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Systematic Revision Within the *Phalanger orientalis* Complex (Diprotodontia, Phalangeridae): A Third Species of Lowland Gray Cuscus from New Guinea and Australia

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ABSTRACT

A study of specimens from the mammal collections of the American Museum of Natural History that were originally assigned to *Phalanger orientalis* sensu lato revealed the presence of three taxa: *P. orientalis* from northern New Guinea, the Bismarck Archipelago, and the Solomon Islands; *P. intercastellanus* from southeast New Guinea, the D'Entrecasteaux Islands, the Trobriand Islands, and the Louisade Archipelago; and a group from southern New Guinea and the Cape York Peninsula of Australia that could not be assigned to either of the two foregoing species. Possession of a distinctive suite of morphological characters warrants recognition of this group at the species level. The characteristics and habitat of the species are described, and the zoogeographic implications of its distribution are discussed.

INTRODUCTION

The taxonomy of the lowland gray cuscuses, small- to medium-sized arboreal marsupials of the family Phalangeridae, has been in a state of flux for many years, a situation that was summarized in some detail by Menzies and Pernetta (1986). The first large-scale phylogentic revision of the cuscuses, by Tate (1945), placed all species in a single genus, *Phalanger*, which was split into three species groups. The largest of these, the ''*orientalis* group'', contained four species: *P. orientalis*, *P. gymnotis*, *P. vestitus*, and *P. celebensis*. The first of these species, *P. orientalis*, was divided into five subspecies, subsumed with-

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in which were a number of taxa previously considered to be of specific rank. These included *P. ornatus* (Gray, 1860), *P. lullulae* (Thomas, 1896), *P. vulpecula* (Förster, 1913), *P. brevinasus*, *P. matsika*, and *P. microdon* (Tate and Archbold, 1935). Subsequent studies (George, 1979, 1982; Ziegler, 1982; Menzies and Pernetta, 1986) resurrected some of these groups as full species, but Tate's basic concept of a single, morphologically diverse species, encompassing cuscuses from the lowlands of New Guinea, together with those of the Solomon Islands, Bismarck Archipelago, Louisade Archipelago, D'Entrecasteaux Islands, Trobriand Islands, South Moluccas, Timor, and the Cape York Peninsula of Australia, has persisted in the literature.

In recent years it has become clear that the apparently homogenous *P. orientalis* of New Guinea, Cape York, and nearby islands may contain within it several populations sufficiently distinct to warrant recognition as species in their own right. Menzies and Pernetta (1986) identified seven populations on the basis of palatal dimensions and non-metric morphological characters, but declined to recognize these as anything more than subspecies of *P. orientalis*. An electrophoretic study by Colgan et al. (1993) showed the existence of two populations within New Guinea that were sufficiently divergent to suggest they represented two species: *P. orientalis* in northern New Guinea and the Bismarck and Solomon Islands, and *P. intercastellanus* in southern New Guinea and the southeast Papuan Islands. The results of the electrophoretic study were supported by an analysis of morphological characters, which can be used to distinguish between the two species (Colgan et al., 1993).

Colgan et al.'s combination of molecular and morphological evidence for the existence of two species within *Phalanger orientalis* sensu lato is compelling. However, the specimens used as the basis of the study are drawn from a comparatively limited sample, taken primarily from offshore islands and a restricted number of sites in mainland New Guinea. There are no specimens from the southern lowlands of New Guinea (including the area known as the Trans-Fly), a region of around 125,000 square miles extending south of the central cordillera between the Kikori and Mimika rivers and encompassing lowland rainforests, seasonally flooded forests, open woodlands, and tropical grasslands. The absence of specimens is perhaps unsurprising, as the area has rarely been visited by Western collectors. Nonetheless, the paucity of material is frustrating, as the few specimens of *P. orientalis* sensu lato collected here are distinctive enough to have been described as a separate subspecies (*P. orientalis mimicus*, Thomas, 1922), a separate species (*P. microdon*, Tate and Archbold, 1935), or even assigned to a different genus (*Strigocuscus mimicus*, Flannery et al., 1987). The results of a discriminant function analysis of metric characters by Menzies and Pernetta (1986) reveal both the clear distinction of the southern New Guinea population of *P. orientalis* from the other New Guinea populations and its affinities with the Cape York population. On this basis, Menzies and Pernetta recognized the two populations as a separate subspecies, *P. orientalis mimicus*.

The American Museum of Natural History possesses a large series of phalangerid marsupials resulting from the eight Archbold Expeditions of 1933 to 1964 to New Guinea and the Cape York Peninsula of Australia (Archbold and Rand, 1935; Rand and Brass, 1940; Archbold et al., 1942; Brass, 1953, 1956, 1959, 1964; Van Deusen, 1978). Recuration of these collections by Musser and Helmut Sommer in the 1990s provided an opportunity to reassess the taxonomy of the lowland gray cuscuses. It became apparent that while the majority of *P. orientalis* sensu lato specimens could be assigned to either *P. orientalis* sensu stricto or *P. intercastellanus*, there remained a set of specimens, collected in the southern lowlands of New Guinea and the Cape York Peninsula of Australia, whose distinctive morphological characteristics fitted into neither of the species described by Colgan et al. (1993). This report describes these specimens, and forms part of series of reports, either published (Musser and Sommer, 1992) or in preparation, that reflect the Department of Mammalogy's efforts to gain a better understanding of the species diversity and zoogeography of mammals in New Guinea.

