SOME COMMENTS UPON H. C. RAVEN'S PAPER: "WALLACE'S LINE AND THE DISTRIBUTION OF INDO-AUSTRALIAN MAMMALS"

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Recently H.C. RAVEN (1935) made an attempt to prove that WALLACE's line is an important zoogeographical boundary as far as the distribution of the Indo-Australian mammals is concerned, and that VAN KAMPEN (1909, p. 13; 1911, p. 544) greatly underestimated the significance and the value of this line when he wrote: ". . . . it becomes evident that such a sharp boundary as Wallace drew does not exist. Not only is there none where he drew it, but no such line exists anywhere in the archipelago" [1]). It is important to note that VAN KAMPEN (1909, p. 13; 1911, p. 544–545) left open the possibility of such a line being drawn to bound the distribution of some single group, for he also wrote: "Of course it is possible [2]) to draw a line which apparently bounds the distribution of some single group . . . . But taking the fauna as a whole it is quite certain that no line may be drawn; but, rather, we may lay out a transition zone in which the fauna of India and that of Australia are mingled, and wherein from the west to the east the Australian components increase more and more in number; and on the other hand the Indian tend to die out" [3]. To prove that the views expressed by VAN KAMPEN are wrong it is, therefore, necessary to show that WALLACE's line forms the boundary for the fauna taken as a whole, and not for a single group only, even though this group is one of those

[1]) This and the following citations are taken from the English translation by BARBOUR.

[2]) In the original Netherlands text VAN KAMPEN wrote "misschien mogelijk" which may be translated as "perhaps possible"; the word "perhaps" was omitted in the translation.

[3]) In 1929 VAN KAMPEN (1929, p. 74-75) was still of the opinion that no sharp boundary can be drawn between the Indian and Australian regions. Celebes and the lesser Sunda Islands are placed by him (l.c., p. 76) in the Oriental region while the remaining (eastern) part of the Archipelago is referred to as Austro-Malayan transition zone. He wrote also that one might even doubt whether it was not more correct to place the whole Archipelago exclusive of New Guinea, in the Oriental region. Several

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used by VAN KAMPEN. But even in proving that WALLACE's line is an important boundary for the distribution of Indo-Australian mammals RAVEN has not completely succeeded.

For zoogeographical studies of this nature it is necessary to have a complete checklist of all the mammals existing in the region under consideration, and the exact distribution of each of the forms must be known. Such a list must be based on a critical study of the all the genera and species involved. As a look at recent publications will show the classification and nomenclature of the Indo-Australian mammals are still so unstable, that it is almost impossible to prepare such a list. It is, therefore, greatly to be appreciated that RAVEN (1935, pp. 208–265) undertook the difficult task of making a list of the mammals of the Indo-Australian and Australian regions. Considering the enormous amount of literature which the author had to study it is not to be wondered that this list, which is the first of its kind, contains a number of errors. As we may expect that this list for long years will be used as the base for further studies, it may be useful to point to some errors which chiefly refer to genera and species in which I have been interested for some time.

In the genus *Suncus* Ehrenb. one subspecies is mentioned twice, once as *Suncus indicus celebensis* (Rev.) (p. 221, no. 54) [1]) and once as *Suncus murina celebensis* (Rev.) (p. 222, no. 58). This is also the case with *Macacus mindanensis apoensis* (Mearns) (p. 236, no. 045) and *Macacus philippinensis apoensis* (Mearns) (p. 236, no. 051), *Sciurus dulitensis dilutes* Miller (p. 242, no. 114*b*; err. typ. for *dilutus*) and *Sciurus notatus dilutus* Miller (p. 243, no. 152)[2]). The sumatran elephant is mentioned as *Elephas indicus sumatranus* Temm. (p. 261, no. 03), while the malayan race of this species

other authors (e.g., DE BEAUFORT, 1926, p. 138; NIERSTRASZ, 1929, p. 338; WEBER, 1928, p. 20) have already referred to the fact that WALLACE's line as a sharply marked boundary between two regions does not exist.

[1]) The numbers between brackets refer to the pages and serial numbers of RAVEN's list.

