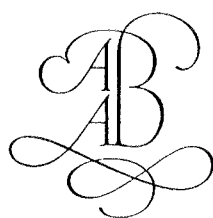


**FAUNAL AND FLORAL MIGRATIONS AND EVOLUTION
IN SE ASIA-AUSTRALASIA**

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Mammals in Sulawesi: where did they come from and when, and what happened to them when they got there?

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ABSTRACT: It is evident that part, at least, of Sulawesi is of Sundaland origin. If there was a dry-land connection between Sulawesi and Sundaland in the Pliocene, this would be compatible with the observation that most of Sulawesi's mammals are endemic at the level of genera, subgenera or well-differentiated species-groups. In some cases their closest relations seem to be with mammals from the Tatro stage of the Siwaliks, presumably via the poorly-known "Siva-Malayan" fauna of Java. Within Sulawesi both altitudinal and geographic speciation are well-marked. The groups in which geographic variation is most easily appreciated are monkeys and squirrels. Combining the data from these groups indicates that species of the southern and southeastern peninsulas separated earliest; those of the central part and the northern peninsula form a single clade. What little is known of the fossil mammals of Sulawesi comes from the Pliocene Walanae Formation on the southern peninsula. Surprisingly, this is not known to contain anoa, babirusa or any of the other present-day endemics, but pygmy elephantids and the giant pig *Celebochoerus*. Until Neogene palaeontology gets started on other parts of Sulawesi we have no explanation for this apparent anomaly, but it has been proposed more than once that Sulawesi was a cluster of separate islands until quite late in geologic time.

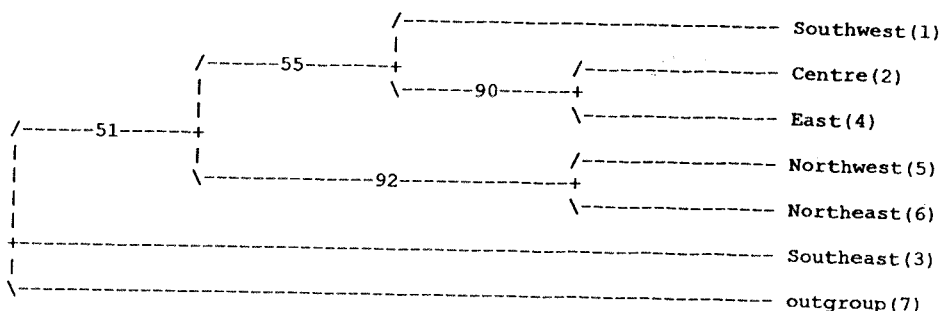
1 INTRODUCTION

Sulawesi is the fourth largest island of the Indo-Australian archipelago. At 189,000 km², it is smaller than New Guinea, Borneo or Sumatra, and larger than Java, Luzon or Mindanao. Its shape is bizarre and spidery. From the central mass a long, thin (20 to 50 km wide) northern peninsula reaches 200 km north, then turns west for 500 km, and northeast again for its final 200 km. Shorter peninsulas project south, southeast and east from the central mass. In each of the four peninsulas mountains rear up to 2700 to 2900 m, and in the central mass of the island altitudes of over 3000 m occur (the highest peak is Nokilolaki, at 3311 m). Raised coral reefs, as much as 700 m. on Butung, and the presence of recent marine clays and sea shells in the Tempe Depression (which separates the southern peninsula from the central mass), indicate a history of local uplift until very recent times.

The Makassar Strait separates it from Borneo to the west; mostly 200 to 300 km wide, this narrows to just over 100 km in the northwest; elsewhere, offshore islands reduce the distances to other islands, though not by all that much. To the north, beginning 50 km offshore, the Sangihe and Talaud archipelagos are strung out for 300 km along an approximately south-north axis, and 250 km beyond them across open water lies Mindanao in the Philippines. To the east Peleng island lies some 20 km offshore, the Sula archipelago begin 50 km beyond that, and the islands of the Maluku group begin about 100 km east and southeast of the Sulas. Three fairly large islands – Butung, Muna and Kabaena – lie off the southeastern peninsula, and another, Salayar, off the southern peninsula, and beyond them the Nusatenggara group are 200 km and more across open sea.

