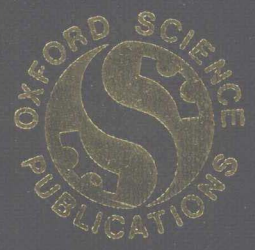

Wallace's line and plate tectonics

Edited by T.C. Whitmore

WALLACE'S LINE AND PLATE TECTONICS

EDITED BY

T. C. WHITMORE
University Research Officer,
Commonwealth Forestry Institute,
Oxford

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OXFORD MONOGRAPHS ON BIOGEOGRAPHY

Editors: W. GEORGE, A. HALLAM, AND T. C. WHITMORE

OXFORD MONOGRAPHS ON BIOGEOGRAPHY

In an area of rapid change, this new series of Oxford monographs will reflect the impact on biogeographical studies of advanced techniques of data analysis. The subject is being revolutionized by radioisotope dating and pollen analysis, plate tectonics and population models, biochemical genetics and fossil ecology, cladistics and karyology, and spatial classification analyses. For both specialist and non-specialist, the Oxford Monographs on Biogeography will provide dynamic syntheses of the new developments.

PREFACE

One of the sharpest zoogeographical divisions in the world divides the Malay archipelago in two. First brought to prominence by the famous naturalist A. R. Wallace in the mid-nineteenth century, Wallace's line, as it soon became named, has tantalized zoologists, and to a milder degree botanists, ever since.

In this book the new understanding of the geological history of the Malay archipelago achieved as a result of the theory of plate tectonics is described in some detail. The implications of this understanding for the interpretation of distribution patterns are then illustrated by consideration of vertebrate animals, palms, and several other plant groups.

It is hoped that the dramatic new discoveries in palaeogeography and their far-reaching implications for biology will interest the wide circle of students of biogeography. At the same time we hope to stimulate both botanists and zoologists to interpret their own research findings against the now considerable knowledge of the geological history of the region. For we think it can now be clearly demonstrated that the distributions of plants as well as of animals bear witness to this history. Thus the book is both for the generalist, and, at the same time, for the specialist in Malesian plants and animals. The conclusion is that, although a fresh look at distributions in the light of recent geophysical findings explains much, there still remain some distribution patterns which are very difficult to interpret. These are the challenges now to be faced.

Oxford
May 1981

T. C. W.

To
Professor C. G. G. J. van Steenis
Professor Emeritus, State University Leiden, Holland, and Director-General,
Flora Malesiana Foundation. Mentor to many Malesian botanists.

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CONTRIBUTORS

M. G. Audley-Charles, Department of Geological Sciences, Queen Mary College, University of London.

The Earl of Cranbrook, Great Glemham House, Great Glemham, Suffolk.

J. Dransfield, Royal Botanic Gardens, Kew.

W. George, Zoology Department, University of Oxford.

A. M. Hurley and **A. G. Smith**, Department of Earth Sciences, Sedgwick Museum, University of Cambridge.

T. C. Whitmore, Commonwealth Forestry Institute, University of Oxford.

NOTE ON PLACE NAMES AND UNITS

In general we follow *The Times atlas of the world, comprehensive edition* (5th edition, revised 1977) but have retained conventional English rendering for major localities, e.g. Celebes (Sulawesi). Place names mentioned in the text are shown on the endpaper map or the map of central Malesia (Fig. 4.9).

Banda Arc. The geological term for the double arc of islands from Flores east through Alor and Wetar and north to Banda (*Inner Banda Arc*) and from Raijua through Timor and the Tanimbar islands then north through the Kai islands and west to Ceram and Buru (*Outer Banda Arc*) (see Fig. 4.9).

Greater Sunda Islands. Borneo, Java, and Sumatra.

Inner Banda Arc. See Banda Arc.

Lesser Sunda Islands (Nusa Tenggara). The geographical term for the islands east of Java from Bali and Lombok eastwards to Damar and Babar (see Fig. 4.9).

Ma. The megayear, 1 000 000 years.

Malaysia. The political State comprising Peninsular Malaysia together with Sabah and Sarawak in northern Borneo.

Malesia. The biogeographical province stretching from Sumatra and the Malay peninsula south of the Kangar–Pattani line (Whitmore 1975) to the Bismarck archipelago.

Moluccas. The geographical term for the islands which occupy the region between Celebes (plus the Talaud and Sula islands, Butung and the Tukangbesi islands), the Lesser Sunda Islands (q.v.), Aru and New Guinea (plus Misool and Waigeo). The biggest Moluccan islands are Halmahera, Ceram, Buru, and Tanimbar (see Fig. 4.9).

