Zusammenfassung
Wir beurteilen die Theorien und Beiträge früherer Autoren auf der Grundlage ihrer Relevanz für den heutigen Erkenntnisgewinn. Mit Blick auf die oftmals unzureichende Klärung der präzisen geographischen Herkunft von Materialproben bei nicht wenigen molekulargenetisch-phylogeographischen Studien (die an aktuellen Arbeiten demonstriert wird), soll die Bedeutung der geographischen »Erfahrungen« (im doppelten Wortsinne) – am Beispiel der Erforschung des australasiatischen Raumes – untersucht werden.


Summary
Science judges on theories and contributions by earlier authors on the grounds of their relevance and heuristic value for current studies and present knowledge. Compiling an abbreviated chronology and highlighting some relevant aspects and events, this paper investigates the importance and implications of geographical «experience» with focus on the historical development of scientific travelling and field research in the Australasian region. The earliest beginnings of European exploration in this area were dominated by expeditions that were initiated, controlled and financed by official, i. e. governmental
Institutions, as is illustrated in the voyages by James Cook in the Indopacific or in the early 19th century by the journeys of naturalists such as Quoy, Gaimard, Lesseon, Hombourn and Jacquinot on board the French L’Épine, La Coquille and L’Astrolabe as well as by naturalists like Darwin, MacGillivray and Hooker on board the British vessels Beagle and Rattlesnake, respectively. Less well known and briefly described here is the Dutch expedition to New Guinea on the Triton. One of its participants, the German-born naturalist Salomon Müller (1804-1864), was the first — albeit largely unknown and forgotten — to discover a pronounced faunistic differentiation within the Malay Archipelago. Müller explicitly described not only a sharp demarcation among the fauna that became later known as Wallace’s line but also a characteristic region known as Wallacea, today both attributed to Alfred Russel Wallace’s discovery of the same phenomena more than a decade later. It will be shown that the general claim, Wallace was the first person to analyze faunal regions in South-East Asia based on the distribution of multiple groups of terrestrial animals does not hold true in more than one respect.

While early expeditions had primarily commercial and/or strategical goals, natural history exploration in Australasia during the late 19th century was largely done by individually travelling naturalists such as Wallace (1823-1913) or, less known Otto Finsch (1839-1917) and Richard Seman (1859-1918). During the early 20th century those were followed in Australasia, for example, by the expeditions of Erwin Stresemann (1899-1972), Berndt Rensch (1900-1990) and Ernst Mayr (born 1904). In particular the three journeys of the latter between 1928-1930 in New Guinea and the Solomon Islands, which will be outlined here, and, thus, the research and observations in situ provided the geographical key for the study of the spatial pattern of animal distribution and for understanding the origin of species and the mechanisms of speciation. It is these geographical data that facilitate insights into complex phenomena in evolutionary biology such as natural selection, faunal regions and their delineation, endemisms and radiations, formenkreise and superspecies, as well as the principle of peripheral isolates and the concept of allopatric speciation. Thus, providing the knowledge on geographical occurrence of faunal and floral elements over vast areas of the globe, has to be considered the main contribution of travelling naturalists toward the development of the modern synthetical theory of evolution. Within the framework of modern phylogeography this core research topic has not lost any of its relevance for the formulation and testing of zoological and evolutionary hypotheses, as is shown in light of the often very inadequate documentation of the geographical origin of certain samples used for molecular genetic and phylogeographic studies.

Introduction

»A country having species, genera, and whole families peculiar to it, will be the necessary result of its having been isolated for a long period, sufficient for many series of species to have been created [...] Therefore the natural sequence of the species is also geographical.«

Alfred Russel Wallace, 1855 (»The Sarawak papers«)

The »Golden Age« of zoology when naturalists on epic journeys travelled through largely unexplored regions of the world, convincingly illustrated, for example, in accounts on the great age of Victorian explorations, is long gone. Today, as it is at least often believed, zoologists only in their laboratories discover the new and unexplored. Especially those systematists who still conduct their research in the field often are misjudged as hopeless romantics who, by profession, satisfy their spirit of adventure and wanderlust. Although often heard, this perception is unfounded. First, the majority of the roughly estimated 13 to 30 (or even up to 100) million animal species is still not yet discovered let alone scientifically described or studied in closer detail. Among this plethora of unknown biodiversity,


2 However, even today relatively large species among the comparatively well-known mammals remain to be discovered, as is illustrated by the Vu Quang bovid Pseudoryx nghetinhensis from Vietnam and the golden-brown mouse lemur Microcebus ravelobensis from Madagascar, to mention only two among many, as well as the many newly described, so-called cryptic species (GLAUBRECHT 2001, pp. 159-173).

3 For recent, well-documented biographies on Wallace, certainly one of the most interesting and least celebrated travelling scientists, see Wilson 2000 and Raby 2001.

4 Rieppel 1705. Rieppel’s »Amboinsische Raritätenkammer« in Dutch was posthumously published in Amsterdam in 1705, with a second and third edition in 1740 and 1741; a Latin edition followed in 1711. A German edition of the second part, viz. on the molluscs of the 1705-issue, was published by Johann Hieronymus Chemnitz and published 1766 in Wien as »Amboinsische Raritäten-Kammer«. Only recently, Rieppel’s book was translated into English in 1999 by E. M. Siegman and published at Yale University Press as »The Ambonese Curiosity Cabinet«. For an account on G. E. Rieppel and the many invertebrate groups rank most prominently. Second, this perception underestimates the importance of the geographical factor for zoology and the development of evolutionary biology. Thus, zoologists have to continue conducting research and explorations in the field not only for discovering species new to science, but also for the determination and evaluation of the distribution of species as providing the systematic and biogeographical foundation for other biological studies.

This paper investigates the contributions of some eminent 19th and 20th century naturalists and the importance and implication of the geographical experiences toward the genesis of biological disciplines. »Experience« is to be understood here in two ways. First, I will briefly give an overview of the contributions of some of the most important explorations and expeditions that were instrumental to set the geographical stage, with a focus on Australasia as one of the biologically richest regions in the world. For example, naturalists such as Salomon Müller, Alfred Russel Wallace, Otto Finsch and Ernst Mayr explored New Guinea in a scientific context including many of the diverse natural history objects. Second, I will investigate the importance of the geographical factor in zoology, highlighting the role that the spatial occurrence of taxa played during the last two centuries for the development of systematic zoology in particular and evolutionary biology in general.

Wallace’s Program, Or the Genesis of Geographical Experience

In order to illustrate this »geographical principle«, the present paper will focus on the Malay Archipelago and the Australasian region. This region, later (and until today) to become mainly associated with the name of the 19th century naturalist Alfred Russel Wallace (1823-1913), is of the richest areas in the world in terms of biological diversity and an ideal area for zoological studies in many respects.

It comes as a surprise that zoology itself learned only relatively late about the significance of the exact determination of the occurrence and distribution of animals. What is here named »Wallace’s program« is, for example, illustrated by one of the earliest faunal accounts from the Indonesian Archipelago. The Dutch merchant, conchologist and founder-malacologist Georg Everhard Rumphius (1628-1702) was certainly one of the greatest tropical naturalist of the 17th century, studying plants and animals of this region. Employed by the Dutch East India Company, he lived since 1654 in the town of Ambon on the Malucian island of Ambon in eastern Indonesia. His famous opus »D’Amboinsche Rariteitkamer« marks the beginning of...
biogeographically orientated studies. Ahead of his time, RUMPF in his »Curiosity Cabinet« not only used the binominal method half a century before LINNÉ established this procedure today considered obligatory in zoological nomenclature. RUMPF was also the first to give a faunistic inventory of a tropical marine fauna and a biological account emphasizing, among others, the living molluscs of the tremendously rich but virtually unknown East Indies region. His magnificent work contains a wealth of first hand information on the biology and ecology of numerous species, thus rendering it the best scientific achievement of the time.

In addition, and in the context here even more important, he recorded the accurate localities of the animals he collected, described and depicted, emphasizing for the first time the geographical origin and the spatial dimension in zoology. After RUMPF'S epic approach to document the exact localities, it was only from the 19th century onward that this procedure was considered indispensable in a scientific publication. However, in spite of this growing tendency to record localities precisely in, for example, conchological monographs, owners of collections at that period were not especially attentive to the identification of the native countries of the shells in their cabinets. This fault is still to be encountered, as von BENTHEM JUTTING pointed out. Although provincialisms were one of the first general features of land plants and animal distributions, these were recorded systematically by only a few of the 19th century scientists, like the zoogeographers SCALTHER (1858) and WALLACE (1876). However, when biologists of this time travelled more and more routinely among different continents, they became impressed by the differences in biotas. Eventually the recognition of limited distributions of distinctive endemic forms suggested a history of local origin and limited dispersal, as revealed in the epitaph by WALLACE in the Introduction. Subsequently, this resulted in the (questionable) task to identify so-called »centers of origin«, to find evidence of historical barriers to dispersal or corridors for faunal exchange and to delimit the earth's biota into faunal and floral regions and provinces.

Far into the 19th century, biologists only gradually began to appreciate the importance of recording exact localities. Although it is often stated, for example, that for the eminent British naturalist Charles DARWIN (1809–1882) the geographical distribution was the key to »unlock the mystery of species«, DARWIN (1845) himself confessed in his journal of the voyage of the Beagle that he initially failed to note the exact location and geographical origin for the birds and reptiles he collected during his brief visit to Galapagos in September and October 1835. Yet did not for some time pay sufficient attention to this statement [by the Vice-Governor of Galapagos, Mr. Lawson, that he could tell from which island any different form was brought],

His contributions to malacology see von MARTENS 1902, von BENTHEM JUTTING 1959 and STRACK and GOULD 1996; for some brief notes see also STRIEBENZI 1951, pp. 37–40. For a long time it was unknown who, after RUMPF'S original drawings had been destroyed during a fire in Ambon in 1687, did the new figures (see, e. g., remark in von BENTHEM JUTTING 1859, p. 193). Yet about at least 42 of the 60 plates of shells and minerals contained in RUMPF'S book were drawn and hand-coloured by the artist and engraver Maria Sibylla MERIAN (1647–1717) (see STRACK and GOULD 1996). For this work she had to arrange the material in a much more static comparative style than in her own, beautifully coloured and biologically insightful opus Metamorphosis Insectorum Surinamensium, also published in 1705 (see e. g. KAUSER 1999).