Sulawesi mammals are heavily Oriental. He also pointed out that there is much diversity within Sulawesi: some mammals have highland and lowland vicariants, but most have distinct variants on the northern, southern and southeastern arms of this spidery-shaped island, and some have still further geographic divisions.

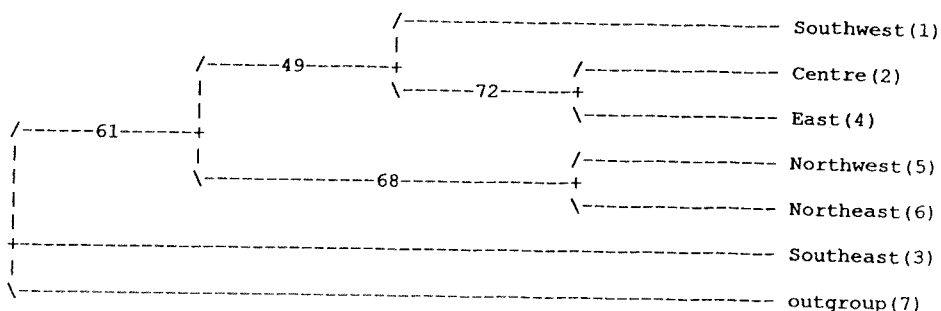
Bootstrap 50% majority-rule consensus tree
(plus other groups compatible with this tree)



(1) UNORDERED

Length 116
Shortest of 1000 random trees, 116
Consistency index* 0.756

Bootstrap 50% majority-rule consensus tree
(plus other groups compatible with this tree)



(2) ORDERED

Length 150
Shortest of 1000 random trees, 149
Consistency index* 0.637

Figure 2. Bootstrap tree, values, and comparative lengths for random tree, based on Sulawesi macaques and squirrels.

There are also fossil mammals known from Sulawesi. The Walanae fauna of southwestern Sulawesi, the only known fossil site, consists of two species of *Stegodon* and (perhaps) one of *Elephas*, and the giant suid *Celebochoerus*, along with a giant tortoise, a crocodile, sharks and stingrays. Size changes, leading in this case to dwarf elephants and giant pigs, are typical of small island faunas, and it was mentioned above that there are indications of marine deposits in the Tempe Depression, suggesting that the southern peninsula was a separate island at one stage in the past. According to Sartono (1979), the Walanae fauna is coeval with Foraminiferal zones N19-20, and so has an age of between 4.6 and 3.0 Ma, i.e. Early Pliocene.

The questions, then, are: how did all these mammals get to Sulawesi, and when; how did present-day geographic patterns of composition and distribution arise; and what happened to those that are known only as fossils?

2 HOW DO THEY RELATE TO MAMMALS ELSEWHERE?

The relationships of the mammals of Sulawesi have been considered by Groves (1976), Musser (1987) and Aziz (1990). Musser (1987) gives lists of both indigenous and non-indigenous mammals.