[2]) In numerous cases the author's names mentioned by RAVEN are not those of the original describers, e.g., the different species of deer described by HEUDE are cited with the author's name "Chinois" (they were described in the "Mémoires concernant l'Histoire Naturelle de l'Empire Chinois"). In other cases the names of later authors, who dealt with the species, have been cited. As far as possible I have corrected them for the use in the present paper.

is mentioned as *Elephas maximus hirsutus* Lyd. (p. 261, no. 04). In several cases a name is given specific rank in one place, while it is mentioned as a subspecies elsewhere in the list, e.g., *Zaglossus bartoni* (Thos.) (p. 208) and *Zaglossus bruijnii bartoni* (Thos.) (p. 208);*Sciurus klossi* Miller (p. 242, no. 129) and *Sciurus nigrovittatus klossi* Miller (p. 243, no. 151); *Sciurus borneoensis palustris* Lyon (p. 242, no. 105) and *Sciurus prevostii borneoensis* Schl. (p. 244, no. 164); *Sciurus tenuirostris* Miller (p. 244, no. 186) and *Sciurus vittatus tenuirostris* Miller (p. 245, no. 193); *Sciurus abbotti* Miller (p. 241, no. 087) and *Sciurus vittatus abbotti* Miller (p. 245, no. 193); *Rattus butangensis* (Miller) (p. 249, no. 158) and *Rattus surifer butangensis* (Miller) (p. 255, no. 328); *Rattus flavidulus* (Miller) (p. 250, no. 195) and *Rattus surifer flavidulus* (Miller) (p. 255, no. 328); *Rattus lancavensis* (Miller) (p. 251, no. 229) and *Rattus vociferans lancavensis* (Miller) (p. 255, no. 355). Another kind of errors is that several times a species is cited under a generic name different from that under which its subspecies are mentioned, e.g., *Scotophilus temmincki* (Horsf.) (p. 234, no. 202), but *Pachyotis temmincki celebensis* Sody and *Pachyotis temmincki panayensis* Sody (p. 234, no. 185); *Uromys littoralis* Lönnb. (p. 256, no. 385), but *Melomys littoralis insulae* Troughton & Le Souef (p. 247, no. 076); *Uromys cervinipes* (Gould) (p. 256, no. 378), but *Melomys cervinipes eboreus* Thomas and *Melomys cervinipes pallidus* Troughton & Le Souef (p. 247, no. 074); *Ictis nudipes* (F. Cuv.) (p. 258, no. 013), but *Mustela nudipes leucocephalus* (Gray) (p. 258, no. 023); *Herpestes brachyurus* Gray (p. 259, no. 054), but *Mungos brachyurus rajah* (Thos.) (p. 259, no. 061); *Herpestes semitorquatus* Gray (p. 259, no. 058), but *Mungos semitorquatus uniformis* Rob. & Kloss and *Mungos semitorquatus semitorquatus* (Gray) (p. 259, no. 064); *Presbytis potenziani* (Bonap.) (p. 237, no. 091), but *Macacus potenziani siberu* (Chasen & Kloss) (p. 237, no. 052). It also occurs that a species is mentioned twice, e.g., *Paradoxurus minax* Thomas (p. 260, nos. 073, 075); *Aonyx cinerea* (Ill.) (p. 258, no. 008) and *Lutra cinerea* Ill. (p. 258, no. 016).

In his list RAVEN mentions several genera, in which he does not incorporate their respective type-species, these being referred to other genera. *Hylopetes* Thomas (1908, p. 6, type: *Sciuropterus* (*Hylopetes*) *everetti* Thos.) is mentioned as a separate genus by RAVEN (p. 238), nevertheless its type is left in the genus *Sciuropterus* F. Cuv. (p. 241, no. 069). The same is the case with the types of the genera *Petaurillus* Thomas (1908, p. 3, type: *Petaurillus hosei* (Thos.)), *Petinomys* [1]) Thomas (1908, p. 6, type: *Sciuropterus* (*Petinomys*) *lugens* Thos.), *Pteromyscus* Thomas (1908, p. 3, type: *P. pulverulentus* (Gthr.)), whose respective type-species are all placed by RAVEN in the genus *Sciuropterus* F. Cuv. (p. 241, nos. 073, 076, 081). *Melomys* Thomas (1922, p. 261) was founded with *Melomys rufescens* (Alst.) as its type; the genus *Melomys* is mentioned by RAVEN (p. 247) as a separate genus, but its type-species is included in the genus *Uromys* Ptrs. (p. 257, no. 400). GRAY (1832, p. 39) described the genus *Pseudomys* with *Pseudomys australis* Gray as only species, which therefore is its type (monotypy); this species is mentioned by RAVEN (p. 249, no. 133) as *Rattus australis* (Gray), but its subspecies is mentioned as *Pseudomys australis oralis* (Thos.) (p. 248, no. 112). *Stenomys* Thomas (1910, p. 507, type: *Stenomys verecundus* (Thos.)) is mentioned as a separate genus (p. 256), but its type-species is entered as *Rattus verecundus* (Thos.) (p. 255, no. 349). *Mesembriomys* Palmer (1906, p. 97) was proposed as a substitute name for *Ammomys* Thomas (1906*a*, p. 83) (non Bonaparte, 1831) of which *A. hirsutus* (Gould) (= *Mus hirsutus* Gould) was the type. The typical form of this species is recorded by RAVEN (p. 246, no. 030) as *Conilurus hirsutus* (Gould), one of its subspecies is mentioned as *Mesembriomys hirsutus rattoides* Thos. (p. 247, no. 081). Moreover the name *Mus hirsutus* Gould, 1842, is preoccupied by *Mus hirsutus* Elliott, 1839, and must be replaced by *Hapalotis gouldii* Gray, 1843 (cf. IREDALE & TROUGHTON, 1934, p. 81).