Outer Banda Arc. See Banda Arc.

Papuasia. New Guinea, the Bismarck archipelago, and the Moluccas.

Sundaic. Pertaining to Sundaland.

Sundaland. The lands of the Sunda continental shelf, west of Wallace's line.

Sunda Shelf. See Sundaland.

Wallacea. The island region in central Malesia which lies between Wallace's line and Weber's line (Fig. 2.3).

West Gondwanaland. That part of Gondwanaland which today forms Africa and South America.

CONTENTS

1 INTRODUCTION

T. C. Whitmore

The revolution in the earth sciences during the last two decades which has resulted from the theory of plate tectonics means that the palaeogeography of the globe during the Mesozoic and Cenozoic is now understood in general terms. Only details remain to be filled in.

This makes possible a profitable new interpretation of plant and animal distributions. For the first time the relative positions of land masses are known at different times in the past. The pattern is known with some certainty, although it is still very difficult to know where coastlines lay because only the stratigraphic record can tell us and this is very incomplete.

One of the classic and best known boundaries of zoogeography is the line, originally proposed in 1858 by A. R. Wallace, which runs through the middle of the Malay archipelago and marks the meeting of essentially Asian and Australian faunas (Chapter 2). The nature of this junction has been subject to much discussion and its exact position has been a matter of dispute. Wallace himself moved his line from west to east of Celebes late in his life, a decision to which new geological discoveries give a certain piquancy.

Until recently the various viewpoints on the palaeogeography and biogeography of the Malay archipelago had to stand or fall on their ability to fit all known facts into a plausible hypothesis. There was no external point of reference. Biologists tended to make geographical reconstructions; and geographers to use biological evidence. But now biologists can for the first time work with a broadly painted background of established palaeogeographical facts, albeit still lacking much fine detail, rather than mere suppositions. The former danger of circular argument, which has so often plagued discussions of biogeography, no longer befogs the scene.

Wegener, in his theory of continental drift, used the evidence of animal distributions in the Malay archipelago and epitomized by Wallace's line to support his view that south-east Asia and Australia had converged (Wegener 1924; and discussion in Hallam 1967). But it was to be nearly half a century before continental drift, reincarnated as plate tectonics and with the powerful evidence of sea-floor spreading as an essential component, became sufficiently well-established to provide this external point of reference for biogeographers.

The major events of global geology which affect the biogeography of the region of Wallace's line are the progressive break up of Gondwanaland from about 140 Ma and the drifting north of the Indian fragment to collide with Laurasia at about 55 Ma[1] (Chapter 3) and of the Australia/New Guinea fragment to collide with the south-east extremity of Laurasia at Celebes at only about 15 Ma, mid-Miocene (Chapters 3 and 4). The boundary between Gondwanaland and Laurasia lies within Celebes or just to its east (Fig. 4.7). Western Celebes is Laurasian, the Makassar Strait lies within Laurasia and has very probably been intermittently bridged from 15 Ma, the late Tertiary, onwards with more land above sea at its southern end. The Inner Banda island arc is Laurasian, the Outer Banda island arc and Moluccas are Gondwanic. Land connections from Laurasian Borneo to Gondwanic New Guinea were continuous or with only narrow sea gaps from some time between the late middle Miocene to late Pliocene (*c.* 12 Ma onwards), and from the Outer to the Inner Banda arc in the middle Pleistocene, 1 Ma, and probably latest Miocene/early Pliocene, 10 Ma, also.

The angiosperms, which first appear as fossils in the Lower Cretaceous, about 120 Ma, are commonly believed to have evolved considerably earlier than that, and somewhere in the region between Assam and Fiji, where the world's richest floras occur. The faunas there too are extremely rich and diverse. But we now see that, contrary to widespread belief, this great richness is not concomitant with long persisting conditions of stability. The new palaeogeographic understanding explodes the supposed cradle of the angiosperms.

The geological history outlined in Chapters 3 and 4 shows that plants and animals could have reached the Malay archipelago without crossing water from one of three sources: Laurasia, Gondwanaland via Australia, or Gondwanaland via India followed by south-eastwards migration. In addition, undoubtedly, some groups are autochthonous, having evolved more or less where they now live.

In this book we explore the present-day distributions of a few groups of plants and animals and interpret them in the light of this insight from palaeogeography. Much can be understood, but enigmas still remain.