- (1) The dwarf buffalo *Anoa* is closely related to (very little advanced on) *Hemibos* from the Tatrot and Pinjor stages of the Siwaliks. Magnetostratigraphic evidence places these stages in the Middle and Late Pliocene, between the beginning of the Mammoth subchron and the end of the Olduvai subchron (Azzaroli & Napoleone, 1981); according to the recent recalibrations, the span would be from 3.20 to 1.78 Ma (McDougall et al., 1992), and actually somewhat later than the Walanae fauna. The occurrence of *Anoa* in the Walanae fauna is not confirmed: isolated teeth found in the vicinity have a different state of fossilization from *in situ* material (Aziz, 1990).
- (2) The babirusa *Babyrousa* is difficult to classify with respect to other pigs, and is generally placed in its own subfamily Babyrousinae (Groves, 1980). It does not occur in the Walanae fauna; some molar teeth thought to be of babirusa are more likely those of *Celebochoerus* (Hooijer, 1954). There is also an "ordinary" pig, endemic at the species level (*Sus celebensis*), living in Sulawesi.
- (3) The giant pig *Celebochoerus* of the Walanae fauna is not related to *Babyrousa*. It was regarded by Hooijer (1954) as related to *Propotamochoerus* from the Dhok Pathan zone of the Siwaliks and elsewhere; this was mainly Late Miocene in age and gone from the Siwaliks by Tatrot times (van der Made & Moyà-Solà, 1989). Aziz (1990, 1993), on the other hand, aligns *Celebochoerus* with the African *Phacochoerus*; it is at any rate quite distinct from any other suid. It is by now well known and represented by most parts of the skeleton; Aziz (1993) figures a magnificent reconstruction of it.
- (4) The Walanae elephants have been ascribed to *Elephas* (= *Archidiskodon*) *celebensis*, *Stegodon trigonocephalus* and *S.sompoensis*, but both Sondaar (1984) and Aziz (1990, 1993) consider the attribution of any fossils to *Elephas* to be in error. *Stegodon trigonocephalus*, an Upper Siwalik species, first appears in Java in the Ci Saat fauna, which is latest Pliocene (Sondaar, 1984).
- (5) The sole carnivore is an endemic giant civet, *Macrogalidia*.
- (6) The macaques (*Macaca* spp.) were considered probably diphyletic by Evans et al. (1999): those of the southwestern and southeastern arms (*M.maura*, *ochreata*, *brunnescens*) versus those of the center, eastern and northern arms (*M.tonkeana*, *hecki*, *nigrescens*, *nigra*). Dr John Trueman (personal communication) has performed a t-PTP test on their dataset, and considers the diphyletic model not secure.
- (7) The tarsiers of Sulawesi (*Tarsius spectrum* group) are the sister-group to those of Sundaland and the Philippines (Groves, 1998). They are not known as fossils on Sulawesi.
- (8) The several species of shrews (*Crocidura*) in Sulawesi represent at least two dispersals: the "old endemics", and a much more recent dispersal resulting in the single species *Crocidura nigripes* (Ruedi et al., 1998). No dates could be placed on either of these two waves, but inferentially the second dispersal must have been an overwater one.

(9) Moore (1959) showed that there are three endemic genera of squirrels in Sulawesi: *Rubrisciurus*, *Prosciurillus* and *Hyosciurus*. Their interrelationships are unknown; they could represent a single, ancient stock, or they could have entered Sulawesi separately. Their species-level taxonomy is unclear.

(10) The Sulawesi murids (Musser, 1987) are very diverse. Some are belong to genera represented in Sundaland (*Rattus*, *Maxomys*, *Haeromys*) or even in the Philippines (*Crunomys*) or Flores (*Bunomys* – see Kitchener et al., 1991), but there are also several endemic genera, not closely related to any elsewhere (*Melasmothrix*, *Tateomys*, *Echiothrix*, *Margaretamys*).

(11) Finally the cuscuses are of two endemic genera (*Ailurops*, *Strigocuscus*), not closely related to any in Australia, New Guinea or Maluku.

There would appear, therefore, to be two faunal layers as far as mammals are concerned. First, there are the “old endemics”, forming genera or species-groups: *Anoa*, *Babirusa*, *Celebochoerus*, *Macrogalidia*, macaques, tarsiers, “old endemic” shrews, the three squirrel genera, the endemic murid genera, and the cuscuses. Secondly, there are the “new endemics”, species of more widespread genera, not too distantly related to species elsewhere: *Sus celebensis*, *Crocidura nigripes*, and some of the other murids. It is interesting to note that not one non-volant mammal species is shared with Sundaland or elsewhere, except for some that are human introductions (deer, palm-civet, commensal rats and mice).

#NEXUS

[Sulawesi biogeography: *Macaca*, *P.leucomus* gp., *P.murinus* gp., *Rubrisciurus*, *Hyosciurus*]

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East      222203021001111201033 1200102020 ?????????? ?????????? ?????????
Northwest 000114131212111210132 1211211012 0200001111 01220101100 ?????????
Northeast 300024141000111320200 0211210011 1120001201 01010011100 00001111
outgroup 000000?000?000000000 000?00200? 000000???0 0???00????? 000?????
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end;
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Figure 3. Character coding for Sulawesi mammals. Characters 1-21 are for *Macaca*, 22-31 for the *Prosciurillus leucomus* group, 32-41 for the *P.murinus* group, 42-52 for *Rubrisciurus*, and 53-60 for *Hyosciurus*.

