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ASSESSING THE TAXONOMIC STATUS OF THE PALAWAN PANGOLIN *MANIS CULIONENSIS* (PHOLIDOTA) USING DISCRETE MORPHOLOGICAL CHARACTERS

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We use discrete morphological characters in a statistical framework to reassess the taxonomic status of the Palawan pangolin *Manis culionensis* relative to the Sunda pangolin *M. javanica*. We recommend that the 15 species-level traits previously proposed in the literature to distinguish the 2 pangolins be replaced by 5 newly defined diagnostic characters related to skull and external scales. Our study supports species-level partition between the Palawan and Sunda pangolins at a frequency of expected polymorphism threshold fixed to 0.10. Isolation through sea level rising (approximately 800,000–500,000 years ago) of proto-Palawan pangolins coming from Borneo through Early Pleistocene land bridges might have promoted the speciation of *M. culionensis*, a Palawan endemic species to be considered of high conservation concern.

Key words: discrete morphological characters, Manidae, *Manis culionensis*, *Manis javanica*, Palawan, pangolin, Pleistocene glaciations, Southeast Asia, species boundaries, taxonomy

Discrete morphological characters—that is, noncontinuous traits reflecting gaps in the pattern of morphological variability among groups of individuals—remain central to systematic biology. Recent developments in phylogenetic analysis have provided new perspectives on the delimitation and interpretation of discrete characters (Gaubert et al., 2005b; Grafen and Ridley 1997; Hlusko 2004; Jernvall and Jung 2000; Lewis 2001; Lovejoy et al. 1999; Pagel 1999; Wiens 1999, 2000, 2001). However, in the absence of a phylogenetic framework, the use of discrete characters remains one of the most common non–tree-based approaches for delimiting species boundaries (e.g., Barnosky and Bell 2003; Helbig et al. 2002). Recent empirical studies also have shown that these traits can be very informative in characterizing hybrid zones (e.g., Daniels et al. 1998; Gaubert et al., 2005a; Rohwer et al. 2001). New tools that explicitly use levels of polymorphism to estimate the discriminative power of discrete characters (Sites and Marshall 2004; Wiens and Servedio 2000) have provided a more rigorous statistical framework to assess the

taxonomic delimitations among groups that have no phylogenetic background (Davis and Nixon 1992; Wiens and Servedio 2000).

Pangolins (Pholidota; Manidae; genus *Manis* Linnaeus, 1758) are an unusual mammalian model because their epidermal scales may clearly identify different species (Pocock 1924). Probably because of these easily measurable external characters, few cranial and postcranial traits have been incorporated into the taxonomy of the genus (Frechkop 1931; Jentink 1882; Patterson 1978; Pocock 1924), which traditionally recognizes 7 species (see Schlitter 1993): *Manis crassicaudata*, *M. javanica*, and *M. pentadactyla* from tropical Asia, and *M. gigantea*, *M. temminckii*, *M. tetradactyla*, and *M. tricuspis* from sub-Saharan Africa.

Although there have been few taxonomic and phylogenetic studies of the genus *Manis* over the past decades (for a notable exception, see Gaudin and Wible [1999]), the status of the Sunda pangolin *Manis javanica* Desmarest, 1822, and the Palawan pangolin *M. culionensis* (Elera, 1915) as separate species remains open to speculation. The Palawan pangolin was 1st listed as a species distinct from *M. javanica* under *Pholidotus culionensis* (Elera 1895). However, most of the subsequent literature and synthetic taxonomic works did not mention the Palawan pangolin or consider it to be a subspecies of *M. javanica* (Corbet and Hill 1992; Ellerman

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TABLE 1.—Species diagnostic characters between *Manis culionensis* and *M. javanica*.

