

Leopard-cats, *Prionailurus bengalensis* (Carnivora: Felidae) from Indonesia and the Philippines, with the description of two new subspecies

By C. P. GROVES

Department of Archaeology and Anthropology, Australian National University, Canberra, Australia

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Abstract

Studied was the geographic variation of leopard-cats (*Prionailurus bengalensis*) in Malaysia, Indonesia and the Philippines. Distinct subspecies can be recognised for: Java and Bali; Sumatra; Borneo; Palawan; and Negros. These show unexpected zoogeographic patterns. On the Malay peninsula a probable hybrid population exists.

Introduction

The leopard-cat, *Prionailurus bengalensis* Kerr, 1792, is one of the most widespread species of the family Felidae, from South Asia through East Asia to the Russian Far East, and Southeast Asia to western Indonesia, and the Philippines (NOWELL and JACKSON 1996).

The Malay/Indonesian distribution covers the Malay Peninsula, Sumatra, Borneo, Java, Bali, and offshore islands. Geographic variation in Indonesia has been treated by BRONGERSMA (1935) and SODY (1949). BRONGERSMA (1935) recognised the following subspecies:

P. b. sumatranus (Horsfield, 1821). Sumatra and P. Tebingtinggi; *P. b. javanensis* (Desmarest, 1816). Java and Bali; *P. b. borneoensis* Brongersma, 1935. Borneo.

SODY (1949) recognised these same subspecies, in addition keeping his options open whether the form from P. Tebingtinggi might not also represent a separate subspecies, *P. b. tingia* (Lyon, 1908).

In the Philippines the species is found in Palawan, Calamianes, Panay, Negros, and Cebu. There has never been a comparison of Philippines leopard-cats with those from any other area. SANBORN (1952) recorded several specimens from Palawan and one from Negros, remarking on the variability within Palawan ("two colour phases, a dark gray and a dull brown"), and noting that the Negros skin was "bright red-brown" and "much larger than any from Palawan". RABOR (1977), who called the species *Felis minuta* Temminck, said only that specimens from Negros "possess brighter colors than those from Palawan".

The aim of this study is to review the species in Indonesia, and to provide for the first time a comparative description of Philippines leopard-cats.

Material and methods

147 skins and 100 skulls of Southeast Asian leopard-cats have been studied in the following collections: Museum Zoologicum Bogoriense, Bogor, Indonesia (MZB); Zoological Reference Collection, Singapore (ZRCS); Sarawak Museum, Kuching, Malaysia (SMK); Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands (RML); Instituut voor Taxonomisch Zoologie, Amsterdam, Netherlands (ZMA); Natural History Museum, London, U.K. (BMNH); Field Museum, Chicago, U.S.A. (FMNH).

The skins were compared visually. The following craniodental measurements were taken: Greatest Skull Length; Condylbasal Length; Bizygomatic Breadth; Postorbital Constriction Width; Interorbital Breadth; Bicanine Breadth; Mandible Length; Upper Carnassial (P^4) Length; Lower Carnassial (M_1) Length. The skull measurements were subjected to Discriminant Analysis using SPSS for Windows (site-licensed to the Faculty of Arts, Australian National University).

Results

Pelage

Compared to leopard-cats from India, Burma and the Indochinese region (here treated as nominotypical *P. b. bengalensis*), those from insular/peninsular Southeast Asia (the Sundaic subregion) have a darker ground colour, especially along the median dorsal zone; smaller spots (which are rarely rosette like); and narrower longitudinal stripes on the nape and withers. Skins from Bangkok, Mergui and Tenasserim (including the type of *Felis tenasserimensis* Gray, 1867) resemble more northerly Burmese and Indochinese skins: off-white ground colour, with larger, more rosette-like spots and broader longitudinal stripes.

Within the Sundaic subregion, there are two strikingly different colour groups:

1) Light grey, with very small spots which are often not very clearly expressed. The three spot-lines along the middle of the back do not form complete stripes, and are thin and close together. Java, Bali, and Palawan.

(a) In Java and Bali the grey is pale, often yellow-grey; the two pairs of longitudinal nape-stripes are of equal width, or the outer pair may be slightly broader.

(b) In Palawan the grey is more ochery-toned; the relation between the nape-stripes is as in Borneo.

2) Warm ochery toned, with larger, clear black spots. The three longitudinal spot-lines are usually fused into complete stripes, or nearly so, and thicker, less close together than in Java or Palawan. Sumatra, Borneo and Negros.