[1] The megayear, see p. xii.

It is now known that during the Pleistocene there have been long periods when the climate of some parts of the world has been drier and more seasonal than today, and that at these times sea-level has been as much as 180 m lower. The two great present-day rain-forest blocks, one centred on Sumatra/Malaya/Borneo and the other on New Guinea, may have been smaller but there are no signs in the Malay archipelago of extensive desiccation (in contrast to both Africa and tropical America). Nevertheless, present-day distribution patterns of plants and animals are likely partly to reflect past differences in climate. The interpretation of range must penetrate this veil and take it, as well as palaeogeographical dispositions of the land, into account.

Our survey of animals focuses on vertebrates, in which Celebes is peculiarly isolated, though more Laurasian than Gondwanic in affinity, more so than islands to its north and south. Any line to be drawn in fact needs to circumscribe Celebes. The inference is that there have always been water barriers in central Malesia (Wallacea), which animal groups have traversed differently dependent on their dispersive ability.

Amongst plants the main investigation is of the palms, richly represented throughout the Malay archipelago. This is a large and complex family which recent study suggests encompasses five main lines of evolution and fifteen natural major alliances. Something is known about both the evolutionary history and the region of origin of the palms and they have been the subject of renewed intensive study in the Malay archipelago since 1965. The group is therefore ideal for an analysis of distribution patterns in the light of palaeogeography. The numerous species, genera, and natural major groups of palms in Malesia provide abundant information which can be set in a global context. It is commonplace that different groups of plants, both genera and families, have different ranges within the archipelago. In the concluding chapter we demonstrate that some of the commonly occurring distribution patterns can be explained in terms of the geographical history, though, as in the palms, many riddles still remain.

We end by discussing briefly one of the remaining major problems of global phytogeography, namely the occurrence of bihemispheric distribution patterns amongst flowering plants which approach or overlap in the Malay archipelago (Fig. 1.1) and have led to the suggestion, now seen to be improbable, that here lies the cradle of the group.

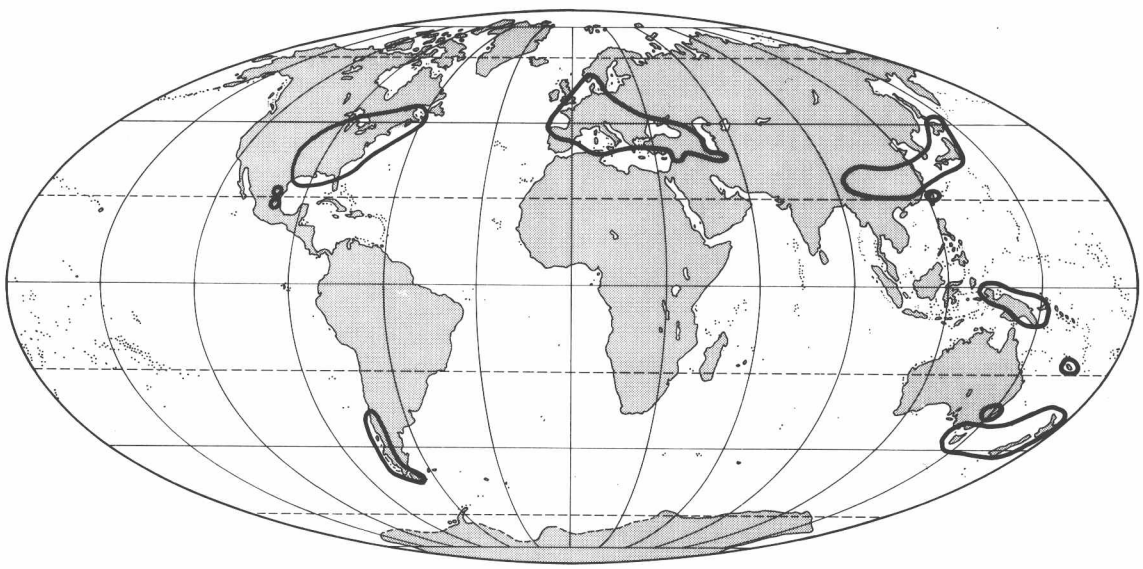

Fig. 1.1. The global distribution of Fagaceae subfamily Fagoideae, the beeches and southern beeches, has a bihemispheric pattern with ranges of the northern and southern genera most closely approaching each other in the Malay archipelago. Mollweide's elliptical equal area projection.