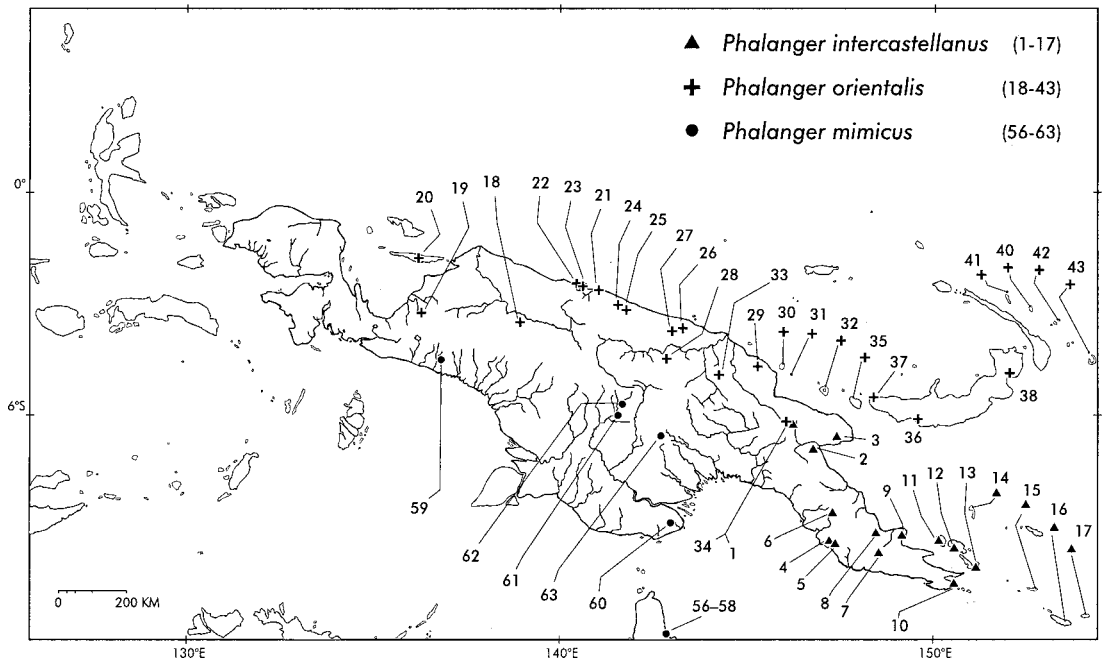

Fig. 1. Collecting localities for specimens of *Phalanger intercastellanus*, *P. mimicus*, and *P. orientalis* in the AMNH collections, and for non-AMNH specimens used in the description of *P. mimicus*. Solomon Islands and Australian localities are not shown on the map. For details of all localities see appendix 1. Locality 33 (= ''New Britain'') is not shown because it is nonspecific.

MATERIALS AND METHODS

Specimens of *Phalanger orientalis* sensu lato from the American Museum of Natural History, Department of Mammalogy (AMNH); the Natural History Museum, London, Mammal Collections (BMNH); and the Bernice P. Bishop Museum (BBM) were examined. A list of specimens is attached as appendix 1. Measurements were taken using vernier calipers. Because the cranium of cuscuses continues to grow throughout adult life (Menzies and Pernetta, 1986) only specimens in which M4 was fully erupted were measured. Dental terminology follows Luckett (1993).

RESULTS

The AMNH collections contain 1162 specimens assigned to *Phalanger orientalis* sensu lato. The main collecting localities for these are listed in appendix 1 and are shown in figure 1. Assignment of specimens from mainland New Guinea to *P. orientalis* sensu stricto and to *P. intercastellanus*, using the diagnostic characters defined by Colgan et al. (1993) resulted in the species distribution seen on the map, with a clear zone of separation at the watershed of the Markham/Ramu Valley. Specimens of both species were collected at Umi River Camp (fig. 1, localities 1 and 34) during the Sixth Archbold Expedition to New Guinea, although this should not be taken as evidence of sympatry. The expedition mammalogist Hobart Van Deusen frequently obtained specimens from local hunters, which could have been brought to the camp from either side of the Markham/Ramu watershed. Dimensions for the skulls of mainland New Guinea populations of *P. intercastellanus* and *P. orientalis* are given in table 1.

A third group of specimens, from the Western Province of Papua New Guinea, could be distinguished from both *P. orientalis* and *P. intercastellanus* by their smaller overall size; their particularly small molars; the presence of a well-developed postparacrista on M1, with a pronounced buccal kink;

TABLE 1
Descriptive Statistics for Cranial and Dental Measurements (mm) for New Guinea Population Samples of *Phalanger orientalis* and *Phalanger intercastellanus*
(Mean and observed range [in parentheses] are listed.)

	Phalanger orientalis [a]			*Phalanger intercastellanus* [b]		
	♂ (*N*=5)	♀ (*N*=2)	pooled (*N*=12)	♂ (*N*=5)	♀ (*N*=3)	pooled (*N*=8)
Breadth across upper canines	16.04 (13.45–19.09)	14.91 (14.17–15.64)	15.24 (13.45–19.09)	15.48 (13.45–16.40)	15.17 (14.00–16.01)	15.32 (13.45–16.40)
Crown length of molar row	18.35 (17.23–20.16)	18.42 (16.94–19.90)	18.17 (16.94–20.16)	19.18 (17.23–19.83)	18.52 (18.70–19.12)	18.85 (17.23–19.83)
Length of third premolar	5.43 (4.56–6.31)	—	5.28 (4.56–6.31)	5.10 (4.56–5.2)	4.98 (4.94–5.01)	5.04 (4.56–5.20)
Breadth of third premolar	4.11 (3.37–4.57)	4.11 (3.71–4.51)	4.10 (3.37–4.57)	4.23 (3.37–4.56)	4.23 (3.92–4.24)	4.23 (3.37–4.56)
Crown length from third premolar to fourth molar	23.78 (22.33–26.47)	22.30 (22.30–22.96)	23.06 (22.30–26.47)	24.42 (22.33–25.24)	23.81 (23.79–24.58)	24.11 (22.33–25.24)
Crown length of premolars	11.89 (10.78–13.29)	11.57 (10.78–13.29)	11.20 (10.78–13.29)	11.89 (10.78–12.42)	11.78 (11.86–12.26)	11.84 (10.78–12.42)
Condylobasal length	82.69 (71.35–96.51)	75.40 (72.70–78.09)	78.17 (71.35–96.51)	83.56 (71.35–86.90)	82.93 (80.30–84.20)	83.25 (71.35–86.90)
Length of nasals	31.85 (26.78–40.43)	29.44 (26.78–32.10)	30.52 (26.78–40.43)	32.34 (26.78–36.57)	32.57 (30.08–32.40)	32.46 (26.78–36.57)
Minimum width of nasals	6.75 (5.33–8.86)	—	6.29 (5.33–8.86)	6.96 (5.33–7.59)	6.59 (5.52–7.66)	6.78 (5.33–7.66)
Posterior width of nasals	13.21 (10.71–15.89)	—	12.35 (10.71–15.89)	13.89 (10.71–15.73)	13.87 (13.38–14.36)	13.88 (10.71–15.73)
Facial exposure of lacrimal (suture to anteriorbital margin)	6.17 (5.30–7.69)	5.22 (3.82–6.62)	5.74 (3.82–7.69)	4.76 (4.25–4.92)	4.95 (4.69–5.39)	4.85 (4.25–5.39)

[a] **Males:** AMNH 151831, 151832, 151838, 194361, 222628. **Females:** AMNH 101998, 198727. **Unknown:** AMNH 109436, 194683–194685, 221350.
[b] **Males:** AMNH 104099, 104148, 108571, 157197, 191189. **Females:** AMNH 108569, 108570, 191190.

the reddish-brown pelage of the females; and most strikingly by the distinctive alignment of the zygomatic arches, which are parallel to the midline of the skull or diverge rostrally, rather than converging rostrally. Skull dimensions for these specimens are listed in table 2.