Species-diagnostic characters	Manis culionensis	Manis javanica
1) Total number of scale rows (middle of the back; following a virtual line that is perpendicular to the anteroposterior axis of the body)	19–21	15–18
2) Size of scales in nuchal, scapular, and postscapular regions[a]	Small	Large
3) Ratio of head and body to tail length (mean ± SD)	1.11 ± 0.03 (n = 5)	1.25 ± 0.13 (n = 20)
4) Ratio of nasal bone to total skull length[b]	< 1/3	> 1/3
5) Posterior region of palatine bone[b]	Weak (i.e., not ventrally inflated; short lateral walls)	Strong (i.e., ventrally inflated; large lateral walls)
6) Posterior extension of zygomatic process[b]	Short, not posterior to sphenopalatine foramen	Long, posterior to sphenopalatine foramen

[a] Shown in Fig. 1.
[b] Shown in Fig. 2.

and Morrison-Scott 1951; Frechkop 1931; Heaney et al. 1998; Jentink 1882; Patterson 1978; Pocock 1924; Schlitter 1993). In contrast, Lawrence (1939) gave a detailed morphological description of *M. culionensis* and argued for its status as a distinct species on the basis of distinct external and cranial states (followed by Sanborn 1952). Another study (Feiler 1998) proposed diagnostic morphological criteria for the Palawan pangolin but invalidated or did not consider most of the observations made by Lawrence (1939). Recently, Esselstyn et al. (2004) considered *M. culionensis* as a valid species, but did not provide diagnostic characters. As a result, these studies do not clearly define the morphological boundaries between *M. culionensis* and *M. javanica*. The establishment of diagnostic morphological characters is crucially important for understanding the evolutionary history of these pangolins and for promoting conservation efforts, because species-level taxa are more likely to benefit from effective conservation plans than are taxa below the species rank (see Hey et al. 2003). The Sunda pangolin is widely distributed across forests of Southeast Asia and Indonesia, whereas *M. culionensis* is considered to be endemic to the lowland rainforests of 2 small Philippine Islands (Palawan and Culion), and the status of its populations is poorly known (Esselstyn et al. 2004; Heaney et al. 1998).

The aim of our study was to reassess the species boundaries between *M. culionensis* and *M. javanica* through the comprehensive observation of museum material. We tested the validity of previously published discrete morphological characters in a much larger number of specimens than were used in previous studies (Feiler 1998; Lawrence 1939). Finally, we defined several new discrete morphological characters that distinguish between the Sunda and Palawan pangolins, and test their discriminative power as species-level markers.

MATERIALS AND METHODS

We 1st defined species-discriminative, discrete characters among the 6 other species of extant pangolins (*M. crassicaudata*, n = 9; *M. gigantea*, n = 8; *M. pentadactyla*, n = 26; *M. temminckii*, n = 11; *M. tetradactyla*, n = 17; and *M. tricuspis*, n = 40; Appendix I). We considered adult specimens only because ontogenetic variations due to juvenile morphology produced bias in estimates of intraspecific variability. We used a digital camera (Nikon CoolPix E4500, Nikon Corporation, Tokyo, Japan) to standardize the assessment of discrete morphological variability among specimens from different museums. We then defined these species-level characters for specimens of *M. culionensis* (n = 9) and *M. javanica* (n = 24). The individuals of *M. javanica* came from throughout its whole range (i.e., Indochinese peninsula, Malaysian mainland, Java, Sumatra, and Borneo islands; Appendix I). Nomenclature of cranial bones followed that of Jollie (1968). We used the statistical method of Wiens and Servedio (2000: equations (1), (2), and (3) and appendix A) to evaluate whether the proposed diagnostic characters were species-distinctive, that is, if there was a significant cutoff in trait frequencies suggestive of low or null gene flow. The data necessary to test this hypothesis consist of the number of observed individuals (n), the total number of characters surveyed (c), and the number of characters that show species-diagnostic traits (k). In short, if $P < 0.05$, the hypothesis that the observed diagnostic characters are either fixed or have an expected polymorphism level below a certain threshold (0.10, 0.05, or 0.01) that reflects species-level differentiation cannot be rejected.

RESULTS

From the observation of 111 specimens representing all species of pangolins, a provisional total of 34 variable characters were identified (data not shown). When this data set was applied to the morphological variability observed between *M. culionensis* and *M. javanica*, we were able to retain 6 discriminative characters from external and skull morphology (Table 1; Figs. 1 and 2).