6 GLAUBRECHT 2000.
7 von BENTHEM JUTTING 1959, p. 183.
8 Brown and LOMONIO 1998; for a brief overview on the historical development in biogeography see e. g. GLAUBRECHT 2000 and literature therein.

and I had already partially mingled together the collections from two of the islands. I never dreamed that islands, about fifty or sixty miles apart, and most of them in sight of each other, formed of precisely the same rocks, placed under the quite similar climate, would have been differently tenanted.

It might have been this confession that led WALLACE to clarify the zoological geography first of the Amazon region and later the Malay Archipelago. Even more important in connection with his co-discovery of the mechanisms of natural selection shared with DARWIN, WALLACE much later recalled in his autobiography that »giving a mass of facts as to the distribution of animals over the whole world, it occurred to me that these facts had never been properly utilized as indications of the way in which species had come into existence.« As BROOKS and SMITH have pointed out, a space-time context for WALLACE'S many observations on animal distribution might have already developed during his travels up the Amazon. Given the insufficient distribution data available at that time, WALLACE apparently decided probably as early as 1846 that an intensive investigation of the facts and plant distribution is needed in order to determine how biological change took place. This is documented, for example, in his 1852 paper on monkeys or his 1853 paper on the occurrence of distinct species of butterflies of the family Heliconidae on opposite banks of the Amazon.

Starting from the observation that the distribution of biological diversity on the face of the earth is neither arbitrary and accidental nor the result of a divine plan, WALLACE (1876) with his systematic approach to the study of the occurrence of animals and plants single-handedly founded biogeography as a science in its own right. Although, of course, biogeography has many and also much earlier roots which cannot be investigated here in more detail, it is nevertheless true that both DARWIN and WALLACE obtained crucial impulses for their formulation of evolutionary theory from zoogeographical observation.

The increasingly detailed knowledge of the geographical distribution of organisms later also provided the indispensable tool for the foundation of the new synthesis in evolutionary biology, as it is first evident, for example, from the seminal accounts by RENSCHE and MAYR. WALLACE'S program of determining the distribution of animals turned into a methodo-
logical research strategy for systematists and biogeographers in particular after the turn to the 20th century. This is marked, for example, in the work of the most eminent ornithologist of the time, Erwin Stresemann (1889–1972),17 who wrote: «Was dem Systematiker einst als ziemlich nebensächlich galt, die Feststellung der geographischen Verbreitung, ist für ihn zu einem wichtigsten Forschungsziel geworden, [um] die genetischen Zusammenhänge der Formen zu erkennen.»18 He later regarded the recognition of geographical variants as most critical and biologically important, since these geographical variants must be considered as instrumental in the speciation process.19 Haffer et al.20 have investigated the scientific development and conceptual contributions to the evolutionary synthesis of the Berlin ornithologist and systematist Stresemann in a series of papers, to which the reader should refer. Here it is sufficient to emphasize that this historical development eventually led to the awareness of the importance of the geographical factor not only for variation and species delimitation, but for speciation and evolution in general.

**Importance of Collections**

Today, exact data on localities and occurrences are still fundamental for biological, in particular (but not exclusively) biogeographical, studies. The determination of species distribution helps in pattern recognition and in process identification. Only accurate distributional data combined with the analyses of the phylogeny of taxa as well as the palaeogeography and palaeoecology of a given region allow us to look back in time. 21 The changed perception of the spatial origin and of natural differentiation in the distribution of animal and plants in the course of two centuries is also reflected in the development of natural history museum collections around the world.

Earlier collections were more or less arbitrary aggregation of curious natural history objects brought back from voyages that were at the beginning not primarily scientific expeditions. These natural science discoveries were housed as so-called _curiosités_ in the various over-sea colonies after the early 1880s. 22 However, even far into the 20th century that character of natural history collections shifted. More and more a research program became visible, leading eventually to a systematic collection effort and also including the exact documentation of the geographical origin of individual items. Recently, Haffer has shown that in the study of birds (which are since then certainly the most well-known vertebrate group in terms of systematics and biogeography) it was the large collections arriving from foreign countries and distant places especially during the second half of the 19th century that turned the attention of European researchers to the study of natural history products from various geographical regions, in this case to exotic ornithology. 23 These collections at the museums, that form the basis for systematic and zoogeographical research on individual and geographic variation as well as biodiversity and evolutionary biology, steadily grew in Germany following the establishment of over-seas colonies after the early 1880s. 24 However, even far into the 20th century, it remained an often heard complaint that locations were insufficiently given, if at all, for specimens sent to museum collections rendering them close to worthless today for scientific purposes. 25

21 Verhandlungen zur Geschichte und Theorie der Biologie, Bd. 9, Berlin: VWB 2002, S. 245-282
Early exploration of Australasia, 1511–1588

In contrast to the later increasingly systematic approach to the study of nature, the earliest objects that found their way back to the natural history collections were more or less arbitrary side products of the earliest explorations. These were not so much motivated by interest in the study of natural products and/or phenomena per se than they were officially initiated and financed endeavours. Although undertaken from a mixture of motives, most expeditions and voyages until the late 18th century were not purely scientific journeys, but were generally military, strategic, and commercial purposes. Here only an abbreviated survey can be given, compiled in Table 1, to which the reader should refer to for more details on the chronology.

In the Australian region this era of strategic explorations begins with the voyages of the Portuguese who were the first Europeans to develop the technology and confidence to sail out of sight of land (with a fair chance of return), using a pivoted compass for direction and an astrolabe (or quadrant) to determine latitude.31 As early as the 16th century they reached the coasts of New Guinea, but apparently successfully concealed their knowledge including the out of sight of land (with a fair chance of return), using a pivoted compass for direction in the discovery of new areas as well as the distribution of geographical knowledge.32

With the formation of a united Dutch trading company in 1602, and after the successful 1615 sea battle at Malacca against the Portuguese, the Dutch took over power in Southeast Asia, ending the century long influence of the former in the Malay Archipelago. Following the journeys of the Spaniard Luis de Torres 1606–1607 and the Dutch William Jansz 1606, who both - each from opposite directions - sailed through the (later to be named) Torres Strait between New Guinea and Australia, the Dutch aggressively searched for sea routes to new markets and assembled their trading empire in the East Indies, extending soon eastward to the coasts of New Guinea and the Moluccas (then called Nova Hollandiae), which they gave their place on the map as New Holland.

Founded at the beginning of the 17th century the Dutch Vereenigde Nederlandse-Oostindische Compagnie managed to establish and maintain itself as a superior colonial power. For almost the next three centuries the VOC was not only dominating exploration but information on natural products in Southeast Asia. Many initial observations and objects reaching Europe have their source in the work of merchants and traders serving for the company. Georg Everhard Rumphius with his personal insight and experiences working in situ is only one, albeit prominent, representative of this era and its specific circumstances. With commercial and trading interests focusing on the exploration of tea, coffee, cacao, cinnamon, and other spices including the most valuable nutmeg it is

31 CLANCY 1995.
32 How printed maps became part of an essential infrastructure to support maritime interests since the Dutch discoveries, and how they record the evolution of geographical knowledge is well-illustrated for the Australian region (which holds a central place in the world stage of cartography) in CLANCY 1995. A general assessment of maps as historical documents can be found in HAMILTON 2001. For the discovery of pre-Coeckian knowledge of Australasian geography see McINTyre 1982.
33 The contribution of Dutch explorers in official duty during this first phase of exploration is illustrated in detail in SCHILDER 1976.
34 For a lively and insightful account of European's competitive run to the aspie islands see for example McINTYRE 1999. Originally, the nutmeg trees grew exclusively on six small and remote islands of the Banda group including the island Run, about 2000 kilometers east of Jakarta. In the 17th century its fruit was believed to cure even the plague, resulting in a 600 fold profit on the markets of Antwerp and London, thus triggering brutal battles between Dutch and British over the possession of the tiny islands. Although today not as much a footnote in world history, an exchange in 1667 between the British and Dutch who traded the island of Manhattan for the nutmeg island of Ternate certainly has changed the face of the earth.

Tab. 1 Strategic-scientific explorations in Australia between 1511 and 1588 – an abbreviated chronology (compiled from various sources)

<table>
<thead>
<tr>
<th>Year</th>
<th>Event</th>
</tr>
</thead>
<tbody>
<tr>
<td>1511</td>
<td>the Portuguese Almeida and Serrano reach Ambon and discover New Guinea.</td>
</tr>
<tr>
<td>1526–1528</td>
<td>the Portuguese Magellan arrives at the Moluccas, reaches 1526 coast of New Guinea, then named Or Nova Guinea (later Nova Guinea by the Spaniard Alvaro de Saavedra 1527 who reached it from the Moluccas).</td>
</tr>
<tr>
<td>1537</td>
<td>the Spaniards Grijalva and Alvarado sail along New Guinea north coast.</td>
</tr>
<tr>
<td>1567</td>
<td>Alvaro MENDANA discovers Solomon Islands (only sighted again much later by CAYEY).</td>
</tr>
<tr>
<td>1595–1597</td>
<td>MENDANA also discovers Marquesas and Santa Cruz Islands.</td>
</tr>
<tr>
<td>1595</td>
<td>first Dutch expedition to East India.</td>
</tr>
<tr>
<td>1598</td>
<td>Olivier van Noorts passes through Malagaias-Strait, crosses Pacific.</td>
</tr>
<tr>
<td>1601</td>
<td>Portuguese Manuel Godinho de EREDIA reaches Melville Island off Australia.</td>
</tr>
<tr>
<td>1602</td>
<td>formation of the Dutch East India Company.</td>
</tr>
<tr>
<td>1606</td>
<td>Willem JANSZ on Daykens sails to New Guineas from Banten, discovers west coast of Cape York Peninsula.</td>
</tr>
<tr>
<td>1606–1607</td>
<td>Pedro HERNANDez de QUIROS discovers the New Hebrides, named «Australia» de Espiritu Santo because thought to be part of the «Great South Land».</td>
</tr>
<tr>
<td>1610–1615</td>
<td>first Dutch voyage to New Guinea.</td>
</tr>
<tr>
<td>1616</td>
<td>Willem Cornellizoon SCHOUTEN and Jacob Le Maire reach Australia's east coast after finding third passage into the Pacific around Cape Horn.</td>
</tr>
<tr>
<td>1619</td>
<td>Frederick HUISMAN and Jacob D'EBEEL reach the «Pacific» of Australia.</td>
</tr>
<tr>
<td>1622</td>
<td>Dutch Leeuwin sails around SW Australia.</td>
</tr>
<tr>
<td>1624</td>
<td>Jan CASTELEN on the Dutch ship Arnhem lands on Australia's north coast, near Darwin.</td>
</tr>
<tr>
<td>1636</td>
<td>Gerard POOL reaches west coast of New Guinea, sails to 14 S.</td>
</tr>
<tr>
<td>1642–1643</td>
<td>Abel JANSZoon TASMAN circumnavigates the area containing Australia, discovers Tasmania («Van-Diemen-Lands»), New Zealand, Tonga and Fiji, Bismarck Archipelago and New Guinea.</td>
</tr>
<tr>
<td>1678</td>
<td>Dutch merchant KEYS travels with three ships to south coast of New Guinea.</td>
</tr>
<tr>
<td>1696</td>
<td>Vlaming reaches estuary of Swan River at Australia's west coast.</td>
</tr>
<tr>
<td>1698</td>
<td>William Dampier discovers New Britain and Dampier's Strait.</td>
</tr>
<tr>
<td>1700</td>
<td>Dampier reaches the NE coast of New Guinea, King Williams Cape («A voyage to New Holland», 1703).</td>
</tr>
<tr>
<td>1767–1769</td>
<td>Philipp CARLBERG's crossing of the Pacific without new discoveries.</td>
</tr>
</tbody>
</table>