(a) In Borneo, the inner pair of nape-stripes is always thinner than the outer, usually markedly so. Occasional individuals are slightly greyer than usual, but do not resemble Javan skins.

(b) In Sumatra, the nape-stripes are of approximately equal width. The colour averages less bright than in Borneo, and the spots are somewhat smaller.

(c) Negros skins resemble those from Borneo, but are darker.

This neat geographic division is spoiled to some degree by skins from the Malay peninsula, which are variable in colour: of the skins in London and Singapore, two are grey like those from Java, four are ochery like Sumatra, and 15 are light fawn like Indo-Burmese skins, while the spots in six of the latter tend towards rosette form. The spots, even if small like those of insular forms, are always "shaded" like other mainland leopard-cats: that is, each spot is lighter (light brown) anteriorly and darker (black or dark brown) posteriorly. The nape-stripes are of equal width; the spot-rows are narrow, less formed, more broken up than in insular specimens.

Table 1. Measurements of *P. bengalensis*

	Negros	Palawan	Mainland	Sumatra	Java	Borneo	Bali
Males							
Greatest skull length							
Mean	88.4	85.2	95.0	89.9	87.5	86.8	83.5
s. d.	1.57	0.97	3.00	3.08	2.95	2.45	2.65
Range	87.0–90.1	84.0–86.7	92.0–98.0	87.0–93.0	86.0–94.0	83.0–90.0	81.0–87.0
n	3	5	3	7	12	8	4
Condylbasal length							
Mean	83.3	77.7	84.0	80.4	80.8	79.4	78.0
s. d.	–	0.68	2.65	3.55	3.77	2.20	2.58
Range	82.0–84.6	77.0–78.4	80.0–85.0	75.0–83.0	77.0–83.0	77.0–82.0	75.0–81.0
n	2	5	3	7	12	8	4
Bizygomatic breadth							
Mean	57.5	54.4	63.7	59.7	56.2	58.3	52.0
s. d.	2.45	2.21	2.08	3.50	2.78	1.44	2.00
Range	55.0–59.9	52.4–58.0	61.0–63.0	55.0–64.0	54.0–60.0	56.0–61.0	50.0–57.0
n	3	5	3	7	12	8	4
Females							
Greatest skull length							
Mean	82.1	79.8	89.7	87.0	82.9	85.1	–
s. d.	–	–	2.73	2.16	3.55	2.97	–
Range	81.1–83.0	–	85.0–92.0	85.0–90.0	76.0–88.0	84.0–88.0	–
n	2	1	6	4	9	7	–
Condylbasal length							
Mean	77.8	72.5	81.8	78.3	72.8	77.1	–
s. d.	–	–	1.60	2.63	4.15	2.69	–
Range	76.5–78.0	–	79.0–82.0	76.0–82.0	66.0–80.0	74.0–82.0	–
n	2	1	6	4	9	6	–
Bizygomatic breadth							
Mean	53.6	49.1	60.2	56.9	51.9	56.6	–
s. d.	–	–	0.75	2.72	2.88	2.97	–
Range	53.2–54.0	–	59.0–61.0	54.0–64.0	49.0–58.0	55.0–62.5	–
n	2	1	6	4	9	8	–
Sexes combined							
P ⁴ length							
Mean	10.0	9.4	9.9	9.8	9.5	9.8	–
s. d.	0.17	0.31	0.35	0.41	0.47	0.71	–
Range	9.9–10.2	9.0–9.9	9.0–10.0	9.0–10.0	9.0–10.0	9.0–11.0	–
n	4	6	8	6	11	8	–
Tail as percent of Head + Body length							
Mean	43.5	48.8	50.1	40.4	46.0	47.0	–
s. d.	–	7.54	5.21	4.43	4.29	4.92	–
Range	–	44–60	44–56	36–47	37–55	40–55	–
n	1	4	7	4	22	11	–

Tail length

Tails are shorter in insular leopard-cats than in those from the mainland, and vary among themselves (Tab. 1). The tail is especially short in the Sumatran and Negros forms, longer in the others; in the Palawan form, it is nearly as long as in those from the mainland.