The isolated populations of the Sunda pangolins (mainland versus Indonesian and Malaysian islands) were morphologically homogeneous, but were distinct from the Palawan pangolin, which was diagnosed as follows: 1) total number of lateral scale rows on back = 19–21; 2) size of scales in nuchal, scapular, and postscapular regions = small; 3) ratio of head and body to tail length = 1.11 ± 0.03; 4) ratio of nasal bone to total skull length < 1/3; 5) posterior region of palatine bone = weak (i.e., not ventrally inflated and short lateral walls); and 6) posterior extension of zygomatic process = short, not posterior to sphenopalatine foramen (see Table 1 for traits in *M. javanica*). None of these characters overlapped between the Palawan and Sunda pangolins except for the ratio of head and body to tail length. This low level of polymorphism (=10%) was due to 2 specimens of *M. javanica* from Indonesia (AMNH 102043 and AMNH 102098) with values of 1.14 and 1.13 cm, respectively. Two cranial characters were polymorphic in other species (character 4 in *M. tetradactyla* and character 6 in *M. pentadactyla*). However, they were strictly discriminative between the other species of pangolins. The estimated *P*-value (Wiens and Servedio 2000) was $P < 0.05$ based on c = 34 observed characters, k = 5 diagnostic characters (because of polymorphism and lower number of observed specimens,

character 3 was not included in this estimation), $n = 33$ observed specimens (9 *M. culionensis* + 24 *M. javanica*), and a 0.10 polymorphism threshold. Therefore, the 5 diagnostic characters between the Palawan and Sunda pangolins significantly supported species-level variability. However, the hypothesis of low or null gene flow was rejected for polymorphism thresholds of 0.05 and 0.01 ($P < 0.05$).

We also were able to assess the taxonomic value of the characters proposed in the literature as species-discriminative between the Palawan and Sunda pangolins (Table 2—11 external and 4 cranial characters). All traits proved to be either polymorphic or erroneously defined. Characters related to tail length, shape of zygomatic process, and lateral margins of pterygoid fossa (Lawrence 1939) can be found as partly reformulated in the species-diagnostic characters derived from this study (Table 1). All the external traits provided by Feiler (1998) were polymorphic or wrongly defined (Table 2).

DISCUSSION

The characterization of morphological variability in an explicit statistical framework allowed us to provide new support for the species-level status of the Palawan pangolin. Following Wiens and Servedio (2000), we assumed that a 10% polymorphism threshold was tolerable for hypothesizing a significant absence of gene flow (i.e., species-level differentiation) between *M. culionensis* and *M. javanica*. We delimited 5 diagnostic, discrete characters based on both scale patterns (2) and skull traits (3). A 6th character based on tail length ratio also may constitute a valuable trait to distinguish between the Palawan and Sunda pangolins, but examination of further specimens will have to be undertaken to evaluate whether or not the observed polymorphism level does not exceed its current value of 10%. Examination of our data did not support the utility of the 15 characters previously proposed to define these species (Feiler 1998; Lawrence 1939), therefore they could not be used as complements to our diagnostic listing. Although our investigations illustrate the need to examine a large number of specimens from multiple museum collections to accurately describe morphological variability, we must point out that our sample size of *M. culionensis* ($n = 9$) is low, reflecting its poor representation in museums worldwide.

