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## Taxonomic Notes on Specimens of the Marsupials *Pseudocheirus schlegelii* and *P. forbesi* (Diprotodontia, Pseudocheiridae) in The American Museum of Natural History

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### ABSTRACT

The rare phalanger, *Pseudocheirus schlegelii*, known only by the holotype obtained from the Arfak Mountains in the Vogelkop region of New Guinea, is now represented by a second specimen in the collection of the American Museum of Natural History. We record our identification and explain its importance in understanding the species integrity of *P. schlegelii*.

American Museum specimens of *Pseudocheirus forbesi* represent a complex that is highly variable in body size as well as pelage color and pattern. The material can be separated into three distinct groups, each diagnosed by a combination of body size and chromatic traits, and each occupying a

discrete geographic region of mainland New Guinea. We document this variation and discuss its significance in the context of understanding whether the *forbesi* complex consists of several species, or represents diagnosable geographic units within a single species ranging from the southeastern highlands to the Vogelkop region. Alternative hypotheses are proposed that, when tested, may offer insights into the real number of species endemic to New Guinea. Documenting this diversity is critical to understanding the evolutionary history of mammals, especially the spectacular marsupial fauna, within the New Guinea region.

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## INTRODUCTION

From 1933 to 1964, the American Museum of Natural History accumulated a large research collection of marsupials from New Guinea. These were obtained by members of the Department of Mammalogy and invited participants from other institutions during seven major expeditions to that island continent sponsored by the late Richard Archbold. This collection has been an important primary source of information for study of New Guinea marsupial taxonomy and evolution. Initial publications reporting results of that research appeared in the 1940s (see Tate, 1937, 1945, 1948a, 1948b, and his other papers cited in those reports), continued sporadically in the next few decades (Van Deusen, 1957, for example) and proliferated in the 1980s and start of the 1990s, signaling renewed interest and critical inquiry into marsupial evolution and biology (some examples are Van Dyck, 1980; Archer, 1981; Groves, 1982; reports in the volumes edited by Archer, 1982, 1987; Menzies and Pernetta, 1986; Springer and Woodburne, 1989; contributions in the volume edited by Seebeck et al., 1990; Flannery, 1990; Menzies, 1991).

This resurgence of research focusing on marsupial distributions, biology, and phylogeny during the last decade coincides with our efforts during approximately that same period to recurate the large collection of marsupials from New Guinea and Australia. Our aims are to correctly identify the specimens (using the most reliable published taxonomic revisions or results of our own primary investigations derived directly from the specimens), to provide safe storage, and to improve access to the collections so they can continue to be utilized by qualified researchers.

From time to time we plan to document some of our observations noted during the recuration. The results will contribute new information about significant aspects of the systematics and geographic ranges of marsupials in the New Guinea and Australian regions, and fresh insights into the patterns of species distributions and possible explanations for them. The present report is the first of the intended series.

Tim Flannery, Tom Griffiths, Colin Groves, Mary Ellen Holden, and Karl Koopman diverted energies from their own research to read the manuscript and provide us with critical and helpful evaluations. Peter Goldberg's usual fine work is reflected in the figures.

*PSEUDOCHEIRUS SCHLEGELII*

In 1884, the systematics of *Pseudocheirus* was summarized by Jentink in a short note with this beginning: "*Pseudocheirus* is a well-defined genus of Phalangers, which, up to this time, embraced three species: *cookii*, *bernsteinii*, and *albertisii*" (p. 109). He went on to discuss the status of two other proposed species, *P. viverrinus* and *P. lanuginosus*, arguing that neither one represented a distinct species but were reflections of variation in pelage coloration and skull morphology of *P. cookii*. In modern view, *cookii* is used to designate a subspecies of the common ringtail opossum, *P. peregrinus*, which occurs in a swath along eastern Australia from Cape York in the north to Kangaroo Island in the south (McKay, 1983: 126).

Jentink continued by briefly describing attributes of the two other species he thought to be valid, *bernsteinii* and *albertisii*. The name *bernsteinii* currently identifies a subspecies of lowland ringtail, *Pseudocheirus canescens*, from the Vogelkop Peninsula of western New Guinea (Flannery, 1990: 166); *canescens*, according to Flannery, "is widespread throughout lowland New Guinea, but it seems to be rare or uncommon over most of its range."

*Pseudocheirus albertisii*, which Jentink recognized and knew only from the Arfak Mountains, is appreciated today as a species of *Pseudocheirops* and a distinctive component of the ringtail fauna endemic to New Guinea. Flannery (1990: 160) noted that it has one of the most unusual geographic ranges of any ringtail, being found only in mossy forest above 1000 m in widely separated regions: the Arfak Mountains of the Vogelkop Peninsula, the Weyland Range, Japen Island, and the North Coast Ranges. For Flannery (p. 160), the "morphological uni-

formity of the species is truly astounding when one considers that the isolation of some populations must have occurred hundreds of thousands if not millions of years ago."

After enumerating characteristics of these recognizable species of *Pseudocheirus*, Jentink (1884: 110) continued:

To these three very good species I have to add a fourth, which is as well characterised as they are. I propose to call it *Pseudocheirus schlegelii* in remembrance of our regretted late Director. This pretty species externally agrees exactly with *Ps. bernsteinii* in all its proportions, and is of the same size. There are only a few differences in color, viz: the head is darker colored and there is no dark stripe on the head; moreover at the base of the ears a light patch is followed by a darker one. Of more significance however are the differences in form of the skull and dentition. The form of the skull calls to mind that part in *Ps. cookii* and *albertisii*; the palate ends close to the last molar and not at some distance behind it as is the case in *Ps. bernsteinii*, moreover all the teeth are stouter (as in *cookii* and *albertisii*) and not so weak as in *bernsteinii*. The length of the upper molar series (with the exception however of the first premolar, which is placed at a certain distance from the other molars in *Ps. bernsteinii*, whereas it is crowded together with the other molars in *Ps. schlegelii*), in the skull of the type-specimen of *Ps. bernsteinii* measures 10 m.m., in the lower jaw the molar series measures 10 m.m., whereas the same parts in a skull of *Ps. schlegelii* of the same size measure respectively 13 and 13 m.m.

