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ARTICLE

AN EARLY PLIOCENE PANGOLIN (MAMMALIA; PHOLIDOTA) FROM LANGEBAANWEG, SOUTH AFRICA

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ABSTRACT—A fossil pangolin is described from the early Pliocene of Langebaanweg, South Africa. Morphological adaptations indicate that the specimen was not arboreal as are the living African species *Manis tricuspis* and *M. tetradactyla*, but was probably ground dwelling and may have engaged in a quadrupedal gait similar to that of the living representatives of the African species, *Manis gigantea*. In addition, it may have used its forelimbs for more extensive digging than does the living African *Manis temminckii*. The tail length, limb bone widths and proportions, and humeral morphology support the assignment of this specimen to *Manis gigantea*, making it the oldest known fossil representative of this species and the only confirmed fossil pangolin from South Africa.

INTRODUCTION

Pangolins (Order Pholidota; Family Manidae) or scaly anteaters are an unusual group of mammals characterized by an outer covering of horny, overlapping epidermal scales and the absence of teeth (Pocock, 1924; Grassé, 1955; Skinner and Smithers, 1990; Gaudin, 1999). They are adapted to a myrmecophagous lifestyle, specialized for feeding on ants and termites. In association with this dietary adaptation, they exhibit robust forelimbs, enlarged claws, and a long, sticky tongue for digging out nests and capturing insects (Kingdon, 1971; Skinner and Smithers, 1990; Gaudin, 1999).

Eight living species of pangolins are known from Asia and Africa, all assigned to the family Manidae. There is disagreement regarding the number of genera to which these species should be allocated (Pocock, 1924; Emry, 1970; McKenna and Bell, 1997; Gaudin and Wible, 1999; Nowak, 1999; Schlitter, 2005). Pending the results of a detailed phylogenetic study of pangolins being undertaken by one of the authors (Gaudin and Emry, in prep.), we will follow Nowak (1999) in referring all extant species to the genus *Manis*. Four species are known from Africa: the four-toed arboreal pangolin *Manis tetradactyla*, the arboreal pangolin *M. tricuspis*, the giant pangolin *M. gigantea* (all co-existing in western and central Africa), and the common pangolin *M. temminckii* (distributed in southern and eastern Africa) (Emry, 1970; Skinner and Smithers, 1990; McKenna and Bell, 1997; Nowak, 1999). The four living Asian species are *M. crassicaudata* from India, *M. pentadactyla* from China and northern South East Asia, *M. javanica* from South East Asia and the East Indies, and *M. culionensis* from the Palawan islands of the Phillipines (McKenna and Bell, 1997; Gaudin and Wible, 1999; Gaubert and Antunes, 2005).

Fossil pangolins are not commonly preserved in the fossil record, but remains have been recovered from the Eocene of Germany (*Eomanis waldi*, Storch, 1978; *Eomanis krebsi*, Storch and Martin, 1994), the Oligocene and the Miocene of Europe (*Necromanis* sp., Helbing, 1938; Koenigswald and Martin, 1990; Koenigswald, 1999), the latest Eocene of North America (*Patriomanis americana* Emry, 1970), the late Eocene (*Cryptomanis gobiensis* Gaudin et al., 2006) and Pleistocene of Asia (Harrison et al., 1961), and the Oligocene and Pliocene of Africa (Klein, 1972; Hendey, 1973; Gebo and Rasmussen, 1985; Pickford and Senut, 1991, 1994). African fossil pangolins have been recorded in Egypt, Uganda, and South Africa. The Egyptian specimen, which is early Oligocene in age (Gingerich, 1992), consists of two terminal phalanges that represent an indeterminate species (Gebo and Rasmussen, 1985). The Ugandan specimen, consisting of a single radius from the Pliocene, was identified as *M. gigantea* (Pickford and Senut, 1991, 1994). Klein (1972) described remains from a Pleistocene deposit in Nelson Bay in the Cape Province of South Africa and identified them as belonging to a pangolin, but this identification was questioned by Skinner and Smithers (1990).

The first positively identified fossil pangolin from South Africa, which is one of the specimens described here (SAM-PQL-21793), was discovered by Hendey (1976) at Langebaanweg and is estimated to be of early Pliocene age. The specimen consists of a partial skull, 21 semi-complete vertebrae, and several long bone elements from all four limbs. Hendey (1976) assigned the specimen to the genus *Manis*, but did not describe it.

There were significant environmental changes during the late Miocene and early Pliocene (Franz-Odendaal, 2002). The Antarctic ice sheet expanded, causing the sea level to drop and a land connection to form across the Straits of Gibraltar. The Mediterranean became a landlocked sea, triggering the 'Messinian salinity crisis' (Loutit and Kennett, 1979). Antarctic glaciation caused temperatures in the southern mid-latitudes to decrease, resulting in the southern African climate changing from tropical to temperate toward the end of the late Miocene. This change in climate was followed by an early Pliocene marine transgression, which re-flooded the Mediterranean basin and caused a regressive ice-phase in Antarctica (Van Couvering, 1976). This change in sea level also facilitated the preservation of terrestrial fossils at Langebaanweg in South Africa (Hendey, 1981a).