The paleobiogeographic data for the Southeast Asian islands provides the framework for a speciation scenario that would have led to the absence of gene flow between *M. culionensis* and *M. javanica*. During the periods of glaciations occurring in the Pleistocene, lower sea levels led to the formation of continental bridges that linked islands now separated by marine areas (Sundaland—Hall 1998; Tougard 2001). The Greater Palawan shelf (including Palawan and Salamian islands—Steppan et al. 2003: figure 1) was the only part of Philippines to be linked to the Sundaland via Borneo, probably from the Early to the Middle Pleistocene (Heaney 1985). The most likely speciation scenario is the migration of a pool of proto-Palawan pangolins from Borneo to Greater Palawan through Early Pleistocene land bridges (in accordance with other terrestrial vertebrate–based scenarios—Heaney 1986; Meijaard 2003;
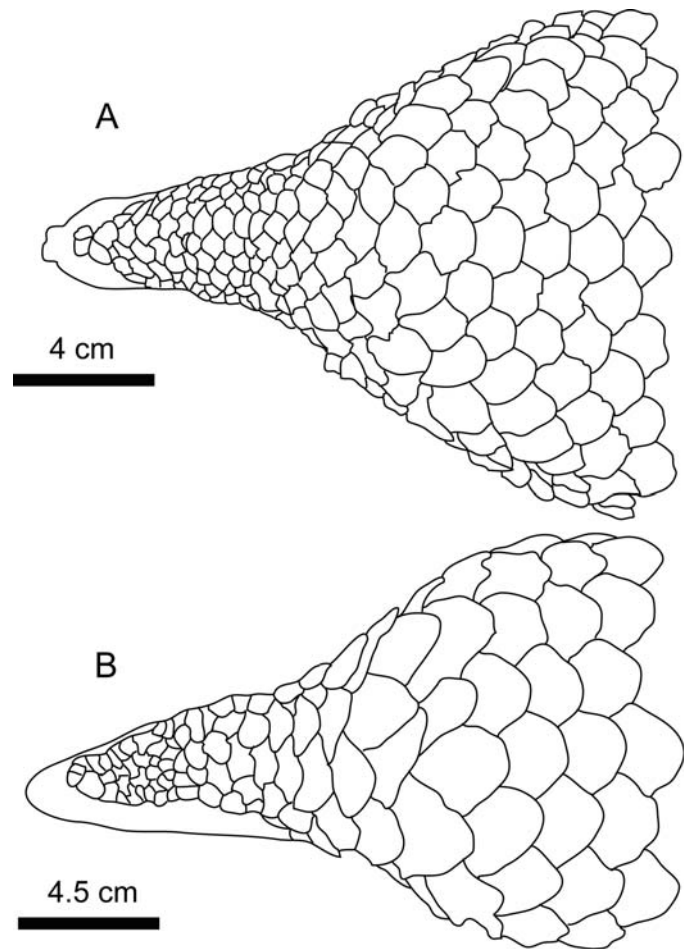

FIG. 1.—Dorsal view of head and scapular region of A) *Manis culionensis* (FMNH 62917; Palawan Island, Philippines), and B) *Manis javanica* (FMNH 33550; Sandakan, Sabah, Indonesia), illustrating diagnostic character 2 (see Table 1). The size of *M. javanica* was adjusted to that of *M. culionensis* for comparative purpose. FMNH = Field Museum of Natural History, Chicago, Illinois.

Tougard 2001) and subsequent isolation after rise of sea level about 800,000–500,000 years ago (EPICA 2004; Rohling et al. 1998). At that period, Palawan would have been separated from Borneo by a narrow water gap that likely would have prevented taxa with low dispersal abilities, such as pangolins, from experiencing gene flow between the 2 islands (Reis and Garong 2001). Because water depth between Borneo and Palawan approximates 145 m, subsequent lowering of sea levels during the 4 last glacial cycles is unlikely to have allowed transmigrations between the 2 islands (Meijaard 2003; Petit et al. 1999; Siddall et al. 2003).