The type specimen of *P. schlegelii*, now registered as 13388 in the collection of the National Natuurhistorisch Museum (Leiden), is an adult male and came from the Arfak Mountains in the Vogelkop region of western New Guinea. Through the years several additional specimens were identified as Arfak ringtails, but all of them proved to be samples of other species and the holotype of *P. schlegelii* remained the only recorded specimen of this distinctive ringtail (Husson, 1964: 559; Flannery, 1990: 169).

We have completed our recuration of the Pseudocheiridae stored in the American Museum of Natural History (AMNH) and have examined and reidentified series of *Pseudocheirops albertisii*, *P. corinnae*, and *P. cupreus* as well as *Pseudocheirus canescens*, *P. caroli*, *P. forbesi*, *P. lewisi*, and *P. mayeri*, from New Guinea; and *Pseudocheirus herbertensis* and *P. peregrinus*, *Pseudocheirops dahli*, and *Hemibelideus lemuroides* from

Australia. Left until last in our study was a mounted ringtail labeled only as *Pseudocheirus*, without any locality data associated with it, and unreferable to any of the other series from either New Guinea or Australia in our collection. To our surprise, its characteristics match those described for *P. schlegelii*, and the mount proves to be the second known museum specimen of this species.

The specimen (AMNH 864) is an adult mounted in the position shown in figure 1. We could not determine its sex. The skull is in the mount and we have not removed it. Length of head and body is 280 mm, length of tail is 266 mm, and length of hind foot (including claw) is 46 mm. We obtained these values by measuring each segment of non-elastic cord that was placed along the ventral surface of the body from nose to anus, from anus to tip of the tail, and from heel to end of the longest digit, including the claw. The head and body length is a gross estimate at best, but tail and hind-foot lengths are more accurate. Length of tail of the holotype of *P. schlegelii* is 250 mm, and length of head and body is estimated to be no longer than 230 mm (Husson, 1964: 560).

Our specimen is somewhat larger than the holotype of *Pseudocheirus schlegelii*, but otherwise could be a twin judged by the close similarity in pelage color and texture, distribution of fur on the tail, and body proportions between AMNH 864 and the holotype. Our evaluation is based on our comparisons of AMNH 864 with samples of all other described species of both *Pseudocheirus* and *Pseudocheirops*, the descriptions of *P. schlegelii* in Jentink (1884) and Husson (1964), and the color plate of the holotype provided by Flannery (1990: 169). The woolly dorsal coat is orange to orange-buff over the head and sides of the body and legs, but is darker over the back—a rusty hue flecked with white, which results from the darker orange-brown hairs that are tipped with white; the same effect is also clearly evident in Flannery's color plate of the holotype of *P. schlegelii*. The bright upperparts give way to a pale buffy orange ventral coat that is broken by a whitish throat and neck and a white patch on the chest. The woolly body fur extends along the tail for about two-thirds of its length, gradually becoming shorter until it is only a pu-



Fig. 1. *Pseudocheirus schlegelii*, AMNH 864.

bescent mantle over the dorsal distal third, a pattern similar to that found in the holotype, as described by Husson (1964).

Coat color of AMNH 864 and the holotype of *P. schlegelii* may have altered somewhat

over the years but it lacks the straw-brown hue so characteristic of bleached coats on mounts exposed too long to light, and the present hues are closely similar to the rich orange characterizing the face and front legs

of *P. forbesi* and the buffy orange on the face and over the underparts of *P. canescens*. A "pretty species" was Jentink's (1884: 110) reaction to *P. schlegelii*, which to him was very similar to *P. canescens* (called *bernsteinii* by Jentink), differing only slightly in color and pattern. We suspect that fresh material would exhibit rich orange-brown fur with backs somewhat darker than AMNH 864 and the holotype of *P. schlegelii*, and buffy orange venters.

Because we did not extract the skull, we can report only that the outline of the upper jaw is typical of that characterizing species of *Pseudocheirus* and not those in *Pseudocheirops*. We have not seen the skull from the holotype of *P. schlegelii*, but we have photographs of it made by George H. H. Tate, and from these prints can see that the premaxillary-maxillary outline has the *Pseudocheirus* conformation. In ventral view, the dental arcade between anterior incisor and premolars is slightly concave in species of *Pseudocheirops*, often pinched in just behind the large front incisor. The same margin in the upper jaw of all species of *Pseudocheirus* forms a gentle unaltered curve. This distinction between the two genera can be seen in Flannery's (1990: 401) illustration of ringtail skulls.

In the past, specimens of *Pseudocheirus mayeri* and *P. forbesi* have been misidentified as *P. schlegelii* (Husson, 1964), and the coat color of *P. mayeri* is said to be very similar to that of the Arfak ringtail (Husson, 1964; Flannery, 1990). To us, the pelage coloration of *P. schlegelii* is more like that of *P. canescens* and the eastern and central New Guinea populations of *P. forbesi* than that of *P. mayeri*. The small-bodied *P. mayeri* has an even dark brown coat that lacks the rich ochraceous hues seen in particular body regions of *P. forbesi* and *P. canescens*, and the frosting over the back caused by the white or pale buff hair tips. Those two species have distinctive facial patterns and body stripes not present in *P. schlegelii*, but are otherwise characterized by grayish brown to orange-brown fur, and orange or buffy patterns on the head, underparts, and legs. This vivid chromatic characteristic is beautifully displayed in Flannery's (1990: 167) color plate of *P. forbesi*. It may be noteworthy that when discussing *P.*

*schlegelii* in his review of *Pseudocheirus*, Tate (1945: 13) suggested that its "true relationships seem to be with the *forbesi* group, or perhaps it is annectant between that and the *canescens-avarus* group."

Of all the species of *Pseudocheirus* known from New Guinea, we compared AMNH 864 most closely with specimens of *P. forbesi*, the painted ringtail. Examples of *P. canescens* are generally smaller than AMNH 864 and the holotype of *P. schlegelii*, and all the specimens of *P. mayeri* we have studied are very much smaller (see the measurements provided by Husson, 1964, and Flannery, 1990). In contrast, specimens of the painted ringtail from the Huon Peninsula and central region of New Guinea are slightly larger in body size than AMNH 864 (see the measurement values listed in table 1). Our specimen of *P. schlegelii*, as well as the holotype, lacks the facial pattern of *P. forbesi* (orange head broken by a dorsal brown or blackish stripe, and a blackish strip extending from the muzzle along the bottom of the cheeks to and surrounding the pinna), and the dorsal brown or blackish stripe along the back that is so characteristic of the specimens we have examined.

