Original investigation

A taxonomic revision of the tigers (*Panthera tigris*) of Southeast Asia

By J.H. Mazák and C.P. Groves

Shanghai Science and Technology Museum (formerly Shanghai Natural History Museum), Shanghai, PR China; and School of Archaeology and Anthropology, Australian National University, Canberra, ACT, Australia

Abstract

The taxonomic affinity of Southeast Asian tigers is re-investigated. Specimens of four traditionally recognized subspecies are examined using various craniological methods, including multivariate craniometric and phenetic analysis. Sumatran tigers differ absolutely (100%) from the geographically neighbouring mainland form *P.t.corbetti*; the Javanese tiger is also 100% distinguishable from the Sumatran. They are therefore regarded as two distinct species (*P.sumatrae*, *P.sondaica*) under the Phylogenetic Species Concept (PSC). The Bali tiger is classified as a subspecies of the Javanese tiger, *Panthera sondaica balica*.
© 2006 Deutsche Gesellschaft für Säugetierkunde. Published by Elsevier GmbH. All rights reserved.

Introduction

The Sumatran tiger (*Panthera tigris sumatrae*) is the only surviving member of the Sunda Islands group of tigers, although its wild population is currently in an extremely precarious state, with a maximum estimate of 500 individuals alive in the wild today (Nowell and Jackson 1996; Seidensticker et al. 1999; Shepherd and Magnus 2004). The determination of subspecific boundaries and patterns of geographic variation are regarded as of critical concern for global tiger conservation management. In recent years, there has been a series of studies attempting to establish and evaluate the current intraspecific tiger taxonomy by using biochemical and molecular genetic approaches (Cracraft et al. 1998; Goebel and Whitmore 1987; Luo et al. 2004; Newman et al. 1985; O'Brien et al. 1987; Wayne et al. 1989; Wentzel et al. 1999). There is, however, considerable divergence among different authors. Cracraft et al. (1998), using complete mitochondrial cytochrome *b* genes of 34 samples, separated living tigers into two distinct species: the mainland tiger (*Panthera tigris*, with no subspecies) and an island species (*P. sumatrae*), using the phylogenetic species concept (PSC). On the contrary, after examining three measures of mtDNA variation, Wentzel et al. (1999) concluded that the living tiger subspecies are genetically very close, suggesting an historic genetic reduction and gene flow among all races until the late Pleistocene; they therefore

disputed the traditional intraspecific tiger taxonomy. Most recently, the five traditional living subspecies were again confirmed by a molecular examination with more extensive samples and objective methods (Luo et al. 2004).

Traditionally, four subspecies of Southeast Asian tiger have been recognized on the basis of skull structure and dimensions, ground colouration and striping, and body size (Hemmer 1987; Nowell and Jackson 1996; Mazák 1968, 1979, 1981).

Their diagnostic features can be summarized as follows:

- *P.t.corbetti*, cranium size somewhat smaller than the nominate form *P.t.tigris*, with a relatively darker ground coloration and more numerous, rather short, narrow and rarely doubled stripes.
- *P.t.sumatrae*, nasal wide and short, occipital plane broad, with numerous, relatively broad stripes.
- *P.t.sondaica*, nasal long and narrow, occiput notably narrow, stripes slightly more numerous than *sumatrae*, and usually long and thin.
- *P.t.balica*, skull shape generally similar to *sondaica*, but much smaller, stripes are on average wider than *sondaica*, and more frequently duplicated, light coloured areas more or less pure white, typically three pairs of short and duplicated transverse stripes on the forehead.

Herrington (1987) maintained the traditional subspecific arrangement through a multivariate craniometric analysis on 45 samples, although some of her results may be interpreted as clinal (Kitchener 1999). Kitchener carried out a series of comprehensive evaluations on the basis of morphological and palaeogeographic analysis, and showed that most geographic variation in tigers is indeed clinal (Kitchener 1999; Kitchener and Dugmore 2000).

In our investigations, specimens of mainland Southeast Asia, the Malay peninsular and Indonesia have been studied using traditional craniometric and qualitative craniological characters. We present below a new taxonomy of Southeast Asian tigers and discuss in particular the systematic status of the Sumatran tiger.