In the genus *Limnomys*, RAVEN (p. 247, nos. 064–067) includes four species; three from the Philippine Islands and one from New Guinea. The name *Limnomys* was first proposed by MEARNS (1905, p. 451) for one of the Philippine species (*L. sibuanus* Mearns). THOMAS (1906*b*, p. 325), who was not aware of this, used the same generic name for a rat from New Guinea (*Limnomys asper* Thos.). A substitute name was proposed by POCHE (1906, p. 326), who replaced *Limnomys* Thomas, 1906 (non Mearns, 1905) by *Parahydromys*. The four species mentioned by RAVEN (p. 247), therefore, must be referred to two genera: *Limnomys* Mearns, which is restricted to the Philippines (TAYLOR, 1934, p. 484) and *Parahydromys*, which is restricted to New Guinea. *Hydromys meeki* (RAVEN, p. 247, no. 054) is probably a misprint for *Hyomys meeki* Thos. under which name it was origi-

[1]) *Petionomys*, RAVEN, p. 239, err. typ.

by RAVEN, we adopt the classification as it has been built up for the group by POCOCK (references in: BRONGERSMA, 1935) the number of genera which occur in the recent fauna of the Indo-Australian Archipelago is raised from one to seven. Though it is very probable that POCOCK has gone too far in the splitting up of the genus *Felis*, it is evident that it is also wrong to include all the cats in one single genus. In the same way it may make a difference whether the genus *Paradoxurus* F. Cuv. is mentioned as containing eighteen distinct species, or the genus being divided into three genera with one species each, and fifteen species being reduced to subspecific rank or being referred to the synonymy of other forms (POCOCK, 1933, 1934).

Of several genera and species we know that in former times their range extended beyond their present day distribution, e.g., the genus *Tapirus* Briss. which does not occur in the recent fauna of Java, but which is known from pleistocene deposits in this island (DUBOIS, 1908, p. 1265; VON KOENIGSWALD, 1934, pp. 191, 193), or the javanese rhinoceros (*Rhinoceros sondaïcus* Desm.) which in prehistoric times extended further eastward in Java than at present (DAMMERMAN, 1934, p. 479). This may also have been the case with other genera and species, and, therefore, it is not impossible that forms which now do not reach further eastward than Java, may have had a distribution which extended farther to the east in former times. Definite proofs to this effect can be furnished by fossils only, and these unhappily are very scarce.

One of the objections which I have against RAVEN's method of proving the validity of WALLACE's line is the following. When enumerating the genera which do not transgress it he does not only count the genera for which this line is apparently the boundary of their range, but he also counts genera from the western part of the Archipelago which do not reach so far eastward. It is true that the latter do not transgress WALLACE's line, but they need not be taken into consideration, as they do not come anywhere near this line, and so probably never had a chance of trying to transgress it. For genera and species which do not reach farther eastward than Sumatra, the boundary is the Sunda-strait, but not WALLACE's line. The same applies to genera which reach Java, but not Bali; for these the Bali-strait is the boundary. If it is allowable to include all the genera

which do not reach eastward of the Sunda- and Bali-straits among those used as evidence to prove the value of WALLACE's line, one could just as well take the whole fauna of the Asiatic continent into consideration. If one wants to prove the presence of an important zoogeographical boundary in the Indo-Australian Archipelago, one must examine the importance of each of the sea-passages between the islands separately, and then it is evident that each of these straits provides a boundary for one or more forms, and that the Indian element in the fauna decreases more or less gradually when going from west to east. As far as our knowledge goes at present the genera *Symphalangus* Gloger, *Rhizomys* Gray, *Capricornis* Ogilby and *Profelis* Severtzow do not reach farther eastward than Sumatra; *Lepus* L., *Lariscus* Thomas & Wroughton, *Pithecheir* Less [1]), *Bandicota* Gray, *Mycteromys* Rob. & Kloss, *Cuon* Hodgs., and the extinct genera *Mececyon* Stremme, *Leptobos* Rütimeyer and *Duboisia* Stremme reached Java, but not Bali; this is also the case with the genera *Tapirus* Briss., *Hyaena* Briss. and *Hippopotamus* L. (subgenus *Hexaprotodon* Falc. & Cautley, extinct), which do not form part of the recent fauna of Java, but of which fossil forms were found in this island. Within the Archipelago the genera mentioned above are restricted to the islands Sumatra and/or Java. There are, however, numerous genera, which have a wider distribution within the Archipelago, but which in the southern part of their range do not reach farther eastward than Java. These genera may also be taken into consideration, when discussing the importance of the Bali-strait as a zoogeographical boundary. Comparison of the number of genera of mammals for which the Bali-strait apparently is the eastern boundary, with the number of genera for which the Lombok-strait is the boundary, we see that five or six times as many genera belong to the first group than to the second one. Therefore it is clear that if we take the number of genera as a criterium, there is perhaps more reason to consider the Bali-strait as an important boundary than the Lombok-strait; this does not only hold good for the distribution of mammals, but also for