Such a remarkable differentiation occurring in a relatively short time (Middle Pleistocene) may seem intriguing in the case of an ancient and morphologically very conserved mammalian lineage such as pangolins (1st fossils dated from Eocene—Gaudin 1999; Storch and Richter 1992), all the more because similar cases of post-Pliocene insular isolation in other species did not result in divergent morphologies. For example, Sri Lankan populations of the Indian pangolin *M. crassicaudata* did not show discrete morphological differentiation from the
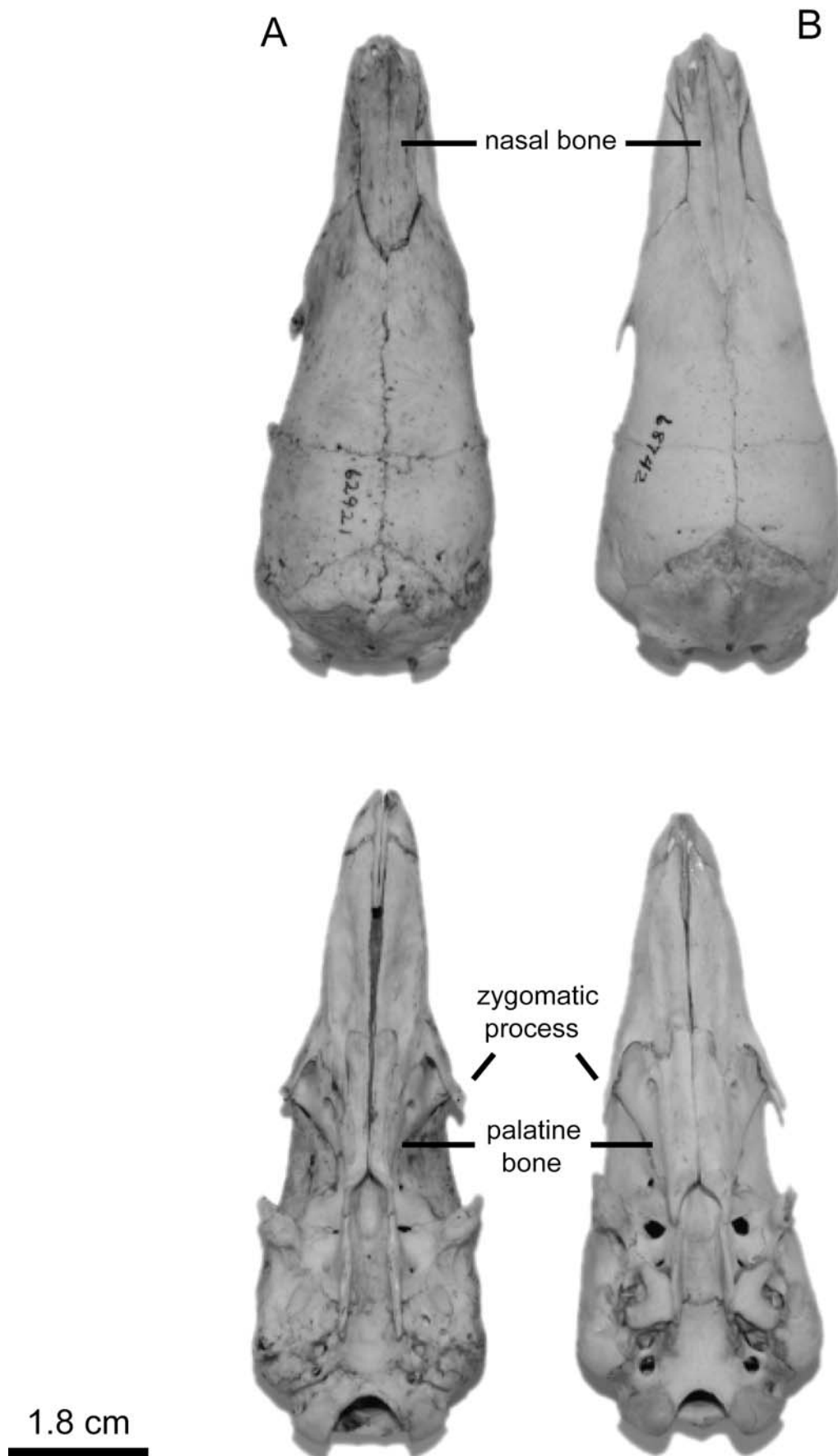
Fig. 2.—Dorsal and ventral views of skulls of A) *Manis culionensis* (FMNH 62921; Palawan Island, Philippines), and B) *Manis javanica* (FMNH 68742; Sandakan, Sabah, Indonesia). Diagnostic characters are indicated (see Table 1). FMNH = Field Museum of Natural History, Chicago, Illinois.

TABLE 2.—Characters proposed in the literature for classifying *Manis culionensis* and *M. javanica* as distinct species. "Polymorphic" means that a given character state exhibited a level of observed polymorphism > 10%.