The Age of Natural Science Explorations in Australasia

1766–1769 | Louis Antoine de Bougainville on La Boussole crosses Pacific, reaches New Hebrides and New Britain, and narrowly misses east coast of Australia, on board botanist PhillipIDIE COMBER. |
1768–1771 | James COOK's first voyage on the Endeavour through the South Pacific, circumnavigating New Zealand, charting Australia's east coast with botanists Joseph BANKS and Daniel CARL SOLANDER. |
### Tab. 1 Strategic-scientific explorations in Australasia between 1511 and 1858 (continuation)

<table>
<thead>
<tr>
<th>Year</th>
<th>Event</th>
</tr>
</thead>
<tbody>
<tr>
<td>1772-1775</td>
<td>James Cook's second voyage on the Resolution and Adventure with naturalists Johann Reinhold Forster and George Forster</td>
</tr>
<tr>
<td>1774-1776</td>
<td>expedition of Thomas Forrest between the southern Philippines and New Guinea, lands near Dorey Harbour</td>
</tr>
<tr>
<td>1776-1780</td>
<td>Cook's third voyage to the Pacific</td>
</tr>
<tr>
<td>1776-1788</td>
<td>French expedition to the Molucas and New Guinea, with naturalist E. Sonnerat (1749–1814), in order to obtain nutmeg trees</td>
</tr>
<tr>
<td>1785-1858</td>
<td>Jean François de Galaup Compte de Lapérouse's voyages on Boussol and Astrolabe in Melanesia and between New Guinea and New Zealand, with naturalist Dupresse</td>
</tr>
<tr>
<td>1788</td>
<td>British settlement (&quot;The First Fleets&quot;) at Sydney Cove</td>
</tr>
<tr>
<td>1789-1794</td>
<td>Spanish South Sea expedition of Malaspina</td>
</tr>
<tr>
<td>1791</td>
<td>MacCluer on Panther and Endeavour sailed along Australia's west coast and surveyed northwest and western coasts of New Guinea</td>
</tr>
<tr>
<td>1791-1793</td>
<td>Antoine Raymond Joseph de Brun D'Entrecasteaux's coastal surveys in Australia and New Guinean waters, Admiralty Islands and New Ireland, on board as naturalist Lallardiere</td>
</tr>
<tr>
<td>1801-1803</td>
<td>Matthew Flinders' Investigateur, circumnavigation and cartography of Australia, a name recommended by him (&quot;A Voyage to Terra Australis, 1814&quot;)</td>
</tr>
<tr>
<td>1800-1804</td>
<td>Nicolas Baudin's French expedition on Geographe and Naturaliste to Australia and the South Sea, with naturalist François Péron</td>
</tr>
<tr>
<td>1817-1820</td>
<td>Louis-Claude de Frémy's world circumnavigation with L'Uranie and La Physicienne, reaches also Timor and Waigeu, with naturalists Quoy and Gaimard, Lesson, Garnot</td>
</tr>
<tr>
<td>1822-1825</td>
<td>Louis Isidore Duperrey's tour around the world on La Coquille, on board Dumont D'Urville, and as pharmacist and naturalist (ornithologist) René F. Lesson</td>
</tr>
<tr>
<td>1826-1829</td>
<td>Jules Sébastien Cesar Dumont D'Urville's voyage on L' Astrolabe through the South Sea, on board Quoy and Gaimard</td>
</tr>
<tr>
<td>1828</td>
<td>Dutch Dourga under Kolff sailed into the (later so called) Princess Marianne Strait at New Guinea's SW peninsula</td>
</tr>
<tr>
<td>1828-1840</td>
<td>Dutch expedition on Trion and Iris to SW coast of New Guinea, with naturalists Salomon Müller, H. C. MacKllet and A. Zippelius (botanist)</td>
</tr>
<tr>
<td>1837-1840</td>
<td>Dumont D'Urville's second voyage around the globe on L'Astrolabe and La Zélée, exploring southwest coast of New Guinea (1839), on board naturalists Humbert and Jacquinet (zoologist and commander on Zélée)</td>
</tr>
<tr>
<td>1843-1846</td>
<td>Samuel with naturalist Arthur Adams</td>
</tr>
<tr>
<td>1846-1850</td>
<td>Owen Stanley's expedition on the Rattlesnake to New Guinea, Louisiane Islands, and north coast of Australia, trying to establish settlement there, with naturalist John MacCallum and Thomas Henry Huxley as assistant surgeon</td>
</tr>
<tr>
<td>1849</td>
<td>Dutch Circ under Bruin-Roos explores north coast of New Guinea</td>
</tr>
<tr>
<td>1858</td>
<td>expedition of the Dutch steamer Eina along New Guinea's coast</td>
</tr>
</tbody>
</table>

### Maritime Expeditions that Later Explore Indo-West-Pacific Waters

<table>
<thead>
<tr>
<th>Year</th>
<th>Event</th>
</tr>
</thead>
<tbody>
<tr>
<td>1857-1859</td>
<td>Austrian expedition around the globe of the Novara, with Johann Zelbor as naturalist and zoologist to the expedition</td>
</tr>
<tr>
<td>1872-1876</td>
<td>Challenger expedition as first geophysical-biological exploration of oceans</td>
</tr>
<tr>
<td>1874-1876</td>
<td>Garele expedition around the world with emphasis on deep sea</td>
</tr>
<tr>
<td>1899-1900</td>
<td>Dutch maritime expedition on Siboga to Indo-West-Pacific</td>
</tr>
</tbody>
</table>

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The invention of the chronometer by John Harrison (1761–1775), who fixed the problem of determination of longitude by using a chronograph, has recently been described by Sorel. 1995.

Raby 1996.

Dance 1971, p. 357.

35 The life and contributions of the 17th century British watchmaker John Harrison (1693–1776), who first solved the problem of determination of longitude by using a chronograph, has recently been described by Sorel. 1995.

36 Raby 1996.

37 Dance 1971, p. 357.
New Zealand and discovering and exploring the east coast of Australia, as well as in 1788 the choice of Botany Bay and (the more hospitable) Sydney Cove, respectively, for a British penal settlement, thus marking the beginning of a new epoch.

While Cook’s first journey to the Pacific is generally considered the first scientific exploration, it is mostly overlooked that the voyage of his French counterpart, Louis Antoine de Bougainville (1729-1811), who visited the Pacific a few months before Cook, with the naturalist-botanist Philibert de Commerson (1727-1773) and an astronomer on board La Boussole, clearly showed the same character. Cook and Bougainville provided the framework for the explorers of succeeding generations, opened up the Pacific and revolutionized existing maps of it. Naval power, science and empire converged with superb economy. Following these explorers, naturalists systematically began to travel, to collect, to study, to draw and to describe the natural productions and biotic diversity protected and sponsored by admiralty and governments.

Beginning with Louis de Bougainville’s voyage around the globe 1766–1769 and comprising the next seven decades, the Australasian region also saw an expansion in scientific exploration accomplished by a series of major French expeditions, accompanied by lavish government-sponsored journals. For example, following the disappearance of Jean Francois Comte de Laperouse (1741–1788), the French coastal surveys in Australia were begun 1791–1793 by Raymond Joseph de Bruin d’Entrecasteaux (1739–1793) with his hydrographer C. F. Beauméps-Beaupré and the naturalist Labillardiere. Later the voyages of Nicolas Baudin (1742–1803) in 1800–1804 to Australia and the South Sea spour des recherches de géographie et d’histoire naturelle, with Louis Claude Freycinet being the expedition’s cartographer, started an important sequence of French navigations. The natural history material collected during Baudin’s expedition was given to the Paris Natural History Museum, with the majority being invertebrates studied by

38 The first man to be officially appointed as naturalist to accompany an expedition to the Pacific, and probably the most competent observer of Pacific natural history in the eighteenth century, as DANCE 1971, p. 355, has pointed out, was Georg Wilhelm Steller (1709-1746) who accompanied several of Vitus Bering’s (1680-1741) expeditions to the north Pacific.

39 Interestingly, the chronology of discoveries and expeditions in Australasia reveals a continuous tradition in the skill of exploration (see Tab. 1), in which accompanying naval officers later became responsible for expediting themselves, eventually leading to new discoveries, with Freycinet serving under Cook, Flinders under Banks, Franklin under Flinders and Stanley under Franklin. The same can be seen in French naval history with Freycinet first serving under Baudin and Dumont d’Urville serving under Duperre before being commander on two marine voyages of his own.

40 RARY 1996, p. 5. The great Pacific voyages and the exploration of Australasia has been accused of being a kind of ecologically imperialism (see GASCIONE 2001 as, for example, illustrated recently in the correspondence of Joseph Banks, botanist on Cook’s first voyage on the Endeavour, who was instrumental in founding the Royal Botanic Garden at Kew near London and who aimed the movement of plants around the world; see CHAMBERS 2000).

41 Instrumental in as well indicative of this process was, in addition to the formation of other learned societies and institutions with the age of Enlightenment and especially after the turn to the 19th century (see, e.g. RARY 1996, p. 7), the founding of the later influential Royal Geographical Society which published its first journal in 1832. The Journal of the Royal Geographical Society was to become the leading scientific medium available for explorers to publish the first news of their discoveries. Also, important contributions concerning the mapping and natural discoveries in the Malay Archipelago appeared here.