Specimens from populations of *Pseudocheirus forbesi* from eastern New Guinea and the Vogelkop are similar in body size to AMNH 864 (see values listed in table 1). The sample from the Vogelkop was collected in the Arfak Mountains where the type of *P. forbesi lewisi* is from (Dollman, 1930). Judging from Dollman's (1930: pl. III) color plate and AMNH 100886, our adult from the Arfak Mountains, the population in the Arfaks is grayish brown, without an orange head, and only tinges of buff on the muzzle, cheeks, and front legs. The dorsal strip along the back is present but diffuse along the margins and inconspicuous. The wide but indistinct mid-dorsal stripe and subdued facial markings of this gray animal contrast starkly with the beautiful unpatterned orange-buff coat of AMNH 864 and its rusty back flecked with white.

We confidently identify AMNH 864 as the second recorded specimen of *Pseudocheirus schlegelii*. This assignment of scientific name to specimen is important because it corroborates the existence of a highly distinctive

species of *Pseudocheirus* and dispels the possibility that the startling chromatic brilliance of the holotype, which prompted Jentink's accolade of "pretty species," is an aberration.

Unfortunately, information concerning the origin of AMNH 864 has been lost. The mount was part of Verreaux's collection that was acquired by the American Museum during the 1880s. The only information associated with it is Verreaux's catalog number, 1230. We suspect, however, that the animal was trapped in the Vogelkop and probably came from the Arfak Mountains. That region was the source of most New Guinea birds and mammals that found their way into the hands of Dutch animal dealers in the 19th century. The holotype of *P. schlegelii* itself was such a specimen; it "was procured (for 10 guilders) on 29 April 1879 from the dealer G. A. Frank, Sr. of Amsterdam" (Husson, 1964: 559).

#### *PSEUDOCHEIRUS FORBESI*

The collection in the American Museum contains series of *Pseudocheirus* that are characterized by morphological, color, and geographical attributes fitting the current definition of *P. forbesi*, the painted ringtail, which is an arboreal herbivore. The specimens exhibit considerable variation in body size as well as fur coloration and pattern that is correlated with particular geographic regions of New Guinea. Recognizing this variation, most workers (Tate, 1945; Laurie and Hill, 1954) have split *P. forbesi* into four subspecies: *P. f. forbesi* ranging from 1000 to 6500 ft in Papua N.G., *P. f. larvatus* from northeastern New Guinea, *P. f. longipilis* from 6500 to 8000 ft throughout the Central Cordillera of Papua N.G., and *P. f. lewisi* from the Vogelkop.

Flannery (1990) also offered this traditional subspecific treatment in his account of the painted ringtail, but to him these divisions were tentative because the subspecies needed careful revision "as there is considerable geographic variation in the species. Animals from eastern New Guinea are less brightly coloured, with subdued facial markings, and the tail and body are similarly coloured. In far western animals, the tail is black, contrasting greatly with the brown body, and the face is strikingly marked in black and orange" (pp.

167–168). One of Flannery's contacts told him there are two kinds of painted ringtails, "a smaller high-altitude one and a larger mid-altitude form." But, wrote Flannery, "whether these forms have any biological reality, and whether they represent any of the named subspecies if they do, remains to be confirmed" (p. 168).

We have been able to sort the American Museum specimens into three groups; two generally conform with the geographic ranges of *lewisi* and *larvatus*, and the third is concordant with the combined distributions of *forbesi* and *longipilis*. We discuss these sets of samples below under the designation of the *forbesi*, *larvatus*, and *lewisi* groups. Some of the specimens consist of a skin associated with either a skull or full skeleton; many represent trophy material (charred crania and dentaries, sometimes associated, usually isolated) and remains of owl pellets; a very few examples are preserved in fluid.

#### *forbesi* group

Specimens in this group constitute true *P. forbesi*, and were collected in the eastern highlands of Papua N.G., from Mount Dayman in the east, northwestward along the Owen Stanley Range, to the highlands just south of Wau (Kaindi and Edie Creek) in the west. All were taken within an altitudinal belt between 950 and 2400 m. Localities and specimens are listed below.

PAPUA N.G., Milne Bay Province. Mount Dayman, Maneau Range: north slope, "middle camp," 1540 m, 158969–158975, 159011, 157244–157263; "top camp," 2230 m, 157235–157243, 159008.

PAPUA N.G., Central Province. Owen Stanley Range: Bellavista, 1450 m, 104117–104119, 104681; Matiska, 950 m, 104123, 104129–104136, 104138, 104357–104360; Mount Tafa, eastern slope, 2070 m, 104108, 104150; Mount Tafa, Mave, 2225 m, 104037 (holotype of *Pseudocheirus forbesi longipilis* Tate and Archbold, 1935); Mount Tafa, west slope, 2400 m, 104036.

PAPUA N.G., Morobe Province. Bulldog Road: Edie Creek, 7000 ft, 221603, 221605; 10 mi south of Edie Creek, 7000 ft, 221604. Kaindi: 9000 ft 191082; Mount Kaindi, 2200 m, 191079–191081.

These specimens generally resemble Flannery's (1990: 167) description of *forbesi* from

TABLE 1

**External Measurements (mm) of Adults from the *forbesi*, *larvatus*, and *lewisi* Groups of *Pseudoechirus* from New Guinea<sup>a</sup>**

(The mean plus or minus one standard deviation, number of specimens in parentheses, and ranges are listed.)