	Manis culionensis		*Manis javanica*	
Characters	Traits from literature	This study	Traits from literature	This study
Color of scales[a]	Dirty yellowish white	Same	Dark	Mostly dark, but some specimens show a mosaic of yellowish and dark parts
Appearance of scales[a]	Thick, few longitudinal striations at base	Polymorphic	Thin, longitudinal striations on upper surface	Polymorphic
Distal border of scales, anterior region of back[a,b]	3-sided	Polymorphic and depending on level of abrasion	Rounded or drawn into a slight point	Polymorphic and depending on level of abrasion
First rows of scales on flanks and limbs[a,b]	Rounded or semicircular	Polymorphic	Long and pointed	Polymorphic
Size of scales on posterior one-half of head[a]	Smaller than rows anterior to eyes	Ambiguous definition (see character 2 in Table 1)	Gradual increase of size toward neck	Same
Diagonal row of 3 scales above most proximal folded scale on lateral margin of tail[a] (similar character for scale behind shoulder)	Middle scale 1.5- to 2-fold as long as overlying scales	Erroneous—state similar to *M. javanica*	Slightly longer than overlying scales	Same
Central row of scales under tail[a]	Width of scales up to 4 times larger than length	Erroneous—might be biased by level of abrasion	?	
Lateral rows of scales of tail[b]	Smooth	Similar sharp appearance in both species	Sharp	Similar sharp appearance in both species
Length of 4th claw relative to 2nd claw on forefoot[a]	Longer	Almost equal	Almost equal	Same
Tail length[a]	Almost equal to head + body length	Inaccurate definition (see character 3 in Table 1)	Two-thirds to three-fourths as long as head + body length	Inaccurate definition (see character 3 in Table 1)
Ear: pinna and fold[a]	Thick, fold well projected	Similar appearance in both species	Less thick, fold less projected	Similar appearance in both species
Shape of skull[a]	Rostrum particularly elongated	Similar appearance in both species	Rostrum less elongated	Similar appearance in both species
Shape of zygomatic process[a]	Peglike projection constricted at base	Inaccurate definition (see character 6 in Table 1)	Slender, flattened and triangular	Inaccurate definition (see character 6 in Table 1)
Posterior margin of palatine bone[a]	Presence of 2 small and rounded knobs	Polymorphic	Absence of knobs	Polymorphic
Lateral margins of pterygoid fossa[a]	Same level as palatine bone	Character partly constituting character 5 in Table 1	Markedly posterior to palatine bone	Character partly constituting character 5 in Table 1

[a] Lawrence (1939).
[b] Feiler (1998).

continental stock (Philips 1926). The present study also failed to find morphological distinction for the Chinese pangolin *M. pentadactyla* between Taiwan and the mainland, and for the tree pangolin *M. tricuspis* between Bioko Island and the African continent. It has been shown that subtle heterotopic shifts in molecular prepatterns may promote additive morphological evolution without implying drastic genetic changes between taxa (Jernvall and Jung 2000; Jernvall et al. 2000). In the case of *M. culionensis*, rapid morphological divergence may have found favorable conditions through the combined effect of founder event and directional selection in a peculiar habitat. Indeed, the presence of a great proportion of rainforest mammalian species from the Late Pleistocene suggests that Palawan was one of the few Southeast Asian areas where rain forests remained continuously until present time, even during the last glacial (Meijaard 2003; but see Reis and Garong 2001). Thus, the Palawan area may have constituted a particular ecosystem that contributed to the morphological differentiation of *M. culionensis*.

The classification of *M. culionensis* as a valid species that is endemic to Palawan and Culion Islands urges the need for further investigations on its distribution and status in the Great Palawan area. The Palawan pangolin is hunted for local consumption and for traditional Chinese medicine (Esselstyn et al. 2004). Given its very restricted range, it should be considered a species of high conservation concern. Our results should be followed up by molecular genetic analyses to better understand the historical processes that shaped these morphological patterns.

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APPENDIX I

Specimens examined.—The specimens used in this study are housed at the American Museum of Natural History, New York (AMNH); the Field Museum of Natural History, Chicago, Illinois (FMNH); the Muséum National d'Histoire Naturelle, Paris, France (MNHN); and the Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany (ZFMK). Material observed for the 2 pangolin species directly concerned in our study (*M. culionensis* and *M. javanica*) is shown in more detail. The postcranial skeleton is referred to as "postcranium."