3 HOW DID THEY GET TO SULAWESI?

Two models of arrival in Sulawesi are possible: by land or across the sea. Groves (1976) drew attention to the “Pulau Laut Centre of Diastrophism” reconstructed by Van Bemmelen (1949), the only geological candidate for a land bridge from Sundaland in the days before Plate Tectonics. The mammals would have had to cross the land-bridge in the late Pliocene, because according to Van Bemmelen it arose at about that time and submerged at the beginning of the Pleistocene. The only Pliocene fauna known from anywhere else in Indonesia was the “Siva-Malayan

fauna" (Ci Saat fauna of Sondaar, 1984) from the lower levels of Java, which in turn was derived from the fauna of the Tatrot zone of the Siwaliks of northern India and Pakistan.

Cranbrook (1981) and Musser (1987), by contrast, could see no evidence that a land bridge had ever existed; for them, the Sulawesi mammal fauna is "depauperate and unbalanced", such as would be typical for one derived by a sweepstake route across a sea barrier, and bats, shrews and rodents are typical of such faunas. Musser (1987) likewise disparaged the idea that the sole Australasian elements, the cuscuses (Phalangeridae), might have clung to moving chunks of Gondwanaland that drifted westward to become part of Sulawesi; why are there no other marsupials on Sulawesi, he asked?

Yet primates and viverrids, at least, would hardly be predicted for a "depauperate, unbalanced" fauna (even if a rather restricted set of each), and particularly significant is that while the affinities of almost all the mammals are with Sundaland, the "old endemics" are relicts, sister-groups of the Sundaland genera, and only the "new endemics" might be derived from within that pool as might be expected if there were chance dispersals across the Makassar Strait. Moreover, while the "new endemics" are the sort of resilient animals that might be expected to cross wide sea barriers - a pig, a shrew, some rats - the "old" endemics are certainly not like this. Most of the broad phylogenetic groups to which the "old endemics" belong are rainforest, yet low sea-level periods, when rafting would have been easiest, are precisely the times when forest cover was most restricted (Heaney, 1991). Similarly, both cuscus genera are primitive, and while the absence of other marsupials is perhaps puzzling, differential (climate-driven?) extinctions are perfectly feasible. So, where does the "Pulau Laut Centre of Diastrophism" stand today?

It has been overtaken by plate tectonics. Geologically, Sulawesi is the result of several collisions of micro-continental fragments from the Australian plate. Hall (1996, Fig.2) depicts Southeast Asian palaeogeography at the end of the Miocene, 5 Ma. Southwestern/central Sulawesi is still part of Sundaland; the southeastern arm has accreted onto this, but the eastern/northern arm fragmented has not yet joined. Two models exist to explain the Makassar Strait. For Hall (1996) and others, the Makassar Strait is attenuated continental crust; the southwestern arm of Sulawesi was alongside eastern Borneo and drifted eastward, probably some time before the Early Miocene although the dating evidence is very poor. For Bergman et al. (1996), however, the Makassar Strait is a foreland basin, pushed down by the loading of the eastern/northern arm micro-continental fragments onto the southwestern/central arm, and this took place in the Late Neogene. But Professor Hall, in a comment during the conference, cautioned against relying on the Makassar Strait, suggesting instead that the land connections with Sundaland would better be sought to the south (Java).

Any of these scenarios could get mammals into Sulawesi dry-shod in time to appear in the Walanae fauna, but whether we can support such an early inferred separation of the Sulawesi endemics from their Sundaland sister-groups is unclear.

4 WHAT HAPPENED WHEN THEY GOT TO SULAWESI?

Most of the present-day mammalian fauna of Sulawesi is, at the generic level, more or less pan-Sulawesi, although some genera, such as the shrew-mice *Melasmothrix* and *Tateomys*, are restricted to high altitudes (Musser, 1987). What is true, however, is that there are marked geographic divisions, and the representatives of many genera and species-groups are taxonomically distinct on the different peninsulae, and often even within them. Full resolution of this geographic variation is a long way off, but some trends are already clear. Neighbouring vicariants can in most instances be shown to differ absolutely so that, even though they may form narrow hybrid zones where their ranges meet, they are most appropriately distinguished at species level.