The study was then expanded to include specimens from the East Papuan Islands, Bismarck Archipelago, Solomon Islands, and the Cape York Peninsula of Australia. Although significantly smaller than the mainland populations of the two species defined by Colgan et al. (1993), it was possible to assign the majority of these specimens to either *P. orientalis* (Bismarck Archipelago and Solomon Islands) or *P. intercastellanus* (East Papuan Islands). However, the Cape York population showed clear affinities with the Western Province specimens, including small size of molars and the alignment of the zygomatic arches, although females of this population lacked the reddish pelage of the New Guinea females. Cranial dimensions of this population are listed in table 2.

Examination of the holotype of *P. orientalis mimicus* Thomas, 1922, in the collections of the Natural History Museum, London, revealed that it possessed the same distinctive cranial characters seen in the Austra-

TABLE 2
Descriptive Statistics for Cranial and Dental Measurements (mm) for New Guinea and Australian Population Samples of *Phalanger mimicus*[a]
(Mean and observed range [in parentheses] are listed.)

	SW New Guinea			Australia		
	♂ (*N*=1)	♀ (*N*=5)	pooled (*N*=6)	♂ (*N*=2)	♀ (*N*=4)	pooled (*N*=6)
Breadth across upper canines	14.34	13.49 (12.62–14.10)	13.92 (12.62–14.10)	15.50 (14.90–16.10)	14.20 (13.40–14.80)	14.85 (13.40–16.10)
Crown length of molar row	16.90	16.57 (16.10–17.04)	16.74 (16.10–17.04)	17.60 (17.40–17.80)	17.00 (16.50–17.30)	17.30 (16.50–17.80)
Length of third premolar	4.79	4.12 (3.74–4.44)	4.46 (3.74–4.79)	5.30 (5.00–5.60)	4.39 (3.79–4.80)	4.85 (3.79–5.60)
Breadth of third premolar	3.60	3.74 (3.51–3.93)	3.67 (3.51–3.93)	3.96 (3.91–4.00)	3.50 (3.26–3.67)	3.73 (3.26–4.00)
Crown length from third premolar to fourth molar	21.71	20.99 (20.29–21.66)	21.35 (20.29–21.71)	23.20 (22.80–23.60)	21.42 (21.09–21.70)	22.31 (21.09–23.60)
Crown length of premolars	10.96	9.52 (9.19–9.69)	10.24 (9.19–10.96)	11.19 (11.10–11.28)	10.13 (8.37–10.91)	10.66 (8.37–11.28)
Condylobasal length	75.70	72.72 (70.60–76.30)	74.21 (70.60–76.30)	79.85 (78.20–81.50)	76.53 (75.20–77.40)	78.19 (75.20–81.50)
Length of nasals	28.50	26.48 (25.31–27.50)	27.49 (25.31–28.50)	31.40 (31.00–31.80)	29.53 (28.20–31.70)	30.46 (28.20–31.80)
Minimum width of nasals	6.43	6.12 (5.78–6.59)	6.27 (5.78–6.59)	7.08 (6.58–7.58)	6.93 (6.48–7.18)	7.01 (6.48–7.58)
Posterior width of nasals	12.06	12.28 (11.80–12.73)	12.17 (11.80–12.73)	15.13 (14.23–16.02)	14.06 (12.22–15.41)	14.59 (12.22–16.02)
Facial exposure of lacrimal (suture to anteriorbital margin)	4.20	3.66 (3.52–3.91)	3.93 (3.52–4.20)	4.08 (4.03–4.13)	3.75 (3.12–4.64)	3.92 (3.12–4.64)

[a] **Males:** AMNH 108905, 154437, BMNH 11.11.11.93. **Females:** AMNH 104400, 104401, 104406, 108904, 154427, 154438, 154440; BBM 103050, 103166.

lian and Western Province specimens at the AMNH. They were also seen in three specimens of "*P. orientalis*" from the Bishop Museum, which were collected on the lower slopes of Mount Bosavi, in the Southern Highlands Province of Papua New Guinea.

DISCUSSION

On the basis of the consistent morphological differences between the southern New Guinea and Cape York populations of *Phalanger orientalis* sensu lato, we recognize a third species of lowland gray cuscus in the *P. orientalis* complex (fig. 2).

Phalanger mimicus (Thomas, 1922)

Phalanger intercastellanus Thomas, 1895.
Phalanger orientalis mimicus Thomas, 1922.
Phalanger microdon Tate and Archbold, 1935.
Phalanger orientalis peninsulae Tate, 1945.

HOLOTYPE AND TYPE LOCALITY: BMNH 11.11.11.93, puppet skin with skull and dentaries of an adult male. Collected by G. C. Shortridge, Parimau, Mimika River, Dutch New Guinea (= Irian Jaya), 4°31′S, 136°36′E, 250 ft, 4 October 1910.

DIAGNOSIS: Skull and teeth small, molars especially so. Lachrymal contribution to the face is short. Zygomatic arches run parallel or diverge from midline of skull rostrally.

Fig. 2. Captive specimen of a female *Phalanger mimicus*. Third Archbold New Guinea Expedition, 1936–1937. Gaima, Western Province, Papua New Guinea.

Well-developed postparacrista on M1, with a pronounced buccal kink. Distinguished from *P. orientalis* and *P. intercastellanus* by its smaller size, lack of convergence of zygomatic arches rostrally, and by well-developed postparacrista. Distinguished from *P. orientalis* by absence of white tail tip in females. Distinguished from *P. intercastellanus* by absence of lingual cingulum on protocone of M2.

DESCRIPTION: Critical skull dimensions are listed in table 2. The most notable feature of the skull is the shape of the zygomatic arches. In all other species of *Phalanger* the arches reach their widest point at the caudal end, near the suture between the jugal and the

squamosal, and converge toward the midline of the skull rostrally. In *P. mimicus* the arches run parallel to the midline, or even diverge rostrally, giving the skull a different shape (fig. 3). In general the skull shows less development of the supraorbital, parietal, and sagittal crests than is seen in other species of the genus; indeed, it is not unusual for the parietal crests to remain unfused, even in very old individuals. The facial extent of the lachrymal is comparatively small, as in *P. intercastellanus*. The frontals are deeply penetrated by the nasal bones; the nasals do not taper abruptly at their caudal extremity, but are rounded (fig. 4). The teeth are remarkably small, even given the overall small size of the animals. In this respect *P. mimicus* is similar to the rare montane Telefomin cuscus, *P. matanim* (Flannery, 1987). The well-developed postparacrista on M1, with its pronounced buccal kink (fig. 5), is seen in several species of *Phalanger*, but not in either *P. orientalis* or *P. intercastellanus*, the two species within which *P. mimicus* was formerly reduced to synonymy.

