

A SECOND EXTINCT BIG CAT FROM THE LATE QUATERNARY OF SRI LANKA

Kelum Manamendra-Arachchi

Wildlife Heritage Trust of Sri Lanka, 95 Cotta Road, Colombo 8, Sri Lanka
Email: kelum@wht.org

Rohan Pethiyagoda

Wildlife Heritage Trust of Sri Lanka, 95 Cotta Road, Colombo 8, Sri Lanka (author for correspondence)
Email: rohan@wht.org

Rajith Dissanayake

23 Ranmoor Gardens, Harrow HA1 1UQ, United Kingdom
Email: rajd@nhm.ac.uk

Madhava Meegaskumbura

Wildlife Heritage Trust, 95 Cotta Road, Colombo 8, Sri Lanka
Department of Biology, Boston University, 5 Cummington Street, Boston, MA, 02215, USA
Email: madhava@bu.edu

ABSTRACT. – A second extinct big cat, tentatively considered to be a tiger (*Panthera tigris*), is recorded from Sri Lanka for the first time from a fossil left lower carnassial found in alluvium near Ratnapura in 1962 and a sub-fossil right middle phalanx ¹⁴C dated to ~ 16,500 ybp, discovered in 1982 in a prehistoric midden at Batadomba Cave, near Kuruwita. The species is diagnosed from the only other big cats known from Sri Lanka, *Panthera pardus* and the extinct *P. leo sinhaleyus* Deraniyagala, 1938. This record significantly advances the timing of dispersal of tigers into the Indian peninsula. Tigers appear to have arrived in Sri Lanka during a pluvial period during which sea levels were depressed, evidently prior to the last glacial maximum ca. 20,000 years ago. The lion appears to have become extinct in Sri Lanka prior to the arrival of culturally modern humans, ca. 37,000 ybp.

KEY WORDS. – Sri Lanka, Pleistocene, tiger, lion, palaeontology, *Panthera tigris*.

INTRODUCTION

Apart from the leopard, which still persists in all natural habitats across Sri Lanka, the only big cat recognised from the island is an extinct lion, known only from two teeth found in alluvial deposits at Kuruwita (06°47'N, 80°22'E) (Fig. 1). Based on these, P. [E. P.] Deraniyagala (1939) erected a new subspecies of lion, *Panthera leo sinhaleyus*, designating a left lower carnassial (M₁) as holotype (the other, a fragment of a right lower canine, in too poor condition to facilitate diagnosis, was lodged as a 'metatype' in NMSL: P. Deraniyagala, 1947).

The lion has been one of the most widespread of all non-commensal mammals, having enjoyed a Pleistocene range that

included Africa, Eurasia, North America and tropical South America (Nowak, 1999: 834). While the fossil record confirms that the species' range in the Indian subcontinent did extend south to the 21st parallel and east to 87° E (Pilgrim, 1931; Dutta, 1976)—approximately a line joining Gujarat to Bengal—there is no evidence of the existence of the lion in Asia east of Bengal or anywhere in peninsular India and Sri Lanka, except for *P. leo sinhaleyus*.

The Holocene range of the tiger, however, extends to the southernmost tip of peninsular India and to all of tropical continental Asia (Hooijer, 1947; Aziz & de Vos, 1999). The apparent absence of evidence of tigers in Sri Lanka and Pleistocene peninsular India has led to the conclusion that tigers arrived in south India "too late to get into Ceylon"

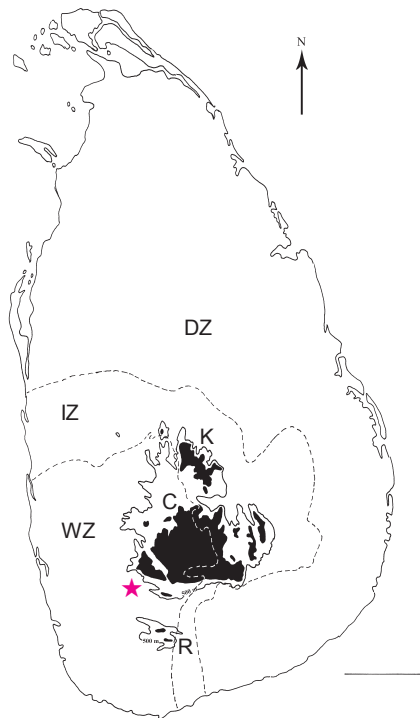


Fig. 1. Map of Sri Lanka, showing location of Batadomba Cave, Kuruwita (star), indicating also the climatic zones: DZ, dry zone; IZ, intermediate zone; WZ, wet zone; the principal mountain ranges: C, Central hills; K, Knuckles hills; and R, Rakwana hills; and the 500 m and 1,000 m contours. Scale bar: 50 km.

(Pocock, 1930) as a result of the India-Sri Lanka land bridge having been submerged since the Late Pleistocene. On the basis of the few known Indian tiger fossils dating to the Holocene (Lydekker, 1886a,b; Sankhala, 1978; Herrington, 1987; Turner & Antón, 1997;) the recent literature too, dates the arrival of tigers in the Indian peninsula only to the end of the last glacial maximum, ca. 12,000 ybp (Hemmer, 1987; Kitchener, 1999; Kitchener & Dugmore, 2000).

Recognizing that “Distinguishing apart the teeth of a tiger from those of a lion is difficult”, P. Deraniyagala (1939) distinguished the holotype M_1 of *Panthera leo sinhaleyus* from those of *P. tigris* entirely by its larger size, concluding that “The Ceylon fossil, although narrower and more elongate, agreed in general size with the lions’ teeth”.

In 1962, second a complete M_1 was discovered in alluvium in the course of excavating a gem pit near Ratnapura. Tentatively identified as having come from a lion, it was lodged in the National Museum’s Ratnapura branch. In 1982, a complete felid right-limb middle phalanx (45.3×20.7×18.5 mm l×w×h) ^{14}C dated to 13,500 ybp and identified tentatively as belonging to a “large lion” (S. [U.] Deraniyagala, 1992; subsequently revised to 16,500 ybp: see S. Deraniyagala, 2001), together with undiagnosable fragments of two other big-cat phalanges and an upper premolar were found in a late Pleistocene midden in Batadomba Cave (Fig. 2), at Kuruwita, a prehistoric human habitation (11,500–37,000 ybp: S. Deraniyagala, 2004). This phalanx clearly does not belong to a leopard.

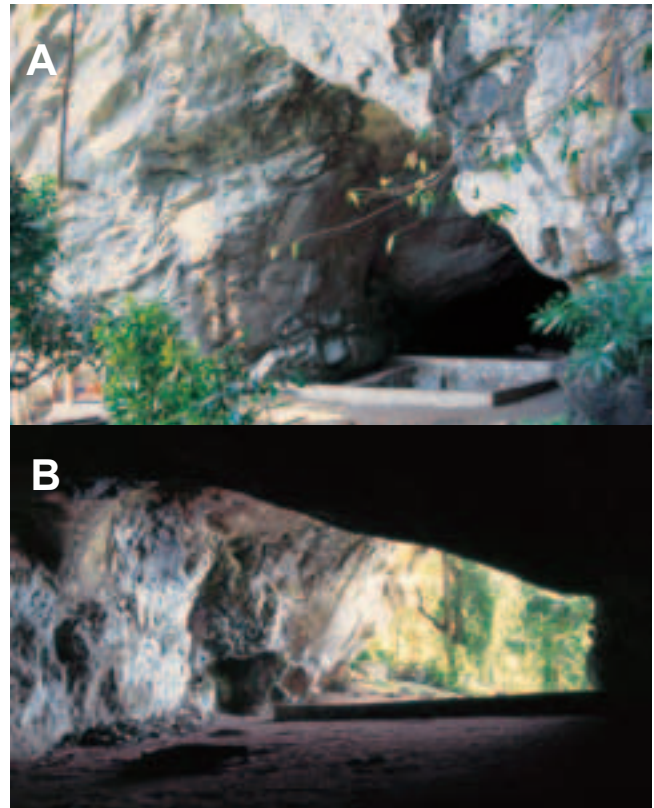


Fig. 2. (A), external and (B), internal views of Batadomba Cave, Kuruwita, Sri Lanka, the source of the tiger phalanx DASL 1982.01.

Here we show that the 1962 Ratnapura M_1 belongs to a tiger, significantly advancing the timing of the dispersal of this species into peninsular India. We also show that the “Batadomba phalanx” belonged to a big cat more closely related to the tiger than to the lion; and confirm from an examination of its holotype M_1 and a large series of recent tiger and lion teeth that *Panthera leo sinhaleyus* was indeed a lion, and that its demise appears to have preceded that of the tiger in Sri Lanka.