Manis culionensis (9).—PHILIPPINES: Palawan Island (AMNH 29745, skull and skin; AMNH 103340, skull and skin; AMNH 203298, skull and skin; AMNH 242095, skull and skin; FMNH 62917, skin; FMNH 62918, skull and postcranium; FMNH 62919, skull, skin, and postcranium; FMNH 62921, skull and skin; MNHN 1884-1822, skull, skin, and postcranium).

Manis javanica (24).—INDONESIA: Java (AMNH 31815, skull and postcranium; AMNH 102041, skull and skin; AMNH 102043, skull and skin; AMNH 102098, skull and skin); Sumatra (MNHN 1911-1717, skin); location unknown (AMNH 101564, skull and skin; AMNH 101532, skull and skin; AMNH 102077, skull and skin). LAOS: (AMNH 87624, skull and skin; FMNH 37989, skull and skin). MALAYSIA: mainland (MNHN 1897-1867, skull and skin); Borneo (AMNH 32637, skull, skin, and postcranium; AMNH 103985, skull and skin; FMNH 68742, skull, skin, and postcranium; FMNH 68743, skull, skin, and postcranium). THAILAND: (ZFMK 95.468, skin). VIETNAM: (MNHN 1899-647, skin; MNHN 1962-2119, skull; MNHN 1974-222, skin). LOCATION UNKNOWN: (AMNH 34882, skull and postcranium; FMNH 33550, skull, skin, and postcranium; FMNH not registered, skin; MNHN 1882-110, skull, skin, and postcranium; MNHN 1985-106, skin).

Other specimens examined.—The following specimens were examined as a 1st step to define species-discriminative, discrete characters among the 6 other species of pangolins (see "Materials and Methods").

Manis crassicaudata (9).—INDIA, PAKISTAN, and SRI LANKA: (AMNH 34255, 150067, 244407; FMNH 57338, 92879, 98232, 98264, 104032; MNHN 1962-1129).

Manis gigantea (8).—DEMOCRATIC REPUBLIC OF CONGO and "AFRICA": (AMNH 53848, 53850, 53853, 53854, 53855, 53859; MNHN 1869-769, 1981-680).

Manis pentadactyla (26).—CHINA, LAOS, TAIWAN, and VIETNAM: (AMNH 26635, 60006, 183148, 184598, 184599; FMNH 32511, 32513, 39284, 39385, 39387, 39388, 46524, 75874, 75875, 75876, 75877, 75878, 75879, 75880, 75880, 94945, 98909, 114387; MNHN 1913-729, 1962-61; ZFMK 50.710).

Manis temminckii (11).—NAMIBIA, SOUTH AFRICA, and "AFRICA": (AMNH 83609, 168954, 168955; FMNH 34610, 35682, 38144, 38225; ZFMK 93.250, 95.464, 95.465, 95.466).

Manis tetradactyla (17).—CAMEROON, CENTRAL AFRICAN REPUBLIC, CONGO, DEMOCRATIC REPUBLIC OF CONGO, GABON, GHANA, IVORY COAST, and "AFRICA": (AMNH 53861, 53866, 150409; FMNH 54447, 62210; MNHN 1872-104, 1899-341, 1942-189, 1958-194, 1962-1173, 1962-60, 1970-437, 1970-438, 1970-439, 1985-101, 1985-103, 1988-268).

Manis tricuspis (40).—CAMEROON, CENTRAL AFRICAN REPUBLIC, DEMOCRATIC REPUBLIC OF CONGO, "DAHOMEY," EQUATORIAL GUINEA (BIOKO ISLAND), GABON, GHANA, IVORY COAST, LIBERIA, NIGERIA, and TOGO: (AMNH 53874, 53931, 55066; FMNH 42678, 42679, 42680, 42681, 62207, 137377; MNHN 1911-1901, 1912-701, 1947-870, 1956-724, 1956-725, 1956-726, 1956-727, 1956-728, 1956-729, 1962-205, 1962-2118, 1962-58, 1962-995, 1967-981, 1970-440, 1970-441, 1970-442, 1990-48, 1992-1859, 1995-1201; ZFMK 61.394, 61.395, 66.651, 66.652, 69.111, 69.113, 69.115, 69.932, 94.467, 99.1151, 99.1152).