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The Langebaanweg locality, situated on the west coast of South Africa, 104 km north of Cape Town (Fig. 1), contains a late Cenozoic succession and consists of up to 120 m of unconsolidated sediments. These sediments include the Elandsfontein Formation, the overlying Saldanha Formation, which is in turn overlain by the highly fossiliferous Varswater Formation. A bedrock Gravel Member (from an unnamed formation) of pre-Tertiary age underlies the Elandsfontein Formation. The Varswater Formation was uncovered during phosphate mining operations during the late 1950s and 1960s, and the exposed area of the mine is referred to as E quarry (Hendey, 1981b). The Varswater Formation is divided into two contemporaneous members; namely, the Quartzose Sand Member and Pelletal Phosphorite Member (Hendey, 1981a). The Quartzose Sand Member (QSM) is an estuarine complex of up to 2 m of floodplain, salt marsh, and tidal flat deposits exposed in E quarry. Both members are thought to be early Pliocene in age (~5 Ma, based on faunal correlations with East African fossil mammal faunas; Hendey, 1973). The Pelletal Phosphorite Member (PPM) consists of phosphatic marine littoral and fluviatile deposits. This study describes the first early Pliocene African pangolin from Langebaanweg, South Africa.

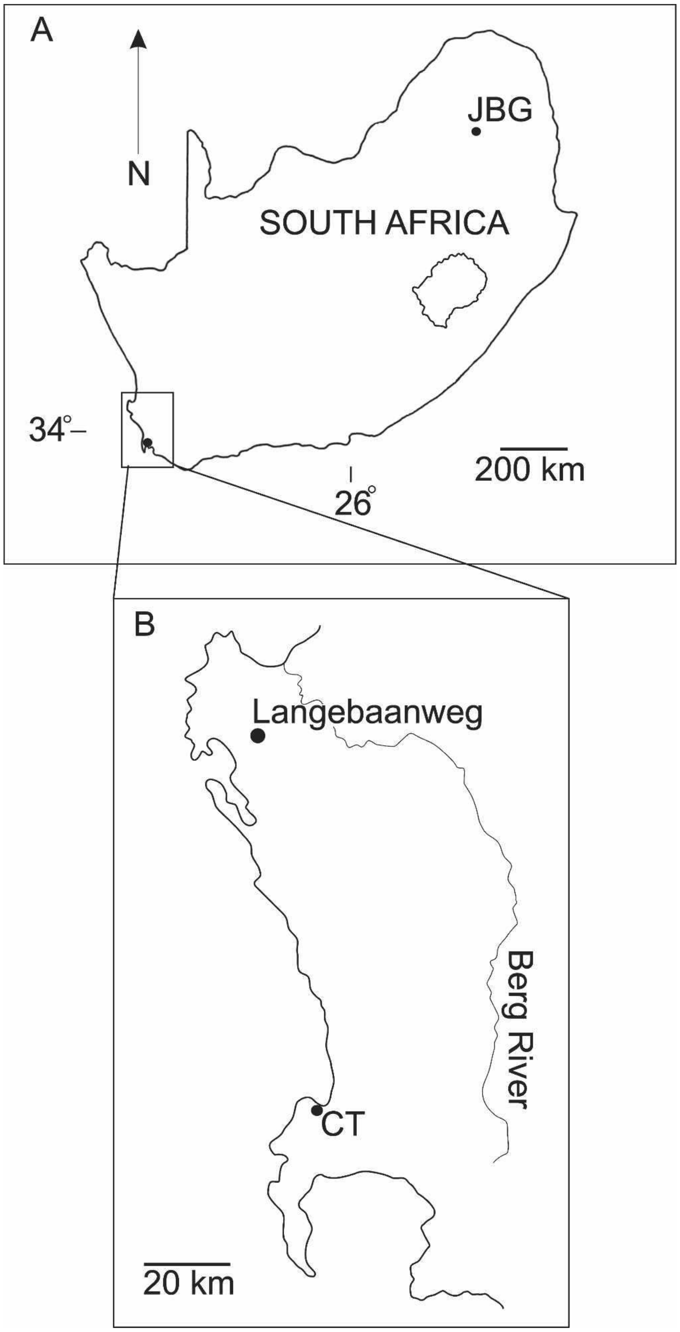

FIGURE 1. **A**, map of South Africa; **B**, Langebaanweg, the locality of SAM-PQL-21793, *Manis gigantea* (modified from Hendey, 1981a). **Abbreviations**: **CT**, Cape Town; **JBG**, Johannesburg.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York; **CM**, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; **FMNH**, Field Museum of Natural History, Chicago, Illinois; **M**, Iziko: South African Museum of Cape Town (Mammalogy); **NMB**, National Museum, Bloemfontein, South Africa; **SAM-PQL**, Iziko: South African Museum of Cape Town (Paleontology Quaternary Langebaanweg); **USNM**, National Museum of Natural History, Smithsonian Institution, Washington, D. C.

Anatomical Abbreviations—**a**, acetabulum; **ac**, anterolateral crest; **af**, articular facet; **c**, cleft; **ca**, capitulum; **d**, depression; **dpt**, deltopectoral crest; **ect**, ectepicondyle; **ef**, entepicondylar foramen; **ent**, entepicondyle; **ethf**, ethmoid foramen; **etl**, ectoturbinal lamellae; **fro**, frontal; **ft**, flexor tubercle; **gf**, glenoid fossa; **gt**, greater tuberosity; **h**, head; **is**, intercondyloid spine; **lt**, lesser trochanter; **nas**, nasal; **op**, olecranon process; **par**, parietal; **pgf**, possible position of postglenoid foramen; **pt**, patellar trochlea; **sf**, sesamoid facet; **sln**, semilunar notch; **sq**, squamosal; **tf**, transverse foramen; **tp**, transverse processes; **tr**, trochlea; **z**, zygopophyses.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order PHOLIDOTA Weber, 1904
Family MANIDAE Gray, 1821
Genus *MANIS* Linnaeus, 1758
MANIS GIGANTEA (Illiger, 1811)
(Figs. 2–6)

Diagnosis—Possesses features common to all extant pangolins, such as elongated, medially canted deltopectoral crest on humerus and fissured ungual phalanges. In addition, shares derived features with extant Manidae not present in other known fossil forms, including a weak lambdoid crest, lack of trochanteric fossa and intertrochanteric crest on femur, lack of fovea on femoral head, lack of distinct raised third trochanter on femur, and distal insertion point for gluteal muscles. Resembles *Manis gigantea* in robust nature of skeleton, tail length, limb bone proportions, and broad olecranon fossa, wide epicondyles, and elongated deltopectoral crest on humerus.