42 For an overview see e. g. DUNMORE 1965-1969.

43 JOSEPH 1804.

The experiences of nature: from Salmon Müller to Ernst Mayr

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The Dutch Triton Expedition 1828

Representing a relatively little known example of government-sponsored, naval exploration during the first half of the 19th century is the 1828 Dutch expedition with A. J. Van Delden to New Guinea on board of the corvette Triton and the colonial schooner Iris under the command of Captains J. J. Steenboom and J. H. Van Boullyce Bastiaanse, respectively. Undertaken by order of the Netherlands’ government, on board of the two ships were also the naturalist Heinrich Christian Macklot (1799–1832) and the botanist A. Zippelius, in addition to Salomon Müller as preparator and the two artists Pieter van Oort and Gerrit van Raalten. They were sent to the East Indies in December 1825, arrived in June 1826 on Java, and finally were ordered the same year. The primary objective of the expedition was to secure Dutch power in western New Guinea in particular against British interests by establishing a settlement on some convenient spot on the west coast of the island. Although Van Delden’s report was never published, detailed accounts of the voyage were given by J. Modera and later Salomon Müller (e.g. 1858) as the sole survivor of this ill-fated expedition.

The Triton expedition did not reach its primary aims due to many adverse circumstances (an unfortunate Verkennung unglücklicher und unvorhergesehener Umstände), but especially due to the failure of finding a suitable landing place for the settlement. In addition, the climate in this region of New Guinea was cold, damp and foggy throughout most of the prevailing southwest monsoon months. Consequently, the majority of the crew including the five scientific men suffered from malaria at their main anchorage, Merkusood at Lobo in Tritons Bay and the Fort Du Bus. After the death of twenty of the ships’ crew and the sickness of about sixty others that made further research impracticable, the expedition was finally forced to return to Kupang on Timor, where the naturalists including Salomon Müller left the expedition with the plan to continue natural history observations in the west part of this island. Based on 13 months stay, Müller in his second volume later reported on the geography and ethnography of Timor. On this island with Zippelius the first member of the scientific party died on December 28, 1828 and was followed by Van Raalten in April 1829, while Macklot was killed during a riot on Java in May 1832 (loosing also his scientific notes). After the last member, Van Oort, died in September 1834, it was only Salomon Müller to return to Europe.

Nevertheless, the Triton expedition was of considerable success in two other respects. First, during this voyage the greater portion of the SW coast was surveyed, being the first detailed cartographic study of New Guinea (Fig. 1), with the Triton and Iris being the first ships to sail into the Princess Marianne Strait from the north. Second, a rich collection of natural history objects from New Guinea were, for the first time, systematically collected and later thoroughly described mainly by Salomon Müller. For example, Modera and Müller both reported on several species of kangaroos (soorte soorten van springhazen), later leading to the description of the new genus Dendrolagus. Among other contributions, this renders Müller and Macklot pioneering biologists and the first Europeans to leave a clear account of a tree-kangaroo in life. In addition to mammals, amphibia, reptiles and fishes, the birds hunted by the expedition’s crew were especially rich, among them birds of paradise, crowned pigeons, and kingfishers. At the end of the voyage, and of a three months’ stay on the coast, our collection was composed of 119 varieties, belonging to 60 different kinds. This material mainly found its way to the Rijksmuseum van Natuurlijke Historie in Leiden, undoubtedly contributing to the fact that, during the 19th century, it held one of the most famous collections.
Salomon Müller and the Foundation of a »Zoological Geography«

»Welcher Unterschied daher in der thierischen Welt jener östlichen Hälfte und der westlichen des Archipels.«

S. Müller (1846)  

The German naturalist Salomon Müller was born on April 7, 1804 in Heidelberg; he also died in Germany, viz. in Freiburg im Breisgau in spring 1864. His parents were Johann Gottlieb Müller, »Bürger und Sattlenneister«, and his wife Maria Elisabeth (maiden name HELFRICHIN). Between 1826 and 1837, Salomon Müller spent eleven of his best years (»elf der schönsten Jahre meines Lebens«) in the Malay Archipelago, thus three years more than Alfred Russel Wallace two decades later. The circumstances of Müller’s employment in the Natuurkundige Commissie van Nederlandsche Indie (member of the Dutch commission of natural history in East India) was described in some detail only by Stresemann. After his return to Europe Müller, who also held a doctor’s title, became Ritter des niederländischen Löwenordens (Knight of the Order of the Dutch Lion) and continued to work in the museum in Leiden.

Having been employed not as naturalist but as »Präparator« to the expedition, he was originally only responsible for stuffing and preparing the collected natural history objects. However, Müller miraculously was not only the sole survivor of the 1828 Triton expedition to New Guinea, but he also remained in the East Indies for nearly another decade and went successfully on several other journeys through the Malay Archipelago before returning on August 22, 1837 to Holland. First, he travelled on Sumatra in 1833–1835. A year later he made a journey from Bandjermasin in the south of Borneo up the river Barito (Soengi Doeson, or Banjer) to Lonton toer just south of the equator, through the region of the sultanat Martapoera and the Lawut-Landen in the province Laut. A detailed report about these journeys on Borneo, undertaken in 1836–1837 in company of Ludwig Horn and the botanist P. W. Korthals, is given in Müller’s first volume of »Reizen en onderzoekingen«, while the journey to New Guinea and his travelling on Celebes, Boeton, Ambon and the Banda Islands is described in the second volume.  

In light of the experiences of the Triton expedition in 1828, and given the obstacles and dangers that remain daunting even for modern biological explorers in many region of Indonesia, it was nothing short of miraculous that Müller — as did Wallace from eight years of travelling in the same region — emerged alive from the East Indies to return to the Netherlands.

As a direct result of the later journeys Müller can be credited with first having cartographed the wide inland from Bandjermasin on Borneo (see Fig. 2). Even more important in our context, he also explored much of the biological diversity not only on New Guinea during the Triton expedition (see above) but also on the Sunda Islands he travelled in the 1830s. The combined

60 S. Müller 1846, S. 114.
61 The few existing biographic dates on Salomon Müller are to be found e.g. in Henze 1993. Stresemann 1939, p. 303, reported in a footnote in his introduction to the history of research on Celebes that up to his research into this matter the year of birth of Müller was unknown (and was indeed hitherto given as »around 1800«) as were his parents and their profession; see also Stresemann 1951, pp. 138 ff.
62 Möller 1846, p. 127.
63 Stresemann 1951, pp. 135–145, 154.
64 Möller 1857

Fig. 2 Salomon Möller first cartographed the wide inland from Bandjermasin on Borneo. From Möller 1857

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experiences and observations on animals from these two geographical regions, in particular on mammals but also birds and reptiles, provided the basis for his later evaluation of a distinctive faunistic division within the Malay Archipelago.

Immediately following his return 1837 and strongly supported by the director of the Rijksmuseum in Leiden, Comenad Jacob Temminck (1778–1858), several faunal elements new to science – from orangutans and marsupials to birds of paradise and varans – were described by Salomon Müller himself, or by Hermann Schlegel (1804–1884; in 1858 to become museum director after Temminck died) and Wilhem de Haan (1801–1855) in a series of illustrated publications.65

To the documentation and descriptions of the findings and the material collected during his travelling, Müller later added two accounts on the geography of animals in the Malay Archipelago that were analytical in its best sense. The first paper written in German (in contrast to his later book on his journeys)66 was published in March and April 1842 in two consecutive issues of the Annalen der Erd-, Völker- und Staatenkunde. Here he begins his detailed analysis of the distribution of mammals on the individual islands of the Sunda group and the Moluccas with the statement that wiewohl alle Inseln, von Java bis Neu-Guinea fast dasselbe Klima haben, und viele von ihnen ziemlich dicht bei einander liegen, ja oft nur durch schmale Meerengen von einander geschieden sind, so besitzt doch jede Insel von einiger Ausdehnung in grösserer oder geringerer Anzahl Gattungen, welche ihr eigenthümlich sind.67

In the subsequent paragraph, he continues: "Es verdient bemerkt zu werden, dass die grossen Sunda-Inseln sehr viele Geschlechter von Säugetieren besitzen, wovon man auf den etwas östlicher gelegenen Molukischen Inseln Keine Spur mehr antrifft, während diesen wieder einige andere eigen sind, die auf jenen ganz und gar vermissen werden."68

After having presented in the first part (published in March 1842) only a brief overview on the distribution of mammals, a second, more detailed account comprising and reviewing the occurrences of particular species of birds, reptiles and amphibians (as later suggested but done only for mammals and birds by Wallace, see below). In his paper Müller recognized it. "The geographic separation – or adig eigentlichen Scheidepunktes, as he stated – starts to the east of Borneo with Celebes and Timor. According to Müller, it is marked, for example, by the westernmost occurrence of marsupials and also the easternmost occurrences of monkeys (except only of the genera Cercopithecus and Cynocephalus), and with Casuar and Megapodius restricted to the eastern part, while peacocks (Pavo) and woodpeckers only occur on the large Sunda Islands. Thus, in contrast to the biota of the east, that of the western part is predominantly comprised of forms from the Asian mainland. For example, the tiger (Felis tigris) occurs on Java and Sumatra but is entirely lacking further east (Müller apparently was unaware of the tiger, today extinct, on Bali)."

65 A series of monographic papers by these three naturalists were edited by C. J. Temminck (for an insight account on his personality and accomplishments see Stresemann 1951, pp. 150–155) and appeared as Verhandlingen über die Naturwissenschaflich der Niederlandeche Oezeezische Bestitzungen. Zoologie in Leiden, published between 1839 and 1845 by the Natuurbundige Commissie in India. Here, Müller often credited Heinrich Christian Macklow (1799–1832) with co-authorship, apparently to honour him for his contributions during the exploration on the Sunda and Timor, although the latter has died before returning. Temminck’s Dutch monograph series contained the very first illustrations of New Guinean animals. Most spectacular is, for example, the two full-page colour plates of the Vogelkop tree-kangaroo Dendrolagus urinus and the Grizzled tree-kangaroo Dendrolagus inustus together with some black-and-white plates, accompanied with the descriptions of the species by Salomon Müller published in a footnote.

66 Müller 1857.

67 Although all islands, from Java to New Guinea, share almost the same climate, and very many of them are rather close to each other, often only separated by narrow straits, each island of some extent possesses in larger or fewer number genera which are peculiar to it. – Translation: M. G.; Müller 1842, p. 252.