The tail wedge of *P. mimicus* is short, as in *P. intercastellanus*. Adult males of the Australian population have upper parts that are gray, with a well-defined dark dorsal stripe finishing well short of the haunches, and silver-tipped guard hairs. Three specimens, including the holotypes of *P. orientalis mimicus* (BMNH 11.11.11.93) and *P. orientalis peninsulae* (AMNH 108905), have an off-white pelage with dark guard hairs. This coloration is often seen in old males of both *P. orientalis* and *P. intercastellanus*. With the exception of aged specimens, however, *P. mimicus* appears to show little or no sex-based color dimorphism, at least in its Australian populations. The situation is less clear for the New Guinea population, because only one adult male, the aforementioned BMNH 11.11.11.93, is known. Females of the New Guinea population have a striking reddish-brown pelage, which was one of the characteristics used by Tate to describe *P. microdon*. Juvenile males also show this coloration, but given the general tendency toward a reddish pelage in juveniles of both *P. orientalis* and *P. intercastellanus*, this may be of limited significance in distinguishing between the species. It is worth noting that, unlike the condition seen in Australian *P. mimicus*, the dorsal stripe continues almost to the base of the tail, albeit becoming more diffuse caudally. The question of whether the differences in pelage between the Trans-Fly and Cape York populations warrant taxonomic recognition cannot be answered without a larger sample from southwest New Guinea.

HABITAT: Rand and Brass (1940) provide descriptions of the southern New Guinea region that contains the collecting localities for *P. mimicus*. In the area along the coast, south of the estuary of the Fly River (which includes the Oriomo River: fig. 1, locality 62), the predominant vegetation type is scrub savanna. Rainforest occurs chiefly as fringing strips of no more than 100–200 m in depth along creeks and streams, and in isolated patches on ridge tops (fig. 6). The rainforest is described by Rand and Brass as ''poor and light'', with some areas that ''could only be described as dense brush''. Savanna trees, including *Acacia* and *Tristania*, intrude into the rainforest. The savannas are dominated by *Melaleuca*; on ridges this genus mixes with *Tristania*, *Eucaplyptus*, and *Acacia* to form savanna forests with a thin, high canopy and a ground cover of grasses. During the rainy season the flat savannas become boggy, and can flood up to a foot (Brass and Rand, 1940). In contrast, the areas around the Palmer River Camp (fig. 1, locality 63) and the Black River Junction (fig. 1, locality 64) in the northern part of Western Province are typified by steep ridges rising up to 100 m above sea level (Brass and Rand, 1940). The vegetation type is classic lowland rainforest rich in epiphytes in both the lower layers and the canopy (fig. 7).

The Australian localities for *P. mimicus* are described by Brass (1953), and bear striking similarities in vegetation to those seen in southern New Guinea. At Shepheard's Battery site, on the Upper Peach River (fig. 1, locality 60), Brass reported that specimens of *P. mimicus* were ''found in numbers'' in the rainforest fringing Bonanza Creek. Rainforest was confined to the margins of the creek, while the remainder of the flats and surrounding ridges were covered in open savanna forests of box, bloodwood, and ironbark trees. In the Iron Range (fig. 1, locality 59)

Fig. 3. Ventral views of crania of **(a)** AMNH 104400, *P. mimicus*; **(b)** AMNH 108569, *P. intercastellanus*; **(c)** AMNH 109435, *P. orientalis*. Natural size.

Fig. 4. Dorsal views of crania of **(a)** AMNH 104400, *P. mimicus*; **(b)** AMNH 108569, *P. intercastellanus*; **(c)** AMNH 109435, *P. orientalis*. Natural size.

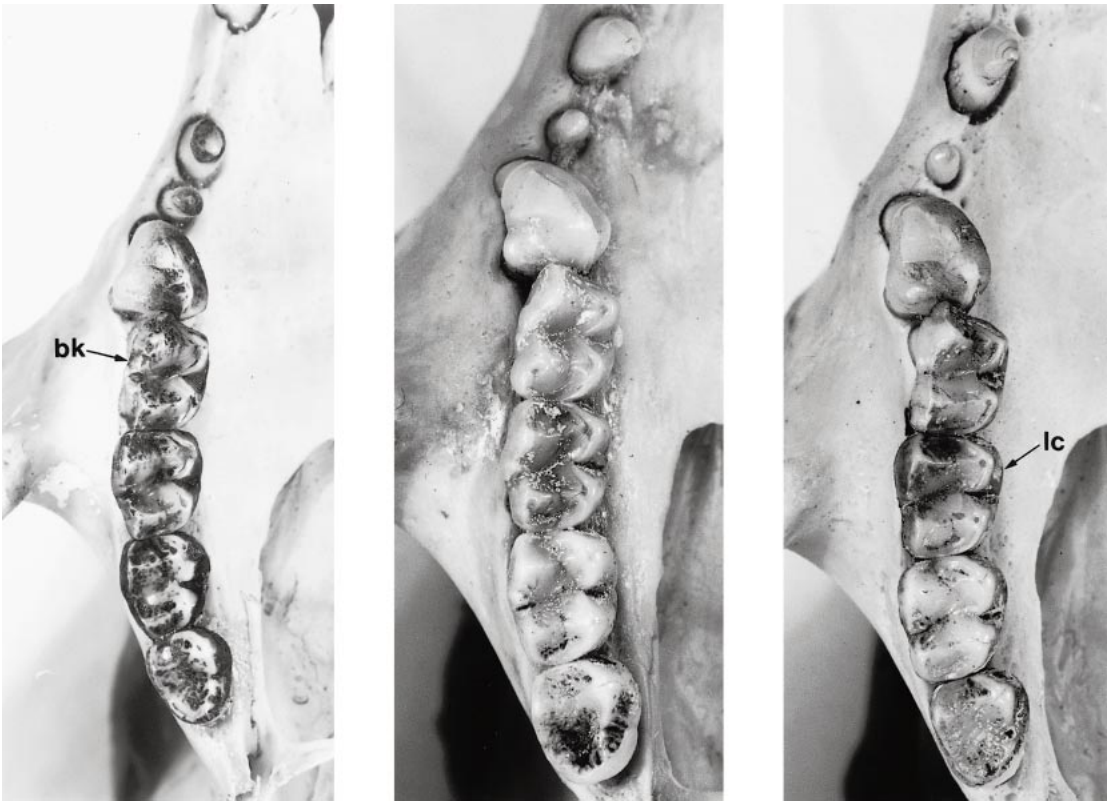

Fig. 5. Right molar tooth rows of **(a)** AMNH 104400, *P. mimicus*; **(b)** AMNH 108569, *P. intercastellanus*; **(c)** AMNH 109435, *P. orientalis*. Abbreviations: **lc** = lingual cingulum of M2; **bk** = buccal kink in postparacrista of M1. Approximately 3.5 × natural size.

lowland rainforests predominated (fig. 8), though there were still patches of open forest in which rainforest was limited to creek margins and gullies. As with the Fly River basin, there was seasonal inundation of the rainforests on the floodplains, in some areas to depths of 6–10 ft (Brass, 1953).