Material Examined—SAM-PQL-21793, which consists of middle, posterior dorsal, and lateral regions of the cranium; 21 caudal vertebrae and several unidentified vertebral fragments; complete right humerus; proximal fragment of right ulna; complete right radius; distal left humerus; almost complete left ulna; almost complete left radius; terminal phalanx from forelimb; complete right and left femora, both missing the greater trochanter; complete left tibia; and fragment of left fibula. SAM-PQL-42760, consisting of several fragments of the midshaft and distal end of a right femur and a caudal vertebra; SAM-PQL-13745, an almost complete right femur with the femoral head missing, a midshaft and proximal region of a left femur, and a caudal vertebra.

Locality and Horizon—E quarry, Piets Pit Bed 2, Quartzose Sand Member, Varswater Formation, Langebaanweg, South Africa, early Pliocene.

Comparative Material—The crania and limb bones of adult representatives of each extant African species, including *M. gi-*

gantea (AMNH 53848, 53851, 53858; USNM 269706), *M. temminckii* (M308; NMB3961; AMNH 168954, 168955; FMNH 35682), *M. tricuspis* (CM 16206), and *M. tetradactyla* (USNM 481806) were examined and measured for comparison with the study specimen.

Description of Skeleton

Cranium—The middle, posterior dorsal, and lateral regions of the cranium are preserved (Fig. 2A, B). In dorsal view, the cranium has a pear-shaped outline, which broadens slightly toward the posterior end. The dorsal surface of the cranium is smooth and a sagittal crest is absent. Postorbital bars are absent. The sutures between the bones are clearly preserved, but because the epiphyses of the long bones are fused, the individual is probably an adult. The median dorsal suture is straight. The frontoparietal sutures do not meet the median dorsal suture at right angles as in *Manis temminckii*, but are angled slightly towards the posterior end of the cranium at the point where they join the dorsal suture (Fig. 2A), as in extant *M. gigantea*. Superficial rugosities are visible on the dorsal surface of the parietals and the squamosals. The lambdoid crest is reduced.

In posterior view, the cranium forms an oval, which is wider than high. The bones of the posterior and ventral regions of the skull are missing. The squamosals are entirely exposed on the lateral and ventro-lateral surfaces of the cranium. The suture between the dorsal edge of the squamosals and the parietals is straight and parallel to the base of the skull, like extant *Manis gigantea*, but unlike that seen in *M. temminckii*, which is slightly concave. The right zygomatic process is preserved. It is directed downward and forward and, as in extant pangolins, does not form a complete arch. The depression on the squamosal for the condyle of the lower jaw is deeper than in *M. temminckii*. The ethmoid foramen, which transmits the ethmoid artery and vein, and the ethmoid nerve during life, is situated slightly more lateral and further forward on the frontal (Fig. 2B) compared to extant *M. gigantea* (Gaudin and Wible, 1999) or *M. temminckii*. The tympanic bones are not preserved. Transverse ridges indicating the remnants of the ectoturbinal lamellae are visible on the ventral surface of the frontals and nasals. The mandible is not preserved.

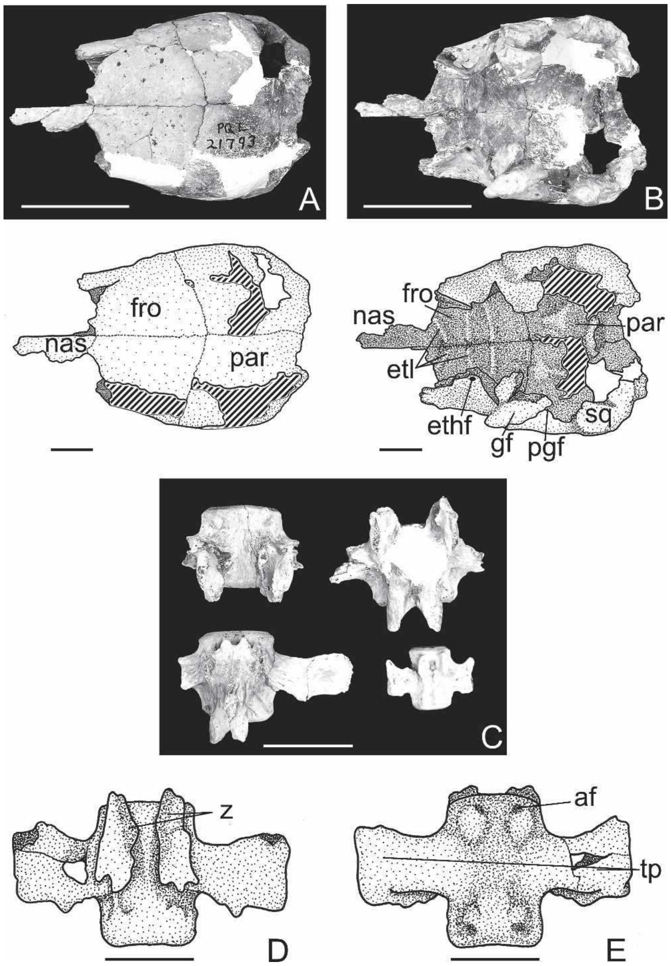

FIGURE 2. Cranium and vertebrae of SAM-PQL-21793, *Manis gigantea*. **A**, dorsal view and interpretative drawing of cranium; **B**, ventral view and interpretative drawing of cranium; **C**, four of the 21 caudal vertebrae in dorsal view. **D**, **E**, interpretative drawings of a caudal vertebra in **D**, dorsal and **E**, ventral view. Scale bar equals 2 cm.