MATERIALS AND METHODS

Materials referred to in this study are deposited in the National Museum of Sri Lanka (Ratnapura) (NMSL); Department of Archaeology, Colombo (DASL); the Field Museum of Natural History, Chicago (FMNH); and The Natural History Museum, London (BMNH).

Osteological terminology follows Turner & Antón (1997); dental terminology follows de Muizon & Cifelli (2000). M_1 = lower carnassial (only those of the left dentary were used).

Measurements. – Metric measurements were made point-to-point, using dial vernier callipers, to an accuracy of ± 0.05 mm. Angles were measured using a protractor, to the nearest 5° .

Carnassials—the following measurements were made: total length (maximum anterior-posterior length of crown, Fig. 3a); inter-apex length (distance between protoconid and hypoconid

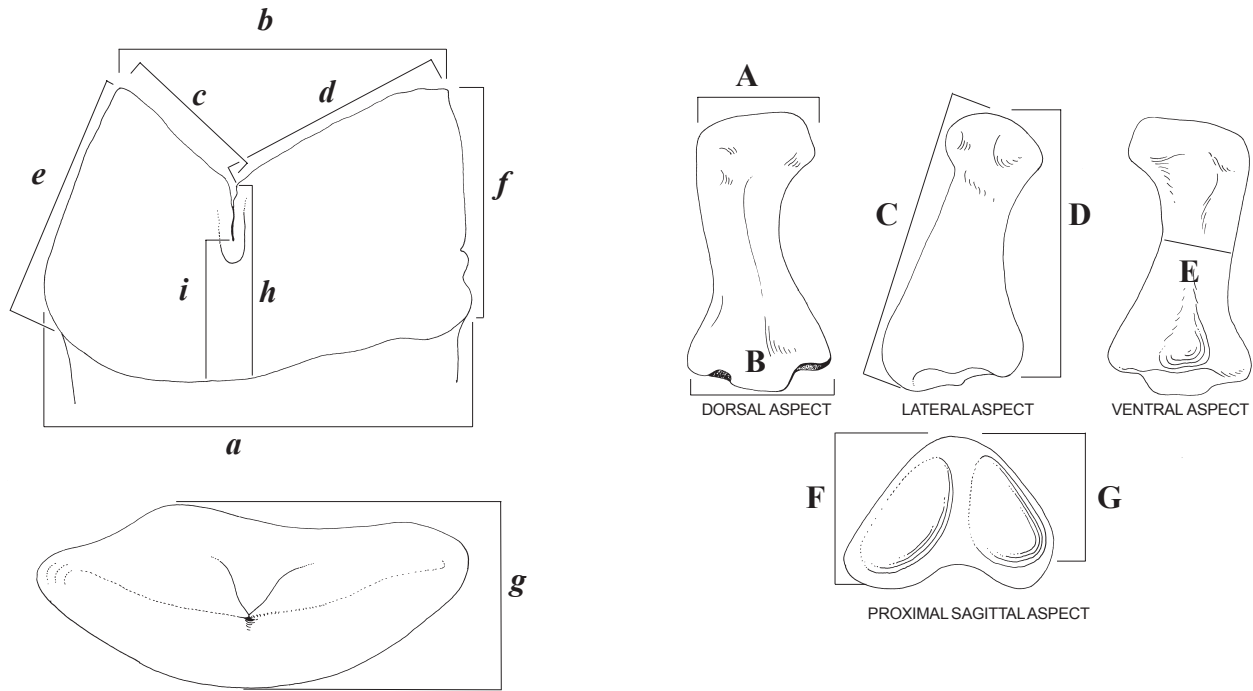


Fig. 3. (Left), measurements of M_1 (buccal aspect; see Materials and Methods): *a*, total length; *b*, inter-apex length; *c*, protoconid length; *d*, hypoconid length; *e*, protoconid height; *f*, hypoconid height; *g*, crown width; *h*, crown depth; *i*, notch depth; and (right) middle phalanx (see Materials and Methods): A, distal width; B, proximal width; C, dorsal length; D, ventral length; E, minimum width; F, maximum height; G, minimum height.

apices, Fig. 3*b*); protoconid length (length along superior edge (blade) of protoconid, Fig. 3*c*); hypoconid length (length along superior edge (blade) of hypoconid, Fig. 3*d*); protoconid height (vertical distance from enamel margin to protoconid apex, Fig. 3*e*); hypoconid height (vertical distance from enamel margin to hypoconid apex, Fig. 3*f*); crown width (maximum labial-lingual width of crown, Fig. 3*g*); crown depth (vertical distance from enamel margin to posterior angle of hypoconid, Fig. 3*h*); notch depth (vertical distance from base of median notch to enamel base, Fig. 3*i*); carnassial angle (angle between superior edges (blades) of protoconid and hypoconid).

Phalanges—the following measurements were made (see Fig. 3): distal width (maximum width of distal articulation, Fig. 3A); proximal width (maximum width of proximal articulation, Fig. 3B); dorsal length (maximum dorsal length, Fig. 3C); ventral length (maximum ventral length, Fig. 3D); minimum width (minimum width of neck of phalanx, Fig. 3E); maximum height (maximum height of proximal articulation, Fig. 3F); minimum height (minimum height of proximal articulation, Fig. 3G).

SYSTAT for Windows XP, Version 11.00.01 was used for the statistical analysis of dental and phalangeal measurements. Principal components analysis (PCA) of the character correlation matrix was used to reduce dimensionality of the morphological variables and to identify those variables that best discriminate between species. Various axis rotations were tested and one selected for optimal interpretability of variation among the characters. Discriminant function analysis (DFA) was used to confirm the results that were obtained from the

PCA and to highlight the variables that best discriminate between groups (lower carnassials and phalanges of recent tigers, recent lions and the fossil examples). Both direct and stepwise methods of discriminant analysis were employed.

TAXONOMY

Panthera leo (Fig. 4; Table 1)

Panthera leo sinhaleyus P. Deraniyagala, 1939.

Material examined. – Holotype, lower left M_1 , BMNH Pal. Dept. M 51883, 30.3 mm dorsal length; “Found immediately above gem sand that was 19 ft below the surface in a Pit at Pan Vila, Edandé Vala, Kuruwita, near milestone 51 on the Kuruwita to Ratnapura Road, Sri Lanka” (06°43' N, 80°23' E, alt. ~ 30 m above sea level), 1936.

Identification. – (See Fig. 4A, B, D). The lower carnassial of *P. leo* is distinguished from that of *P. tigris* most easily by having only a single horizontal notch on the lower half of its distal surface, see Fig. 4A, B, D (vs. two in *P. tigris*: see Fig. 4I). The carnassials of *P. leo* may also be distinguished from those of *P. tigris* by having the talonid as a fairly well-developed cusplet (vs. talonid elongate, swollen, in *P. tigris*); the aboral protoconid slope convex in appearance (vs. the smooth longitudinal ridge on aboral protoconid gives the slope a flat or concave appearance in *P. tigris*); the saddle of the talonid trough relatively short and shallow (relatively long and deep in *P. tigris*); and the inferior enamel margin curved