68 It deserves to be mentioned that the larger Sunda islands possess many genera of mammals which are absent from the more eastward located Moluccan islands, whereas on the latter islands again some others occur that are lacking entirely on the former islands. – Translation: M. G.; Müller 1842, p. 252.

69 Müller 1842, p. 289.

70 Müller 1842, p. 289.
71 Müller 1846, p. 119.
72 Müller 1846, pp. 109–110.
73 The Indian Archipelago therefore is divided along its length in respect to geography and natural history into two parts of unequal spatial extent. The western larger half comprises the islands of Borneo, Sumbawa, Java, Sumatra and the peninsula of Malacca; the eastern half only islands of second and third rank, namely Celebes, Flores, Timor, Gilolo and maybe Mindanao as the outer boundary. – Translation: M. G.
(ii) The transitional zone he found to be on the islands of Celebes, Flores, Timor and Buru, recognizing the fauna and flora of the Spice Islands or Moluccas as being already predominantly Australian with the marsupials as the most characteristic elements, among them members of Phalanger. »Diesen Übergangsstreifen bilden die Inseln Celebes, Flores, Timor und Buru; er liegt also zwischen dem 136 und 145 Meridian-Grade östlich von Ferton,' making especially the Moluccas in terms of their zoology most closely related to New Guinea and New Holland.25 As another most typical faunal element he considered the Babirussa endemic to Sulawesi.

In addition to the examples among the mammalian taxa and their distributions across the archipelago that he provided, MÜLLER in the first quantitative approach also summarized that about 175 mammalian taxa are known altogether from the Malay Archipelago, including the Malacca Peninsula and New Guinea. While 50 species – mainly the largely mobile chiroptera – occur over the entire region, he stated that less than 30 live exclusively in the eastern part.26 In another example, MÜLLER noted for the woodpeckers that 16 species occur on Java, Sumatra, and Borneo while on Celebes there is only one species (Picus fulvus) and Picidae are entirely lacking on Timor and the Moluccas.27 He summarized that among the reptiles there are 70 to 80 species that live in the eastern part of the Malay Archipelago including New Guinea, Celebes and Timor, whereas about 120 species occur in the western part.

Finally in a concluding remark, MÜLLER outlined the heuristic value of field research in the Indonesian Archipelago, stating that numerous islands especially in the eastern part remained as terra incognita. »Man ersieht daraus, welch ungemein fruchtbaren und interessantes Feld dieselbe [Welthandlung] der Natursuchtung darbietet.«

Analysing MÖLLER's writings28 it is beyond doubt that he – and not Alfred Russel WALLACE as generally believed – was first to discover the faunistic division between Asia and Australia. As testimony of their parallel and independent observations, MÖLLER amazingly states – even on a taxon-by-taxon basis – the same examples among the faunal elements that later were utilized by WALLACE to illustrate the same peculiar faunal distinction. I am unaware of any references to Salomon MÜLLER in WALLACE's writings or that of most of his contemporaries discussed in the following section; and we should conclude, therefore, that WALLACE apparently had no knowledge of the work and publication of the former. However, STRESEMANN noted that WALLACE might have been stimulated by MÖLLER's 1846 account, but failed to give any evidence for this assumption.29

Notwithstanding, the fact that MÜLLER published his main contributions to science in German and Dutch does not justify the now century long and virtually complete ignorance of his earlier and parallel discovery that dominates particularly the contemporary Anglo-Saxon literature. It is not an unusual but, nevertheless, astonishing fact that MÜLLER's contribution has been completely forgotten, as is revealed in the vast majority of biological, biogeographical and biographical accounts. He has also been overlooked by historians of science; for example, any mention is missing from recent influential works on the history of biology.30 I was unable to find – even in German literature – more than an occasional and marginal reference to him and his biogeographical contribution.31 In addition, only MAYR (1944), SIMPSON (1977) and recently BRANDON-JONES (1998) and OOSTERZEE (1997) briefly mention Salomon MÜLLER. For example, the latter author stated that »Müller [sic!] in 1846 defined a line based essentially on ecology, devoting the remaining book to WALLACE and the discovery of his line. As in the latter book, WALLACE is not only credited and cited as being first to discover this faunal demarcation, but he is also generally considered as »father of biogeography.« However, to the same degree that WALLACE shares with DARWIN the discovery of natural selection as the driving force of evolution, Salomon MÜLLER shares with WALLACE the discovery of a distinct faunal demarcation line and an intermediate zone with endemic elements in the Malay Archipelago as well as the founding of zoological geography as a biological discipline.

Alfred Russel Wallace and Wallace's Line

It was, nevertheless, WALLACE – and not MÜLLER – who opened the scientific world's eyes to its biological diversity after having travelled 14000 miles within the Malay Archipelago on some 60 to 70 separate journeys and sending back to England a total of over 125000 specimens.32 The theories he worked out during and after his travels in the East Indies dwelt essentially on spatial relationships, the reason to consider WALLACE as being, fundamentally, a geographer. Consequently, geographical information was instrumental for WALLACE both for his biogeographical as well as evolutionary contributions to biology. In several seminal papers and books he developed innovations in the historical reconstructions of faunas and, thus, implemented zoological geography as a biological discipline within the framework of evolutionary theory.33

It is, as SMITH correctly stated,34 usually little appreciated how strongly natural processes are constrained by the necessity of having to take place in a three-dimensional space, and WALLACE's skill at spatial analysis is best illustrated by his contribution to the biogeography of the Australasian region. He first developed the greater picture of a fundamental faunal difference between the western and eastern islands of the Malay Archipelago in his landmark paper on the natural history of the Aru Islands, off the coast of New Guinea.35 This paper re-

82 For example, in the writings of FINSCH 1865, RENSCH 1936 and STRESEMANN 1939, 1951.
83 OOSTERZEE 1997, p. 34.
84 For example BROWN and LOMOLINO 1993, RABY 2001.
85 WALLACE 1869, see also RABY 1996, 2001.
86 The term zoological geography has been used both by MÖLLER 1846 and WALLACE 1860 in the titles of their respective papers. In addition, MÖLLER 1846, p. 119, also used geographical zoology when suggesting a research program to investigate the regional fauna of the East Indies. SMITH 1991, p. 218, in his introductory remarks to WALLACE's contribution to biogeography differentiated these two terms as the former trying an historical reconstruction of faunas while the latter looks into the »spatial aspects of phylogenies«. It is highly unlikely that, given the lack of any indication on evolutionary ideas, at least MÜLLER could have meant his terms in this latter sense.
88 WALLACE 1857.
presents his first major treatise on the method of biogeographical analysis and is in many respects the birth of the new approach to that subject.99

Describing his biological observations WALLACE noted that "this difference [of the faunas in the Malay Archipelago], must be well marked, is not one of species, but of genera, families, and whole orders. Yet, it would be difficult to point out two countries more exactly resembling each other in climate and physical features."90 Not very much later WALLACE went on with a large-scale analysis of faunal patterns, writing on the zoogeography of the Malay Archipelago.91 However, as often in his writing, he anticipated the main subject of this classical paper a year earlier in a letter to the ornithologist and editor of the journal Isis, Philip Lutley SCLATER (1829–1913), who published the letter the same year.92 In concert with observations from his travelling and collecting animals specimens in the East Indies, his first contribution to a systematic regional biogeography was directly triggered by SCLATER’s (1858) paper on the geographical distribution of birds.

This paper by the latter author was highly influential for shaping WALLACE’s concept as to how and where to locate the precise boundary between the Asian and Australian biotas. According to SCLATER, his system should reflect the most natural primary divisions of the earth’s surface, taking the amount of similarity or dissimilarity of organized life solely as our guide. While coarse, SCLATER’s formal approach of schematically dividing the earth’s terrestrial surface into six biogeographical regions was based on the distribution of birds (but mainly restricted to passerines due to believed lower dispersal abilities). It had a major impact on zoogeography and on biogeography in general.93 This early approach was immersed in the prevailing view of the earth’s stability in the form of fixed continents and permanent ocean basins and, thus, from today’s perspective represents the so-called classical-descriptive era of biogeography (in contrast to the late 20th century analytic-phylogenetic era).94

Nevertheless, SCLATER’s scheme turned out to be of enormous heuristic value. WALLACE not only perfectly agreed[d],95 but also believed that the six zoological provinces will be confirmed by every other department of zoology as well as by botany. Commenting on the precise boundaries of the suggested regions, WALLACE here for the first time suggested his later famous line to delimit the Indian (= Oriental) Region.96 His south-eastern limits I draw between the islands of Bali and Lombok, and between Celebes and Borneo, and the Moluccas and the Philippines.97 WALLACE, repeating that the same division will hold good in every branch of Zoology,98 later marked out the precise limits of the two faunal regions in the Malay Archipelago by contrasting individual taxa. Despite his claim that the regional limit will be followed by most (if not all) groups of animals, he only discussed mammalia and birds. Therefore, WALLACE does not surpass the general approach presented 14 years earlier by MÜLLER for four vertebrate classes (see above). Albeit having more detailed knowledge on the distribution of individual taxa, the general claim that WALLACE was the first person to analyze faunal regions based on the distribution of multiple groups of terrestrial animals99 ultimately does not hold true in two respects.100

It should be mentioned explicitly here, though, that WALLACE correctly drew his demarcation line that separates the Oriental and Australian fauna between Bali and Lombok and Borneo and Celebes.101 In contrast, MÜLLER had assumed for the southern part that the faunal division should lay further east, i. e. east of Sumbawa, while he clearly saw the fundamental faunal difference between Borneo and Celebes.102

This distinct perception also has relevance in light of the question about the causation of this pronounced faunal division. While we do not have any indication that MÜLLER ever thought about it, or at least addressed this aspect, it is worthwhile to briefly examine the development of WALLACE’s thought on this matter. It is occasionally assumed that, although WALLACE’s line directly corresponds to deep water marking the limit of historical land connections among the major East Indian islands and between them and the Southeast Asian mainland, WALLACE did not realize this.103

However, this is apparently only true for his earlier writings. Indeed, in his 1860 paper he stated that there is nothing in the aspect or physical character of the lands to lead us to expect such a difference; their physical and geological differences do not coincide with the zoological differences. There is a striking homogeneity in the two halves of the Archipelago.104 In contrast, after his return to London in 1862 WALLACE increasingly thought about and argued for a parallel between faunal similarities and the continental extensions, i. e. shelves. It was Charles DARWIN, having communicated WALLACE’s 1860 paper to the Linnean Society in 1859, who in August 1859 mentioned in a letter to WALLACE (then still in Indonesia) a close relation between depth of water and the degree of biological affinity.105 DARWIN cited a paper by George Windsor EARLE (1813–1865),106 who travelled in the Indian archipelago between 1832–1834107 and published a paper on the physical structure and arrangement of the Indian Archipelago.108 This paper is accompanied by a map showing the existence of shallow seas