In general, the shape of the cranium differs from those of both *Manis tricuspis* and *M. tetradactyla* in that the epitympanic recess in the squamosal is significantly less inflated laterally and posteriorly. The cranium of SAM-PQL-21793 is similar in shape to that of *M. temminckii*, but with an estimated skull length of 117 mm, it is slightly larger than *M. temminckii* (average skull length 84 mm; Kingdon, 1971) and is significantly larger than the cranium of *M. tricuspis* (average skull length 74 mm; Kingdon, 1971). However, it is smaller than the skull of the extant *M. gigantea* (average skull length 155 mm; Kingdon, 1971).

Vertebrae—Twenty-one semi-complete caudal vertebrae (Fig. 2C) and several fragments, consisting of zygopophyses and broken transverse processes of specimen SAM-PQL-21793, as well as two partially preserved caudal vertebrae of specimens SAM-PQL-13745 and SAM-PQL-42760 are preserved. The tail of SAM-PQL-21793 is at least 630 mm in length, which is longer than the average *Manis temminckii* tail length (413 mm; Kingdon, 1971) and also longer than the average tail length of *M. tricuspis* (463 mm; Kingdon, 1971). The tail length of specimen SAM-PQL-21793 is, however, comparable to that of extant *M. gigantea* (average tail length 625 mm; Kingdon, 1971).

All the vertebrae have neural arches, spines, zygopophyses, and transverse processes, in varying degrees of preservation, which decrease in size towards the end of the tail. The last few caudal vertebrae are not preserved. The individual caudal vertebrae are larger than those of adult *M. temminckii* and the transverse processes are shorter, anteroposteriorly wider and angle back more than those in *M. temminckii*. In these respects these vertebrae resemble those of extant *M. gigantea*. The transverse crest for muscle attachment on the dorsal surface of the transverse processes is sharper and larger than that found in *M. temminckii*, but is again similar to the condition in *M. gigantea*. The width of a centrum near the sacrum is approximately 85% its vertebral length, but the length of the centra increases towards the end of the tail, similar to what is seen in *Manis temminckii* (90%). It is not known whether a similar condition is present in *M. gigantea*. The centra are dorsoventrally flattened and the articular facets are oval. The articular facets for the chevrons on the ventral side form short, paired processes, but the chevrons themselves are not preserved. The neural arches are low, but are generally not preserved in their entirety.

Scapula—A fragment of the glenoid fossa and part of the acromion from the left scapula is preserved (Fig. 3H; Fig. 4A). The glenoid fossa is concave for the articulation with the head of the humerus and is approximately 23.5 mm wide.

Humerus—Humeri from both forelimbs show some form of pathology (Fig. 3A, D). Only the distal region of the left humerus is preserved, but it has almost completely lost the shape typical of pangolin humeri.

The right humerus is complete, but exhibits several small protuberances grouped together at the distal end on the posterior surface. It measures 88.4 mm in length and in size falls between that of the extant *M. gigantea* measured in this study

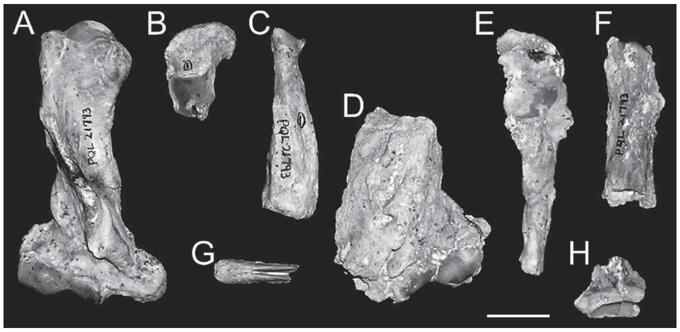

FIGURE 3. Forelimb and pectoral girdle of SAM-PQL-21793, *Manis gigantea*. **A**, right humerus, posterior view; **B**, right ulna, posterior view; **C**, right radius, lateral view; **D**, left humerus, posterior view; **E**, left ulna, posterior view; **F**, left radius, lateral view; **G**, terminal phalanx, dorsal view; **H**, glenoid fossa of left scapula, anterior view. Scale bar equals 2 cm.