Taxon and locality	LHB	LT	LHF
<i>Forbesi</i> group			
Mt. Dayman	249.1 ± 16.74 (19) 209–278	258.6 ± 18.44 (10) 240–272	37.2 ± 1.08 (19) 35–39
Owen Stanley Range	271.6 ± 14.40 (8) 255–301	262.5 ± 18.42 (8) 237–283	35.4 ± 3.62 (8) 30–40
Kaindi Region	246 (1)	253 (1)	39 (1)
<i>Larvatus</i> group			
Kratke Mts.	284.5 ± 18.75 (11) 242–300	296.9 ± 13.13 (11) 275–316	44.4 ± 0.92 (11) 42–45
Mt. Michael–Purosa	277.0 ± 10.05 (7) 258–291	285.7 ± 19.42 (7) 272–327	45.4 ± 1.62 (7) 43–48
Mt. Wilhelm–Mt. Otto	309.4 ± 11.91 (7) 292–328	318.4 ± 18.33 (7) 295–343	48.6 ± 1.62 (7) 46–50
Mt. Hagen–Nondugl	—	—	—
Mt. Rawlinson	292.7 ± 19.35 (3) 281–315	301.3 ± 15.04 (3) 284–311	45.7 ± 0.58 (3) 45–46
Cromwell Mts.	286.7 ± 14.28 (7) 267–310	286.0 ± 15.79 (7) 271–320	45.0 ± 2.00 (7) 43–48
Star Mts.	—	—	—
<i>Lewisi</i> group			
Arfak Mts.			
100886	—	—	—
100885	—	—	—

<sup>a</sup> Abbreviations: LHB, length of head and body; LT, length of tail; LHF, length of hind foot. Values were obtained from tags attached to stuffed study skins.

eastern New Guinea. Upperparts of the body on adults are dark brownish gray in some specimens, brownish buff in others. A wide dark stripe, diffuse along its margins, runs along the back and rump. The head is buffy orange, its brightness accentuated by a black swath extending from the muzzle across the bottom of each cheek to behind the eye and around the top of the ear. Most individuals lack a middorsal head stripe; others have a pale and inconspicuous middorsal brownish streak. The tail fur ranges from brown to dark brown and contrasts with coloration of the body coat but not as strikingly as seen in specimens of the *larvatus* group where the tail fur is blackish brown and the color contrast between body and tail is stunning.

Specimens in the *forbesi* group are also smaller compared with those in the *larvatus* cluster. These differences are most apparent

when adults of comparable age are compared (figs. 2, 3). Among external measurements, for example, length of hind foot does not exceed 40 mm in *forbesi*, while the range is 42–50 mm in *larvatus* (table 1). Differences in body measurements are only evident when comparing specimens of comparable ages because there is so much variation in size that is correlated with age in *Pseudoechirus*, even among animals in full adult pelage. To obtain a more stringent estimate of size differences, one that was not so influenced by age in lengths of body and skull dimensions, and one that would involve a larger proportion of each sample, we tested the differences between crown lengths of various tooththrows: the distance from the anterior margin of the second upper premolar to the back of the fourth molar, from the anterolabial margin of the first upper molar to the posterior mar-

TABLE 2

**Dental Measurements (mm) of Adults from the *forbesi*, *larvatus*, and *lewisi* Groups of *Pseudocheirus* from New Guinea<sup>a</sup>**

(The mean plus or minus one standard deviation, number of specimens in parentheses, and ranges are listed.)

Taxon and locality	PM2-M4 <sup>b</sup>	M1-3	pm1-m4
<i>Forbesi</i> group			
Mt. Dayman	15.5 ± 0.36 (18) 14.9–16.2	9.1 ± 0.24 (18) 8.7–9.5	15.2 ± 0.41 (18) 14.4–16.0
Owen Stanley Range	16.0 ± 0.50 (14) 15.3–17.1	9.4 ± 0.44 (14) 8.8–10.1	15.9 ± 0.44 (14) 15.2–16.7
Kaindi Region	16.1 ± 0.55 (6) 15.4–16.9	9.6 ± 0.28 (6) 9.2–10.0	16.1 ± 0.52 (6) 15.5–16.9
<i>Larvatus</i> group			
Kratke Mts.	17.2 ± 0.35 (11) 16.5–17.6	10.2 ± 0.26 (17) 9.9–10.8	16.7 ± 0.36 (11) 16.1–17.4
Mt. Michael–Purosa	16.9 ± 0.55 (8) 16.0–17.5	10.2 ± 0.32 (9) 9.9–10.7	16.6 ± 0.54 (8) 15.8–17.5
Mt. Wilhelm–Mt. Otto	17.5 ± 0.34 (20) 16.8–18.2	10.3 ± 0.35 (28) 9.7–10.6	17.1 ± 0.20 (10) 16.7–17.3
Mt. Hagen–Nondugl	17.5 ± 0.38 (27) 16.9–18.3	10.4 ± 0.35 (28) 9.7–11.0	17.3 ± 0.40 (26) 16.6–18.2
Mt. Rawlinson	17.6 ± 0.48 (6) 17.1–18.4	10.5 ± 0.22 (8) 10.2–10.8	17.2 ± 0.44 (26) 15.7–18.0
Cromwell Mts.	17.4 ± 0.43 (94) 16.6–19.2	10.3 ± 0.31 (103) 9.5–11.0	17.0 ± 0.33 (84) 16.0–17.7
Star Mts.	15.8 ± 0.36 (3) 15.4–16.1	9.3 ± 0.39 (4) 8.8–9.7	15.7 ± 0.42 (3) 15.2–16.0
<i>Lewisi</i> group			
Arfak Mts.			
100886	15.2	8.5	—
100885	—	9.0	—

<sup>a</sup> Abbreviations: PM2-M4, length of maxillary toothrow from second premolar to fourth molar; M1-3, length of first three molars; pm1-m4, length of mandibular toothrow from first premolar to fourth molar. Values were obtained with dial calipers graduated to tenths of millimeters.

<sup>b</sup> We tested significance of differences between means by *t*-tests. No significant differences (probability greater than .05) existed among means from the three localities within the *forbesi* group, and among means within the *larvatus* group except the sample from the Star Mountains, in which the mean was significantly smaller (probability .01–.001) than means from the other *larvatus* samples. In contrast, means of samples from the *forbesi* group are significantly smaller (probability equals .01–.001 or less) than means from all samples in the *larvatus* group except that from the Star Mountains.

gin of the third upper molar, and from the front edge of the third lower premolar to the back edge of the fourth lower molar. The length of the mandibular row is generally correlated with length of the upper toothrow. We measured length of the first three molars because this is the measurement given by Thomas (1887: 146) for the holotype of *forbesi*. Lengths of toothrows in the *forbesi* samples are significantly shorter than those in samples of *larvatus* (table 2).