Babyrousa has distinct taxa on the northern peninsula (with no differentiation along it), in the center, on the Togeian Islands, and on the Sula Islands and Buru. Groves (1980) classified them all as subspecies of a single species, but the northern and Togeian taxa at least are diagnosably distinct and should rank as distinct species, *Babyrousa celebensis* and *B.togeanensis* respectively. The species *B.babyrussa* occurs on the Sula Is. and Buru, to both of which it has been introduced, but as we know so little of babirusa from other parts of the Sulawesi mainland it is not possible to say from where it actually originated. Finally a single skull from central Su-

lawesi may or may not represent the species known otherwise only as a subfossil from the southern peninsula, *B. bolabatuensis*.

Characters for *Macaca*

1. Crown hair (not lengthened, short but erect, short crest, long crest), O
2. Cheek tufts (absent, short, bushy) O
3. Gluteal fields (absent, small, large) O
4. Rump patch (absent, present but not bushy, pale and bushy) O
5. Ischial callosities (flat, stand out) U
6. Tail length cf head + body (>50, 28-46, 24-34, 5-12, 3-6) O
7. Baculum length, mm (16-22, 20-25) O
8. Baculum dorsoventral basal diameter, mm (1.7-2.5, 2.2-3.0, 3.3, 3.3-4.8?, 4.5-4.8) O
9. Dorsal colour (brown, black)
10. Colour of shanks (as body, slightly paler, much paler) O
11. Colour of forearms (as body, slightly paler, much paler) O
12. Age-greying (none, slight, much) O
13. Colour of ventral skin (pale, black)
14. Tail hair (thick, sparse)
15. Relative muzzle length (61% or less, 62% or more)
16. Lateral ridges on muzzle (absent, weak, strong) O
17. Relative zygomatic breadth (>65, 60-65, 60) O
18. Malar surface (flat, convex)
19. Temporal margin of malar (broad, narrow, very narrow) O
20. Depth of supraorbital ridges (5-6, 6-7, 7-8, 9 or more) O
21. Sagittal crest height in old males, mm (absent, 1-2, 3, 5-6) O

Table 1. List of characters used in cladistic analysis of Sulawesi macaques. The states (primitive to derived) are in parentheses. O = Ordered, U = Unordered (for multistate characters).

Groves (1969) divided anoa into a lowland and a mountain species, *Bubalus* [perhaps, preferably, *Anoa*] *depressicornis* and *quarlesi* respectively, but the picture is probably more complicated than this. Thus Sugiri and Hidayat (1996) recorded at least one specimen, from G.Nokilolaki in central Sulawesi, whose appearance and karyotype were unlike any previously known. The differentiation between the common lowland and mountain anoa is very deep; Kakoi et al. (1994) found that two lowland and eight mountain anoa, from Surabaya and Raganun zoos, differed in five amino acid residues in the β haemoglobin molecule, and hypothesized that they may have already diverged before they entered Sulawesi.

But the best-marked geographic variation is found in macaques and squirrels. The macaques are divided into at least seven distinct species in different parts of Sulawesi (Fooden, 1969). I listed 21 morphological characters, including some that distinguish Sulawesi macaques from other members of the *Macaca nemestrina* group (Table 1), and ran a trial cladistic analysis using PAUP. The results (Fig. 1) did not entirely fit with those of Evans et al. (1999), but some of the bootstrap values are low.

I made preliminary examinations of Sulawesi squirrel skins, in the Natural History Museum (London), Rijkmuseum van Natuurlijke Historie (Leiden), and American Museum of Natural History (New York). All of the genera show distinct geographic variation. Limited diversity has been described for *Hyosciurus* and none whatever for *Rubriciurus*, but some variation none the less exists, although I cannot document it fully because material from some parts of Sulawesi is very limited. In the genus *Prosciurillus*, by contrast, a number of species and subspecies have been described, and these fall into three well-marked species-groups: the large, brightly-coloured squirrels of the *P. leucomus* group; the smaller, drab-agouti forms of the *P. murinus* group, among which (unlike the *P. leucomus* group) size differentials permit occasional sympatry; and the rare but widespread *P. weberi*. I analysed the first two groups separately, but I could not detect any noticeable geographic variation in the very sparse available material of *P. weberi*, so I excluded it from the analysis. The characters are listed in Table 2.