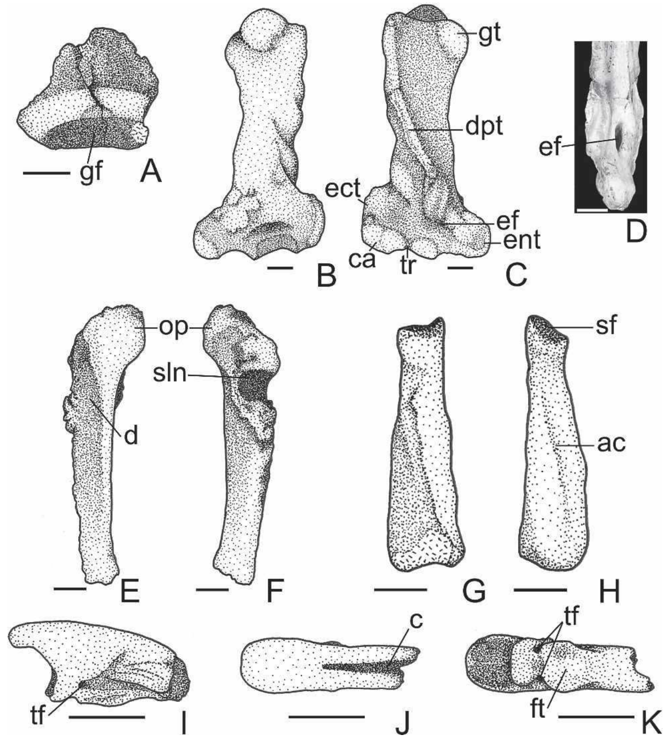

FIGURE 4. Interpretative drawing of the scapula and forelimb of SAM-PQL-21793, *Manis gigantea*. **A**, glenoid fossa of left scapula in anterior view; **B**, **C**, **D**, right humerus in **B**, anterior, **C**, posterior and **D**, lateral view showing the entepicondylar foramen; **E**, **F**, left ulna in **E**, anterior view, and **F**, medial view; **G**, **H**, right radius in **G**, medial view and **H**, lateral view; **I**, **J**, **K**, terminal phalanx in **I**, right lateral view, **J**, dorsal view and **K**, ventral view. Scale bars equal 1 cm, except D, equals 2 cm.

(79% the length of *M. gigantea* and 20% longer than *M. temminckii*, Table 1). The bicipital ridges, forming the upper parts of the anterior and medial borders of the shaft of the bone, are enlarged (possibly pathological). The elongated, medially canted deltopectoral crest extends distally to the entepicondylar bridge and is folded over toward the medial side of the bone (Fig. 4B, C). This is also observed in extant Manidae as well as in the North American Eocene pangolin *Patriomanis* (Emry, 1970; Rose and Emry, 1993), the Asian Eocene pangolin *Cryptomanis* (Gaudin et al., 2006), and in the European *Necromanis* from the Phosphorites of Quercy (Emry, 1970; Koenigswald and Martin, 1990; Koenigswald, 1999). The crest is broad with a flat surface that has been weathered away slightly. A groove, which was probably for the tendon of the biceps muscle, passes through the crest in the distal region just above the entepicondyle. The deltopectoral crest with its groove is similar in appearance to that of *Patriomanis* (Emry, 1970). A second groove on SAM-PQL-21793 begins at the midshaft on the posterior surface and extends distally round the bone to the anterior surface just above the ectepicondyle. Neither this groove nor the groove on the deltopectoral crest is present in the living African pangolins except *Manis gigantea,* which has both grooves. A groove at the distal end of the deltopectoral crest is present in the extant Asian species *M. javanica*. The entepicondylar foramen, which is absent in *M. temminckii*, but present in all other extant Manidae, is present in this specimen (Fig. 4D). The depression on the postero-medial side of the deltopectoral crest that supports the biceps muscle is deeper than that seen in extant Manidae. On the posterior side of the humerus, slightly above the trochlea, lies a deep transverse groove, the olecranon fossa, for the elevated superior margin of the semilunar notch ('anconeal process') of the ulna. The olecranon fossa is broad, similar to *Patriomanis* and differs from that of extant Manidae. The greater tubercle extends farther proximally than the lesser tubercle, like in *Patriomanis* (Rose and Emry, 1993) and extant Manidae. The profile of the trochlea is convex, similar to *M. tetradactyla* and *M. tricuspis*, and differs from that of *M. gigantea* and *M. temminckii*, where the profile of the trochlea is straight. In *Patriomanis* (Emry, 1970) and the extant Asian species, the profile of the trochlea is concave. The epicondyles are similar to those of *M. gigantea*, *Necromanis* (Koenigswald and Martin, 1990; Koenigswald, 1999) and *Eomanis* (Storch and Martin, 1994). On the whole, the right humerus of specimen SAM-PQL-21793 is notably robust and most similar to *M. gigantea*.

The left humerus (Fig. 3D) is severely pathologic. The trochlea, part of the entepicondyle, and the entepicondylar foramen are clearly visible. However, the distal region of the deltopectoral crest is a bulbous expanded region instead of a distinct crest. A large pit lies just above the entepicondylar foramen and a deep crevice extends up the postero-medial edge of the crest. Several pits are also visible on the distal posterior surface of the bone.

Ulna—Only the proximal region of the right ulna, consisting of the olecranon process and semilunar notch, is preserved (Fig. 3B). The left ulna is almost complete, with only a tiny portion of the distal end missing (Fig. 3E; Fig. 4E, F). It measures 75.2 mm in length and is closest in length to *M. temminckii* (65.5 mm) and *M. tricuspis* (60.2 mm) (Table 1). A deep depression is observed on the lateral surface of the left ulna (Fig. 4E), between the semilunar notch and the posterior border. There is a flat articular surface, the radial notch, between the semilunar notch and the deep lateral depression, below which lies a notch that is probably for the insertion of the biceps. All these characteristics are similar to those of living pangolins.

Radius—A complete right radius (Fig. 3C; Fig. 4G, H) and the proximal end of the left radius (Fig. 3F) are preserved, although the left radius has some form of pathology. The right radius is more robust compared to living pangolins. The proximal end has a cup-like capitular surface, a lateral sesamoid facet (Fig. 4H), a medial trochlear extension, and a proximal ulnar facet, as in extant Manidae, *Patriomanis* (Emry, 1970), and *Necromanis* (Helbing, 1938). The sesamoid facet is also slightly visible in proximal view, similar to the extant Manidae and unlike *Patriomanis*. The shaft of the radius in anterior view becomes distally expanded into a well-developed crest. The distal end is wider

TABLE 1. Limb bone measurements (minimum and maximum values in parentheses) and ratios for SAM-PQL-21793, *Manis gigantea*, and the four extant African pangolin species, *Manis gigantea* (AMNH 53848, 53851, 53858, USNM 269706). *Manis temminckii* (AMNH 168954, 168955, FMNH 35682, M308, NMB 3961), *Manis tricuspis* (CM 16206), and *Manis tetradactyla* (USNM 481806).