This smaller-bodied animal with the subdued facial markings and slightly contrasting body and tail coloration is apparently the only kind of painted ringtail in the region from Edie Creek and Kaindi southeastward to Mount Dayman, although two scientific names have been applied to samples from there. The earliest name of course is *forbesi*, proposed by Thomas (1887: 146) for a specimen collected in the Astrolabe Mountains at 2000 ft. We have not seen the holotype,



but Thomas, in his scanty description, characterized it as lacking the "dark central streak on the head, with a large black patch in front of as well as behind the ear," and indicated the length of the first three molars (we presume they were the uppers because all the rest of the measurements provided are from the cranium only) to be 8.8 mm. The facial pattern is typical of our specimens from southeastern New Guinea, and length of the first three molars falls within the range of variation exhibited by our samples from Mount Dayman and the Owen Stanley Range (table 2). This information from the original description of the holotype combined with the morphological and chromatic traits of our series leads us to identify our samples from southeastern New Guinea as *Pseudoechirus forbesi*.

Tate and Archbold (1935: 4) proposed *longipilis* as a subspecies of *P. forbesi*. The holotype was obtained on Mount Tafa at 2225 m, and Tate and Archbold characterized their new form as the "mountain representatives of *Pseudoechirus forbesi* but with long, very dense pelage." They explained that

evidence favoring the recognition of this mountain race of *forbesi* rests upon the type and a second male (topotype, but from 2400 meters) of equal age and possessing similar characters of pelage. Lack of anatomical characters in the skull to accompany the differences in the fur only emphasizes the view that *longipilis* is purely an offshoot of *forbesi* adapted to conditions in the highlands. The two races may intergrade, but the fact that a specimen of typical *forbesi* taken from the eastern slope of Mt. Tafa only a few hundred meters lower than *longipilis* is in no respect intermediate indicates that the latter is likely to be an upland race distinct from the lowland race *forbesi*.

Less than ten years later, when he reviewed the known species of *Pseudoechirus*, Tate (1945) had received no new material of *forbesi* but mentioned that the altitudinal range of the form was apparently from 1600 to 6500 ft. In his account of *P. f. longipilis*, he noted that this subspecies was still known only by the two males from Mount Tafa that were the basis for the original description of *longipilis*, and that the altitudinal range extended from 6500 to 8000 ft. To Tate (1945: 11), the "very dense silky pelage contrasts strongly with that of the series from altitudes lower than 6000 ft."

We have compared the two specimens Tate assigned to *longipilis*, the series upon which he based his contrasts between *forbesi* and *longipilis*, and large series collected subsequent to Tate's tenure at the American Museum. We simply cannot distinguish the two specimens collected on Mount Tafa from specimens in samples obtained elsewhere along the southeastern Cordillera. To our eye, the pelage of the two ringtails from Mount Tafa is slightly longer and feels thicker than that on specimens from lower elevations in the same region—as Tate (1937) noticed—but the difference is slight. We detected no significant contrasts in thickness and texture of pelage between samples from high elevations and lower places in other areas. On Mount Dayman for example, samples from 1540 m are indistinguishable in pelage traits from those collected at 2230 m. Slight differences in fur length and texture do exist among samples, but in our material those contrasts may only reflect different ambient temperatures and not morphologically differentiated populations with discrete geographic ranges.

We do not have samples of *forbesi* from highlands west of those mountains in the Wau area where Edie Creek and Kaindi are located, approximately 146°40'E. The closest sample west of the Wau region is from the Kratke Mountains, 90–100 km away, which are part of the Central Cordillera, but specimens from there have the diagnostic features we associate with the *larvatus* group, which we write about below.

#### *larvatus* group

The name *larvatus* is a combination of the Latin *larva*, one meaning of which is mask, and the suffix *atus*, meaning "having the nature of," that together aptly describe the ringtail from west of the Wau area. So striking is the facial pattern on these animals that both of the other scientific names applied to this group, *capistratus* and *barbatus* (Tate, 1937, 1945), also allude to facial markings. That masked orange-buff head with its prominent middorsal blackish streak set against a rich brownish gray body, buffy orange front legs, and black tail characterize the animals in our collection from highlands in the Huon Pen-