Material and methods

In the present investigation we studied 111 adult skulls (including young adult) from the ranges of the four described Southeast Asian tiger subspecies: *P.t.corbetti*, *P.t.sumatrae*, *P.t.sondaica*, *P.t.balica*. All specimens are used for morphometric analysis and 48 samples were photographed and compared visually afterwards for a phenetic study. A large dataset of skull measurements was donated kindly by the late Dr. Vratislav Mazák to C.P.G. J.H.M studied and measured tiger specimens from nearly all major Chinese collections, and in the 1970s C.P.G in company with V. Mazák, examined specimens in London and Leiden, (including the types of *corbetti*, *sumatrae* and *sondaica*), and also examined specimens in Budapest, Singapore and Cibinong. Many of our colleagues kindly examined the specimens in several important Eurasian museums on our behalf.

Specimens studied were from the following collections:

UK: The Natural History Museum (formerly British Museum of Natural History), London: ♂♂ 30.5.22.1, 21.12.29.1, 10.3.10.8, 33.4.1.203, 32.5.2.1, 51.755, 31.7.30.1, 33.7.9.4, 30.1.4.2, 19.11.12.13, 34.334, 12.11.10.1, 20.11.14.2, 1937.12.1.1, 1937.4.12.194, 1937.4.12.198, 114.R, 37.12.1.2, 38.3.14.5; ♀♀ 30.5.22.2, 10.3.10.9, 32.5.2.2, 30.1.4.3, 56.5.6.54, 32.11.9.1, 30.1.4.1, 47.450, 35.4.6.2, 35.4.6.1, 35.4.6.3, 47.449, 1937.4.12.199, 1939.1643a, 38.3.14.6

Germany: Senckenberg Museum, Frankfurt: ♀♀ 2576; Museum für Naturkunde, A. Humboldt, Berlin: ♂♂ A 1408a, 28794, B-1, 19659, 28793; ♀♀ A 61.10, A.7.02, 14830, 7620, A 2695, 14367, 14369

France: Muséum National d'Histoire Naturelle, Paris: ♂♂ 1962-2858; ♀♀ 162-2862, 149-331, 164-248; Muséé d'Histoire Naturelle, La Rochelle: ♂♂ M159

The Netherlands: Zoölogisch Museum, Amsterdam: ♂♂ 1039, 9175, 1382, 9178, S560, S562, 1829; ♀♀ 9176, 991, 1827, 9183, 9179; Naturalis (formerly National Museum of Natural History), Leiden : ♂♂ 11633, "e", 4694, 264/Q, "d"; ♀♀ 3319, 2202, 4697, 872, "h", 806/15755, "j", no number

Czech Republic: National Museum, Prague: ♂♂ no number (date 23.XI.1978); ♀♀ no number (date 25.VI.1960)

Sweden: Naturhistoriska Riksmuseet, Stockholm: ♂♂ no number (date 1939); ♀♀ 3714

Belgium: Institute Royal des Sciences Naturelles de Belgique, Brussels: ♂♂ 9323/907E; ♀♀ 164/906, 941/907, 806/907r, 9323/9078
Hungary: Budapest Natural History Museum, Budapest: ♂♂ 4250.17
Russia: Zoological Institute of the Russian Academy of Science, St.Petersburg: ♂♂ 5737; ♀♀ 25616
China: Institute of Zoology, Academia Sinica, Beijing: ♂♂ H717, H 920, H1033, H1037, H1038, H1121; ♀♀ H1116, H1034, H1035, H1036; Kunming Institute of Zoology, Academia Sinica, Kunming: ♂♂ 90157; ♀♀ 61022; Shanghai Science and Technology Museum, Shanghai: ♂♂ 608/20646, 1355/24335, 899/3947, 1356/807; ♀♀ 3611
Singapore: Zoology Department, University of Singapore: ♂♂ 765; ♀♀ 764, 1904
Indonesia: Zoological Museum Cibinong: ♂♂ 6836, ♀♀ 2428

Craniometric characters were adapted from Mazák (1967, 1976) and are abbreviated as follows:
GLS: Greatest skull length; CBL: Condylobasal length; BL: Basal length; IFB: Infraorbital breadth; RB: Rostral breadth; IOB: Interorbital breadth; POB: Postorbital breadth; BZB: Bizygomatic breadth; MB: Mastoidal breadth; SOB: Supraoccipital breadth; OH: Occipital height; GLN: Greatest nasal length; P4L: Upper carnassial length; CP4L: C-Pm4 length ; ML: Mandible length; MH: Mandible height; M1L: Lower carnassial length; Cm1L: C-m1 length.
Additionally, J.H.M selected six polymorphic qualitative skull characters from the literature (Hemmer 1969; Mazák 1976, 1979; Mazák et al. 1978; Mazák 1979; Schwarz 1912), which were applied in a subsequent phenetic analysis; these characters are:

C1. Shape of supraoccipital bone – a. narrow; b. intermediate; c. broad
C2. Shape of occiput – a. more or less acute triangular shape; b. obtuse triangular shape
C3. Nasal – a. long and narrow; b. short and wide
C4. Form of lateral margin of occiput (lambdoidal crest) – a. obviously concave in the middle region; b. not or slightly concave in the middle region
C5. Shape of sagittal crest – a. not well convex, upper outline more or less straight; b. well convex, upper outline concave
C6. Upper margin of supraoccipital bone – a. clearly isosceles triangle; b. intermediate; c. much more rounded

In a previous study (Mazák 2004) it was confirmed that there is marked sexual dimorphism in the skulls of tigers; we therefore treated the sexes separately in all skull analysis. All craniometric data were analysed using SPSS 11.5 software. Statistics include univariate statistics (mean, standard deviation, and range), univariate and bivariate graphs, and multivariate analysis. Discriminant analysis (DFA) was performed to assess the efficacy of the selected variables and build a predictive pattern of different group memberships. Because not every measurement could be taken on every skull, we ran a number of DFA with different combinations in order to maximize either sample size or number of variables.

We developed an approach to manage the polymorphic qualitative skull characters which we call "character state variation analysis". Character states are coded as (0,1,2), the range of scores is taken to correspond with the degree of variation of one character. After coding we obtain an original numerical matrix, from which we calculate the difference within and between geographic groups (in this way we can measure the proportional difference between putative subspecies).

Subsequently, the difference within each group and between geographically neighbouring groups (i.e. the difference within *corbetti*, compared with the difference between *corbetti* and *sumatrae*) were determined through an independent-sample T test. Finally, using Z-scores to standardize the matrix, we calculate the dissimilarity coefficient and construct a dendrogram (either an UPGMA cluster analysis with STATISTICA 5.0 software, or Neighbour-joining [NJ] using MEGA 2.1 software) to reveal the phylogenetic relationships among Southeast Asian tigers.

The narrowness of the occiput and width of the nasals are two diagnostic features which have been emphasized in much previous work (Brongersma 1935; Hemmer 1969; 1976, 1979; Pocock 1929; Schwarz 1912, 1913; Seidensticker 1986; Sody 1932, 1949) to identify, respectively, the Java and Sumatran tigers. In this research we have further determined whether these characters are correlated with skull dimensions through an allometric analysis, and applied the allometric equation

$$Y = aX^b$$

where a is the regression coefficient, b is the value of the coefficient of allometry and X is either occiput height (SOB to OH) or condylobasal length (GLN to CBL). To address allometry, skull variables were log transformed, and a linear regression by the least squares estimation method was undertaken.

We use the phylogenetic species concept (Cracraft 1983, 1997) for specific determination, and employ the 75% rule for subspecific recognition; for detailed criteria of subspecies classification we refer

to the interpretations of O'Brien and Mayr (1991) and O'Brien (1996, in Nowell and Jackson 1996).

Results

Basic statistic parameters (means, standard deviations) of craniometric variables of both sexes are given in table 1.

Multivariate analysis

Male group

A one-way ANOVA shows that the following variables differ significantly ($P < 0.0001$) among geographically neighbouring male groups: SOB (*F*-value 43.845), GLN (*F*-value 12.546), POB (*F*-value 12.042), C-P4L (*F*-value 9.591), P4L (*F*-value 8.245), OH (*F*-value 8.104) and IFB (*F*-value 7.25) (Fig. 1).