Element	M	SAM-PQL-21793 n = 1	*M. gigantea* n = 4	*M. temminckii* n = 5	*M. tricuspis* n = 1	*M. tetradactyla* n = 1
Humerus	total 1	88.4	112.5 (105.5–119.7)	70.8 (68.1–73.5)	57.5	52.5
	prox w	29.1	37.6 (35–40.2)	22 (21–22.7)	16.5	13.2
	ms w	18.2	18.1 (17.1–19.1)	10.4 (9.4–11.4)	10.3	7.8
	dist w	46.3	56.8 (52.8–60.7)	33.5 (31.4–35.6)	26.6	22.2
	l/prox w	5.1	3	3.2	5.5	6
	l/dist w	1.9	2	2.1	2.2	2.4
	l/ms w	4.9	6	6.8	5.6	6.7
Ulna	total 1	75.2	108.2 (97.3–119.2)	65.5 (62.8–68.1)	60.2	50.9
	prox w	22.4	23.2 (22.1–24.4)	14.7 (12.6–16.7)	11.9	6.1
	ms w	17	9.2 (8.6–9.7)	6.3 (4.4–8.1)	3.6	3.4
	dist w	12.3	9.1 (8.5–9.7)	6.7 (5.3–8)	4.3	3.8
	l/prox w	5.4	4.7	4.5	5.1	6.3
	l/dist w	6.1	11.9	9.7	14	13.4
	l/ms w	4.4	11.8	10.4	16.7	15
Radius	total 1	58.9	76.3 (66.5–86.1)	44.7 (43.2–46.2)	43.8	41.5
	prox w	11.1	20 (18.9–20.9)	9.9 (8.93–10.9)	9.7	8.2
	ms w	12.1	7.8 (7.8)	6 (4.7–7.3)	5	3.7
	dist w	17.5	20.2 (18.3–22.1)	12.6 (10.2–14.9)	8.8	7.7
	l/prox w	5.3	3.8	4.5	4.5	5.1
	l/dist w	5.4	3.8	3.5	5	5.4
	l/ms w	4.9	9.8	7.5	8.8	11.2
Femur	total 1	114.1	139.7 (129.3–150.2)	107.5 (103–112)	59	54.1
	prox w	>46.2	59.1 (55.5–62.8)	41 (38.2–43.8)	21.4	19
	ms w	22.2	23.7 (21.4–26)	15.8 (14.7–16.8)	9.1	7.7
	dist w	37.7	49 (48–50.1)	31 (29.9–32.2)	18	15.4
	l/prox w	—	2.4	2.6	2.8	2.9
	l/dist w	5	2.9	3.5	5.3	5.5
	l/ms w	5.1	6	6.8	6.5	7
Tibia	total 1	95.8	121.5 (109–133.9)	86.8 (82.5–91)	67.5	56.2
	prox w	32.5	41.4 (38.9–43.9)	28.4 (27–29.8)	17.7	15.3
	ms w	12.8	14.1 (12.9–15.2)	9 (7.6–10.4)	5.6	4.8
	dist w	25.9	37.4 (35.8–39)	21.5 (20–23)	15.8	14.7
	l/prox w	2.9	2.9	3	5.8	5.7
	l/dist w	5.7	3.2	4	4.3	5.8
	l/ms w	7.5	8.6	9.6	12.1	11.7
Fibula	total 1	—	111.4 (97.2–125.6)	78.9 (74.2–83.5)	63.7	50
	prox w	—	12 (11.5–12.3)	11.1 (5.9–16.3)	4.8	4
	ms w	11.3	5 (4.7–5.2)	4.1 (3–5.2)	2.4	2.3
	dist w	—	15 (13.7–16.2)	11.6 (8.7–14.5)	7.1	6.2
	l/pox w	—	9.3	7.1	13.3	12.5
	l/dist w	—	7.4	6.8	7	6.1
	l/ms w	—	22.3	19.2	26.5	21.7

Measurements (in mm) were made using Mitutoyo digimatic calipers. Abbreviations: dist, distal; l, length; M, measurement; ms, midshaft; prox, proximal; w, width.

than the proximal end and has a single cup-like transverse articular surface. Two pits are observed on the lateral surface towards the distal end. The radius measures 58.9 mm in length and falls between that of the *M. gigantea* (76.3 mm) and *M. temminckii* (44.7 mm) (Table 1).

The left radius is larger and thicker than the right radius and is slightly deformed (Fig. 3F). Pits are common and include a particularly large one on the medial surface towards the proximal end. A distinct diagonally oriented longitudinal ridge, which is not present on the right radius, extends down the lateral surface of the bone. Pathological bone also extends slightly onto the proximal articular surface.

Phalanx—Part of a terminal phalanx is preserved, but the tip is missing (Fig. 3G; Fig. 4I, J, K). The phalanx shows the characteristic bifid pattern of pangolins. It is large and curved, and probably belongs to the digging third digit of one of the forelimbs. Ventrally, there is a round, but relatively flat tubercle for the attachment of the flexor tendon (Fig. 4K). This tubercle is not as bulbous as in *Manis tetradactyla* (Gebo and Rasmussen, 1985) or *M. temminckii*, is rounder in shape compared to that of *M. pentadactyla* (Gebo and Rasmussen, 1985), but is similar to that of *M. gigantea*. The transverse foramen opens onto the plantar surface, similar to *M. pentadactyla* and *M. gigantea* (on manual ungual phalanx III), and unlike *M. tetradactyla* (Gebo and Rasmussen, 1985) and *M. temminckii*. The articular surface of the phalanx is strongly concave with two grooves.