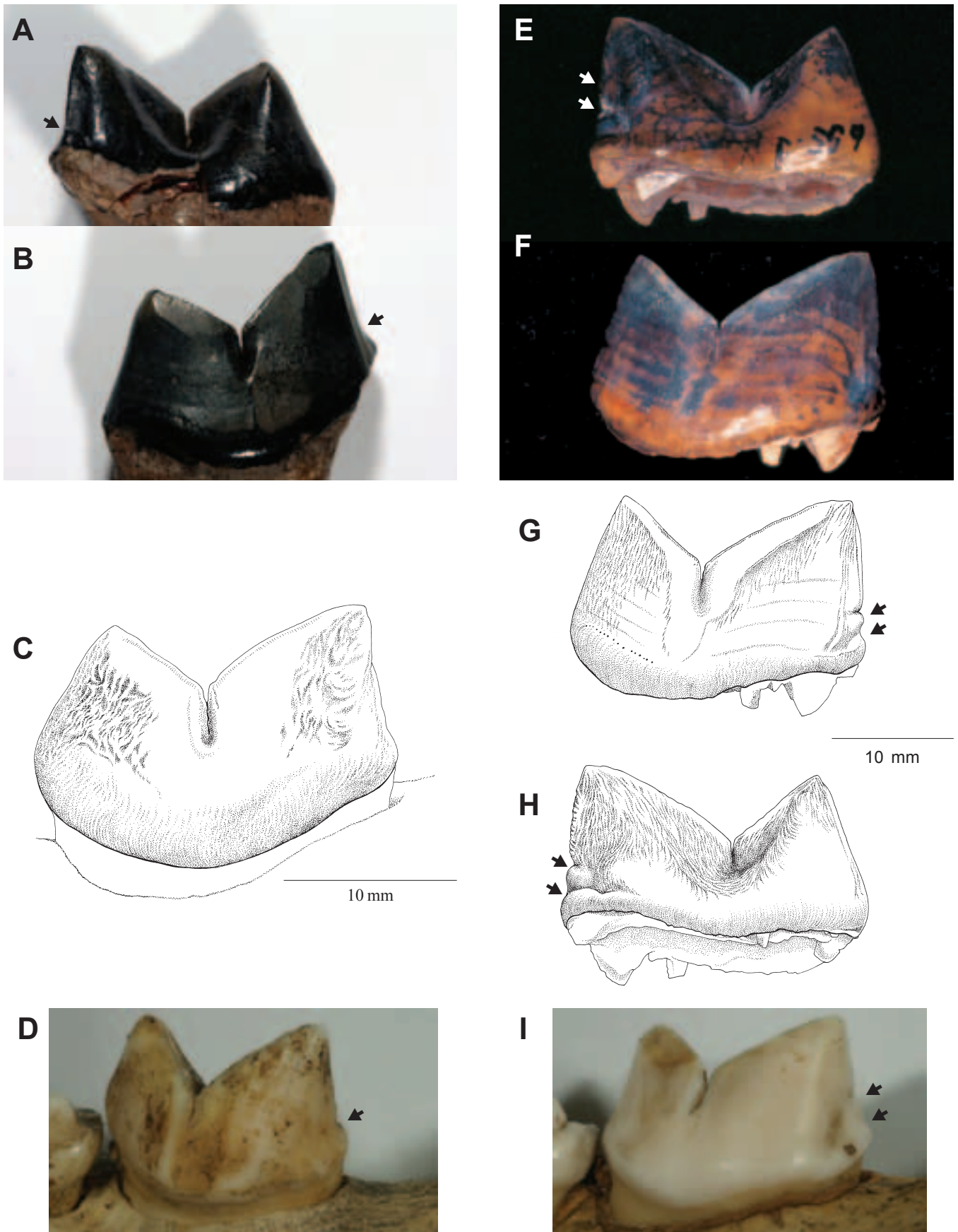


Fig. 4. Left lower M_1 : A, lingual aspect, *Panthera leo sinhaleyus*, holotype, BMNH Pal. Dept. M 51883; B, buccal aspect, *P. l. sinhaleyus*, holotype, BMNH Pal. Dept. M 51883; C, buccal aspect, *P. pardus*, NMSL uncat., Sri Lanka; D, buccal aspect, *P. l. persica*, female, BMNH 31.4.13.2, Gir Forest, India; E, lingual aspect, *P. tigris*, NMSL (Ratnapura), F559; F, buccal aspect, *P. tigris*, NMSL (Ratnapura), F559; G, buccal aspect, *P. tigris*, NMSL (Ratnapura), F559; H, lingual aspect, *P. tigris*, NMSL (Ratnapura), F559; I, buccal aspect, *P. t. tigris*, BMNH 79.11.21.197, India. Arrows indicate notches on distal surface.

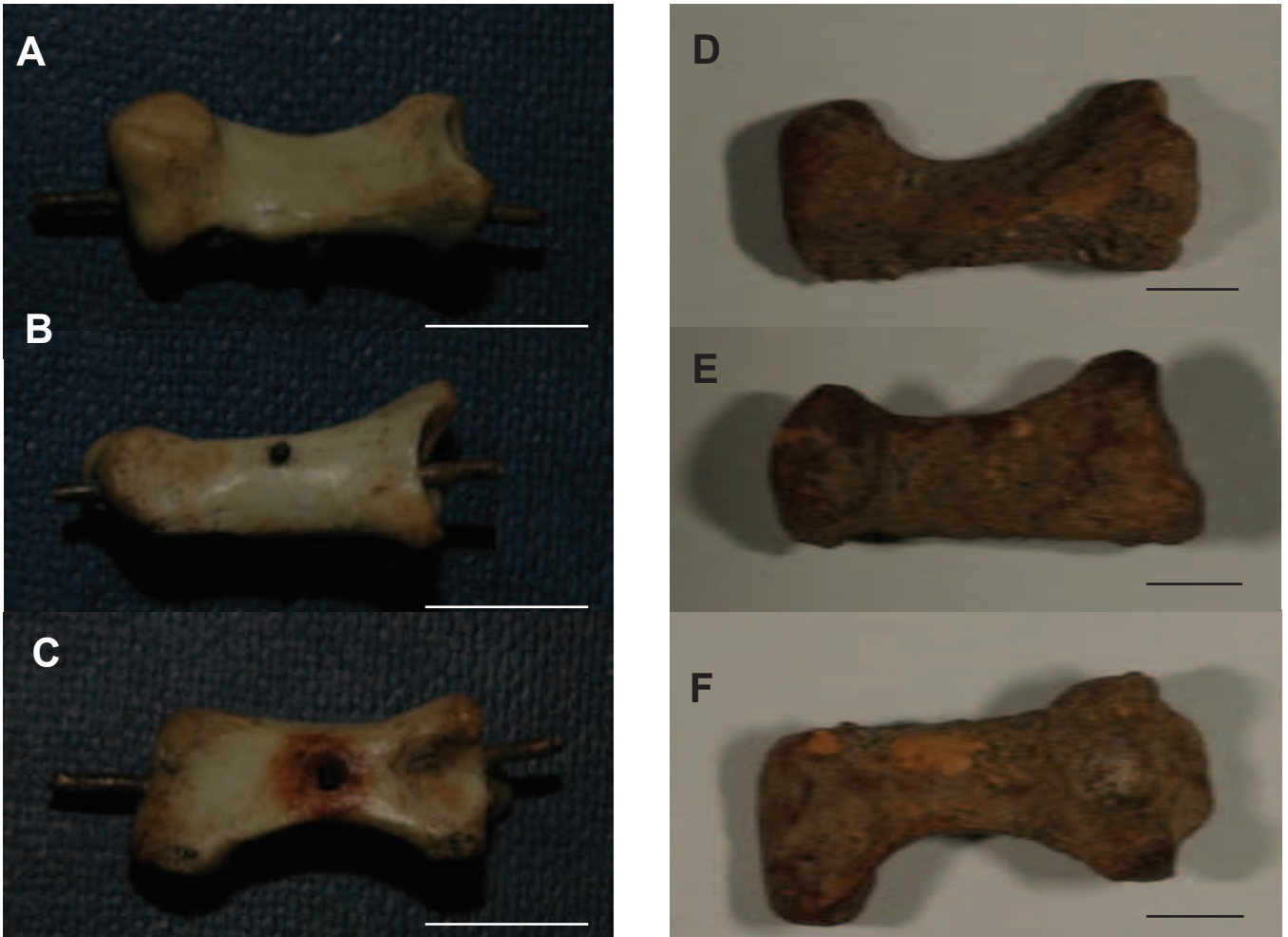


Fig. 5. A–C, dorsal, lateral and ventral aspects respectively, of right middle phalanx of *Panthera pardus*, NMSL uncat., Sri Lanka; D–F, dorsal, lateral and ventral aspects respectively, of right middle phalanx of *Panthera tigris*, DASL 1982.01, Batadomba Cave, Kuruwita, Sri Lanka. Scale bars = 10 mm.

downwards (vs. inferior enamel margin relatively straight in *P. tigris*).

Measurements of holotype M₁, BMNHM 51883 (in mm). Total length, 30.3; inter-apex length, 19.9; protoconid length, 9.3; hypoconid length, 14.2; protoconid height, 17.2; hypoconid height, 15.0; crown width, 15.3; crown depth, 14.2; notch depth, 9.7; carnassial angle, 105°.

Note. – The Sri Lankan lion was allocated to a distinct subspecies *P. leo sinhaleyus* by P. Deraniyagala (1939), but there is insufficient information to determine how it might differ from other subspecies of *Panthera leo*; for the purposes of the present paper therefore, we consider this taxon as *P. leo*.

Panthera tigris
(Figs. 4, 5; Table 1)

Material examined. – Lower left M₁, NMSL (Ratnapura) F559, length 25.7 mm, Lindagava Kumbura, Muvagama, Ratnapura (06°40'30" N, 80°24'12" E, alt. ~ 30 m above sea level), Sri Lanka, 20 May.1962. Complete sub-fossilised middle phalanx, DASL1982.01, 45.3×20.7×18.5 mm (l×w×h) from Stratum 5; two fragments of phalanges (DASL1982.02–03) from Stratum 4; and

one fragment of an upper premolar (DASL.1982.04) from Stratum 4, excavated from a midden in Batadomba Cave (see Fig. 2), Kuruwita (06°47' N, 80°23'E, alt. 460 m), Sri Lanka, 1982.