Skulls and teeth

Skull size of males decreases in the sequence Mainland–Sumatra–Negros–Java–Borneo–Bali–Palawan, with overlaps between the ranges of all but the smallest and largest taxa (Tab. 1). In females the sequence is different, so that sexual size difference, as indicated by mean condylobasal length in female as a percentage of that in male, is much more in Java (90.1%) and Palawan (93.3% – but only one female skull available) than in other populations (97.1–97.4% in Mainland, Sumatra and Borneo, 98.6% in Negros).

The skull is narrower in Java and Palawan than in other populations. The two Philippine forms have much less development of cranial crests, so that Greatest Skull Length (prosthion to opisthocranion) is comparatively less compared to condylobasal length than in the Indonesian and mainland forms; this is especially marked in Negros.

The carnassials (represented in table 1 by P^4 , for which larger samples are available than for M_1) average smaller in Java and Palawan than in other populations.

Discriminant Analysis using all adult and late-juvenile crania (Fig. 1) separates four groups: Negros, Palawan, Java, and Sumatra/Borneo/Mainland. Palawan is intermediate between Negros and the two other clusters. Function 1, on the abscissa, accounts for 48.3% of the total variance; it does not correlate strongly with any of the original variables, but weakly contrasts mandible length, condylobasal length and interorbital breadth with post-orbital breadth. Function 2, along the ordinate, accounts for 29.1% of the variance; it is largely a size function, emphasising breadth measures more than length. Restricting the analysis to adults only reduced the dataset too much to achieve meaningful results.

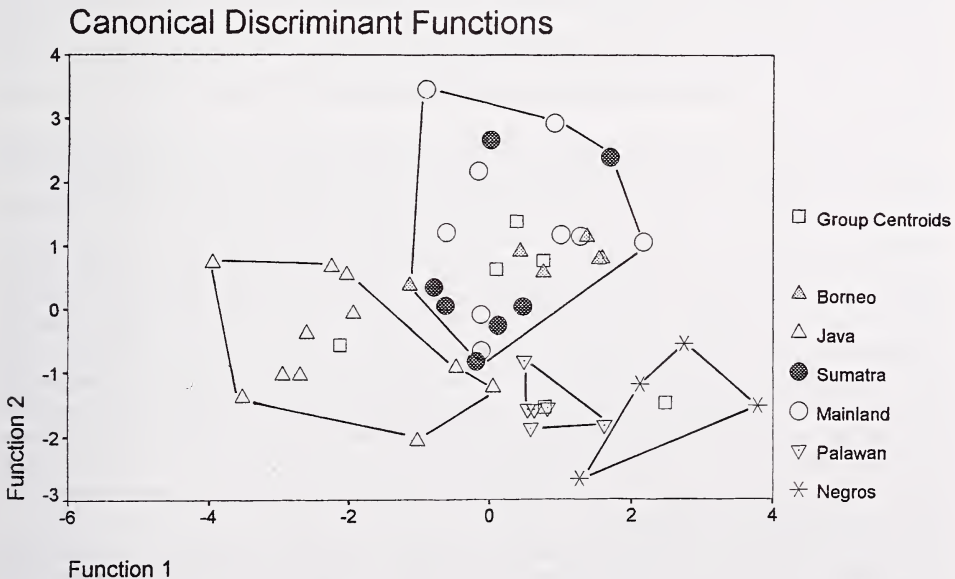


Fig. 1. Plot of First and Second Discriminant Functions for skull and tooth measurements of Southeast Asian leopard cats (*Prionailurus bengalensis*).

Thus, the insular leopard-cats divide into two phenetic groups on several characters: colour and pattern, sexual dimorphism, skull shape, and upper carnassial size. In Java and Palawan colour is greyer, the spotted pattern is less marked, male-female size difference is more marked, skulls are narrower, and P^4 is shorter. In Sumatra, Borneo and Negros colour is more ochery, spots are blacker, there is less size difference between the sexes, skulls are broader, and the upper carnassial is longer. The total-evidence approach to cranial morphology, however, shows that the Negros cranium is the most distinctive, and the Palawan form is intermediate between Negros and the two different (Java, Sumatra-Borneo-Mainland) western Sundaland forms.

Discussion

The relationships of each of the insular forms now need to be discussed.

(a) Philippines. There is an interesting zoogeographical problem. HEANEY (1985, 1986) has surveyed the zoogeographic affinities of the Philippines; only in the case of Palawan is there evidence for a former land-bridge to Sundaland (= the shallow-water islands of western Indonesia), and Palawan does possess a distinctly Sundaic mammalian fauna, whereas Mindanao and Luzon show high endemism. The fauna of Negros is very poorly known; only 13 mammal species other than bats are recorded. On this admittedly limited evidence, faunal similarity indices cluster Negros with the Philippine (non-Palawan) Faunal Province, specifically with Luzon and Mindoro.