COMMENTS: A number of authors have recognized the distinctive nature of the lowland gray cuscuses from southern New Guinea (Thomas, 1922; Tate and Archbold, 1935; Menzies and Pernetta, 1986; Flannery et al., 1987; George, 1987). Particularly noteworthy among these earlier studies is that of Menzies and Pernetta (1986), who used a discriminant function analysis of metric characters (largely drawn from the palatal region) to distinguish different populations of *P. orientalis* sensu lato. Their analysis revealed first, the clear distinction of the southern New Guinea population of *P. orientalis* from the other New Guinea populations and, second, its affinities with the Cape York population. On this basis, Menzies and Pernetta recognized the two populations as a separate subspecies, *P. orientalis mimicus*. Our study supports the results of their analysis, the only difference being their retention of *mimicus* within *P. orientalis*. Except for its consistently smaller size, Menzies and Pernetta could find no distinctive characters to separate the taxa. In fact, as we have demonstrated, the qualitative differences in cranial morphology between *mimicus* and the other populations of *P. orientalis* sensu lato are at least as great as those that define a number of well-established species of phalangerids, and are certainly sufficient to justify separation at the species level.

The systematic placement of *P. mimicus* is problematic. The characteristics that were originally proposed by Flannery et al. (1987)

Fig. 6. Aerial view of the Oriomo River area (locality 60), photographed during the Third Archbold New Guinea Expedition, 1936–1937. In the foreground is savanna, with patchy woodlands of *Melaleuca* and *Eucalyptus*. Lowland rainforest is concentrated in a band along the line of the Oriomo River, which can be seen running from left to right in the top part of the photograph.

Fig. 7. Lowland rainforest, Fly River, 5 mi below Palmer Junction (locality 61). Photographed during the Third Archbold New Guinea Expedition, 1936–1937.

as the basis for inclusion of the species in *Strigocuscus* have proved unreliable, being for the most part either age related, homoplastic, or just poorly defined (Springer et al., 1990; Norris, 1992). Despite its original placement within *P. orientalis* sensu lato, there is little in the way of morphological evidence to link *P. mimicus* to either *P. orientalis* or *P. intercastellanus*, although sex-based color dimorphism in the New Guinea population of *P. mimicus* may be an indicator that the three taxa form a coherent group. Links with other species of *Phalanger* are equally tenuous. The small molars of *P. mimicus* are similar to those of the apparently rare and enigmatic Telefomin cuscus, *P. ma-*

Fig. 8. Rainforest, Iron Range, Cape York Peninsula (locality 57). Photographed during the 1948 Archbold Cape York Expedition.

TABLE 3
Austral Elements of the New Guinea Mammal Fauna
(Species compiled from Flannery [1995], and Hitchcock [1998]; habitat information from Strahan [1993].)

Species	Habitat
Sminthopsis archeri [a]	tall, mixed savanna
Sminthopsis virginiae	open savanna woodland
Isoodon macrourus	monsoon woodlands and grasslands
Largorchestes conspicillatus [a]	open forests, open woodlands, grassland
Macropus agilis	open forest and adjacent grasslands
Thylogale stigmatica [a]	rainforests, wet sclerophyll forests, scrub
Phalanger mimicus	patchy rainforest, lowland rainforest
Pteropus alecto	mangrove swamps, patchy rainforest
Pteropus scapulatus [a]	eucalypt woodland
Scotorepens sanborni	understory of coastal forests
Taphozous flaviventris [b]	eucalypt forests, scrub
Mormopterus loriae [b]	open forests, rainforest canopies
Chalinolobus nigrogiseus [b]	open woodland, wet sclerophyll forest
Rattus sordidus	tropical grassland, open forest, rainforest clearings
Pseudomys delicatulus [a]	grassland, sclerophyll forests, woodland
Conilurus penicillatus [a]	open woodland, eucalypt woodland, monsoon forest
Xeromys myoides [a]	mangrove swamps, grassy swamps

[a] Trans-Fly region and Australia only.
[b] Southeast New Guinea and Australia only.

tanim (Flannery, 1987), which also shows deep penetration of the frontals by the nasal bones. However, *P. matanim* lacks the distinctive zygomatic morphology of *P. mimicus*, and has long, lax fur and a broad dorsal stripe, more like the pelage texture and pattern of the midmontane *P. vestitus*. The well-developed postparacrista of M1, although absent in both *P. orientalis* and *P. intercastellanus*, is seen in such a wide range of phalangerids as to make it virtually useless as a phylogenetic character. In contrast, the distinctive alignment of the zygoma is not seen in any other species of phalangerid, although it does occur in some species of pseudocheirid possums (for example *Pseudochirops cupreus* and *Pseudochirulus canescens*).

One of the distinctive features of the Trans-Fly biota is the heavy presence of Australian elements in the fauna (Flannery, 1995). (These are listed in table 3.) The underlying biogeographic reasons for this relate to the tectonic history of New Guinea. In contrast to the central cordillera and Huon Peninsula, which were formed as an arc of volcanic islands upthrust by the northward drift of the Austral Plate, the southern plains have always formed part of the Austral Plate. At many times in the past 2 million years, most recently during the late Pleistocene (ca. 20,000 years ago), the Trans-Fly has been continuous with Australia (Flannery, 1995). From this point of view, the existence of a distinctive species of *Phalanger* spanning the Trans-Fly plains and Cape York is unsurprising. Nonetheless, the distribution of *P. mim-*

icus raises some interesting questions of zoogeography, which are worth considering in more detail.

Based on the distribution of mammals, Flannery (1995) recognizes three zoogeographic provinces in New Guinea, which correspond closely to the island's underlying geological structure and history. The Oceanic Province includes the Vogelkop Peninsula; Weyland Mountains; Japen Island; and the Cyclops, Bewani, and Torricelli Ranges. The Austral Province is defined by Flannery as the Trans-Fly plains, the Moresby Region, and the coastal grasslands that run southeast from there toward Milne Bay, and then along the northern coast as far west as Popondetta. Finally, there is the Tumbunan Province, an entity originally proposed by Schodde and Calaby (1972), and encompassing rainforest and alpine grassland. The boundary between the Austral and Tumbunan Provinces ''can be conveniently regarded as the interface between woodland with gallery rainforest and more dense rainforest'' (Flannery, 1995). None of these provinces are continuous geographically; Flannery divides the Tumbunan Province into four discrete subprovinces (Eastern, Western, Central, and Huon; Flannery, 1995), and a similar case could be made for dividing the Austral Province fragments into Trans-Fly, Northeastern, and Southeastern subprovinces.