Identification. – (See Figs. 4, 5). The lower carnassial of *P. tigris* is distinguished from that of *P. leo* most easily by having two horizontal notches on the lower half of its distal surface (vs. a single notch in *P. leo*). The carnassials of *P. tigris* may also be distinguished from those of *P. leo* by having the talonid elongate and swollen (vs. talonid a fairly well-developed cusplet, in *P. leo*); the aboral protoconid flat or concave in appearance as a result of the smooth, longitudinal ridge on its buccal side (vs. aboral protoconid slope convex in appearance in *P. leo*); the saddle of the talonid trough relatively long and deep (vs. saddle of talonid trough relatively short and shallow in *P. leo*); and inferior enamel margin relatively straight (vs. inferior enamel margin curved downwards in *P. leo*).

Principal components analysis (Fig. 6) with unrotated axes on the correlation matrix of morphometric characters from the phalanges of recent tigers, recent lions and the Kuruwita right middle phalanx (DASL 1982.01) shows that the fossilized example does not overlap with the recent

Table 1. Proportional measurements of lower left carnassials of *Panthera tigris* (Ratnapura M₁, NMSL-R F559); ten recent *P. tigris*; holotype of M₁ *Panthera leo sinhaleys* (BMNH M 51883); and 27 recent *P. leo* (details of recent specimens listed in Comparative Material).

	tiger				lion			
	NMSL-R F559 M ₁	min.	max.	s.d.	BMNH M 51883 holotype M ₁	min.	max.	s.d.
inter-apex length (% of crown length)	75.5	60.2	75.5	4.4	65.7	64.1	84.0	4.2
protoconid length (% of crown length)	40.9	30.7	40.9	3.0	30.7	30.2	40.4	2.8
hypoconid length (% of crown length)	54.9	44.0	54.9	3.3	46.9	41.5	58.3	4.2
protoconid height (% of crown length)	54.1	50.7	61.4	3.7	56.8	48.6	61.7	3.4
hypoconid height (% of crown length)	51.8	43.2	55.0	3.6	49.5	47.2	59.4	3.0
crown width (% of crown length)	51.0	47.7	59.4	3.0	50.5	47.7	55.6	1.9
crown depth (% of crown length)	47.5	41.3	53.8	14.1	46.9	38.3	51.7	3.7
notch depth (% of crown length)	31.9	28.3	38.2	2.5	32.0	23.4	34.9	2.6
inter-cusp angle (degrees)	105	90	115	8	105	100	120	5
protoconid length : hyperconid length (%)	74.5	64.2	74.8	3.6	65.5	63.4	80.0	4.0
crown depth : protoconid height (%)	87.8	76.7	96.4	6.0	82.6	72.4	99.3	7.1
crown depth : hypoconid height (%)	91.7	84.7	112.5	8.7	94.7	72.1	108.8	9.7
notch depth : crown depth (%)	67.2	60.0	73.8	4.2	68.3	57.3	76.2	5.9

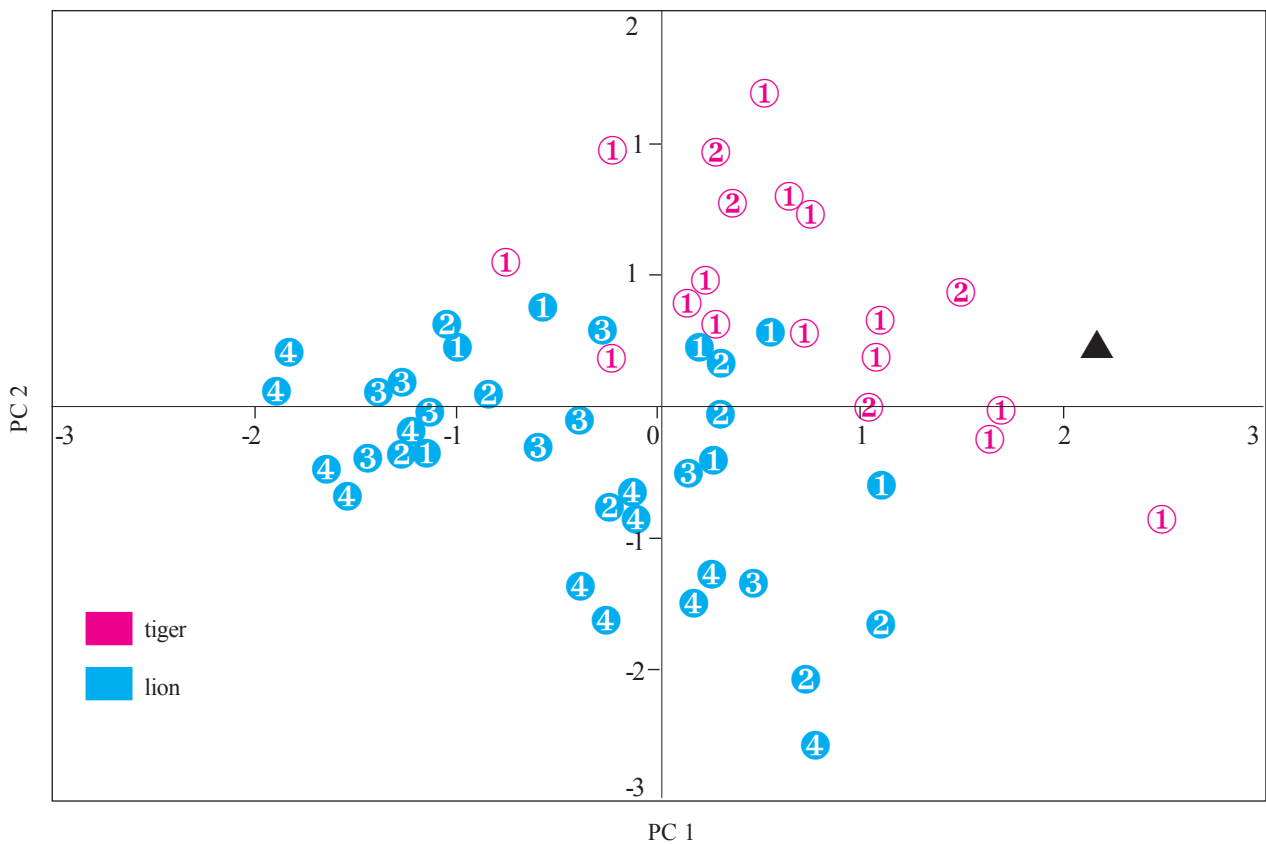


Fig. 6. Plot of principal components 1 and 2 of seven metric variables of the Kuruwita right middle phalanx, DASL1982.01 (black triangle), and available middle phalanges of pes and manus of two recent specimens of *P. tigris* (open magenta circles) and four recent specimens of African and Asian *P. leo* (solid cyan circles) (for specimen details see Comparative Material).

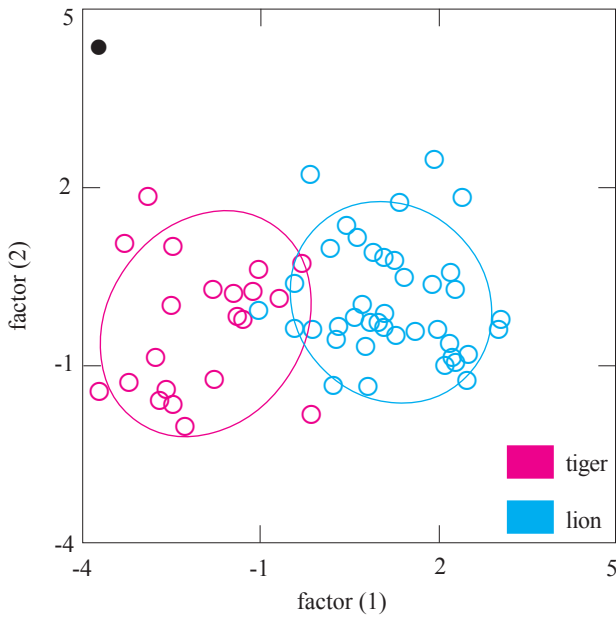


Fig. 7. Canonical variables plot of discriminant function analysis of available middle phalanges of pes and manus of two recent specimens of *P. tigris* (magenta open circles), four recent specimens of African and Asian *P. leo* (cyan open circles) and right middle phalanx from Batadomba Cave, Kuruwita (solid black circle); 95% confidence ellipses are centered on the centroid of each group. For specimen details see Comparative Material.

lions on the PC 1 axis. The PC 1 axis, which explains about 65% of the total variation, represents maximum height (factor score 0.955), proximal width (factor score 0.948) and distal width (factor score 0.936). These dimensions were larger in the Sri Lankan fossil big cat than in recent lions. The PC 2 axis, which explains about 17% of the total variation, represents minimum width (factor score 0.722) and dorsal length (factor score -0.520). The fossil overlaps with—and cannot be distinguished from—recent lions on the PC 2 axis.