On the other hand there is emerging evidence that Negros, together with Cebu and Panay which lie on the same shallow-water shelf, does have its own endemic suite of species, including a deer (*Cervus alfredi*), a pig (*Sus cebifrons*), a shrew (*Crocidura negrina*) and a cloud-rat (*Crateromys heaneyi*). But none of these species, unlike the leopard-cat, has a direct Sundaland affinity; rather, they are all either vicariants of Luzon-Mindanao taxa, or else primitive relicts which have presumably been replaced elsewhere in the Philippines by later invaders from outside the region. The leopard-cat in Negros appears to be unique in having no conspecifics (no close competitors) in the Luzon and Mindanao faunal regions; either the species once inhabited these other islands and has gone extinct there, or else it has dispersed directly, overwater, from Palawan or from Borneo (via the Sulu chain?). The cranial evidence suggests that Palawan is the source; the pelage data would favour Borneo.

(b) Borneo and Sumatra. Consistent, if minor, differences exist between the Bornean and Sumatran leopard-cats. They appear to be correctly assigned to distinct subspecies.

(c) Bali. Limited evidence suggests that the leopard-cat of Bali differs on average only from that of Java. Subspecific distinction is probably not warranted.

(d) Mainland. The leopard-cat of the Malay peninsular is closely similar to that of the Indo-Chinese region. This differs from most mammals: a Malay-Sumatran affinity is more usual (reviewed by LEKAGUL and MCNEELY 1977). A few facts, such as the occurrence in the Malay peninsula of individuals with a more Sumatran-like colouring, suggest the former presence of a common Sundaic form there, since swamped by gene-flow from the north. Despite average differences, it is not possible to distinguish the peninsular leopard-cat from the common mainland Southeast Asian one; whether this in turn is distinct from the Indian subspecies, nominotypical *bengalensis*, is outside the scope of this study. The "Mainland" sample of leopard-cat studied for comparative purposes for this study will be designated simply "cf. *bengalensis*".

(e) Java. The grey, rather pale-spotted pelage of the Java population is duplicated only in Palawan; nowhere else in the entire range of the species does a comparable morph occur. On the other hand it is not dissimilar to the pelage of congeneric *Prionailurus rubiginosus* and *P. viverrinus* (though in the latter the markings are more nearly

black). The difference between the grey and ochery morphs could actually be genetically very simple; the grey morph in some respects recalls the chinchilla mutation at the C locus which reduces yellow pigmentation and occurs in several species of felids (ROBINSON 1978); the difference in the present instance would be that it has become fixed (independently?) in two different *P. bengalensis* populations, and in two entire species of the same genus. This hypothesis proposes that a chinchilla mutation is at the base of these pelage features, not that it is responsible for them in their entirety.

In conclusion, the following subspecies may be recognised in the insular and peninsular Southeast Asian region (Malaysia, Indonesia, Philippines):

***Prionailurus bengalensis javanensis* (Desmarest, 1816)**

Distribution: Java and Bali.

Specimens seen: Skins: Java: BMNH 27; ZRCS 1; MZB 26; Bali: BMNH 5. Skulls: Java: MZB 11; BMNH 6; RML 8; Bali: BMNH 4.

Diagnosis: Grey with very small, longitudinally elongated, poorly expressed spots; nape-stripes of equal width, or outer pair slightly broader; median dorsal spot-lines very close together. White midfacial streak extends from forehead to muzzle; white cheek zone not clearly demarcated with black stripes; throat collars poorly marked. Tail length averaging 46% of head plus body; tail spots especially vaguely marked. Skull length in males equivalent to other Indonesian subspecies, but that of females much smaller, hence unusually sexually dimorphic (female condylobasal length only 90% that of male); skull relatively narrow; upper carnassial averaging shorter than other Indonesian forms.

Notes: Colour in Java is light grey or grey-yellow with just a hint of tawny, occasionally with pinky-ochery tones. The spots tend to be reddish-toned. Balinese specimens are even greyer, spots even less distinct, than the average from Java, though not outside the Java range; male skull averaging smaller, but ranges and standard deviation limits overlap.