2 WALLACE AND HIS LINE

W. George

Wallace discovered the dramatic change in fauna which occurs in the middle of the Malay archipelago while he was still living there. His views on the exact position of the demarcation line changed with time. They were expounded in a letter to Bates in 1858; then in a series of publications which spanned the half century between 1859 and 1910. His discoveries have continued to tax the minds of zoogeographers who have proposed various refinements of the original discovery. Wallace realized the enigmatic nature of Celebes and, in searching for an interpretation, recognized the importance of an understanding of the palaeogeography of the region. His views and those of others provide a historical introduction to present-day understanding of both the palaeogeography and biogeography of the region.

The first indication that there were zoological regions, conforming to the major land masses of the world and brought into being by slowly evolving continents and slowly evolving animals, may be found in a letter that Alfred Russel Wallace sent from the island of Amboina in the eastern part of the Malay Archipelago in January 1858 to Henry Bates who was then back in London from his South American travels. 'In the Archipelago', he wrote, 'there are two distinct faunas rigidly circumscribed, which differ as much as those of South America and Africa, and more than those of Europe and North America. Yet there is nothing on the map or on the face of the islands to mark their limits. The boundary line often passes between islands closer than others in the same group. I believe the western part to be a separated portion of continental Asia, the eastern the fragmentary prolongation of a former pacific continent' (Marchant 1916).

Later that year, P. L. Sclater divided the world into six avifaunal regions. Unlike Wallace, he believed in stability and creation. But 'it is not yet possible', he wrote, 'to decide where the line runs which divides the Indian Zoology from the Australian' (Sclater 1858). Sclater included the Philippines, Borneo, Java, and Sumatra in the Indian region; and New Guinea, New Zealand, and some Pacific islands in the Australian region.

Wallace read Sclater's paper and congratulated him on his classification but proposed some emendations to boundaries between regions. In March 1859, Wallace argued that the boundary between the Indian and Australian 'zoology' should run between the islands of Bali and Lombok: because barbets reach Bali and not Lombok and cockatoos reach Lombok but not Bali. 'This, I think, settles that point.' Wallace then used parrots to run the boundary between Borneo and Celebes. He was amazed that two regions 'which have less in common than any other two upon the earth' should be separated by no major physical or climatic barrier. It seemed to confirm his belief that the western isles had once been part of Asia and that the eastern ones, including Celebes. Timor, the Moluccas and New Guinea, were remnants of a vast Pacific-Australian continent, but he had reservations about Celebes which he argued was peculiar and might represent fragments of a very ancient land which 'may have been connected at distant intervals with both regions' (Wallace 1859). Later that year, he described the ornithology of north Celebes and noted that it contained more Javanese species than Moluccan. He concluded that the island is 'one of the most interesting in the world to the philosophical ornithologist' (Wallace 1860*a*).

Wallace had been following Sclater in dividing the world into regions according to the distribution of birds but, in 1860, he decided that the world could be divided into regions that would 'hold good in every branch of zoology'. He sent a paper to England which was communicated to the Linnean Society by Charles Darwin (Wallace 1860*b*). In it he argued on the basis of his knowledge of mammals, birds, and insects for the division of the world into discrete faunal regions. The boundary between Bali and Lombok was retained in spite of his limited knowledge of the Bali fauna. The Moluccas were associated definitively with New Guinea and Australia. He had further reservations about Celebes which he attached to a vast Indo-Asian continent ('the last eastern fragment') and supposed that its main colonizations had been across the sea. 'Facts such as these', he wrote, 'can only be explained by a bold acceptance of vast changes in the surface of the earth.'

Wallace looked for an interpretation of faunal distribution in the light of past evolutionary events. But this new and dynamic approach was limited because he had only modern faunas from which to reconstruct the past. No other line of reasoning was possible because there was

nothing known of either the palaeogeography or the palaeontology of the Malay archipelago and no obvious physical differences between the islands.

However, his account of a visit by his assistant Charles Allen to the Sula Islands (Fig. 4.9), reported to the Zoological Society of London in 1862, showed how effective this approach was (Wallace 1862). The Sula Islands had a mixture of Moluccan and Celebesian forms which, because of their geographical position, did not surprise Wallace. But he noticed that there were far more Celebesian components of the fauna than Moluccan: according to his calculations, nearly double. So he concluded that the Sula Islands are an outlying fragment of Celebes and must have had a connection with that island in the past.

On further consideration, Wallace later associated the island of Buru with the Sula Islands: the presence of such animals as the babirusa pig (Fig. 7.2) and the megapode brush turkeys made it likely that these islands once had a connection (Wallace 1869).