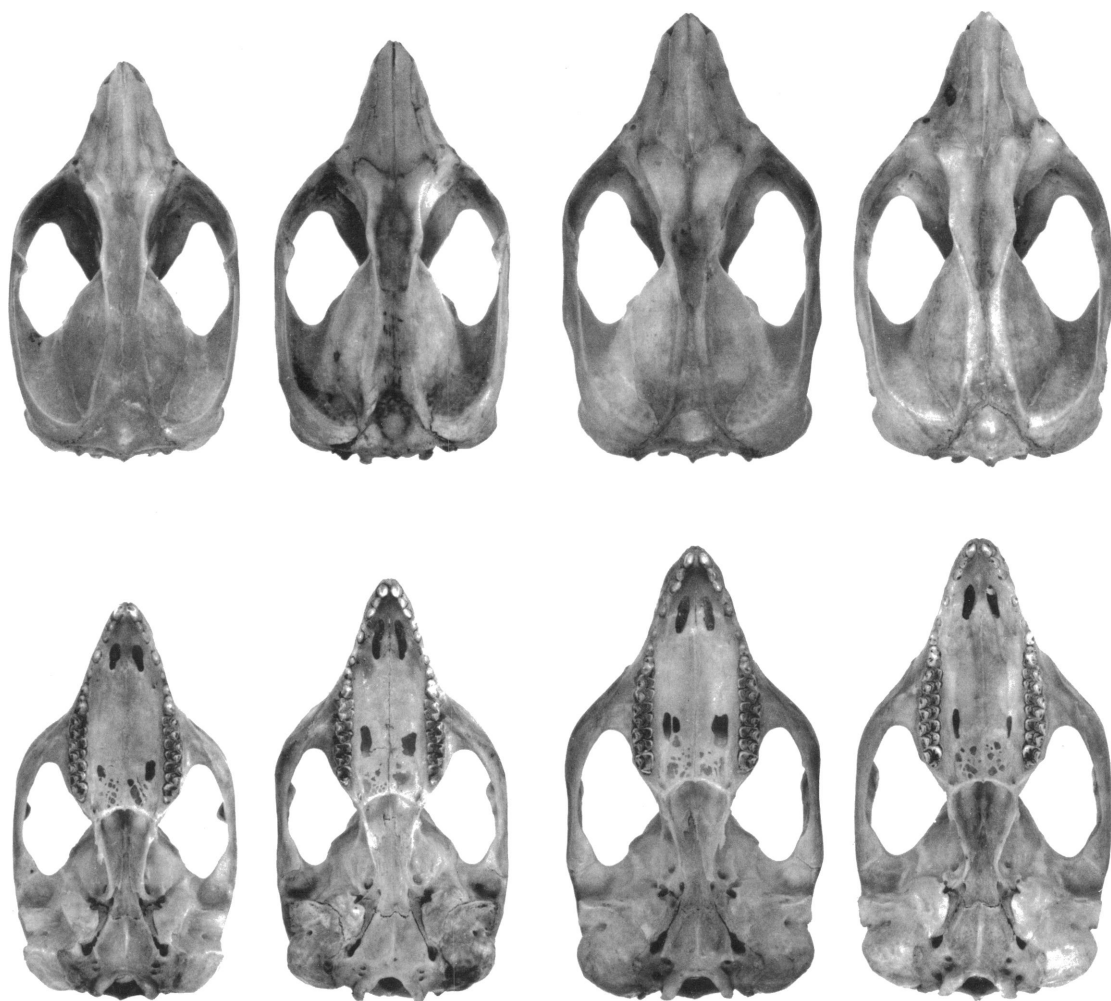


Fig. 2. Dorsal and ventral cranial views ( $\times 1$ ) of *Pseudocheirus* adults from New Guinea. The two on the left represent the *forbesi* group from (left to right) Mount Dayman (AMNH 157235) and Matiska in the Stanley Owen Range (AMNH 104131). The two on the right are members of the *larvatus* group from (left to right) the Kratke Mountains, Central Cordillera (AMNH 191125) and the Cromwell Mountains, Huon Peninsula (AMNH 194778).

insula, the Torricelli Mountains, and the Central Cordillera from the Kratke Mountains in the East to the Star Mountains in the west. These specimens come from an altitudinal range between 1350 and 3000 m. They are listed below.

PAPUA N.G., Eastern Highlands Province. Kratke Mountains: 1385 m, 191119; Arau, 1400 m, 191110–191117, 193152; Kassam, 1350 m, 191118, 191120–191128. Okapa area, Purosa, 1970 m, 191104–191109. Vicinity of Oburra, about 20 mi south of Kainantu, 4000–7000 ft,

221619. Mount Michael: Gono, 2000 m, 191099; northeast slopes, 10,200 ft, 191096–191098, 191100–191103, 193150, 193151. Mount Otto, Collins' Sawmill, 2800 m, 191094, 191095. Mount Wilhelm, Pengagl Creek, 9100 ft, 191084–191089, 191091. Unggai Division, Yaviyufa, above 6000 ft, 195155.

PAPUA N.G., Western Highlands Province. Kumbor Range: 156166. Vicinity of Nondugl: 193171, 156189–156191, 156194, 156195, 156198–156200, 156202, 156203, 156273, 156275, 156279, 156280. Mount Hagen: 155746, 155747, 155752, 155753, 155755,

155758, 155760, 155761, 155986, 155989, 156001, 156005, 156052, 156093, 156094, 156300, 156301, 251030–251036. Mount Wilhelm: 155905, 155906, 155910, 155912, 155913, 155916, 155918, 155919, 155923, 155924, 191093; 11,000 ft, 191083, 191092, 191093, 193148, 193149; Piunde-Aunde Creek, 191090, 193147.

PAPUA N.G., Madang Province, Schrader Mountains: Kaironk Valley region, Jimi Valley, 7900 ft, 251130; Gulkm, upper Aunjang Valley, 7600 ft, 251245–251247.

PAPUA N.G., Morobe Province, Huon Peninsula. Mount Rawlinson, 1370 m: 195973, 195983, 195984–195986, 195996, 195998–195008, 196012, 196013, 196021, 196022; Gang Creek, 4300–4600 ft, 194770–194777, 195159, 195160. Berakwaiyu, 1490 m: 196032. Ogeramang: 196030. Sevia (Siwea), 5000 ft: 79775, 79776, 79784, 99884. Saruwaged Mountains, Iloko area, 1680 m: 196045, 196046, 196054. Cromwell Mountains: Indagen area, 1830 m, 196033–196036 and 196047–196050; Mount Upusenga, above 2100 m, 196394; Mount Ulur Camp, 7800 ft, 251361–251602, 194778–194785, 195157, 195158, 195161–196165.

PAPUA N.G., West Sepik District. Torricelli Mountains, Mount Somora, 3000 ft, 198067.

IRIAN JAYA, Star Mountains, Sibil Valley, 1250 m, 221730, 221731, 221732, 221734, 222047.

If any population of *Pseudocheirus* deserves the common name painted ringtail it is this one, as a glance at Flannery's (1990: 167) color plate of an animal from the Telefomin region will attest. Not only do specimens of *larvatus* differ from those we identify as *forbesi* from the southeastern highlands of New Guinea in their conspicuous facial markings (contrasts also noted by Tate, 1937), richer pelage hues, and greater contrast between color of body and tail fur, but they also average significantly larger in body size (tables 1, 2; figs. 2, 3), quantitative differences we have already explained.

Two other scientific names have been applied to specimens from the highland region where our samples were taken. No data exist, however, indicating that more than one kind of animal occurs in the middle elevations and higher mountains of the Huon Peninsula, Torricelli Mountains, and adjacent regions of the Central Cordillera (also see Flannery and Seri, 1990). This conclusion was originally announced by Tate (1937, 1945) when he arranged *capistratus* and *barbatus* as syn-

onyms of *P. forbesi larvatus*, a treatment followed by subsequent workers (Laurie and Hill, 1954; Flannery, 1990) and endorsed by us.

Although our samples support the hypothesis that only one kind of painted ringtail occurs in the region, they do not present absolute uniformity in body size and color pattern among specimens of a given age group or among samples from different highland areas. On the Huon Peninsula, for example, adults from Mount Ulur in the Cromwell Mountains have dark grayish brown upperparts and the typical striking facial markings. Those from Gang Creek on Mount Rawlinson have buffy brown upperparts and the dorsal head stripe is not as dense or well defined. However, no significant differences in mean length of hind foot (table 1) or mean length of maxillary tooththrow (table 2) exist between the two samples.

Some specimens we assign to *larvatus* approximate examples of *forbesi* in size. One old adult from Mount Rawlinson (AMNH 196004) that is represented by only a dentary has a tooththrow 15.7 mm long, which falls within the range of *forbesi* (table 2) and is the only specimen out of 26 from Mount Rawlinson that is so small. Four young painted ringtails from the Star Mountains agree with *larvatus* in prominence of facial markings but have a paler tail and shorter tooththrows (table 2).