Pelvis—A fragment of the left pelvis consisting of part of the acetabulum with a lower portion of the pubis is preserved (Fig. 5E; Fig. 6A). The fragment shows that the pubis is larger and more robust compared to *Manis temminckii* or *Manis tricuspis* (Kingdon, 1971).

Femur—Both femora of SAM-PQL-21793 are nearly complete, with only the greater trochanters missing (Fig. 5A, B). Total length is 114.1 mm (82% the length of *M. gigantea* and 9.4% longer than *M. temminckii*, Table 1). As in extant Manidae, the femoral head has no fovea, whereas a fovea is present in *Patriomanis*, *Cryptomanis* and *Necromanis* (Emry, 1970; Koenigswald, 1999; Gaudin et al., 2006). The trochanteric fossa and intertrochanteric crest are absent. The lesser trochanter is distinct and posteromedially placed (Fig. 6B, C). The third trochanter is absent, which differs from *Necromanis*, *Cryptomanis*, and *Patriomanis* where the third trochanter is salient (Emry, 1970;

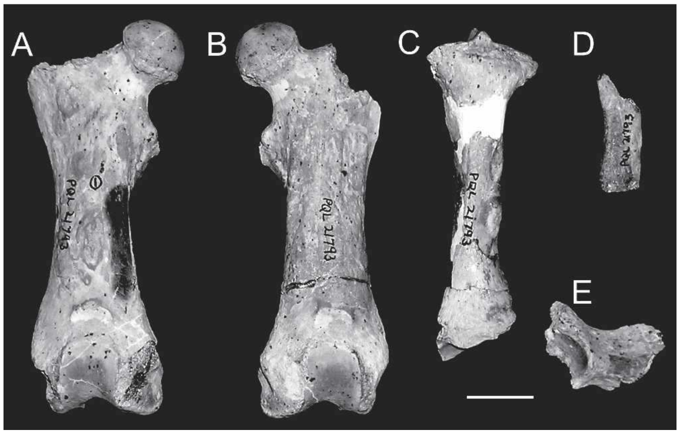

FIGURE 5. Hind limb and pelvic girdle of SAM-PQL-21793, *Manis gigantea*. **A**, left femur, posterior view; **B**, right femur, posterior view; **C**, left tibia, anterior view; **D**, left fibula, medial view; **E**, acetabulum of left pelvis. Scale bar equals 2 cm.

Koenigswald and Martin, 1990; Koenigswald, 1999; Gaudin et al., 2006). In specimen SAM-PQL-21793, the gluteus maximus muscle probably inserted on the lateral surface of the shaft just above the lateral condyle, as in extant Manidae. The third trochanter is more proximally situated in *Necromanis*, *Cryptomanis*, and *Patriomanis* (Emry, 1970; Koenigswald and Martin, 1990; Koenigswald, 1999; Gaudin et al., 2006). A digital fossa at the root of the neck, which is beneath the curved tip of the greater trochanter and gives attachment to the tendon of the obturator externus muscle, is absent. This is unlike *Necromanis* (Emry, 1970), but similar to the condition in extant Manidae. The shaft of the femur is anteroposteriorly compressed and the patellar trochlea is directed towards the head (Fig. 6B), as in extant Manidae. The distal end is more compressed anteroposteriorly than in the living pangolins. The femoral fragments of SAM-PQL-13745 (midshaft width 19.2 mm) and SAM-PQL-42760 (upper midshaft width 21.5 mm) are similar to the femora of specimen SAM-PQL-21793.

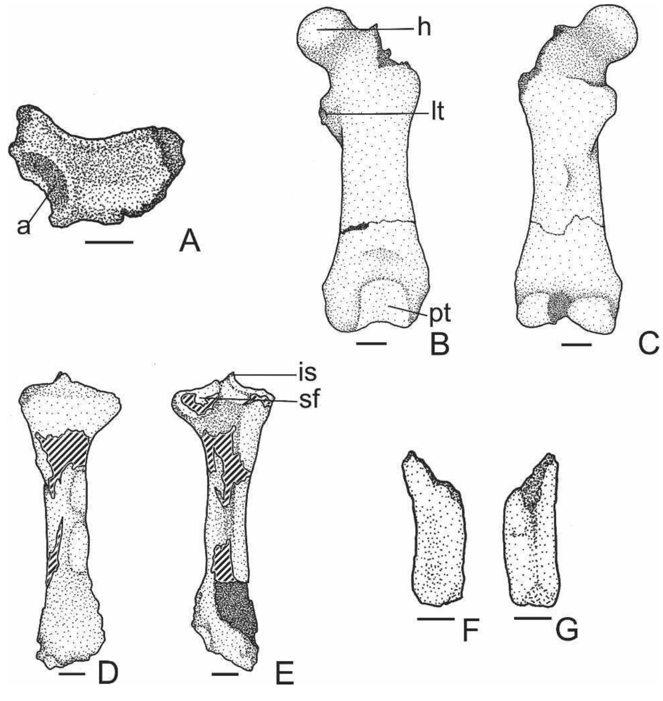

FIGURE 6. Interpretative drawing of the pelvis and hind limb of SAM-PQL-21793, *Manis gigantea*. **A**, acetabulum of left pelvis; **B**, **C**, right femur in **B**, anterior view and **C**, posterior view; **D**, **E**, left tibia in **D**, anterior view and **E**, posterior view; **F**, **G**, left fibula in **F**, medial view and **G**, lateral view. Scale bars equal 1 cm.