Table 1. Skull measurements of Southeast Asia tigers

		♂♂				♀♀			
		Corbetti	*Sumatrae*	*Sondaica*	*Balica*	*Corbetti*	*Sumatrae*	*Sondaica*	*Balica*
GLS	M	328.61	316.22	321.32	301.53	290.53	276.67	278.19	260.4
	SD	17.78	16.89	10.52	9.16	9.98	10.21	9.14	7.52
	R	294.2–365	292.4–339	306–338	295–312	273.3–304.8	263–294	260–292	252–266.5
	n	18	10	19	3	21	16	17	3
CBL	M	288.89	281.07	284.09	270.93	259.01	246.94	248.91	235.83
	SD	11.77	12.85	8.64	7.0	8.68	8.43	8.32	5.97
	R	266–312.5	263–299.6	269–297.5	266.5–279	243–272	235.3–264.5	234–262	229–240
	n	18	10	19	3	21	16	17	3
BL	M	270.52	264.39	265.73	251.57	242.38	231.71	232.52	218.8
	SD	12.29	12.74	8.24	5.58	8.85	8.06	7.34	6.16
	R	245.8–294.3	246–283	250–278.5	248–258	224.9–253.5	220–247.5	219–244.3	212–224
	n	18	10	19	3	21	16	16	3
RB	M	92.61	93.48	93.19	87.93	83.13	80.02	80.21	74.2
	SD	4.15	4.53	3.66	2.72	4.0	4.31	3.56	2.79
	R	85.5–101.9	87.5–100.5	88.4–99.4	85.8–91	77–92.68	72.5–88.2	75.5–86.5	71–76.1
	n	18	10	19	3	21	16	16	3
IFB	M	80.79	85.79	80.38	76.57	76.08	74.68	71.01	69
	SD	4.88	3.22	2.94	0.74	4.32	4.22	2.69	
	R	73–90.5	80.5–90	75.4–86	76–77.4	68.62–82.9	67–84.7	66–75.8	
	n	19	11	20	3	21	16	17	1
IOB	M	66.47	63.24	61.44	61.4	58.82	52.84	53.45	54
	SD	6.38	3.39	3.12	4.0	4.78	2.59	3.22	1.41
	R	52–75	59–70	56–66.5	58.7–66	48.2–66.47	48–57.6	47–59	53–55
	n	19	11	20	3	21	16	17	2
POB	M	60.6	57.68	54.85	56.83	59.72	55.55	54.06	56.75
	SD	3.74	3.07	2.45	1.93	3.04	2.3	1.59	2.47
	R	53.1–68.5	52–61.8	50.8–61.8	55.3–59	52.09–66	51.5–59.3	50–56.5	55–58.5
	n	18	11	20	3	20	15	17	2
BZB	M	222.97	216.54	218.42	210.47	195.6	183.16	186.28	176
	SD	16.09	11.98	12.79	7.65	8.57	11.2	8.4	10.61
	R	184.6–247.4	202.5–238	198–243.7	202.7–218	178–207.4	168–199.7	166–200	168.5–183.5
	n	18	11	20	3	20	15	17	2
MB	M	126.14	122.91	123.39	114.67	113.0	110.13	109.32	100.6
	SD	6.34	6.38	4.86	2.47	3.16	6.3	3.93	1.44
	R	115–140	114.5–132	114–131	113–117.5	106.6–118.8	100.5–119	101.5–115	99–101.8
	n	19	10	20	3	20	15	17	2