Back in London, Wallace read a paper to the Royal Geographical Society in 1863 on the geography of the Malay Archipelago. This was mainly deduced from zoogeographical distributions but he also considered the depth of the oceans round the islands, the distribution of volcanoes and coral islands in the archipelago which had made it an unstable area for long periods of time, the vegetation of the islands and their climate. Wallace argued that it was an area of change, of evolution.

The 100 fathom (180 m) line running between Borneo and Celebes made Borneo part of an Asian continent. On similar evidence, New Guinea and the Aru Islands were part of an Australian continent (Fig. 2.1) as G. W. Earl(e)

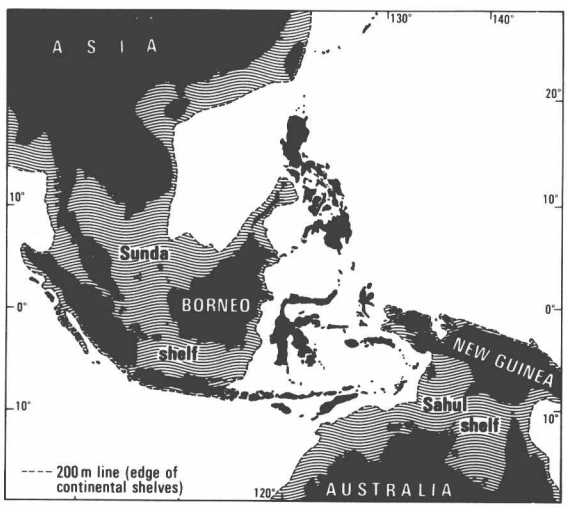

Fig. 2.1. The Sunda and Sahul continental shelves. (From Whitmore 1975.)

had already noticed in 1845. Zoological evidence was used to put the intermediate islands in one region or the other. Celebes and all islands to the east, including the outer Banda Arc islands, were therefore put in the Australian region. The Philippines, though deficient in many striking Asian mammals such as gibbons and rhinoceroses, were part of an Asian continent. In the south, the line ran between Bali and Lombok.

Moreover, in this paper Wallace had changed his mind about Celebes: in 1860 Celebes was the outlying eastern fragment of an Indo-Asian continent, in 1863 it was the farthest westward extension of an Australian continent. This revision was based on the remarkable differences Wallace had observed and later substantiated between the faunas of Borneo and Celebes, in spite of their geographical closeness: differences in mammals (no hedgehogs and only viverrid carnivores on Celebes, for example), differences in birds (no trogons or barbets but megapodes on Celebes), differences in insects (green–gold *Pachyrhynchus* weevils absent from Borneo) (Wallace 1863, 1869, 1880) (Figs 2.2 and 2.3).

In an 1865 article on the pigeons of the Malay Archipelago he confirmed that Celebes had associations through the Sula Islands with the Moluccas and New Guinea. He recognized a centre of pigeon diversification on New Guinea which extended outwards to include the Solomon Islands to the east and the Moluccas and Timor to the west. For example, the range from the Pacific islands to north Celebes of the brown-backed ground pigeon *Chalcophaps stephani* put Celebes into the eastern subregion of the archipelago. But there were other pigeons on Celebes, like the green pigeons *Treron*, whose affinities were with the western islands. 'Celebes', he decided, 'is a very isolated and remarkable island, which, from the variety and peculiarity of its productions, appears to be the remnant of some extensive land, which existed anterior to the present distribution of land and water in the surrounding regions' (Wallace 1865).

In his 1863 paper Wallace drew a red line on the map passing down the Makassar Strait. To the west, he wrote 'Indo-Malayan region' and, to the east, he wrote 'Austro-Malayan region'. This became 'Wallace's line' in 1868 when T. H. Huxley in a paper on gallo-columbine birds referred to a 'boundary in question'. It was supposed to 'coincide with what may be called "Wallace's line" between the Indian and Papuan divisions of the Malay Archipelago'. It did not 'coincide' in the north for in his own figure Huxley's line passed to the west of the Philippines but whether this was intentional is not clear from the text. Whatever the intention, it resulted in *two* Wallace's lines: one to the east of the Philippines and one to their west (Fig. 2.4).

Later, Wallace reproduced his 1863 line in his great

work *The geographical distribution of animals*: it still ran to the east of the Philippines (Wallace 1876).

