward than Lombok. This was one of the weightiest arguments which Wallace used. However, cockatoos live in the Philippines, and thus well to the westward of his own line. Weber points out that the fauna of the Lesser Sunda Islands is in large part an impoverished Indian one derived from Java, beside which there occurs a small element from Celebes (along the Flores bridge). So also by the same means has come a slight infiltration of Philippine forms. Here also we find a few Papuan or Australian species. Timor appears, indeed, to have received some animals directly from New Guinea or Australia (birds, *Hyla*).

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