Stepwise backward DFA (Fig. 7) shows that the fossilized phalanx is distinct from but closer to recent tigers than recent lions. This analysis correctly classified 100% of the fossil example, together with 93% of recent lions and 91% of recent tigers (Wilks' lambda 0.2009; $p = 0.000$). The first canonical variable best discriminates the groups and accounts for 88% of total dispersion of the groups (eigenvalue 2.542). The second canonical variable accounts for 10% of the dispersion (eigenvalue 0.35). In the canonical variables plot, the centroid for the fossil phalanx is (-3.727, 4.345), and those for recent lions (1.193, 0.063) and recent tigers (-1.913, -0.299). The first canonical variable represents mostly proximal width (standardized canonical discriminant function (SCDF) -1.573) and minimum height (SCDF -1.055). The second canonical variable represents mostly maximum height (SCDF -2.213) and minimum width (SCDF 2.164). There is a slight overlap on the first canonical variable between recent tigers and the fossil example, but no overlap between this and recent tigers or lions on the second canonical variable. Thus, according to the DFA, some of the variables of the second canonical variable could

be used to distinguish the fossilized tiger from recent tigers and recent lions: indeed, a review of the measurements shows that the distal width of the fossil example does not overlap with those of either recent lions or tigers. While assigning this phalanx tentatively to a tiger, we consider it possible that this may represent an as yet unknown species of big cat.

Measurements of M_1 , NMSL (Ratnapura) F559 (in mm). Total length, 25.7; inter-apex length, 19.4; protoconid length, 10.5; hypoconid length, 14.1; protoconid height, 13.9; hypoconid height, 13.3; crown width, 13.1; crown depth, 12.2; notch depth, 8.2; carnassial angle, 105°.

Measurements of right middle phalanx, DASL 1982.01 (in mm), width of distal articulation, 20.1; width of proximal articulation, 20.7; dorsal length, 45.3; ventral length, 42.4; minimum horizontal width, 11.3; outer height of proximal articulation, 18.5; inner height of proximal articulation, 12.5.

COMPARATIVE MATERIAL

Panthera tigris, phalanges: BMNH 1884.1.22.6, female, "Deccan", N=16; BMNH 114.K.K., male, "Mizapore, Decca[n]", N=7; FMNH 31153, sex undetermined, "Allapalli, India", N=15. Left lower carnassials: BMNH 82.12.10.1, male, "Bengal"; BMNH 10.7.21.1, female, "south-west India"; BMNH 29.11.2.1, sex undetermined, "North Canara, Bombay" [sic]; BMNH 8.8.11.19, sex undetermined, "North China"; BMNH 88.8.7.1, male, "Afghanistan"; BMNH 13.5.11, sex undetermined, "West China"; BMNH 1849.7.27.4, sex undetermined, "India"; BMNH 79.11.21.197, sex undetermined, "India"; BMNH 1938.8.12.3, male, "India"; BMNH 1884.10.30.3, sex undetermined, "India".

Panthera leo, phalanges: BMNH 68.657, female, Zambia, N=9; BMNH 1932.6.6.4, male, "Tanganyeka", N=8; BMNH 1952.11.13.1, female, "India", N=8; BMNH 1952.11.13.1, male, "India", N=9; BMNH 1932.6.6.4, male, "Tanganyeka", N=7; FMNH 15530, sex undetermined, "Africa", N=4; FMNH 73.175, female, "Africa", N=8. Left lower carnassials: BMNH 31.2.1.5, female, "Bechuanaland"; BMNH 19.7.7.942, female, "Natal"; BMNH 35.3.16.1, male, "Northwest Rhodesia"; BMNH 31.2.1.4, male, "Bechuanaland"; BMNH 25.6.17.12, sex undetermined, "NE Transvaal"; BMNH 30.12.3.1, male, "E. Transvaal"; BMNH 45.136, female, "India"; BMNH 34.11.1.4, male, "E. Transvaal"; BMNH 25.6.17.5, sex undetermined, "NE Transvaal"; BMNH 25.6.17.7, sex undetermined, "NE Transvaal"; BMNH 25.6.17.9, sex undetermined, "NE Transvaal"; BMNH 57.2.24.1, female, "India"; BMNH 31.4.13.1, male, "India"; BMNH 31.1.5.1, male, "India"; BMNH 31.1.5.2, male, "India"; BMNH 31.4.13.2, female, "India"; BMNH 1642 a, sex undetermined, "Moshonaland"; BMNH 1893.5.20.1, male, Zimbabwe; BMNH 35.3.16.2, male, "Northwest Rhodesia"; BMNH 34.11.1.3, female, "E. Transvaal"; BMNH 31.2.1.6, female, "Bechuanaland"; BMNH 93.5.21.1, sex undetermined, "Bechuanaland"; BMNH 1893.5.20.1, sex undetermined, "Zimbabwe"; BMNH 19.7.15.32, sex undetermined, "S. Rhodesia"; BMNH 87.5.16.1, male, "south of Victoria Falls"; BMNH 25.6.17.10, sex undetermined, "NE Transvaal"; BMNH 1992.167, male, Transvaal.

Panthera pardus, NMSL uncat., manus right 4th-digit middle phalanx and left lower M_1 , sex undetermined, Sri Lanka.

DISCUSSION

P. Deraniyagala (1939) did not explain explicitly how he diagnosed the holotype M_1 of *Panthera leo sinhaleyus* as belonging to a lion, though he justified its allocation to a distinct subspecies of lion by its being “narrower and more elongate” than those of recent lions in the BMNH collection. It appears that he based his species-identification essentially on Brongersma (1935), confirming this through the examination also of two recent tiger carnassials in the BMNH collection. His conclusion that the BMNH M 51883 M_1 belongs to a lion and not a tiger was supported by Hemmer (1966b) and also by our own examination.

We exclude the possibility of the Kuruwita-Ratnapura M_1 and phalanx belonging to the only other Sri Lankan big cat, the leopard (*P. pardus*), as the carnassials and phalanges of leopards are immediately distinguishable from those of lions and tigers in both morphology and size (Figs. 4, 5). The length of the lower carnassial of the largest leopard we examined was 18.4 mm, significantly short of even the smallest lion (23.5 mm) and tiger (25.0 mm) measured. The largest middle phalanx in the leopard, in the 3rd or 4th-digit of the pes, at 22.7 mm dorsal length, is significantly smaller than even the smallest tiger (31.2 mm) and lion (22.9 mm) measured. Fossil leopards are known from an archaeological context (see below), and are not different in size from recent ones. We note, however, that old museum collections of big cats may be biased towards larger animals, which may have been preferred by the sport hunters who acquired these specimens.

The phalanges of tigers and lions lack non-overlapping proportional measurements, although they separate well in multivariate space (see Fig. 6). At 45.3 mm dorsal length, the Batadomba phalanx is significantly (9.3%) longer than the longest recent *P. leo* phalanx measured in the BMNH collection; these average 32.8 mm (s.d. = 4.4, range 22.9–41.1 mm, N=40) in dorsal length. The dorsal lengths of the measured tiger phalanges averaged 37.4 mm (s.d. = 6.5, range 14.3–46.1, N=23). Unfortunately, we could find no way of discriminating between the middle phalanges of the digits of pes and manus, or determining the digit to which the Batadomba phalanx belongs, though based on its large size, we suspect it belongs to digit 3 or 4.

Given their close relationship (O’Brien et al., 1987), the diagnosis of lions from tigers based on bone fragments alone is challenging (see also Turner & Antón, 1997). While lion and tiger carnassials do not separate clearly in mensural statistics, Herrington (1987: fig. 4a) showed them to be distinct in shape in occlusal view. We were, however, unable unambiguously to distinguish lion and tiger carnassials using principal components analysis and discriminant function analysis based on the seven measurements made (see Fig. 3a–g, and Comparative Material for details of measured examples). The left lower carnassials of recent lions, tigers and the fossil examples used in this analysis cannot be distinguished from each other with confidence by either PCA or DFA. Principal components analysis served to demonstrate that M_1 F599, the holotype carnassial of *P. l. sinhaleyus*, and

those of recent lions and tigers show considerable overlap on both PC axes. Recent lion and tiger carnassials could not be unambiguously discriminated from each other in DFA, which correctly classified only 81% of the recent lions and 80% of the recent tigers (Wilks’ lambda = 0.5093; $p = 0.0293$). Inclusion of the fossil teeth together with the recent lion and tiger carnassials gave a similar result. DFA correctly classified 100% of the holotype of *P. l. sinhaleyus* and 100% of F599, 70% for recent tigers and 41% for the recent lions (Wilks’ lambda = 0.3046; $p = 0.20$). Here the standardized canonical discriminant functions were greatest for inter-apex length (0.953) and crown depth (-0.719). Owing to their inconclusive outcomes, the dental PC and DFA plots are not shown.