Wallace had put Celebes in the 'Austro-Malayan region' in 1863 and 1876 but he argued that, if the species and genera which are common to Celebes and the surrounding islands are considered, 'we must admit that the connexion seems rather with the Oriental than with the Australian region'. However, he also argued that, if the proportion of species and genera present to those absent is considered, 'we seem justified in stating that the Austro-Malay element is rather the most fully represented'. From this, Wallace concluded that Celebes had probably never been united by extensive land to either the east or the west (Wallace 1876).

By the time *Island life* appeared in 1880, Celebes had become an 'anomalous island' along with New Zealand. Its poor mammal fauna, although much of it of Asian derivation, made it unlikely that the island had formed part of an Asian continent for more than a short period of time. Or perhaps, he argued, it had been no more closely linked than by a string of islands. But 'the question at issue can only be finally determined by geological investigations'. To Wallace, the bird fauna of Celebes appeared more Australian than to later investigators but the island, 'both by what it has and what it wants, occupies such an exactly intermediate position between the Oriental and Australian regions that it will perhaps ever remain a mere matter of opinion with which it should properly be associated' (Wallace 1880).

Wallace's last word on Celebes came in 1910 when he decided that his famous line should be redrawn: 'I came to the conclusion that Celebes was really an outlier of the Asiatic continent but separated at a much earlier date, and that therefore Wallace's line must be drawn east of Celebes and the Philippines' (Wallace 1910).

By the early twentieth century, other lines, shown on Fig. 2.4, had appeared among the islands based on the distribution of one group of animals or another (George 1964; Simpson 1977). Other than Wallace's, the only one that has persisted is Weber's line of 1904. This line was based on the distribution of molluscs and mammals and conformed, more or less, to the 100 fathom (180 m) sea line in the east of the archipelago.

Thus, two shallow water lines had been recognized (Fig. 2.1) and many authors maintain that, as these lines delineated ancient continents, it was possible that there had always been only ocean and islands in between. Consequently, each island had obtained a characteristically peculiar and unique fauna. For this reason, Dickerson (1928) proposed that the island area should be considered as a separate region (a suggestion already made by Wallace in 1863) and gave it the name Wallacea.

Wallace's line has persisted amongst zoologists as an important concept. It has much less utility to botanists. There is a disjunction at the Makassar Strait, with 297 genera of flowering plants reaching their eastern limit there, but the boundary between Java plus the Lesser Sunda Islands and the rest of the archipelago is of equal importance (van Steenis 1950). There are approximately 2300 genera of flowering plants in total in the archipelago and for the great majority Wallace's line is unimportant.

Some zoologists, like Raven in 1935, considered the validity of Wallace's line on the basis of the proportion of mammals that had crossed the line going east compared with those that had not and came to the conclusion that Wallace's line marked a boundary which was the eastern limit of the great majority of East Indian mammals, like rhinoceroses and elephants. Others made their assessment on the proportion of western and eastern elements to be found on each island in Wallacea. Thus, Rensch in 1936, following Mertens (1934), calculated that 88 per cent of Celebes reptiles, 80 per cent of the amphibia and 88 per cent of the butterflies were of western origin which was a similar proportion to that found on Lombok and more than twice as high as for the Kai Islands. Following the same line of argument for Australo-Malayan birds, Ernst Mayr calculated that 67.6 per cent of the passerines were from the west and decided that 'there is no doubt, Celebes must be included with the Oriental region' (Mayr 1944).

After a detailed examination of the lines and of Wallacea, Mayr along with several authors, at a Linnean Society discussion (Scrivenor *et al.* 1943), concluded that Weber's line was a better boundary between the faunas of the two great regions than Wallace's line although the butterflies, for example, left Celebes as anomalous as ever (Corbet 1943). Thus, the conclusion was reached that most of the modern fauna in Wallacea consists of more Asian types than Australian.

Other authors have taken an ecological approach to boundaries. Already, in 1846, Salomon Müller had drawn a line very similar to Wallace's but which he determined ecologically pointing out, for example, that arid conditions run eastwards from Java to Tanimbar and affect the vegetation. In 1857, Zollinger ran a similar floristic line from east of Timor to east of Celebes. And Wallace pointed out, in 1863, that the islands could be classified according to whether they were forested or not, those to the west of his line together with Celebes and New Guinea having essentially forest biomes and the rest more arid conditions. Lincoln (1975), studying the birds of Bali and Lombok, came to the conclusion that Wallace's line marks the division between a rich continental fauna associated with high rainfall, forests and varied habitats and an impoverished fauna associated with low