Early biogeographic models for New Guinea's mammal fauna (for example, Ziegler, 1977) assumed that the island was the center of diversity for rainforest-adapted marsupial species, which went on to establish limited outlying populations in Australia, most notably on Cape York. Subsequent discoveries in the fossil record of Australia, particularly in the Oligo-Miocene deposits at Riversleigh (Archer et al., 1991), revealed that a diverse fauna of rainforest mammals was present in Australia for much of the Tertiary, thus generating a competing hypothesis for the center of species diversity. In this model, New Guinea's marsupial fauna is seen as a relict distribution of the formerly widespread Australian rainforest marsupials, with New Guinea acting as a refugium from the increasing aridity of Australia during the Pleistocene and Holocene (Archer et al., 1991). The fauna of the Austral Province was seen as containing more recent arrivals, better adapted to the diverse habitat of open woodland, gallery rainforest, savanna grasslands, and swamps found in the Trans-Fly and in coastal areas of southeast New Guinea.

At first sight, *P. mimicus* would appear to fit conveniently into the group of Austral Province species confined to the Trans-Fly subprovince of New Guinea and to northern Australia (table 3), an inhabitant of patchy rainforest surrounded by open woodlands and savanna. However, it is also found in lowland rainforest areas (i.e., the Palmer River, Black River, and Mount Bosavi localities), more typical of the Tumbunan Province. That being the case, what defines the boundary between the ranges of *P. mimicus* and *P. intercastellanus*? Both species are found in lowland rainforest, and *P. intercastellanus* has been reported in wooded savanna in the Port Moresby area (Menzies and Pernetta, 1986). Clearly, habitat specialization alone cannot explain the distribution of the two species.

Discussing the boundary between *P. orientalis* and *P. intercastellanus* in the Markham-Ramu area, Colgan et al. (1993) noted that a number of other lowland mammal species and subspecies pairs abut in this vicinity, and postulated an underlying zoogeographic barrier. Similar examples exist for the *P. mimicus*/*P. intercastellanus* boundary; these include the closely related *Melomys* species *M. levipes* (SE New Guinea) and *M. lorentzii* (Trans-Fly); two subspecies of *Rattus leucopus, R. l. dobodurae* (SE New Guinea) and *R. l. ringens* (Trans-Fly); two subspecies of the gray dorcopsis, *Dorcopsis luctosa luctosa* (Trans-Fly) and *D. l. beccarii* (SE New Guinea); and two subspecies of spotted cuscus, *Spilocuscus maculatus chrysorrhous* (SW New Guinea) and *S. m. goldei* (SE New Guinea) (Taylor et al. 1982; Flannery, 1994, 1995; Menzies, 1996). All these pairings involve species that occur in lowland rainforest, and cannot be explained by fragmentation of the savanna grasslands and open woodlands of the Austral Province. Like the boundary between *P. orientalis* and *P. intercastellanus*, it is possible that the range of *P. mimicus* is limited at its eastern extent by some as yet undiscovered zoogeographic bar-

rier. Unfortunately, and in contrast to the Markham-Ramu area, the mammal fauna of the western portion of Papua New Guinea's Gulf Province (the likely zone of contact between *P. mimicus* and *P. intercastellanus*) has not been extensively sampled (Flannery, 1995, Map 11).

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APPENDIX 1: GAZETTEER AND SPECIMENS

We have listed the localities of all specimens of *Phalanger intercastellanus*, *P. mimicus*, and *P. orientalis* in the collections of the AMNH, together with those of specimens from other institutions that were studied for this project. The number preceding each place corresponds to the same-numbered locality on the map in figure 1. Place-names and elevations are taken from specimen tags or published expedition summaries. Flannery (1995); Laurie and Hill (1954); HOUSND (1944); and USBGN, Indonesia (1982) were the sources consulted for coordinates. For a few localities it was necessary to estimate coordinates from expedition summaries, and these coordinates are labeled ''estimated''. In cases where the name of the locality has changed, or where a locality is known by more than one name, the alternate name is shown in parentheses. Where the spelling of the locality on the specimen tag differs from that used in the published gazetteer, the tag spelling is noted in quotation marks. Sites in Irian Jaya are referred to by the names used before the political transfer of Netherlands New Guinea to Indonesia, with the Indonesian name following in parentheses. The Dutch names are embedded in the taxonomic literature of New Guinea mammalogy and refer to well-known type localities and places visited during the major biological surveys of the 20th century.

PHALANGER INTERCASTELLANUS

1. PAPUA NEW GUINEA, Morobe Province. Upper Markham Valley, Umi River Camp (6°5′S, 146°10′E), AMNH 191194, 193137–193138.

2. PAPUA NEW GUINEA, Morobe Province. Lower Markham Valley, Oomsis Creek (6°40′S, 146°48′E), AMNH 191189–191192; Gurakor (6°49′S, 148°37′E), 650 m, AMNH 193135–193136; Atzera Range (= ''Atzara, West Northwest of Lae'': 6°37′S, 146°55′E), AMNH 192696.

3. PAPUA NEW GUINEA, Morobe Province. Huon Peninsula, Finschhafen (6°35′S, 147°50′E), AMNH 195948–195949, 195952–195956, 195958; Yapang (= Japang: 6°25′S, 147°30′E), AMNH 195860–195861; Maran (6°25′S, 147°20′E), AMNH 195827, 195829; Masba Creek (6° 30′S, 147°30′E), 2000 ft, AMNH 194739–194741, 195169; Mount Rawlinson (= Mount Zegunung: 6°30′S, 147°15′E), AMNH 195652, 195654, 195658, 195664, 196683, 195693, 195698–195699, 195701, 195721, 195740, 195764, 195781, 195783; Ogeramnang (6°25′S, 147°20′E), AMNH 195847.

4. PAPUA NEW GUINEA, Central Province. Port Moresby (9°28′S, 147°10′E), Baubauguina Plantation, AMNH 191188, 192713.

5. PAPUA NEW GUINEA, Central Province. Astrolabe Range (9°33′S, 147°26′E), Baruari Rest House, AMNH 108541–108542, 108569–108571.

6. PAPUA NEW GUINEA, Central Province. Wharton Range, Belavista (= ''Bellavista'': 8°31′S, 147°4′E), AMNH 104120; Deva Deva (8°32′S, 146°58′E), AMNH 104115; Mafulu (= Mafula: 8°31′S, 147°0′E), 1250 m, AMNH 104099–104100, 104121, 104148; Matsika (8°34′S, 146°55′E), 950 m, AMNH 104102–104103, 104127, 104364; Ononge (8°40′S, 147°15′E), AMNH 104092–104151.