Hemmer (1966a: 23; trans. Colin Groves, in litt.) showed that lion and tiger molars could be differentiated on the basis of several subtle morphological character states, as follows. Lion—“The talonid is a fairly well-developed cusplet, and the aboral protoconid-slope usually appears convex; the trough is narrow, the saddle of the notch is usually low and the inferior enamel margin on the buccal side is curved downwards.” Tiger—“The talonid is an elongated swelling and the diminutive hypoconid is bordered by a notch, so that the aboral edge of the protoconid appears mostly concave; the protoconid is narrow, the trough is wide and the saddle of the notch is usually high; the inferior enamel margin on the buccal side is fairly straight.” We found these character states to be consistent across all 27 lion and 10 tiger left lower carnassials examined, but note that they are difficult to translate into mensural data of statistical value using the measurement techniques employed here.

The most reliable binary character state for distinguishing the lower carnassials of tigers from lions is the horizontal notch on the lower half of the posterior face of the tooth. Lions have one such notch (see Fig. 4C), whereas tigers have two (see Fig. 4G); see also Hemmer (1966a: pl. 7). The Ratnapura M_1 , however, has the lower of these notches more prominent (Fig. 4H) than those on the recent tiger teeth examined (see Fig. 4G), a character that may have taxonomic significance. It is possible also that dental characters have undergone change in these cats during the past 16 millennia (see Szuma, 2003, for evidence of dental variation in the Red fox in the decadal time frame).

We cannot be certain that the Batadomba phalanx (DASL 1982.01) and the Ratnapura M_1 (NMSL F559) belong to the same species. While we are confident that the Ratnapura M_1 belongs to a tiger, the Batadomba phalanx, while separating distinctly from the lion, is clearly distinct also from the tiger. At 45.3 mm dorsal length, this phalanx is less than 2% shorter than the longest of the 23 BMNH tiger phalanges (46.1 mm, from a female, BMNH 1884.1.22.6, from the “Deccan” [peninsular India]), which suggests that this cat was comparable in size to the tiger. Pending the availability of further evidence, we choose to assign both the M_1 and the phalanx to a single species, tentatively the tiger. While conceding that the large size of the Batadomba phalanx could be the result of taphonomic bias, the size of the Sri Lankan cat appears to have been remarkable given that insular *P. tigris*

populations (e.g. in the Sunda Islands) have generally been noted to be smaller than their mainland counterparts (Luo et al., 2004).

The assignment of the Batadomba phalanx to *P. tigris* adds confidence to our diagnosis of this species from Sri Lanka, especially since trade in tiger teeth has been implicated in prehistoric records of the tiger in islands such as Borneo, where there is no other evidence of their presence and no apparent reason for their extirpation (Wilkinson & O'Reagan, 2003). Indeed, the presence of sharks' teeth in the Batadomba Cave middens (pers. obs.), more than 50 km from the sea, indicates that teeth may have played a role in commerce even in prehistoric Sri Lanka. However, the discovery of the Ratnapura tiger M₁ in alluvium, together with hippopotamus and rhinoceros fossils, demonstrates that tigers did indeed occur in the island.

Based on present-day submarine topography, a functional land bridge between Sri Lanka and India requires a sea-level lowering of only ~ 10 m. Sea levels were ~ 120 m below present-day levels at the last glacial maximum ca. 20,000 ybp (Siddall et al., 2003), thus facilitating a more than 80 km-wide terrestrial connection. It appears likely that sea levels were sufficiently depressed during the final ~ 200,000 years of the Pleistocene to have supported a land connection between Sri Lanka and India for all or most of that time (Bossuyt et al., 2004), and probably until 5,000–10,000 ybp (S. Deraniyagala, 1992; Anderson, 1998; Yokoyama et al., 2000).

While the present data push back the date of arrival of tigers in peninsular India, they do not facilitate a conclusion as to when these big cats first arrived in the peninsula. Tigers are known from Java around two million ybp (Hemmer, 1987), and may have reached India and Sri Lanka at any time during the Pleistocene or Late Pliocene, though the lack of fossil evidence does not permit a conclusive resolution of this question. Indeed, there is no known barrier to the dispersion of tigers into the Indian peninsula during the Pleistocene, though Kitchener & Dugmore (2000) speculated that the widespread presence of short grasslands may have resulted in the tiger being altogether absent, or present only in very small numbers, during this period, surviving successive glacial maxima in refugia such as the moist forests of the south-western Western Ghats mountains. The wet zone of Sri Lanka may have provided another such refugium.

It appears however, that despite the existence of a land bridge, an ecological impediment to the dispersion of moist-forest faunas between the mainland and Sri Lanka did exist for much of the past 500,000 years (Bossuyt et al., 2004), though the nature of this barrier is not known. Although the climatic history of South Asia is not well documented, there is evidence that the climates of peninsular India and Sri Lanka experienced protracted desiccation during Pleistocene glacial maxima (S. Deraniyagala, 1992; Pant & Rupa Kumar, 1997), possibly resulting in desertification of the land bridge between India and Sri Lanka for much of that time. Even during the present relatively pluvial period, southern India and northern Sri Lanka are remarkably dry, precipitation being seasonal and rarely

exceeding 1,500 mm yr⁻¹, with a vegetation of tropical dry shrub-land, a habitat not associated with tigers. In view of tigers having appeared in Sri Lanka, established a population sufficient to have justified hunting, and then become extinct at the end of the last glacial maximum, we suspect that their entry to Sri Lanka (and therefore peninsular India) may have coincided with a pluvial phase during or prior to the previous interglacial, ca. 70,000–200,000 ybp, their apparent absence from Pleistocene India during this period being a sampling artefact.

There is no fossil evidence in Sri Lanka that facilitates dating of the appearance on the island of leopards, which arrived in Asia 170,000–300,000 ybp (Uphyrkina et al., 2001; Meijaard, 2004). The leopard is known, however, from cave middens, including those at Batadomba Cave, ¹⁴C dated to 31,000 ybp (S. Deraniyagala, 1992), suggesting that it co-existed with the tiger in Sri Lanka for several thousand years before the latter disappeared. Leopards are also known from the Pleistocene of India, from Billa Surgam cave in Karnul (Andhra Pradesh State) and alluvial deposits at Susunia (West Bengal State) (Saha et al., 1984). The case in Sri Lanka appears to have been the reverse of the model proposed by Wilkinson & O'Reagan (2003), which suggests that tigers were responsible for the extirpation of leopards on Bali, if indeed leopards did reach that island.

Despite the existence of a Pleistocene land bridge, there are no records from Sri Lanka, either fossil or recent, of several present-day south Indian large mammals, such as the wolf (*Canis lupus*), nilgai (*Boselaphus tragocamelus*), four-horned antelope (*Tetracerus quadricornis*) and blackbuck (*Antelope cervicapra*). There is fossil evidence however, of the late Pleistocene presence in the island of the dhole (*Cuon javanicus*) (P. Deraniyagala, 1958), which has since been extirpated. The gaur (*Bos gaurus*), also known from middens at Batadomba Cave (S. Deraniyagala, 1992), appears to have persisted longer, becoming extinct only in historical times (Knox, 1681: 78). In India and Southeast Asia, the range of the tiger completely overlaps that of the gaur (Corbet & Hill, 1992), the latter serving as a prey species for the former (Lekagul & McNeely, 1988).