We do not have specimens of painted ringtails from that vast region of Irian Jaya between the Star Mountains and Vogelkop, and a corresponding gap is reflected in Flannery's (1990) map. In this distributional picture, the sample of *lewisi* from the Vogelkop region is isolated from members of the *forbesi* and *larvatus* groups in geography, and also in morphology.

#### *lewisi* group

This taxon is represented in the collection of the American Museum by two specimens from the Arfak Mountains on the Vogelkop Peninsula: an old adult (AMNH 100886) from Siwi, 800 m, and a juvenile (AMNH 100887) collected at Ditschi, 1100 m. Both were reported by Tate (1945: 12) in his review of *Pseudocheirus*.

Dollman (1930: 431) described *lewisi* as a

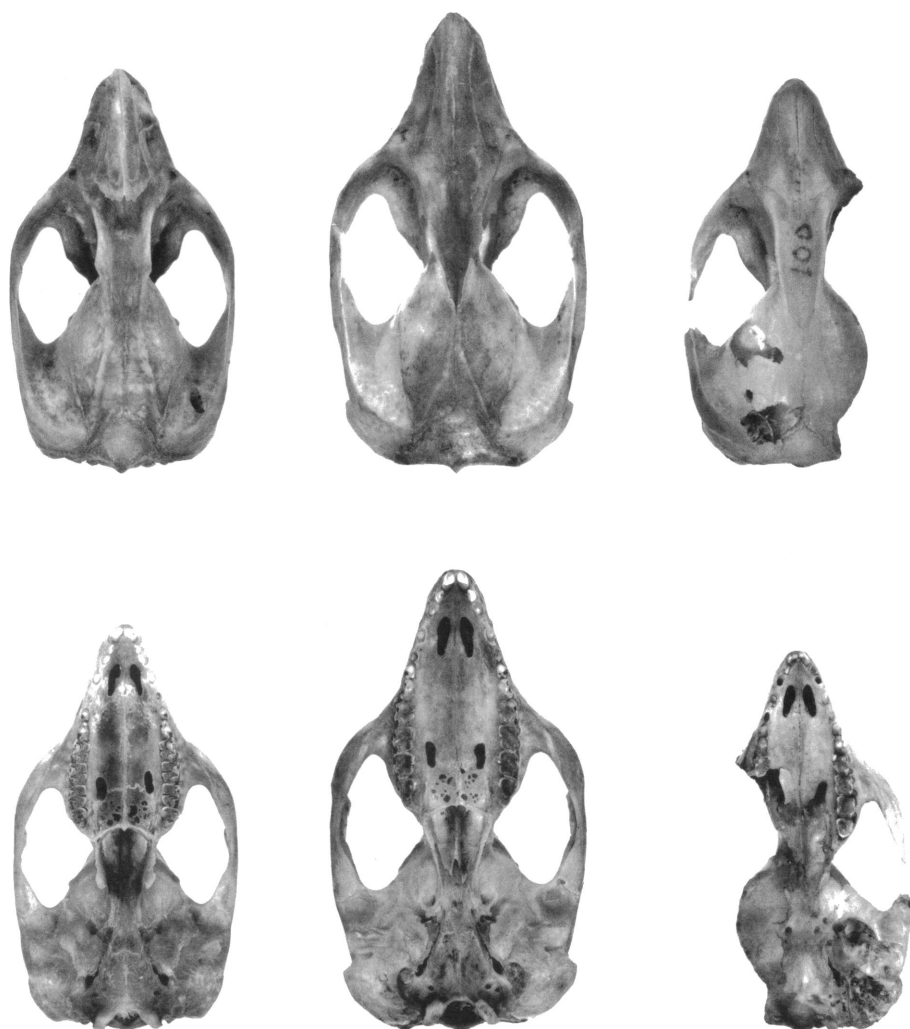


Fig. 3. Dorsal and ventral cranial views ( $\times 1$ ) of *Pseudocheirus* adults. **Left:** AMNH 157250, a member of the *forbesi* group from Mount Dayman in the southeastern arm of New Guinea. **Middle:** AMNH 191084, representing the *larvatus* group from Mount Wilhelm in the Central Cordillera of Papua. **Right:** AMNH 100886, a member of the *lewisi* group from the Arfak Mountains in the Vogelkop region of western New Guinea.

species of *Pseudocheirus* and characterized it as "related to *Pseudochirus forbesi* Thos., but distinguished by the absence of all rufous on the head, and the coat being considerably greyer throughout." Its dimensions, Dollman noted, were similar to those of *forbesi*, not *larvatus*; both these forms were considered separate species when Dollman was working. He also provided a color plate, rendered by himself, of *lewisi*, and the chromatic qualities of the animal portrayed there are very much like our adult from Siwi.

Judged by our material and Dollman's description and color plate, *lewisi* adults are small-bodied (table 2; fig. 3) with grayish brown fur over upperparts of head and body as well as proximal half of tail, pale buffy gray underparts, a very pale tinge of buff along outer margins of the front legs, and no distinct facial markings. The gray over the head is interrupted only by dark brown on the muzzle, a brown patch in front of the ear, and a pale buffy circle around the bottom of each ear. The even grayish brown of the back

is broken by a narrow and inconspicuous brown dorsal stripe. The distal half of the tail is brown instead of grayish.

The juvenile from Ditschi, which is clothed in long and woolly fur and in which the fourth molar had not yet erupted, is brighter than the adult. The face and head is gray and without a dorsal stripe or mask, but the dorsal coat is rich buffy brown and unbroken by any dorsal dark streak. Tone of the ventral coat is similar to that in the adult, and the proximal half of the tail does not contrast with color of the back but the distal half is darker, a pattern also found on the adult.

With such a small sample, we are unable to appreciate the actual range of variation in body size and pelage color and pattern in this ringtail which has only been recorded from the Arfak Mountains. If the specimens available for study are a reliable index of the morphological and chromatic traits of the Arfak population, then that animal is clearly very different from samples of the larger-bodied and strikingly patterned *larvatus*. The sample of *lewisi* resembles those of true *forbesi* in body size (table 2), and in its subdued facial markings, but still lacks the rich hues and buffy orange heads characterizing specimens from the southeastern highlands of eastern New Guinea. Overall, the contrasts between *lewisi* and the other two groups of painted ringtails in pelage coloration and pattern is greater than the distinctions between some species of *Pseudocheirus*, *P. forbesi*, and *P. canescens*, for example.