[1]) On the strength of the evidence given by PALMER (1904, p. 538) I have used the generic name *Pithecheir* Lesson (1838?). The Nomenclator Animalium Generum et Subgenerum, however, mentions 1840 as the date of publication. Should this prove to be right, then the name should be replaced by *Pithechir* Müller, 1839.

that of reptiles and amphibians (MERTENS, 1928). Another point to which already VAN KAMPEN drew attention is that if we want to find an important zoogeographical boundary between two regions, this line must not be the eastern boundary for the western forms only, but it also should be the western boundary for the eastern ones. While a number of genera reach the eastern limit of their distribution on Bali, this cannot be said of the whole of the Indian element, some genera and species occurring farther eastward on the Lesser Sunda Islands. Neither is WALLACE's line the boundary for the most typical australian element in the fauna of the Lesser Sunda Islands, i.e., the marsupial genus *Phalanger* Storr. This genus was mentioned by EVERETT (in HARTERT, 1897, p. 514) as perhaps occurring on Flores, and from this island it is mentioned by HECK (1920, p. 167) and MERTENS (1929, p. 29). This record, however, needs confirmation, and should it prove to have been erroneous, the westernmost locality in the Lesser Sunda Islands would be Timor [1]).

No one will deny that important differences exist between the mammological fauna of Borneo and that of Celebes, but even this part of WALLACE's line is transgressed by several Indian forms, and RAVEN arrives at the conclusion that the mammalian fauna of Celebes in its chief characters is Indian. Celebes is a very good example of an island showing a mixed fauna; besides a number of endemic forms of mammals, the fauna contains a number of oriental forms with a wider distribution, as well as some Australian forms (e.g., *Phalanger* Storr). The Makassar-strait may be said to be the western boundary for the distribution of the Australian forms, but though a great number of oriental genera do not transgress it, it cannot be regarded as a sharply marked boundary for the Oriental element. The part of WALLACE's line which passes through Makassar-strait perhaps approaches nearest to what may be expected of a zoogeographical boundary. Still it has no value as a boundary separating two zoogeographical regions, but only as an expression of the fact that Celebes and Borneo did not have a direct connection, at least not in the time the present fauna developed (cf. DE BEAUFORT, 1926, p. 138).

If it is considered sufficient evidence for the presence of an

[1]) cf. Mertens, Zool. Jahrb., Syst., vol. 68, pts. 4-5, August 1936, p. 278.

important zoogeographical boundary that a great number of genera do not pass it, the western boundary for the Australian element must be laid just west of New Guinea, for of the most typical Australian mammals, the Marsupialia, only very few genera occur on the islands west of New Guinea; the genus *Phalanger* Storr is the only one that reaches Celebes, the Sangir Islands, and the Lesser Sunda Islands. Thus drawing a line to bound the distribution of the majority of the eastern forms and one to bound the distribution of the majority of the western forms, we would get two lines which enclose a region of which the fauna is an impoverished Indian one with a few eastern forms. In fact numerous lines may be drawn, each bounding the distribution of a single genus or of a group of genera with the same range; these lines may run parallel for some distance, but generally they diverge or cross each other in other parts of the Archipelago. This shows that a sharply marked boundary separating the Indian and the Australian regions does not exist, and that any attempt to draw such supposed boundaries is a hopeless task.

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ON DEVELOPMENT, GROWTH AND DISTRIBUTION OF CARCINIDES MAENAS (L.)

BY

G. J. BROEKHUYSEN JR.

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INTRODUCTION

The investigation dealt with in the present paper took place at the Zoological Station of the "Nederlandsche Dierkundige Vereeniging", Den Helder, where I was working from the latter half of 1933 until July 1936.

The original aim of this investigation was to try and analyse and to explain the distribution of *Carcinides maenas* (L.), which, at least in the surroundings of Den Helder, appeared to be very characteristic. Everything seemed to point to the distribution of this animal being susceptible to comparatively small differences in salinity.

As full-grown crabs were less suitable animals for experimental