While tigers occur in a diversity of 'closed' habitats ranging from tropical rainforests through mangrove swamps to tall grasslands, lions are associated mainly with 'open' habitats such as savannah, grassy plains and scrub (Nowak, 1999: 825, 832). The other fauna recorded from the same midden as the Batadomba phalanx include the land snails *Acavus* and *Paludomus*, the carp *Tor khudree*, the jungle fowl *Gallus lafayettii*, gaur, and a variety of smaller mammals such as monkeys and porcupines (S. Deraniyagala, 1992: 314; pers. obs.). While many of these species occur in all Sri Lankan forest types, members of the endemic Sri Lankan mollusc genus *Acavus* are restricted to closed-canopy monsoon or 'rain' forest (Hausdorf & Perera, 2000). The late Pleistocene fauna of the Ratnapura area also included a now-extinct hippopotamus, *Hexaprotodon sinhaleyus* and rhinoceroses, *Rhinoceros sinhaleyus* and *R. kagavena* (see P. Deraniyagala, 1963; S. Deraniyagala, 1992). Teeth of *R. sinhaleyus* (= *R. sondaicus*: see Laurie et al., 1983), from Adavatta, Lunugala



Fig. 8. The lion in Sri Lankan art. Stylized lions such as this one at Anuradhapura (6th century, AD) are common in Sri Lanka—evidently the work of sculptors who had not seen the living animal.

(Sri Lanka) have been thermoluminescence dated to $80,000 \pm 20,000$ ybp (S. Deraniyagala, 2004). Indeed, *R. sondaicus*, the Javan rhinoceros, is a rainforest species (whereas the Indian rhinoceros, *R. unicornis*, is typical of the floodplains ecosystem of the terai). These data suggest that the late Pleistocene habitat of Kuruwita comprised swampland and moist, closed-canopy rain forest that seems to have persisted until large-scale clearing commenced ca. 150 ybp: elsewhere in the range of these species, such habitats are associated closely with tigers, but not with lions.

Further, rhinoceros, hippopotamus and lion remains are not represented in Sri Lankan cave middens: they seem to have disappeared before the occupation of these caves by early modern humans. (The records of lion remains in the Batadomba Cave middens—see S. Deraniyagala, 1992—are erroneous: the Batadomba phalanx, here attributed to a tiger, is the only specimen in sufficiently intact condition as to facilitate definitive identification). The lions therefore appear to have been victims of the advancing rainforests and dense monsoon forests that accompanied the pluvial phase that saw the advent of the tiger in Sri Lanka. While the Kuruwita and Ratnapura fossils show that lions and tigers were sympatric in this area, however, there is no evidence to suggest they were syntopic.

The Late Pleistocene is also significant because it was during this time that the initial dispersion of modern humans occurred. Although stone tools probably dating back to the Mid-Pleistocene have been found (S. Deraniyagala, 1992), the

earliest direct evidence of modern humans in Sri Lanka dates to ca. 37,000 ybp (S. Deraniyagala, 2004). Whether hunting pressure was sufficient to extirpate tigers from the island, however, is open to question: there is no direct evidence to support or refute the idea that modern humans impacted negatively on the fauna, resulting in ‘prehistoric overkill’ sensu Martin (1984).

Extinctions on islands have generally been associated more with predation and prolonged attrition (“sitzkrieg”) than with environmental change (Barnosky et al., 2004; Guthrie, 2004). While hunting may have impacted on the population of tigers in Sri Lanka, habitat loss too, might have been an important determinant. Premathilake & Risberg (2003) show from a study of pollen that at Horton Plains, a present-day tropical montane rainforest (2,100 m a.s.l., ~40 km distant from Kuruwita), that a significantly cooler climate dominated 24,000 ybp, giving way to grasslands 18,000 ybp, semi-deciduous seasonal forest establishing itself about 14,000 ybp, with the final transformation into rainforest taking place only about 9,000 years ago. Ungulate prey of 5.3–63.8 animals km^{-2} are required to support typical tiger densities of 3.2–16.8 100 km^{-2} (Karanth et al., 2004; Karanth & Stith, 1999). Both reduced prey density and shrinkage of dense forest (resulting from desiccation during the last glacial maximum) may significantly have reduced the range and population of the tiger in Sri Lanka, with human predation accelerating its demise. Opposing phases of climate-driven habitat flux appear to explain the disappearance of both the lion and the tiger from Sri Lanka, leaving this territory to the only truly generalist Asian big cat, the leopard. Even today, leopards are ubiquitous in Sri Lanka, persisting in all natural habitats and many anthropogenic ones, from sea level to montane cloud forest at up to 2,400 m a.s.l.

P. Deraniyagala (1939) supported his assignment of the Kuruwita M_1 to a lion rather than a tiger in part because of the “almost complete lack of a reference to the tiger in Ceylon’s art, legend and folk lore when compared with the frequent appearance of the lion in these fields...” (P. Deraniyagala, 1958: 87). The appearance of the lion in Sri Lanka’s art, legend and folklore, however, cannot serve as evidence of the presence of lions in the island during historical times. The majority ethnic group of Sri Lanka, the Sinhalese, derive their name from ‘sinha’, the Sanskrit for lion; the name of the island being a corruption of “si[n]hala-dweepa”, which translates as “island of the lion race”. This association with lions appears to have originated from Indo-Aryan colonisers of the island in the sixth century BCE. “The original home of the first Indo-Aryan immigrants to Sri Lanka was probably north-west India and the Indus region” (de Silva, 1981: 3). As it happens, north-west India remains the only part of the subcontinent in which lions have been reported during historical times. As P. Deraniyagala (1958) himself points out, the lions in Sri Lankan art are heavily stylised and were evidently the work of sculptors who had not seen the living animal (see Fig. 8).

The frequency with which the ‘sinha’ root appears in Sri Lankan place names cannot be used as evidence for the former occurrence of lions there. Singapore, which derives from the Sanskrit ‘sinha’ (= lion) and ‘pura’ (= city), and Singaraja (=

lion king) in Bali are two prominent instances where the lion has infiltrated the etymology of places in which its has never existed, thanks to the spread of Indo-Aryan culture. That such place names should be commonplace in Sri Lanka while being almost entirely absent in peninsular India (where, too, they ought then to have been present) is also evidence of an origin based on culture and not the physical presence of lions.

ACKNOWLEDGEMENTS

We thank Colin Groves (Australian National University, Canberra) and David Polly (Queen Mary, University of London) for critical review that served significantly to improve the manuscript; and are further grateful to the former for helpful discussion and for translating the portion of Hemmer (1966a) quoted in the text. Richard Sabin, Norman McLeod, David Gower, J. J. Hooker, Daphne Hills and Andy Carrant (all of BMNH); and Bill Stanley and Robert F. Inger (FMNH) provided access to material, hospitality and guidance during visits to their institutions. We are grateful also to Siran U. Deraniyagala, former Director General of Archaeology, Sri Lanka, for inviting K. M.-A. to work on the identification of fossil animals in the Department's collection, for the loan of specimens, and for helpful discussion.