Table 1 (_continued_**)**

		♂♂				♀♀			
		Corbetti	Sumatrae	Sondaica	Balica	Corbetti	Sumatrae	Sondaica	Balica
SOB	M	69.83	68.14	54.88	52.87	62.39	59.76	48.58	48.5
	SD	4.91	6.51	3.18	1.89	3.68	4.79	2.44	1.8
	R	60.5–78	60.5–83.4	50–62.4	51.4–55	56.5–72.5	53–68.2	44–52.5	46.5–50
	n	19	10	20	3	20	15	17	2
OH	M	100.63	95.08	95.48	84.67	86.44	81.37	81.99	71.63
	SD	7.12	6.55	3.09	4.04	2.62	4.93	2.91	1.76
	R	85.5–114	86.5–109	91–102	81–89	80–94.1	74.5–91.5	77–86	70–73.5
	n	19	10	15	3	19	15	13	3
GLN	M	109.46	96.97	106.21	102.0	97.64	86.62	90.39	84.5
	SD	6.48	4.73	3.15	7.81	4.76	4.47	3.8	5.22
	R	101–121	90–103.5	100.4–110	97–111	85.8–104.5	81–93.6	84–95.5	78.5–88
	n	19	10	15	3	19	15	13	3
ML	M	217.47	208.9	213.17	201.37	195.15	183.41	185.37	173.67
	SD	10.49	10.4	8.21	7.48	6.14	8.63	7.34	7.75
	R	193–233	196–223.5	198–226	196.7–210	186.02–203.3	174–201.5	172–197.3	166–181.5
	n	17	10	19	3	18	16	17	3
MH	M	110.44	104.56	108.38	102.23	93.21	85.49	87.76	79.3
	SD	8.04	4.66	7.54	7.4	5.91	5.0	4.93	
	R	90.5–128.8	95.5–110	96–117.5	97–110.7	84.43–104	78.3–97	79–97	
	n	17	10	19	3	18	16	17	1
P4L	M	35.61	33.75	34.25	34.6	32.86	30.78	31.35	30.57
	SD	1.05	1.28	1.11	0.36	1.1	1.19	0.68	0.81
	R	33.4–37.2	32–35.5	31.89–36	34.3–35	30–35	29–33	30–32.5	29.7–31.3
	n	20	11	19	3	21	14	16	3
CP4L	M	98.61	94.77	94.27	90.93	90.92	84.06	83.78	82.27
	SD	3.59	3.44	2.66	2.72	3.15	3.01	2.04	3.52
	R	94–104.2	89.5–99.4	89–99	88.8–94	86–97.5	77.8–90	80–87	79–86
	n	20	11	19	3	21	14	16	3
M1L	M	26.43	25.99	25.76	25.33	24.72	23.51	22.8	22.4
	SD	1.2	1.51	0.82	0.65	1.27	2.66	0.95	0.57
	R	24–28.1	23–28.4	23.5–27	24.7–26	21.93–26.75	21–32.2	21–24	22–22.8
	n	17	10	19	3	17	15	15	2
CM1L	M	115.04	110.82	111.74	107.33	105.63	98.81	99.63	96.5
	SD	3.41	4.56	3.08	4.16	4.43	3.59	3.6	2.12
	R	109.5–120.9	103–116.7	107–117	104–112	96.87–113.07	91.5–105	94.5–106	95–98
	n	17	10	19	3	17	15	15	2

As revealed by the discriminant analysis (Fig. 2), three subspecies groups are clearly separated, with no overlaps: _P.t.corbetti_, _P.t.sumatrae_ and _P.t.sondaica_. _P.t.sondaica_ and _P.t.balica_ are also somewhat separate, but with overlapping dispersions. Most specimens of _corbetti_ are localized on the right side of the plot, _sondaica/balica_ samples are on the left, while _sumatrae_ occupies an intermediate position on DF1 but is totally distinct on DF2. Function 1 and 2 summarize 64.5% and 30.6% of total variance, respectively.
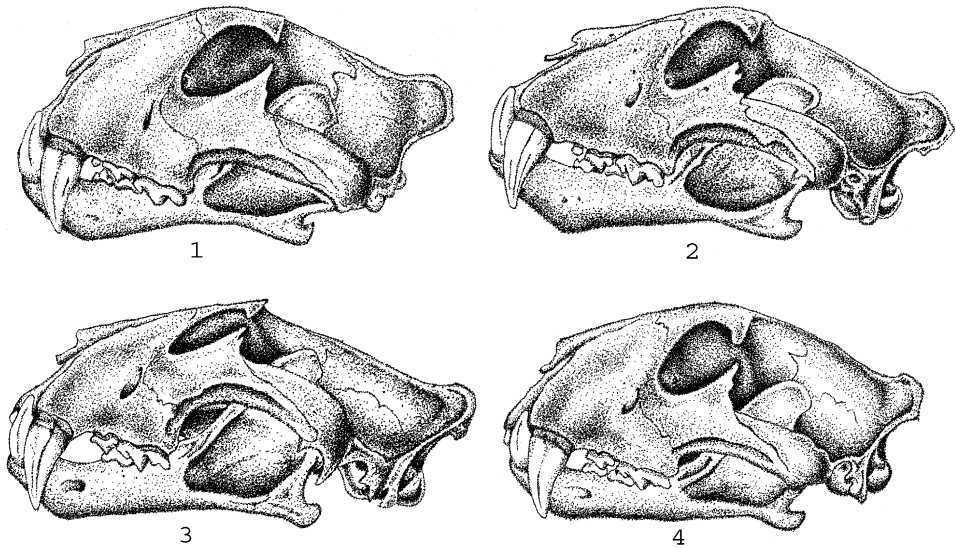
Fig. 1. Lateral view of skull of adult males of Southeast Asian tigers: (1) Indochinese tiger *P.t.corbetti*, holotype (BM 33.4.1.203), from "Quang-Tri" in Vietnam, greatest skull length 322.6 mm; (2) Sumatran tiger *P.sumatrae* (ZMA No.1039), from "Palembang" in Sumatra, greatest skull length 331.5 mm; (3) Javanese tiger *P.sondaica* (ZMA No.1829), from Java, greatest skull length 317.3 mm; (4) Bali tiger *P.s.balica* (BM 38.3.14.5), from Bali, greatest skull length 295 mm.
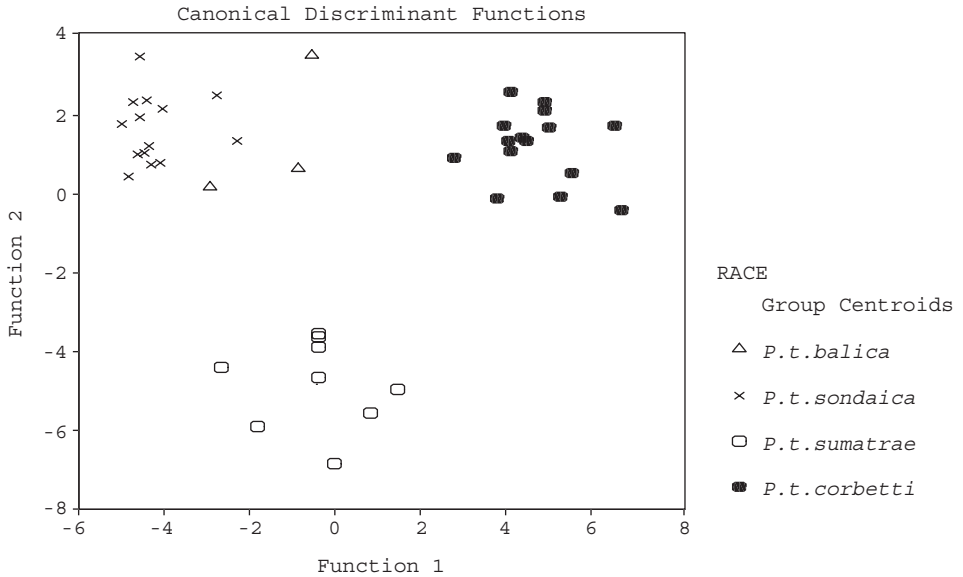
Fig. 2. Plot of Discriminant Function analysis of male Southeast Asian tigers.