Characters for *Prosciurillus leucomus* group

1. Colour of flanks (fawn-agouti, more reddish, red-agouti) O
2. Colour of midback (as flanks, more ochery, strongly chestnut) O
3. Light postauricular spots (no, yes)
4. Colour of ear-backs (as body, black, white) U
5. Ear-tufts (absent, slight, long)
6. Colour of feet (as body, paler [more orange])
7. Colour of underside (reddish, red-yellow, grey, creamy) U POLARITY
UNCERTAIN
8. Grey bases on underside (barely visible, markedly showing through)
9. Tail banding (absent, vague striations, marked bands)
10. Head + body length, mm (<165, 170-172, >176) O POLARITY UNCERTAIN

Characters for *Prosciurillus murinus* group

1. Colour of upperside (brown, yellower, redder) U
2. Colour of hair shafts (brown, yellow, red) U
3. Colour of underside (creamy, [red-]grey, red) U
4. Colour of ear-backs (as body, white)
5. Hair on ear-backs (sparse, dense)
6. Colour of feet (agouti as body, paler)
7. Head + body length, mm (ca 105, 120-130, 130-140, >160) O POLARITY
UNCERTAIN
8. Tail length, mm (<85, 95-100, 105-110, >115) O
9. Hindfoot length, mm (<30, 30-31, 32-34) O
10. Tail banding (weak, striking)

Characters for *Rubrisciurus*

1. Banding of dorsum (agouti, more saturated)
2. Colour of dorsum (not red, red-brown, deep brown) O POLARITY
UNCERTAIN
3. Colour flanks (maroon-red, brighter red, deep fiery rufous) O
POLARITY UNCERTAIN
4. Colour of tail (maroon, reddens towards tip, blackish) O POLARITY
UNCERTAIN
5. Posterior half of dorsum (as anterior, more blackish)
6. Colour of ears (dark maroon brown, reddish black, black) O
7. Colour of underside (gingery, maroon-red) POLARITY UNCERTAIN
8. Condylbasal length, mm (<63, 63-64, >64) O POLARITY UNCERTAIN
9. Tail length, mm (<180, >185) POLARITY UNCERTAIN
10. Hindfoot length, mm (<61, 62-67, >68) O POLARITY UNCERTAIN
11. Maxillary toothrow length, mm (<12.7, >12.9) POLARITY UNCERTAIN

Characters for *Hyosciurus*

1. Colour of upperside (fuscous, maroon red)
2. Tail (as body, brindled)
3. Colour of hands and feet (darkened, blackish)
4. Colour of underside (pale yellowish, white) POLARITY UNCERTAIN
5. Border of light zone of underside (irregular, regular) POLARITY
UNCERTAIN
6. Tail length, mm (<120, >120) POLARITY UNCERTAIN
7. Hindfoot length, mm (48.5-51, 50-55) POLARITY UNCERTAIN
8. Greatest skull length, mm (50-57, 57-57.5, >60) O POLARITY
UNCERTAIN

Table 2. Lists of characters used in cladistic analysis of Sulawesi squirrels. Notations as for Table 1.

Then, as an experiment (suggested by Dr John Trueman), I ran a "total evidence" cladistic analysis combining data for both macaques and squirrels, using a generalized outgroup. The resulting trees are given in Fig.2. The consistency index for the Unordered run is 0.81 (excluding uninformative characters, 0.756), and for the Ordered run is 0.673 (excluding uninformative characters, 0.637). The length of the tree is in both cases equal to the shortest of 1000 random trees. The basic distinction, with over 50% bootstrap value, is between the southeastern peninsula and the rest: does this suggest that the southeastern arm was, early on, isolated from the rest of Sulawesi?

There are many problems awaiting study. When did the "old endemics" arrive, and was it really early enough to get them across when (part of) Sulawesi was connected to Sundaland? And why have anoa and babirusas not turned up in the Walanae fauna? Were there, perhaps, two "old endemic" waves, and the second, the one which survives, replaced the first, the *Stegodon* plus *Celebochoerus* fauna? How did geographic differentiation take place – was there a phase in which, as Fooden (1969) surmised, Sulawesi was not one but a series of islands? When did the cuscuses arrive; was it really on the Australian plate fragments?

All these questions relate strongly to the basic question: what, actually, is the meaning of Wallace's Line?

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