7. PAPUA NEW GUINEA, Milne Bay Province. Maneao Range (= ''Maneau Range''), Mount Dayman, Gwariu River 1 mi. south of Biniguni Camp (9°40′S, 149°16′E), 200 m, AMNH 157212, 158964–158965; Bottom Camp (= Number 3 Camp: 9°45′S, 149°20′E), 700 m, AMNH 157209–157211, 159004–159005.

8. PAPUA NEW GUINEA, Milne Bay Province. Moi Biri Bay, Baiawa (9°35′S, 149°28′E), 40 m, AMNH 157208.

9. PAPUA NEW GUINEA, Milne Bay Province. Cape Vogel Peninsula, Dabora (9°43′S, 150°3′E), sea level, AMNH 157205–157207, 158999–159000; Menapi (9°46′S, 149°57′E), sea level, AMNH 157192–157204, 158966–158967, 159001–159007.

10. PAPUA NEW GUINEA, Milne Bay Province. Milne Bay, Mornuna Plantation (10°30′S, 150°30′E, estimated), 50 m, AMNH 199502.

11. PAPUA NEW GUINEA, Milne Bay Province. D'Entrecasteaux Islands. Goodenough Island, Bolubolu (= Bolu Bolu: 9°22′S, 150°20′E), sea level, AMNH 157213–157216, 158995–158996; east slopes, AMNH 158209–158214; east slopes near Arafuia (9°20′S, 150°14′E), AMNH 158266–158286; east slopes near Wakonai (9°19′S, 150°15′E), AMNH 158271–158274; east slopes, Camp number 2 (= ''Camp number 1'': 9°20′S, 150°15′E), 900 m, AMNH 157225–157226, 158968; mountains near Garuwata, AMNH 158216–158256, 158258–158265; south slopes, Mount Oiamadawa'a (9°18′S, 150°14′E), AMNH 158215; Top Camp (9°21′S, 150°13′E), 1600 m, AMNH 157217–157219, 157221; 1400–1500 m, AMNH 157220, 157222–157224; Goodenough Island, AMNH 79803, 158257, 160219–160221.

12. PAPUA NEW GUINEA, Milne Bay Province. D'Entrecasteaux Islands. Fergusson Island, Agamoia (9°33′S, 150°37′E), 200 m, AMNH 159907–159910, 190800–190806; mountains between Agamoia and Ailuluai (9°37′S, 150°34′E), 700 m, AMNH 159906, 190794–190799; Deidei (9°40′S, 150°52′E), sea level, AMNH 159911–

159912, 159555, 190807–190808; Iamele #1 (9°33′S, 150°32′E), 15 m, AMNH 159897–159905, 190785–190793.

13. PAPUA NEW GUINEA, Milne Bay Province. D'Entrecasteaux Islands. Normanby Island, Waikaiuna (10°4′S, 150°58′E), 20 m, AMNH 159551–159554, 159852–159854, 190773–190784.

14. PAPUA NEW GUINEA, Milne Bay Province. Trobriand Islands. Kiriwina Island, Liluta (9°33′S, 150°37′E, estimated), 10 m, AMNH 159557–159558, 159575–159576, 190713–190714, 190852–190857, 199501.

15. PAPUA NEW GUINEA, Milne Bay Province. Louisiade Archipelago. Misima Island, north slopes of Mount Sisa (10°39′S, 152°49′E), AMNH 159961, 190809–190812.

16. PAPUA NEW GUINEA, Milne Bay Province. Louisiade Archipelago. Sudest Island (= Tagula Island), Joe Landing (= Inagailaui: 11°27′S, 153°30′E, estimated), AMNH 190528–190529, 190813–190814; Mount Riu (11°31′S, 153°25′E), AMNH 190815; Rambuso (11°28′S, 153°33′E), sea level, AMNH 159556, 190530, 190816–190826; Sudest Island, AMNH 79835.

17. PAPUA NEW GUINEA, Milne Bay Province. Louisiade Archipelago. Rossel Island, Abaleti, 50 m, AMNH 190827–190835, 190584–190586; Jinjo (''Jinju'': 11°19′S, 154°18′E), sea level, AMNH 190846–190851, 190589–190593; Mount Rossel (11°22′S, 154°13′E), 700 m, AMNH 190587–190588, 190836—190845.

PHALANGER ORIENTALIS

18. IRIAN JAYA. Idenburg River, Bernhard Camp (3°30′S, 139°15′E): 4 km southwest of Bernhard Camp, 850 m, AMNH 152710, 151838, 151852; 6 km southwest of Bernhard Camp, 1200 m, AMNH 151831–151832.

19. IRIAN JAYA. Weyland Range (= Pegunungan Kobowre: 3°50′S, 135°43′E), Gebroeders Mountains, 6000 ft, AMNH 101998.

20. IRIAN JAYA. Japen Island (= Pulau Yapen: 1°45′S, 136°10′E), AMNH 26799–266836; Dawai River, 5 km northeast of Samberbaba (1°50′S, 136°42′E), AMNH 221714.

21. IRIAN JAYA. Hollandia (= Jayapura: 2°32′S, 140°43′E), AMNH 109434–436, 109653, 151818, 152711.

22. IRIAN JAYA. Cyclops Mountains (= Pegunungan Cycloop: 2°30′S, 140°32′E), AMNH 109443, 151969.

23. IRIAN JAYA. Lake Sentani (= Danau Sentani: 2°36′S, 140°34′E), AMNH 109432–109433, 152824.

24. PAPUA NEW GUINEA, Sandaun Province. Bewani Mountains (3°14′S, 141°12′E): Mount Menawa, 2800–5400 ft, AMNH 198061; Utai (3°22′S, 141°34′E), 650 ft, AMNH 198116.

25. PAPUA NEW GUINEA, Sandaun Province. Torricelli Mountains (3°41′S, 142°27′E): Mount Nibo, 2300–3200 ft, AMNH 198062.

26. PAPUA NEW GUINEA, East Sepik Province. Prince Alexander Range, Mount Turu, Ambukanja (3°37′S, 143°19′E), 2100 ft, AMNH 198122–198125; 3760 ft, 198127–198129.

27. PAPUA NEW GUINEA, East Sepik Province. Maprik (3°38′S, 143°03′E), 500 ft, AMNH 193289.

28. PAPUA NEW GUINEA, East Sepik Province. Headwaters of the Karawari River (4° 36′S, 143°E), AMNH 222659.

29. PAPUA NEW GUINEA, Madang Province. Adelbert Range. Wanuma (4°46′S, 145°19′E), AMNH 199093–199129, 199968; 2200 ft, AMNH 198739–198740; Kaibugu (4°55′S, 144°56′E), 460 ft, AMNH 198731; Atitau (4°46′S, 145°20′E), 3800 ft, AMNH 198736–198737; Maratambu, 2100 ft, AMNH 194361; Okamundu (''13 miles WSW Atitau''), 1950 ft, AMNH 198735; Adelbert Range, AMNH 251052.