Function 1 is positively correlated with SOB, MH, CBL, GLN and P4L, while on Function 2 cranium size (CBL, GLS), mandible height (MH) and the nasal length contribute most information. There is no overlap between the *corbetti*, *sumatrae* and *sondaica* dispersions, with 100% correct classification (Tabs. 2 and 3).

When the supraoccipital breadth is compared (Fig. 3), it is clear that the mainland Southeast Asia group (*corbetti*) is obviously broader than that of Java and Bali group with nearly no overlap between them. The Sumatran group is similar to *corbetti*, and much wider than *sondaica* and *balica*.

Figure 4 compares the greatest nasal length of skulls of *corbetti*, *sumatrae*, *sondaica* and *balica*. *Sumatrae* is shorter than both *corbetti* and *sondaica*, but there is some overlap. *Sondaica* falls within the interquartile range of *corbetti*. There is a difference in median value between *sondaica* and *balica*; the median value of *balica* appears close to *sumatrae*, but this simply reflects its absolutely small size (Tab. 1).

Female group

Interestingly, we found that there are more variables that are significantly different ($P < 0.0001$) between female groups than

between males through an analysis of variance (ANOVA). Among them the following variables have high F-values, and differentiate between groups: SOB (F-value 45.782), C-P4L (F-value 28.286), GLN (F-value 20.698), OH (F-value 18.687) and P4L (F-value 15.045). There is no significant difference ($P > 0.001$) for interorbital breadth (IOB), infraorbital breadth (IFB), rostral breadth (RB), mandible height (MH) and lower carnassial length (M1L).