100 Today it is known that far from all taxa show distributional boundaries corresponding precisely to WALLACE’s line; other lines have been described to accommodate them. For an overview and relevant literature see, for example, OOSTERZEIT 1997. A recent discussion using limnic gastropods and references to additional literature is given in GLAUBRECHT 2000.
101 See, for example, his maps in WALLACE 1863, 1876.
102 MÜLLER 1846.
103 For example Brown and LOMOLINO 1998, p. 308. For a recent account on the biogeography of the Indonesian Archipelago and possible underlying palaeogeographical causations summarizing current knowledge see HALL and HOLLOWAY 1998.
104 WALLACE 1860, p. 175.
106 As CAMERINI 1993, p. 716, pointed out, the spelling of EARL(B)’s name varied in his own publications and references to him by contemporary authors.
107 See EARLE 1837.
108 EARLE 1845.
between the Asiatic mainland and the larger Sunda Islands on the one hand and New Guinea and Australia on the other hand. Later, Wallace in his own paper on the physical geography addressed this important finding but argued vehemently against Earle’s hypothesis of Australia being once part of Asia. The combination of his own biological observations with the increased geographic knowledge unfolding since around the mid 19th century that even allowed first hypotheses on causal explanations of zoogeographical patterns, eventually enabled Wallace to more fully document and analyse the distribution of animals than anyone before him. This is illustrated by his development of a detailed and very precise map of the earth’s biogeographic regions continued to be used today. Thus, although many of the concepts enunciated by Wallace were introduced by earlier scientists, it was Wallace – based on the available geographical experience – who then for the first time restated, documented and interpreted them in an evolutionary context.

In the context of the development of evolutionary theory, Camerini has recently examined how maps were instruments of thought and as visual components of the conceptual framework. Mapping faunal boundaries since Wallace’s time served not only as a method for organizing and communicating faunistic data but was also a potential and increasingly powerful device in providing and compiling the data in support for modern evolutionary argumentation. Interestingly, this approach has only been taken up again about half a century later by the pioneers of the modern or synthetic evolutionary theory as will be shown in a section further below, with the German-born Ernst Mayr playing a key role in this process precisely a century after Müller.

### Travelling Naturalists on New Guinea

With Alfred Russel Wallace a gradual but highly significant change takes place over the course of the second half of the 19th century. As Rasy pointed out, for the new generation of individual scientific travellers, Alexander von Humboldt (1769–1859) and Aimé Bonpland (1773–1858) with their journeys to South America, have served as a role model for many successors to come (less so for various reasons but also deserving mention, Maria Sibylla Merian). The details of Wallace’s development in respect to the problem of land connections and differentiation of faunal regions are investigated by Rickman (1977).

109 Interestingly, Wallace apparently attended a meeting on 8 February 1853 of the Zoological Society in London, where Earle gave a note on the zoology of the Malay Peninsula (see Rasy 2001, p. 86). In an earlier footnote Earle 1845, p. 363, referred to the fact – as rather a singular circumstances – that kangaroos, that were first in 1828 discovered in New Guinea, also occurred on the Asiatic mainland and the larger Sunda Islands on the one hand and New Guinea and Australia on the other hand. Later, Wallace in his own paper on the physical geography addressed this important finding but argued vehemently against Earle’s hypothesis of Australia being once part of Asia. The combination of his own biological observations with the increased geographic knowledge unfolding since around the mid 19th century that even allowed first hypotheses on causal explanations of zoogeographical patterns, eventually enabled Wallace to more fully document and analyse the distribution of animals than anyone before him. This is illustrated by his development of a detailed and very precise map of the earth’s biogeographic regions continued to be used today. Thus, although many of the concepts enunciated by Wallace were introduced by earlier scientists, it was Wallace – based on the available geographical experience – who then for the first time restated, documented and interpreted them in an evolutionary context.

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### Tab. 2 Scientific travellers to Australasia in the years 1833-1930, with focus on New Guinea – some examples (compiled from various sources)

<table>
<thead>
<tr>
<th>Year</th>
<th>Traveller</th>
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<tbody>
<tr>
<td>1833-1835</td>
<td>Salomon Müller travelled on Sumatra</td>
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<tr>
<td>1836-1837</td>
<td>Salomon Müller travelled in South Borneo with L. Horner and P. W. Korthals</td>
</tr>
<tr>
<td>1839-1848</td>
<td>Franz Wilhelm Jungius’s journeys on Java and Sumatra</td>
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<tr>
<td>and 1855-1864</td>
<td></td>
</tr>
<tr>
<td>1854-1856</td>
<td>Alfred Russel Wallace’s journey through the Malay Archipelago</td>
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<td>1855-1856</td>
<td>Andreas Fedor Joachim in the Philippine Archipelago</td>
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<td>Otto Finsch’s first journey to the Cape York Peninsula, Torres Strait Islands, and south coast of New Guinea</td>
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<td>Richard Simon’s journey to study monotremes, marsupials, and lung-fish in Australia with visit to New Guinea</td>
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109 Interestingly, Wallace apparently attended a meeting on 8 February 1853 of the Zoological Society in London, where Earle gave a note on the zoology of the Malay Peninsula (see Rasy 2001, p. 86). In an earlier footnote Earle 1845, p. 363, referred to the fact – as rather a singular circumstances – that kangaroos, that were first in 1828 discovered in New Guinea, also occurred on the Asiatic mainland and the larger Sunda Islands on the one hand and New Guinea and Australia on the other hand. Later, Wallace in his own paper on the physical geography addressed this important finding but argued vehemently against Earle’s hypothesis of Australia being once part of Asia. The combination of his own biological observations with the increased geographic knowledge unfolding since around the mid 19th century that even allowed first hypotheses on causal explanations of zoogeographical patterns, eventually enabled Wallace to more fully document and analyse the distribution of animals than anyone before him. This is illustrated by his development of a detailed and very precise map of the earth’s biogeographic regions continued to be used today. Thus, although many of the concepts enunciated by Wallace were introduced by earlier scientists, it was Wallace – based on the available geographical experience – who then for the first time restated, documented and interpreted them in an evolutionary context.

In the context of the development of evolutionary theory, Camerini has recently examined how maps were instruments of thought and as visual components of the conceptual framework. Mapping faunal boundaries since Wallace’s time served not only as a method for organizing and communicating faunistic data but was also a potential and increasingly powerful device in providing and compiling the data in support for modern evolutionary argumentation. Interestingly, this approach has only been taken up again about half a century later by the pioneers of the modern or synthetic evolutionary theory as will be shown in a section further below, with the German-born Ernst Mayr playing a key role in this process precisely a century after Müller.

### Travelling Naturalists on New Guinea

With Alfred Russel Wallace a gradual but highly significant change takes place over the course of the second half of the 19th century. As Rasy pointed out, for the new generation of individual scientific travellers, Alexander von Humboldt (1769–1859) and Aimé Bonpland (1773–1858) with their journeys to South America, have served as a role model for many successors to come (less so for various reasons but also deserving mention, Maria Sibylla Merian and Charles de La Condamine [1701–1774]). Not only have later naturalists themselves repeatedly referred to these earliest individual scientific travellers, but their function as a role model has also been stressed by many historians of science. For example, Rasy gave an insightful account on the triumvirate of Amazonian naturalists, Henry Walter Bates (1825–1892), Alfred Russel Wallace and Richard Spruce, who are representative of a second group of scientific explorers. With Ida Laura Pfeffer (1797–1860), Charles M. Allen (1823–1892) and Frederick Smith (1805–1879), those naturalists and their assistants working in the Malay Archipelago next to Wallace have been portrayed by Baker. A compilation of some of these scientific travellers in Australasia is given in Table 2.
Most of these travelling naturalists, so characteristic for the second half of the 19th century, were not sponsored directly by the government, like HUXLEY or DARWIN attached to Royal Naval survey ships. They were not salaried, essentially independent and solitary, self-financing with mostly only additional support from either learned societies or institutions for which they worked. They were straying in beetles and birds and monkeys and dried plants who needed to collect extensively even to pay their expenses, let alone to secure a possible income for the future. These members of a new species of freelance, self-financing collectors were truly "scientific entrepreneurs," as RABY so aptly has named them, and brought to attention the riches of the previously virtually unknown biota of the regions they explored. In addition, their journeys and works were highly influential and slowly helped — via their material and observations brought back to Europe as well as their reports and studies — to reshape the world of natural history. For example, Franz Wilhelm Junghuhn (1809–1864) travelled between 1839 and 1848 and again between 1855 to 1864 on the Sunda Islands Java and Sumatra, on which he systematically studied geology and geography, vegetation and climate, thus following the path outlined only a few years earlier by MÜLLER. For the Philippine Islands — that archipelago WALLACE never reached despite earlier plans — we should mention Andreas Fedor JAGOR (1817–1890) who travelled there as one of the first naturalists in the years 1859 and 1860. He was followed in 1863–1865 by Karl SIMPER (1832–1893). Celebes (today Sulawesi) was explored by the Swiss naturalist and ethnographer Fritz SARASIN (1859–1942) together with his cousin Paul SARASIN (1856–1929). They started traveling together in 1883 on a journey to Ceylon; Fritz SARASIN in 1910–1912 also explored New Caledonia and the Loyalty Islands. From the plethora of travelers and their journeys all over the world, only very few can be mentioned here, and this should also be restricted to the region of New Guinea. Although having a long history of individual and scattered discoveries, this island continent remained seldom visited through most of the 19th and far into the subsequent century (see Tab. 2). Given the close proximity to the heavily travelled Moluccas which attracted the attention of earlier maritime powers, this fact is remarkable even in light of New Guinea's history of discovery. To mention only one example, WALLACE (1869) during his eight years in Indonesia only spent about five months in 1858 near Dorey Harbour at the northwest coast of New Guinea, curiously enough at exactly the same time and location as the Dutch expeditions. Nevertheless, both these travelling naturalists and entrepreneurs«, as THOMAS later coined the term «archetype entrepreneurs», as RABY so aptly has named them, and brought to attention the riches of the previously virtually unknown biota of the regions they explored. For example, Franz Wilhelm Junghuhn (1809–1864) travelled between 1839 and 1848 and again between 1855 to 1864 on the Sunda Islands Java and Sumatra, on which he systematically studied geology and geography, vegetation and climate, thus following the path outlined only a few years earlier by MÜLLER. For the Philippine Islands — that archipelago WALLACE never reached despite earlier plans — we should mention Andreas Fedor JAGOR (1817–1890) who travelled there as one of the first naturalists in the years 1859 and 1860. He was followed in 1863–1865 by Karl SIMPER (1832–1893). 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To mention only one example, WALLACE (1869) during his eight years in Indonesia only spent about five months in 1858 near Dorey Harbour at the northwest coast of New Guinea, curiously enough at exactly the same time and location as the Dutch expedition. In the late 19th century it was the Italian botanist Odoardo BECCARI (1843–1920), who in 1872–1876 and again in 1875 explored this large island and later published a travel account. Among those explorers and adventurous naturalists who contributed to the knowledge of New Guinea's fauna and flora, thus ranking most prominently as being of extraordinary merit, are also Luigi D'ALBERTIS (who made natural history collections on New Guinea for Giacomo Marquis DORIA's Museo Civico di Storia Naturale in Genoa), Michael Oldfield THOMAS from the Zoological Department at the British Museum in London (who, however, never visited the island but named about 2900 mammal genera, species and subspecies, among them about 2000 taxa from New Guinea) and later GeorgeTopic from the American Museum of Natural History in New York (who carried out field work in conjunction with Richard ARCHBOLD). Mostly unknown, in contrast, are two German naturalists, who — at different times — also explored natural history on New Guinea, viz. Otto FINSCH (1839–1917) and Richard SEMON (1859 to 1918). Both were undoubtedly successful with respect to scientific output, albeit from different points of view.