30. PAPUA NEW GUINEA, Madang Province. Karkar Island (4°40′S, 145°59′E), AMNH 220351–220714.

31. PAPUA NEW GUINEA, Madang Province. Bagabag Island (4°49′S, 146°13′E), AMNH 221194–221349, 221565–221574.

32. PAPUA NEW GUINEA, Madang Province. Long Island (5°20′S, 147°8′E), AMNH 99827, 99828, 99892–99899, 236799–236823.

33. PAPUA NEW GUINEA, Madang Province. Schrader Range, Pasinkam (''Pasinkap, 13 mi NE Aiome'': 5°1′S, 144°50′E), 280 ft, AMNH 198724, 198727–198729; Simbai River (5°16′S, 144°31′E), Nduimba Creek, AMNH 194682–194685.

34. PAUPA NEW GUINEA, Morobe Province. Upper Markham Valley, Umi River Camp (6°5′S, 146°10′E), AMNH 191913.

35. PAUPA NEW GUINEA, Morobe Province. Umboi Island (= Rooke Island: 5°35′S, 148° 0′E), Arot, AMNH 23683–236833; AMNH 99891, 236824–236829.

36. PAPUA NEW GUINEA, West New Britain Province. Whiteman Range, Aliwo (= Aliwu: 6°12′S, 149°34′E), 500 ft, AMNH 194530–194534; Camp 6 (= Iambon; 6°4′S, 149°48′E), 1600 ft, AMNH 194357, 194407–194409; Camp 8 (5°57′S, 149°49′E), 1800 ft, AMNH 194352; Camp 11 (5°47′S, 149°49′E), 3700 ft, AMNH 194354–194356; Camp 14 (= Muia; 6°10′S, 149°46′E), AMNH 194358, 194412–194413; south slope of Whiteman Range, 2000 ft, AMNH 194353.

37. PAPUA NEW GUINEA, West New Britain

Province. Mount Talawe (5°31′S, 148°24′E), AMNH 221429.

38. PAPUA NEW GUINEA, East New Britain Province. Wide Bay, Baining Mountains, Balayang (4°47′S, 151°58′E), 2500 ft, AMNH 99852–99854; Marlo River, AMNH 99873–99876.

39. PAPUA NEW GUINEA, province unknown. New Britain. AMNH 99801–99803, 221451.

40. PAPUA NEW GUINEA, New Ireland Province. Lihir Group, Lihir Island (3°4′S, 152°34′E), Landolowit, AMNH 99745–99746.

41. PAPUA NEW GUINEA, New Ireland Province. Tabar Group, Tabar Island (2°55′S, 152°0′E), AMNH 99834–99836.

42. PAPUA NEW GUINEA, New Ireland Province. Tanga Group, Boang Island (3°22′S, 153°18′E), AMNH 99837.

43. PAPUA NEW GUINEA, North Solomons Province. Nissan Islands (= Green Islands, Nissan Atoll), Nissan Island (4°30′S, 154°13′E), AMNH 79793–79799.

44. PAPUA NEW GUINEA, North Solomons Province. Buka Island (5°15′S, 154°37′E). 100 ft, AMNH 193645–193650; Mungai Plantation AMNH 99882, 99883.

45. PAPUA NEW GUINEA, North Solomons Province. Bougainville Island, Angana, near Kieta (6°13′S, 155°37′E), AMNH 193644; Buin (6°49′S, 155°43′E), AMNH 79790–79792, 79848, 79849; Numa Numa, AMNH 79800, 83952; Bougainville (6°0′S, 155°0′E), AMNH 99885.

46. SOLOMON ISLANDS, Western Province. Treasury Islands, Mono Island (7°20′S, 155°34′E), AMNH 79921–79924, 79932–79936, 79874.

47. SOLOMON ISLANDS, Western Province. New Georgia Islands, Vella Lavella (= Mbilua: 7°45′S, 156°40′E), AMNH 79939.

48. SOLOMON ISLANDS, Western Province. New Georgia Islands, Ghanongga (= Ranongga: 8°4′S, 156°34′E), AMNH 79863, 79864, 79925–79930, 79938, 79940.

49. SOLOMON ISLANDS, Western Province. New Georgia Islands, Gatukai Island (8°46′S, 158°10′E), AMNH 79887, 79888.

50. SOLOMON ISLANDS, Western Province. New Georgia Islands, Rendova Island (8°31′S, 157°19′E), AMNH 79809–79813.

51. SOLOMON ISLANDS, Isabel Province. Molakobi (= Bikolia Island: 7°22′S, 158°7′E), AMNH 79937.

52. SOLOMON ISLANDS, Guadalcanal Province. Komachu Island (= ‘‘Komanchi’’, ‘‘Komanchu Island’’: 9°49′S, 160°49′E), AMNH 79750, 79873.

53. SOLOMON ISLANDS, Malaita Province. Malaita (= Mala Island: 9°0′S, 161°0′E), AMNH 92150; 1500 ft, AMNH 99967; 3000 ft, AMNH 99968–99971.

54. SOLOMON ISLANDS, Makira Province. Makira (= Bauro Island, San Cristobal: 10°35′S, 161°45′E), AMNH 75190.

55. SOLOMON ISLANDS, province unknown. AMNH 199506, 90082–90084.

PHALANGER MIMICUS

56. AUSTRALIA, Queensland. Cape York, 30 mi. north of Coen (14°00′S, 143°10′E), AMNH 108904, 108905.

57. AUSTRALIA, Queensland. Cape York, Iron Range (12°45′S, 143°15′E), AMNH 154427, 154428.

58. AUSTRALIA, Queensland. Cape York, Upper Peach River, Bonanza Creek (13°45′S, 143°20′E), Shepheard’s Battery site, 800 m, AMNH 154437–154440, 154503, 155086, 155087.

59. IRIAN JAYA. Mimika River, Parimau (4°31′S, 136°36′E), 250 ft: BMNH 11.11.11.93.

60. PAPUA NEW GUINEA, Western Province. Oriomo River: Dogwa (8°53′S, 143°04′E), AMNH 104400, 104401, 104405, 104406, 104477, 104674–104676, 104848, 104849; Oriomo River (9°03′S, 143°10′E), BBM NG-29401.

61. PAPUA NEW GUINEA, Western Province. Fly River: 5 mi below Palmer Junction (5°54′S, 141°33′E), AMNH 105210.

62. PAPUA NEW GUINEA, Western Province. Fly River: 1 mi below the mouth of the Black River (5°38′S, 141°48′E), AMNH 105209.

63. PAPUA NEW GUINEA, Southern Highlands Province. Mount Bosavi (= Mount Leonard Murray: 6°35′S, 142°52′E): north-northwest slopes, 700 m, BBM NG-103050, 103166.