### Significance

Our purpose here is not to argue for species status for each of the three groups of samples, but to simply note the character variation in some morphological and chromatic traits among samples of the *forbesi* complex in the collection of the American Museum, and reveal how this variation is related to geography. Our brief exposition of variation and localities provides enough information to allow marsupial systematists to test the following alternative hypotheses.

1. The three groups of samples represent three species.
2. Each of the three groups of specimens

reflects a distinctive population (which would be translated into taxonomic arrangement by recognizing each as a subspecies of *P. forbesi*) that is morphologically and geographically diagnosable but not genetically isolated from the other two.

3. Samples of the *forbesi* and *larvatus* clusters represent geographic and morphological variants of one species, but the specimens of *lewisi* are from a population that is genetically incompatible with members of the other two.

The morphological and color characteristics of specimens from highlands above 3000 ft between the Wau region and the Kratke Mountains, 90–100 km apart (see map in fig. 1 of Brass, 1964) can be used to test the integrity of all three hypotheses. Assuming populations of painted ringtails occur in the area and can still be sampled, or that specimens are available from other institutions, examples should demonstrate that *forbesi* and *larvatus* either retain their size and pattern traits in parapatric (either at the same or different elevations) or sympatric contact, or reveal intergrading patterns of variation reflecting some degree of gene exchange.

We note that the characteristics in samples of *larvatus* from mountains on the Huon Peninsula are closely similar to those in series of *larvatus* from the Central Cordillera, yet these highland regions are separated by the Markham and Ramu rivers (see fig. 1 in Brass, 1964, for a good visual contrast between highlands and river valleys). For an animal with a recorded altitudinal distribution that does not extend lower than about 1300 m, the river valleys at 300 m to sea level would appear to form a barrier to distribution and gene exchange. This is not reflected in the samples, at least at the gross level of character-state analyses we employed. By contrast, no significant barrier is evident in the highlands of the Central Cordillera between the Kratke Mountains, where samples of *larvatus* have been obtained, and the Wau region, the most northeasterly area where our samples of *forbesi* were collected. Possibly this observation is significant in the context of falsifying those parts of each hypothesis concerning the *forbesi* and *larvatus* proposals.

Testing the status of the Vogelkop *lewisi* relative to *larvatus* and *forbesi* in each hypothesis is more difficult. Specimens of paint-

ed ringtails from the vast expanse of mountains and coastal forests between the Star Mountains (which straddle the border between Papua N.G. and Irian Jaya) and the Vogelkop region in the far West are not represented in the collection of the American Museum. A similar expanse without specimen records is also indicated on Flannery's (1990: 168) distribution map. If our collections and the locality dots on the map reflect actual distributions of members of the *forbesi*, *larvatus*, and *lewisi* groups on New Guinea, then the painted ringtail is absent from nearly all of the western half of that island continent. The gap may be real because the few regions of Irian Jaya that have been intensely surveyed have not produced specimens of the *forbesi* complex: examples are the expeditions to the Snow Mountains (Archbold et al., 1942), the Wissel Lakes area (the *Pseudocheirus* were reported by Husson, 1964), the Weyland Mountains (Stein, 1933a, 1933b, 1933c), and other regions in what was called Dutch New Guinea (see results reported by Jentink, 1908, and Thomas, 1911, for example). Furthermore, Irian Jaya has received significant survey attention, as is shown by Flannery's (1990: 37) map of all collecting localities for mammals in New Guinea. Some of the major expeditionary efforts, especially the 1938–1939 Archbold Expedition to the Snow Mountains (which included the Hollandia region on the north coast and an altitudinal transect from lowlands along the Idenburg River to high elevations at Lake Habbema and slopes of Mount Wilhelmina) resulted in the acquisition of large series of mammals, including several species of *Pseudocheirus*, but examples of the *forbesi* complex were not among them. Relative to the *forbesi* and *larvatus* groups, the Vogelkop population is distinguished and isolated by its grayish coat that is nearly devoid of facial or body patterns, but also by its small body size compared with *larvatus*, and the great geographic distance between it and *larvatus*, the closest of the other painted ringtail groups. The morphological gap is real and if the distributional hiatus is also a reality and not an accident of sampling, then *lewisi* is clearly now prohibited from gene exchange with *larvatus* by geography; detecting whether potential genic compatibility or isolation exists may

require larger samples or other kinds of data and analyses.

We record two final observations. First, the small, subtly patterned and grayish *lewisi* may represent the primitive condition among populations of ringtails if large size, bright coloration, and striking facial markings as well as marked body and tail contrasts are derived. Determining polarities of such traits in groups of New Guinea marsupials (and other mammals) is important. Such information can be used to test the significance of patterns in the geographic distributions of species and their diagnostic characters, such as the possible centrifugal pattern of speciation for New Guinea tree-kangaroos recently discussed by Groves (1990).

Second, samples of *lewisi* have been recorded from the Arfak Mountains and nowhere else. Among endemic New Guinea mammals, *lewisi* shares such a distinction only with *Pseudocheirus schlegelii*. The only other New Guinea endemic that is apparently restricted to the Vogelkop region, but not to the Arfak Mountains, is the black tree-kangaroo *Dendrolagus ursinus* (Groves, 1982; Flannery, 1990). What is the significance of this pattern? At the other end of New Guinea, the distributional relationships between the *forbesi* and *larvatus* groups resemble the distribution of subspecies of *Dendrolagus dorianus* (Groves, 1982, 1990; Kawai, 1989). The dull-colored subspecies of *Dendrolagus dorianus* (*dorianus*) is found in the southeastern arm of New Guinea, a range approximating that of the *forbesi* group of painted ringtails. The brightly colored subspecies of *D. dorianus* (*notatus*) occurs to the west (but not on the Huon Peninsula) over an area that generally resembles the distribution of the *larvatus* group of *Pseudocheirus*. Do these generally concordant distributions have significance in interpreting the historical evolution of these mammalian groups, and are there other species with similar ranges? Careful study of specimens in museums may hold the answers to these questions.

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