***Prionailurus bengalensis sumatranus* Horsfield, 1821**

Distribution: Sumatra, including the offshore island of Tebingtinggi.

Specimens seen: Skins: BMNH 4, including the type of *sumatrana*; ZRCS 2; MZB 8. Skulls: MZB 3; ZRCS 3; RML 2; ZMA 3.

Diagnosis: Less bright ochery than *borneoensis*, with smaller spots; nape stripes of approximately equal width; dorsal spot-rows close together, tend to coalesce into continuous but thin longitudinal stripes. Tail short, averaging 40.4% of head plus body. Underparts creamy-white; well-spotted on chest, upper belly, and inner aspect of hindlegs; inner surface of forelegs less well-spotted, but always two dark bands across humerus. White mid-facial streak extends well onto muzzle. Dark cheek stripes, demarcating white zone of cheeks above and below, very thick; lower stripes turn medially and form a collar across upper throat, with a second collar behind this. Skull broader than *javanensis*; less sexually dimorphic (female condylobasal length 97.4% of male; upper carnassial averaging longer).

Notes: BRONGERSMA (1935) regarded *Felis tingia* Lyon, 1908, from P. Tebingtinggi, as a probable synonym of *sumatranus*. At the same time he described a skull and "several" skins (the latter from photographs) from Nias, considering it possible that they could represent a separate subspecies; since that date, however, no further evidence of this putative taxon has become available.

***Prionailurus bengalensis borneoensis* Brongersma, 1935**

Distribution: Borneo.

Specimens seen: Skins: BMNH 11; ZRCS 1; SMK 21; MZB 3. Skulls: MZB 2; ZRCS 6; SMK 16; RML 1; BMNH 7.

Diagnosis: Rich ochery colour, darkened in middorsal region, with comparatively large, clearly marked black spots; inner pair of nape-stripes always thinner than outer, usually markedly so; median dorsal spot-lines joined into stripes, completely or nearly so. Underparts, throat, facial markings similar to *sumatrana*. Tail averaging 47% of head plus body. Skull as *sumatrana*, but slightly smaller.

Notes: Two skins in the Sarawak Museum are noticeably greyer than any other, and a few others tend towards a greyish tone; but colour is never as grey as in *javanensis*, and the spots are larger and blacker than the latter.

BRONGERSMA (1935) discussed the name *Felis undata* Desmarest, often previously used for this subspecies. He concluded that, the type being lost and the description well-nigh indeterminable (it may even refer to a feral domestic cat), this name cannot be used for any taxon of leopard-cat.

***Prionailurus bengalensis cf. bengalensis* (Kerr, 1792)**

Distribution: Mainland Southeast Asia, from the Malay peninsula north at least into Burma and the Indochinese peninsula.

Specimens seen: Skins: BMNH 9; ZRCS 12. Skulls: ZRCS 9; BMNH 3.

Localities: Specimens examined for this study are from Seremban, Negri Sembilan; Tebing Tingii, Kelantan (N.B. this is not P. Tebingtinggi in Sumatra); Johore; K. Kangsar, Perak; Melaka; Selitar.

Diagnosis: Colour usually light fawn, even creamy-toned, on flanks, somewhat contrasting with tawny tone in mid-dorsal region; spots often comparatively large, though rarely as large as *bengalensis*, but always of "shaded" type; nape-stripes of equal width or the inner pair somewhat thinner than the outer; dorsal spot-rows narrow, ill-formed, tend to be broken up. Tail length about half that of head and body. Skull larger than insular subspecies, and not very sexually dimorphic (female condylobasal length 97.4% of male).

Notes: Colour is more variable than in the insular forms; it is usually as above, but occasional specimens are grey as *javanensis* or ochery as *sumatrana*. As is common in Indochinese populations of *bengalensis*, both large-spotted and small-spotted forms occur, though the spots are rarely as large or rosette-like as in Indochina, while the stripes are less broad and the colour is less pale. The spots in the small-spotted type resemble *sumatrana* except that they are "shaded" like the large-spotted type: that is, they are light brown anteriorly, becoming dark brown posteriorly.

As suggested above, the most plausible interpretation of this variability would seem to be that gene-flow from further north in Southeast Asia has overwhelmed, but not yet entirely submerged, a population formerly of Sundaic affinity.