LITERATURE CITED

- Anderson, R. C., 1998. Submarine topography of Maldivian atolls suggests a sea level of 130 metres below present at the last glacial maximum. *Coral Reefs*, **17**: 339–341.
- Aziz, F. & J. de Vos, 1999. The fossil faunas from the Citarum area, West Java, Indonesia. *Deinsea*, **7**: 21–32.
- Barnosky, A. D., P. L. Koch, R. S. Feranec, S. L. Wing & A. B. Shabel, 2004. Assessing the causes of Late Pleistocene extinctions on the continents. *Science*, **306**: 70–75.
- Bossuyt, F., M. Meegaskumbura, N. Baenerts, D. J. Gower, R. Pethiyagoda, K. Roelants, A. Mannaert, M. Wilkinson, M. M. Bahir, K. Manamendra-Arachchi, P. K. L. Ng, C. J. Schneider, O. van Oomen & M. C. Milinkovitch, 2004. Local endemism within the Western Ghats–Sri Lanka Biodiversity Hotspot. *Science*, **306**: 479–481.
- Brongersma, L. D., 1935. Notes on some recent and fossil cats, chiefly from the Malay Archipelago. *Zoologische Mededelingen*, **8**: 1–89.
- Corbet, G. B. & J. E. Hill, 1992. *The mammals of the Indomalayan Region: a systematic review*. Oxford Univ. Press, Oxford. viii+488 pp.
- de Muizon, C. & R. L. Cifelli, 2000. The “condylarths” (archaic Ungulata, Mammalia) from the Early Palaeocene of Tiupampa (Bolivia): implications on the origin of South American ungulates. *Geodiversitas*, **22**: 47–150.
- de Silva, K. M., 1981. *A history of Sri Lanka*. Oxford University Press, Delhi. xx+603 pp.
- Deraniyagala, P. E. P., 1939 (1938). Some fossil animals from Ceylon, Part II. *Journal of the Royal Asiatic Society (Ceylon Branch)*, **34**: 231–239.
- Deraniyagala, P. E. P., 1947. Some fossil animals from Ceylon, Part V. *Journal of the Royal Asiatic Society (Ceylon Branch)*, **37**: 221–230.
- Deraniyagala, P. E. P., 1958. *The Pleistocene of Ceylon*. Ceylon National Museums, Colombo. ix+164 pp., 58 pl.
- Deraniyagala, P. E. P., 1963. Some mammals of the extinct Ratnapura Fauna of Ceylon Part V, with reconstructions of the hippopotamus and the gaur. *Spolia Zeylanica*, **30**: 5–25, pls. 1–5.
- Deraniyagala, S. U., 1992. *The prehistory of Sri Lanka: an ecological perspective*. Memoir 8, 2nd ed. Archaeological Department, Colombo. 813 pp.
- Deraniyagala, S. U., 2001. *The prehistory of Sri Lanka: an ecological perspective: Addendum 1B*. www.the-prehistory-of-sri-lanka.de, accessed 15 Feb. 2005.
- Deraniyagala, S. U., 2004. *Prehistoric basis for the rise of civilization in Sri Lanka and southern India*. Sri Lanka Deputy High Commission in Chennai. 28 pp.
- Dutta, A. K., 1976. Occurrence of fossil lion and spotted hyena from Pleistocene deposits of Susunia, Bankura District, West Bengal. *Journal of the Geological Society of India*, **17**: 386–391.
- Guthrie, R. D., 2004. Radiocarbon evidence of mid-Holocene mammoths stranded on an Alaskan Bering Sea island. *Nature*, **429**: 746–749.
- Hausdorf, B. & K. S. Perera, 2000. Revision of the genus *Acavus* from Sri Lanka (Gastropoda: Acavidae). *Journal of the Malacological Society of London*, **66**: 217–231.
- Hemmer, H., 1966a. Untersuchungen zur Stammesgeschichte der Pantherkatzen (Pantherinae). Part 1. *Veröffentlichung des Zoologische Staatssammlung München*, **11**: 1–121.
- Hemmer, H., 1966b. Fossilbelge zur Verbreitung und Artgeschichte des Löwen, *Panthera leo* (Linné, 1758). *Säugetierkundliche Mitteilungen*, **15**: 289–300.
- Hemmer, H., 1987. The phylogeny of the tiger (*Panthera tigris*). In: Tilson, R. L. & U. S. Seal (eds.), *Tigers of the world: the biology, biopolitics, management, and conservation of an endangered species*. Noyes Publications, Park Ridge. Pp. 28–35.
- Herrington, S. J., 1987. Subspecies and the conservation of *Panthera tigris*: preserving genetic heterogeneity. In: Tilson, R. L. & U. S. Seal (eds.), *Tigers of the world: the biology, biopolitics, management, and conservation of an endangered species*. Noyes Publications, Park Ridge. Pp. 51–61.
- Hooijer, D. A., 1947. Pleistocene remains of *Panthera tigris* (Linnaeus) subspecies from Wanh sien, Szechwan, China, compared with fossil and recent tigers from other localities. *American Museum Novitates*, **1346**: 1–17.
- Karant, K. U., J. D. Nichols, N. S. Kumar, W. A. Link & J. E. Hines, 2004. Tigers and their prey: predicting carnivore densities from their prey abundance. *Proceedings of the National Academy of Sciences*, **101**: 4854–4858.
- Karant, K. U. & B. M. Stith, 1999. Prey depletion as a critical determinant of tiger population viability. In: Seidensticker, J., S. Christie & P. Jackson (eds.), *Riding the tiger: tiger conservation in human-dominated landscapes*. Cambridge University Press, Cambridge. Pp. 100–113.
- Kitchener, A. C., 1999. Tiger distribution, phenotypic variation and conservation issues. In: Seidensticker, J., S. Christie & P. Jackson (eds.), *Riding the tiger: tiger conservation in human-dominated landscapes*. Cambridge University Press, Cambridge. Pp. 19–

- 39.
- Kitchener A. C. & A. J. Dugmore, 2000. Biogeographical change in the tiger, *Panthera tigris*. *Animal Conservation*, **3**: 113–124
- Knox, R., 1681 (2nd ed., 1989, J. H. O. Paulusz, Ed.). *An historical relation of the island Ceylon*. Tissara Prakashakayo, Dehiwala. lii+688 pp.
- Laurie, W. A., E. M. Lang & C. P. Groves, 1983. *Rhinoceros unicornis*. *Mammalian Species*, **211**: 1–6.
- Lekagul, B. & J. A. McNeely, 1988 (2nd ed.). *Mammals of Thailand*. Association for the Conservation of Wildlife, Bangkok. li+758 pp.
- Luo, S. –J., J. –H. Kim, W. E. Johnson, J. van der Walt, J. Martenson, N. Yuhki, D. G. Miquelle, O. Uphyrkina, J. M. Goodrich, H. B. Quigley, R. Tilson, G. Brady, P. Martelli, V. Subramaniam, C. McDougal, S. Hean, S. –Q. Huang, W. Pan, U. K. Karanth, M. Sunquist, J. L. D. Smith & S. J. O’Brien, 2004. Phylogeography and Genetic Ancestry of Tigers (*Panthera tigris*). *PLOS Biology*, **2**: 2275–2293.
- Lydekker, R., 1886a. Preliminary note on the Mammalia of the Karnul caves. *Records of the Geological Survey of India*, **19**: 120–122.
- Lydekker, R., 1886b. The fauna of the Karnul caves. *Palaeontologica Indica*, Ser. 10, **4**: 23–58, pls. 7–11.
- Martin, P. S., 1984. Prehistoric overkill: the global model. In: Martin, P. S. & R. G. Klein (eds.), *Quaternary extinctions: a prehistoric revolution*. University of Arizona Press, Tucson. Pp. 354–403.
- Meijaard, E., 2004. Biogeographic history of the Javan leopard *Panthera pardus* based on a craniometric analysis. *Journal of Mammalogy*, **85**: 302–310.
- Nowak, R. M., 1999. *Walker’s Mammals of the World* (6th ed.). Johns Hopkins University Press, Baltimore. Vol. 1, pp. i–li+1–836+ i–lxx.
- O’Brien, S. J., G. E. Collier, R. E. Benveniste, W. G. Nash, A. K. Newman, J. M. Simonson, M. A. Eichelberger, U. S. Seal, D. Janssen, M. Bush & D. E. Wildt, 1987. Setting the molecular clock in Felidae: the great cats, *Panthera*. In: Tilson, R. L. & U. S. Seal (eds.), *Tigers of the world: the biology, biopolitics, management, and conservation of an endangered species*. Noyes Publications, Park Ridge. Pp. 10–27.
- Pant, G. P. & K. Rupa Kumar, 1997. *Climates of South Asia*. Wiley, New York. 344 pp.
- Pilgrim, G. E., 1931. The fossil Carnivora of India. *Palaeontologica Indica*, **18**: 1–232.
- Pocock, R. I., 1930. Tigers. *Journal of the Bombay Natural History Society*, **33**: 505–541.
- Premathilake, R. & J. Risberg, 2003. Late Quaternary climate history of the Horton Plains, central Sri Lanka. *Quaternary Science Review*, **22**: 1525–1541.
- Saha, K. D., S. Banerjee & B. Talukder, 1984. Occurrence of fossil *Panthera pardus* Linn. from the Pleistocene deposits of Susania, Bankura, West Bengal. *Bulletin of the zoological Survey of India*, **6**: 257–259.
- Sankhala, K., 1978. *Tiger! The story of the Indian tiger*. Collins, London. 224 pp.
- Siddall, M., E. J. Rohling, A. Almogi-Labin, Ch. Hemleben, D. Meischner, I. Schmelzer & D. A. Smeed, 2003. Sea-level fluctuations during the last glacial cycle. *Nature*, **423**: 853–858.
- Szuma, E., 2003. Microevolutionary trends in the dentition of the Red fox (*Vulpes vulpes*). *Journal of Zoological Systematics and Evolutionary Research*, **41**: 47–56
- Turner, A. (& M. Antón, illustr.) 1997. *The big cats and their fossil relatives*. Columbia University Press, New York. xxvii+234 pp.
- Uphyrkina, O., W. E. Johnson, H. Quigley, D. Miquelle, L. Marker, M. Bush & S. J. O’Brien, 2001. Phylogenetics, genome diversity and origin of modern leopard, *Panthera pardus*. *Molecular Ecology*, **10**: 2617–2633.
- Wilkinson, D. M. & H. J. O’Reagan, 2003. Modelling differential extinctions to understand big cat distributions on Indonesian islands. *Global Ecology and Biogeography*, **12**: 519–524.
- Yokoyama, Y., K. Lambeck, P. De Deckker, P. Johnston & L. K. Fifield, 2000. Timing of the last glacial maximum from observed sea-level minima. *Nature*, **406**: 713–716.