The zoologist R. SEMON, who was a student of Ernst HAECKEL in Jena, published, in addition to his famous scientific works on the biology, in particular the ontogeny and embryology, of monotremes, marsupials and lung-fishes, a travel report about his exploration in New Guinea, New Guinea and some Indonesian islands. In contrast, the travels and scientific contributions of the ethnologist and zoologist Otto FINSCH from Bremen remained essentially obscure, not the least caused by the fact that only scattered reports were published in less known and less-widely distributed German journals, but especially due to the lack of a comprehensive scientific account and/or narrative given by the author himself. Apart from a compilation on New Guinea and an annotated list of his writings, his extensive journeys 1872–1882 and 1884–1885 to the South Sea, Australia and New Guinea and its circumstances are often forgotten today. Again, however, it was STRESEMANN who dedicated an entire chapter in his account on the history of ornithology to FINSCH and his contributions to the natural sciences. Nevertheless, both these travelling naturalists and entrepreneurs«, as THOMAS later coined the term «archetype entrepreneurs», as RABY so aptly has named them, and brought to attention the riches of the previously virtually unknown biota of the regions they explored. For example, Franz Wilhelm Junghuhn (1809–1864) travelled between 1839 and 1848 and again between 1855 to 1864 on the Sunda Islands Java and Sumatra, on which he systematically studied geology and geography, vegetation and climate, thus following the path outlined only a few years earlier by MÜLLER. For the Philippine Islands — that archipelago WALLACE never reached despite earlier plans — we should mention Andreas Fedor JAGOR (1817–1890) who travelled there as one of the first naturalists in the years 1859 and 1860. He was followed in 1863–1865 by Karl SIMPER (1832–1893). Celebes (today Sulawesi) was explored by the Swiss naturalist and ethnographer Fritz SARASIN (1859–1942) together with his cousin Paul SARASIN (1856–1929). They started traveling together in 1883 on a journey to Ceylon; Fritz SARASIN in 1910–1912 also explored New Caledonia and the Loyalty Islands. From the plethora of travelers and their journeys all over the world, only very few can be mentioned here, and this should also be restricted to the region of New Guinea. Although having a long history of individual and scattered discoveries, this island continent remained seldom visited through most of the 19th and far into the subsequent century (see Tab. 2). Given the close proximity to the heavily travelled Moluccas which attracted the attention of earlier maritime powers, this fact is remarkable even in light of New Guinea's history of discovery. To mention only one example, WALLACE (1869) during his eight years in Indonesia only spent about five months in 1858 near Dorey Harbour at the northwest coast of New Guinea, curiously enough at exactly the same time and location as the Dutch expedition. In the late 19th century it was the Italian botanist Odoardo BECCARI (1843–1920), who in 1872–1876 and again in 1875 explored this large island and later published a travel account. Among those explorers and adventurous naturalists who contributed to the knowledge of New Guinea's fauna and flora, thus ranking most prominently as being of extraordinary merit, are also Luigi D'ALBERTIS (who made natural history collections on New Guinea for Giacomo Marquis DORIA's Museo Civico di Storia Naturale in Genoa), Michael Oldfield THOMAS from the Zoological Department at the British Museum in London (who, however, never visited the

118 RABY 1996, p. 79.
119 WALLACE 1869.
120 A single comprehensive account on the history of discovery in New Guinea is lacking, but several more or less extensive overviews can be found, for example, in MÜLLER 1857, FINSCH 1865, WICHMANN 1910, STRESEMANN 1954 and PRODIN and GREISSIT 1982.
121 cf. introductory remark in MÜLLER 1858, p. 264.
122 WALLACE 1869.
123 BECCARI 1924.
Although geographical isolation as an essential condition in the formation of species has been stressed as early as the second half of the 19th century, in particular by the German entomologist Moritz Wagner, it was largely ignored by many zoologists and evolutionary biologists over the following decades. In the late 1930s Mayr realized how important the presentation of a massive documentation in favour of geographical speciation would be, given the then often prevailing Lamarckian views and in particular Richard Goldschmidt's thesis of systemic mutations and the ignorance of the importance of geographical speciation in the United States.

Therefore, according to his own account, he took a leading role in this process after having taken up the viewpoint of earlier workers in Germany, such as the entomologists Karl Jordan and Moritz Wagner and the ornithologists Ernst Harttert and Erwin Stresemann, who all suggested that geographical separation plays the primary role among isolating factors. Mayr supported their basic tenet that there is no speciation without separation, ultimately leading to his well-known and seminal contributions.

Mayr's strong claim of geographical separation, that forms the basis of his 1942 synthesis, undoubtedly also has its roots in his early field experiences in the South Sea. He combined those in the most fruitful way with the idea on geographical separation which was during this time, as Mayr stated "official philosophy in the bird department of the Berlin Museum" where he had grown up. However, astonishingly there is not a single comprehensive account on his early and adventurous travels. Mayr only gave three published reports on the scientific results of his New Guinea trips and one, very cursory account on the Solomon journey. In the course of an ongoing effort by the present author to reconstruct the detailed itinerary from various sources (including Mayr's publications, correspondence and museum collection notes), the exact date and routes of his journeys were compiled in order to allow further research into the genesis of his thought about the importance of geography for evolution.

Early Beginnings in Germany

After having studied medicine in Greifswald since 1923, Mayr in February 1925 decided (on Stresemann's recommendation) to study zoology at the Friedrich-Wilhelm University in Berlin (later to be named Humboldt University), where he — under the supervision of the renowned systematist and curator of ornithology at the Natural History Museum in Berlin, Erwin Stresemann (1889–1972) — completed a dissertation on the range expansion of the European serin finch Serinus canaria. This already was a study with a clear systematic-geographic focus. He had exactly 16 months to finish this PhD thesis, before he became assistant at the Berlin Natural History Museum on July 1, 1926. Although he was mostly absent on field research or later as research associate in New York in 1931 and 1932, Mayr officially remained (albeit unpaid) in this position until the end of July 1932.

As revealed by their extensive scientific correspondence, it was under the influence of his teacher and friend Stresemann in Berlin that Mayr first became aware of the importance of reproductive isolation. Stresemann's ideas and concepts strongly facilitated the development of his views of the species concept and speciation phenomena in the late 1920s and early 1930s. In addition, it was Bernhard Rensch (1900–1990) who also worked as curator at the Berlin museum and who's book on geographical races and the problem of species formation was highly influential to Mayr when he read it in 1930 after returning from the Solomon Islands.

Prior to his field work as naturalist, there had been no time to allow for a minimum of thinking about such "extraneous matters as the mechanisms of evolution," as Mayr later put it, and "like Darwin we believed in a categorical difference between continuous and discontinuous variations. However, and apparently even forgotten by Ernst Mayr himself, his geographical thinking has very early roots as revealed in a letter by him to Erwin Stresemann, dating from May 12, 1924. A reproduction of a hand-drawn sketch by Mayr in the letter is provided in Figure 3.

Fig. 3. Detail of a letter by Ernst Mayr to Erwin Stresemann, dating from May 12, 1924, with a hand-drawing illustrating his early ideas as to the formation of species and the role of geographical isolation in this process (from the Handschriftenabteilung of the Staatsbibliothek Preußischer Kulturbesitz in Berlin (Nachlass Stresemann; 150).

131 Wagner 1868.
132 See for discussion, e.g. Jordan 1905, Mayr 1980.
134 Mayr 1940, 1942.
137 Mayr 1943.
138 Bases on this research, a large-scale map was assembled and presented during the 10th annual meeting of the Deutsche Gesellschaft für Geschichte und Theorie der Biologie at the Museum für Naturkunde of the Humboldt University in Berlin in June 2001; the detailed itinerary and a map will be published elsewhere.
139 See Mayr 1926.
As is illustrated, MAYR has anticipated the importance of geography in the struggle to solve systematic questions in the context of species concepts and speculation. He also suggested possible explanations and solutions depicting this ecologically based, historical-dynamic interpretation on the origin of geographical variation of species. HAFFER has extensively investigated this early development of MAYR’s thinking showing that MAYR in 1924 has already outlined to STRESEMANN a research program that he would eventually conduct on his own.144 Consequently, one can come to the conclusion that, already during his early Berlin years, it was clear to MAYR where naturalists would have to look for evidence and for examples to test their hypotheses.

MAYR’s Expeditions to New Guinea and the Solomon Islands, 1928–1930

Far into the 20th century New Guinea has remained an enormous, largely unexplored island continent.145 During the International Congress of Zoology in Budapest in autumn 1927, Lord Walter ROTHSCHILD (1868–1937),146 who then held the largest private collection of birds in the world at the Zoological Museum in Tring near London, and Dr. Leonard C. SANFORD (1868–1950), trustee of the American Museum of Natural History in New York, on STRESEMANN’S initiative invited MAYR for a collecting expedition to northern New Guinea. In February 1928 MAYR left for the South Sea, and did not return until the end of April 1930. He was twenty-three years old then, had never been on an expedition before and was admittedly inexperienced in bird collecting.147 Nevertheless, prior to his trip, he enthusiastically studied the bird fauna of New Guinea in the museum collections in Tring and Berlin to acquaint himself with the birds known from the island.