***Prionailurus bengalensis rabori* new subspecies**

Type: FMNH 74326, adult female, skin and skull, from Canlaon, Negros Oriental. Collected by D. S. RABOR, 24th April 1953.

Distribution: Negros; presumably also Cebu and Panay, whence the species has been recorded.

Specimens seen: Skins: BMNH 2; FMNH 5. Skulls: BMNH 2; FMNH 9.

Diagnosis: Dark ochery to buffy fawn in colour, less bright than *borneoensis* especially in median dorsal region; spots large (but smaller than *borneoensis*), dark; median dorsal spot-rows forming nearly continuous stripes; median nuchal stripes very broad, median pair much narrower than lateral pair, failing to reach shoulders. A single black collar between interramal area and throat (posterior collar missing). White face streak short, does not extend far onto muzzle. Tail more clubby than other insular forms; its length (in a single specimen, the type) 43.5% of head and body. Skull of male averaging larger than Indonesian forms, of female equivalent in size to *sumatrana* and *borneoensis*, but poorly crested in both sexes so that Greatest Length is low compared to Condylbasal Length; skull somewhat narrower than latter two, but not as narrow as *javanensis*. Upper carnassial averaging longer than other insular forms. Measurements of type (in mm): Greatest Skull Length 81.1, Condylbasal Length 76.5, Bizygomatic Breadth 53.2, Postorbital Constriction 23.9, Interorbita Breadth 14.0, Bicanine Breadth 19.6, Mandible Length 52.8, P⁴ length 10.2, M₁ length 6.9; Total Length 396, Tail 120, Hindfoot 15, Ear 17.

Notes: SANBORN (1952) and RABOR (1977) called Philippine leopard-cats *Felis minuta* Temminck, 1825, noting but not formalising differences between cats from Negros and Palawan. As correctly recorded by BRONGERSMA (1935), the syntypes of this species (in the Leiden Museum) are from Java and are examples of *P. b. javanensis*.

Etymology: for the late DIOSCORO S. RABOR, doyen of the Filipino mammalogy (and ornithology) community. Professor RABOR died in 1995, after a long illness. His long and active career has inspired a flourishing school of faunal studies and conservation action in the Philippines, and spawned a new generation of wildlife enthusiasts.

Prionailurus bengalensis heaneyi new subspecies

Type: FMNH 62896, nearly-adult male (with speno-occipital synchondrosis not fully fused), skin, skull and skeleton, from Puerto Princesa, Palawan. Collected by H. HOOGSTRAAL, May 5th, 1947.

Specimens seen: Skins: BMNH 1; FMNH 9. Skulls: BMNH 2; FMNH 3.

Diagnosis: Colour grey-fawn with small, dark brown spots on flanks; inner pair of nape-stripes always thinner than outer, both pairs reaching back to scapular level; dorsal spot-lines usually incomplete, close together, thin. White midfacial streak long, reaching muzzle. Tail long, averaging 48.8% of head and body; only vaguely spotted. Skull small in male, and even more so in female; condylbasal length of single available female only 93.% of male average; skull even narrower than in *javanensis*, though fairly broad across muzzle. Upper carnassial smaller than any other insular subspecies.

Measurement of type (in mm): Greatest Skull Length 85.1, Condylbasal Length 78.4, Bizygomatic Breadth 52.4, Postorbital Constriction 22.1, Interorbita Breadth 12.7, Bicanine Breadth 21.5, Mandible Length 55.0, P⁴ length 9.6, M₁ length 7.3.

Notes: Both SANBORN (1952) and RABOR (1977) noted that there is a difference in colour between Palawan and Negros cats, but neither made a taxonomic distinction, presumably having insufficient material.

Etymology: For LARRY R. HEANEY, leading expatriate connoisseur of the Philippine mammal fauna.

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Zusammenfassung

Die Bengalkatzen (Prionailurus bengalensis) Indonesien und den Philippinen, mit Beschreibung zweier neuer Unterarten.

Die Bengalkatzen (*Prionailurus bengalensis*) Südostasiens zeigen ein unerwartet komplexes biogeographisches Muster. Zwei neue Unterarten werden von den Philippinen beschrieben; die Populationen von der Malayischen Halbinsel sind sehr variabel und könnten das Resultat einer Hybridisierung zwischen sundaischen und Festlandindividuen sein.

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Author's address: COLIN P. GROVES, Department of Archaeology and Anthropology, Australian National University, Canberra, A. C. T. 0200, Australia

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