Tibia—The left tibia is complete apart from a missing fragment towards the distal end on the posterior surface (Fig. 5C). The tibia is similar to that of living pangolins although it does appear to be slightly less slender towards the distal end. It measures 95.8 mm in length (79% that of *M. gigantea* and 9% longer than that of *M. temminckii*; Table 1). The proximal end is transversely expanded, similar to extant Manidae and *Patriomanis* (Emry, 1970; Fig. 6D, E). There is a sharp intercondyloid spine on the proximal surface between the two articular surfaces (Fig. 6E). The median condylar surface of the bone is slightly convex, whereas the posterior surface beneath the lateral condyle is distinctly concave and forms a deep depression. This depression continues down the posterior surface to approximately midshaft. There is a sesamoid facet (Fig. 6E) on the posterior surface of the proximal end of the bone for a sesamoid bone found in the tendon of the popliteus muscle, as in extant Manidae, *Patriomanis* (Emry, 1970), and *Cryptomanis* (Gaudin et al., 2006). The anterior surface of the tibia is damaged and it is not possible to assess the cnemial crest.

Fibula—Only a fragment of the proximal midshaft of the left fibula is preserved (Fig. 5D; Fig. 6F, G). It is significantly wider than that of *Manis temminckii* and even that of *M. gigantea* (Table 1). The fibula is laterally flattened as in extant Manidae, but it cannot be determined whether the shaft curves as it does in the extant Manidae.

DISCUSSION

Hendey (1976) classified specimen SAM-PQL-21793 as *Manis*, but did not identify the specimen to species level. This specimen shows several morphological differences from the arboreal *Manis tricuspis* and *M. tetradactyla*, as well as the terrestrial species, *M. temminckii*. For example, the absence of a laterally and posteriorly expanded epitympanic recess within the squamosal suggests that this specimen does not belong to either *M. tricuspis* or *M. tetradactyla*. The tail length differs from *M. tricuspis* and the phalanx shape and position of the transverse foramen in the phalanx differs from that of *M. tetradactyla*. Specimen SAM-PQL-21793 is also significantly larger and more robust than the arboreal species *M. tricuspis* and *M. tetradactyla* (total lengths and widths, Table 1). Several features including the robust nature of the skeleton (limb bone widths), and morphology of the cranium (e.g., position of sutures, the ethmoid foramen, squamosal depression), humerus (e.g., presence of entepicondylar foramen, profile of the trochlea), and phalanx morphology (e.g. phalanx shape, position of transverse foramen) indicate that this specimen also differs from *M. temminckii*.

Furthermore, the proportion of forelimb to hind limb length in specimen SAM-PQL-21793 differs from *M. tricuspis, M. tetradactyla*, and *M. temminckii*. The forelimbs in the arboreal *Manis tricuspis* and *M. tetradactyla* are slightly shorter than the hind limbs (forelimb length [humerus + radius] to hind limb length [femur + tibia] = 0.8). The forelimb to hind limb ratio in the more terrestrial *M. gigantea* is 0.72. The forelimbs in *Manis temminckii* are significantly shorter than the hind limbs (forelimb length to hind limb length = 0.59). *Manis temminckii* tends to walk mostly on its hind limbs and does not dig extensively. The forelimb to hind limb length ratio in specimen SAM-PQL-21793 is 0.7 and is most similar to extant *M. gigantea* (0.72). Specimen SAM-PQL-21793 was probably ground dwelling and engaged in a quadrupedal gait, similar to *M. gigantea*.

Although SAM-PQL-21793 shares a few features with *Patriomanis, Cryptomanis*, *Necromanis*, and *Eomanis* not found in extant pangolins, it shares an even greater number of derived features with the extant Manidae not known to occur in other fossil pangolins. The specimen exhibits several morphological differences from extant *Manis gigantea* (e.g., the position of the ethmoid foramen on the frontal, trochlea profile in humerus), but it has several features, including the robust nature of the skeleton, tail length, and humeral morphology, that identify this specimen as a fossil representative of *M. gigantea*. We recognize that the skull length of SAM-PQL-21793 is smaller than the skull length of *M. gigantea* and that the lengths of the long bone elements fall between those of *M. gigantea* and *M. temminckii*. However, the midshaft widths of all the limb bones of SAM-PQL-21793 measure closest to *M. gigantea*, highlighting the robust nature of the skeleton and further suggesting that SAM-PQL-21793 resembles *M. gigantea*. Pickford and Senut (1991) discovered a complete fossil pangolin radius from Uganda that was identified as *M. gigantea* and was estimated to be between 3.6 and 3.45 Ma in age (middle Pliocene). Specimen SAM-PQL-21793 is estimated to be approximately 5 Ma in age (early Pliocene) and thus, represents the oldest specimen of *M. gigantea* yet known. Gaudin and Wible (1999) (on the basis of a cladistic analysis using 67 cranial characters) suggested that the extant African pangolins should be placed in separate genera. They suggested that the two arboreal African species, *M. tetradactyla* and *M. tricuspis*, be placed in the genus *Phataginus*, and the two terrestrial African species, *M. gigantea* and *M. temminckii*, be placed in the genus *Smutsia* (Gaudin and Wible, 1999). This suggestion has not yet been formalized because Gaudin and Wible (1999) concede that a wider range of characters, including those from the postcranial skeleton and soft tissues, should also be studied. However, if confirmed, their results suggest that specimen SAM-PQL-21793 would be the oldest representative of a formally recognized genus *Smutsia*.

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