These journeys of Ernst MAYR have been referred to as »Rothschild-Expedition nach Niederländisch-Neu Guinea« (1928), as an »Expedition der Universität Berlin in das Mandatsgebiet Neu Guinea« (1928–1929) and as »Whitney-Expedition des American Museum of Natural History zu den Solomon Inseln« (1929–1930). Although they were carried out in immediate succession, they had quite different sources of financing and, particularly the last, a different character.

(i) The journey to Dutch New Guinea (today Irian Jaya) from April to October 1928 was covered by a grant given by Lord ROTHSCHILD with the purpose of collecting for his museum in Tring and for the AMNH. Ernst MAYR only gave two brief narrative accounts on the first part of his travels, the trip to the Arfak and Wandammen Mountains in the Vogelkop Peninsula of NW New Guinea, and to the Cyclops Mountains, also in the Dutch New Guinea.153

(ii) The subsequent voyage to the former German Mandated New Guinea (today in Papua New Guinea) from October 1928 to June 1929 was supported by a grant from the German Forschungsgemeinschaft der Deutschen Wissenschaft. MAYR explored the Saruwaged Mountains and Herzog Mountains; the material from there was for the Berlin Museum.148

(iii) Finally, the expedition to the Solomon Islands from July 1929 to February 1930 was financed as part of the Whitney South Sea Expedition. This latter journey was originally not planned by MAYR; it only turned out in May 1929 as a welcome opportunity while he was collecting in the Herzog Mountains at the northeast coast of New Guinea. This expedition was part of a long-term venture financed by Harry Payne WHITNEY (1872–1930) from New York, who thus enabled systematic bird collecting trips during the 1920s and until 1939 on all islands of the South Sea.150 For this Solomon Islands trip we only have a cursory narrative but should note here that MAYR participated in the collecting of birds on the three previously poorly or unexplored islands of Choiseul, Malaita and San Cristobal.156

Case Studies from Birds

Initially, MAYR was especially interested in the bird forms of the different mountainous regions on northern New Guinea. During his expeditions he visited five of these ranges, three of them are in today’s Irian Jaya (i.e. Arfak, Wandammen, and Cyclop Mountains), the other two (the Saruwaged and Herzog Mountains) are in Papua New Guinea. The scientific results including the description of new bird species and subspecies have been published between 1931 and 1945 in a series of about 20 papers, contributing to the other results of the Whitney South Sea Expedition. A first summarizing account on the systematics and distribution of birds from Polynesia was published in German,157 followed by a fieldguide on the birds of the Southwest Pacific.158

However, beyond doubt the most important outcome of MAYR’s geographical experience in the South Sea was the two accounts on speciation in birds and on the evolution and the origin of species;159 these are mainly based on examples from the birds and geographical data he collected during his early travels, thus during the scientific work that takes us into the field.160 What was the Galapagos for Charles DARWIN and the Atu Islands for Alfred Russel WALLACE, New Guinea and the Solomon Islands would become for Ernst MAYR, perhaps with the significant difference that the latter was well prepared to discover the many zoogeographical examples and their suitability to serve as evolutionary biology model cases in the field. Owing to their spatial separation and, correlated with this, the rapid evolutionary changes observable, insular habitats – either on isolated mountain ranges or on oceanic islands in particular in an archipelago setting – provide natural laboratories for zoological studies. MAYR has illustrated and discussed many of these examples among the bird fauna of Oceania and New Guinea, as for example those from birds of paradise (Paradisaeae) on New Guinea and some adjacent islands, or from the whistlers or whistlikeheads (Pachycephala pectoralis).164 HAFFER has again

149 For field biologists New Guinea still is a biological treasure trove par excellence; for a recent account on the biogeography and ecology of the biota of New Guinea see, e.g. GREISSIT 1982. The same holds true for the archipelago of the Solomon Islands, still one of the most remote and biologically undiscovered regions. Only until recently, with the monograph of MAYR and DIAMOND 2001, this has started to change, at least for the avifauna.
150 A biography can be found in ROTHSCHILD 1983.
151 MAYR 1930, p. 20.
152 See e. g. JAIN 1998, p. 898.
153 MAYR 1930, 1932, HAFFER 1930.
examined some of these case studies in the light of Mayr's contribution toward the evolutionary synthesis in the late 1930s and 1940s. General evaluations of Mayr's scientific contributions based on his geographical experience have been repeatedly presented recently initiating quite an industry following Mayr's 90th birthday. Thus, we can only conclude here that his experience and roots as a travelling naturalist as well as systematist and zoogeographer eventually placed him in a prominent position for his synthetic accounts on the concept of species and on geographically induced mechanisms involved in speciation. His and others detailed research on the spatial occurrence of faunal elements and the geographical variation in situ provided the key for our present biogeographical and evolutionary biology knowledge, including such phenomena as natural selection, faunal regions and their delineation, endemisms and radiations, formenkreise and superspecies, as well as the principle of peripheral isolates and the concept of allopatric speciation.

The Importance of the Geographical Factor

Despite a long tradition in exploration and even during the golden age of natural scientific expeditions, biogeographical experience and information has long remained a deficiency. Nevertheless, as I tried to show above, with Rumpf's (1705) epic work Raritietskammer we see some very early approaches, often and long overlooked. Only with what is described here as WALLACE's program the significance of spatial pattern and how these changed over time became paramount. The idea of travelling to gather facts about living animals and the idea of using these facts alone to build a theory about the living world has simply not entered the mind of many scientists prior to naturalists such as Darwin and Wallace.

One major result of Wallace's but also of Müller's earlier exploration for example in the Malay Archipelago was the clarification of zoological geography; in this case the discovery commemorated by the description WALLACE's line and WALLACEa¢s. Their foundation of biogeography by carefully observing and noting the local occurrence and distribution in particular of animals rendered the geographic factor instrumental in providing the basis for the genesis of evolutionary theory only later taken up as key elements by the naturalists of the Stresemann circle with Rensch and Mayr. Thus, the geographical experience - in both senses of the word - became paramount and should be regarded as one of the most significant contributions of naturalists toward the modern synthetic theory of evolution.

Within the framework of modern phylogeography this core research area in systematic biology has not lost any of its relevance for the formulation and testing of zoological and evolutionary hypotheses, as can be seen in the often very inadequate documentation of exact geographic origin of samples used for modern molecular genetic and phylogeographic studies.

Caveats

This important and influential contribution of travelling naturalists - and with it the significance of the determination of the precise geographical origin of specimens and, thus, the spatial distribution and dimension of species - has fallen into oblivion, not only among historians

162 Haffer 1997, pp. 74–85

of science but also among zoologists. However, it is not only from an historical perspective that the geographical factor is most relevant even for modern evolutionary biological studies, as science judges on theories and contributions by earlier authors on the grounds of their relevance and heuristic value for current studies and present knowledge.

Considering recent developments, including molecular genetic techniques in phylogeographic studies, as a systematist one should be highly concerned with the ignorance of WALLACE's principles, i.e. to precisely determine the geographical origin of each specimen under study. This is illustrated, to use only one example from one of WALLACE's favourite animals of the Malay Archipelago, by recent molecular genetic studies as to the question about the number of species of orangutan on Borneo and Sumatra.

According to common knowledge, only one species Pongo pygmaeus occurs in Southeast Asia, with two subspecies living on the islands of Borneo (P. p. pygmaeus) and on Sumatra (P. p. abelii). Molecular geneticists repeatedly reached the conclusion that there might be more than this one species, postulating distinct species status for each of the separate island populations on Borneo and Sumatra. However, the same authors admitted in their papers that, unfortunately, they were not able to control for the geographical origin of the specimens they studied. Consequently, these papers were quickly criticized not only for having sampled only a single specimen each, but also for having taken DNA samples from zoo animals for which the precise origin was indeed unknown. Thus, although it remained unsolved whether the animals for which separate species status was suggested came from either Sumatra or Borneo, these molecular papers made it successfully through the peer-review process and were published in renowned international scientific journals. Finally, this debate ended with the suggestion that for these studies the precise locations should be given and the deposited specimen samples made generally accessible.

Conclusion

With this proposal, eventually molecular geneticists advance to a procedure that became a corner stone of the practice of so-called classic systematists since the scientific travels of naturalists in the 19th century. Thus, now the most modern discipline in biology also joins this long and important tradition in zoology. This fact lends further proof to the proposition that WALLACE's geographical principle - the historical development of which was outlined in the present paper - has lost nothing of its paramount importance for the formulation of zoological and evolutionary biological hypotheses.

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References


Darwin, C.: Journal of Researches into the Geology and Natural History of the Countries Visited during the Voyage of H.M.S. Beagle. London: Cultura 1845


Finch, O.: Neu-Guinea und seine Bewohner. Bremen: Müller 1865


Haffer, J.: Ornithological research traditions in central Europe during the 19th and 20th century. J. Orn. 142 (Sonderheft 1), 27-93 (2001)


MAYR, E.: A tendfoot explorer in New Guinea. Reminiscences ofan expedition or birds in the primeval forests of the Arfak Mountains. Natural History 32, 83–97 (1932)


MAYR, E.: Speziation phenomena in birds. American Naturalist 74, 249–278 (1940)


MAYR, E.: A journey to the Solomons. Natural History 52, 30–37, 48 (1945)


MÜLLER, S.: Reizen en onderzoekingen in de indischen archipel, gedaan op last der Nederlandsche Indie-bescheiden, tussehen de jaren 1828 en 1836. Part I and II. Amsterdam: Frederik Muller 1857


RENSCH, B.: Die prinzipi geographischer Rassenkreise und das Problem der Artbildung. Berlin: Borntraeger 1929
Matthias Glaubrecht


Other non-printed sources

Signatur S III, MAYR, E.: Personalakte

Dr. rer. nat. Matthias GLAUBRECHT
Museum für Naturkunde of the Humboldt University Institute of Systematic Zoology Invalidenstrasse 43
10115 Berlin Germany
Phone: +49 (0)30 20 93 85 04
Fax: +49 (0)30 20 93 85 28
E-Mail: matthias.glaubrecht@rz.hu-berlin.de