The discriminant analysis shows a similar result (Fig. 5) to that of the males. Three clusters can be clearly distinguished: *P.t.corbetti*, *P.t.sumatrae* and *P.t.sondaica/P.t.balica*. *Sondaica* and *balica* tend to form a single group. Functions 1 and 2 contain 57.8% and 33.1% of total variance, respectively. In Function 1, as shown by the standardized coefficients of the discriminant functions, supraoccipital breadth (SOB) and mandible length (ML) exhibit most positive weighting. *Corbetti* and most specimens of *sumatrae* are separated from the *sondaica/balica* cluster on this function. Absolute size and nasal length are predominant in Function 2, with condylobasal length (CBL), greatest length (GLS), bizygomatic breadth (BZB) and greatest nasal length (GLN) positively weighted. The Sumatran tiger is therefore distinguished from *corbetti* and *sondaica* by a
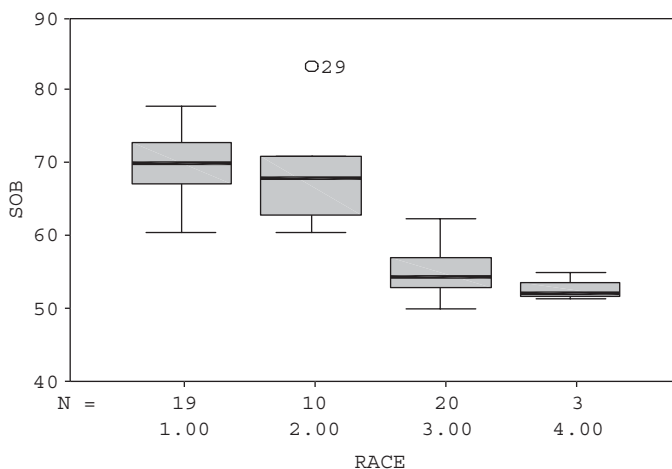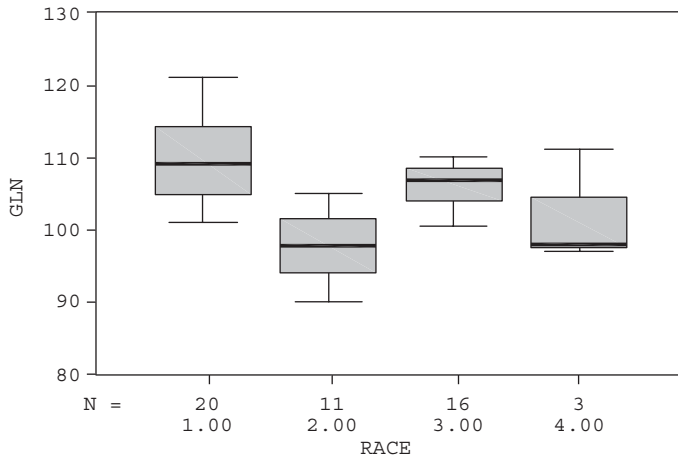

Fig. 3. Box-plot for supraoccipital breadth of skull for male Southeast Asian tigers: (1) *corbetti*, (2) *sumatrae*, (3) *sondaica*, (4) *balica*.

Fig. 4. Box-plot for greatest nasal length of skull for male Southeast Asian tigers: (1) *corbetti*, (2) *sumatrae*, (3) *sondaica*, (4) *balica*.

Table 2. Loadings of variables on DF 1 and 2 from DFA analysis for Male group

	Function	
Craniometric variable	1	2
GLS	−2.562	1.714
CBL	0.903	2.273
BL	− 0.162	− 4.699
RB	− 0.835	0.712
IFB	0.022	− 1.733
IOB	0.545	0.101
POB	0.643	0.392
BZB	− 1.056	− 0.699
MB	− 1.025	0.828
SOB	1.787	− 0.233
OH	0.729	− 0.818
GLN	0.927	0.977
ML	0.587	0.690
MH	1.108	1.091
P4L	0.795	− 0.186
C-P4L	− 0.006	− 0.176
M1L	0.016	0.390
C-m1L	− 0.319	− 0.250
% Variance Explained	64.5	30.6

Table 3. Loadings of variables on DF 1 and 2 from DFA analysis for Female group

	Function	
Craniometric variable	1	2
GLS	0.505	1.089
CBL	−1.390	2.743
RB	−1.281	−0.485
BZB	−0.723	1.464
SOB	1.009	−0.856
OH	0.758	−0.603
GLN	0.235	0.979
P4L	0.381	0.007
BL	0.822	−4.651
MB	−1.057	−0.056
ML	1.180	−0.220
C-P4L	0.512	0.815
% Variance Explained	57.8	33.1

relatively small skull size, narrower zygomatic arch and short nasal bones (Tab. 4). The box-plots for supraoccipital breadth and greatest nasal length in female groups (not shown) were generally similar to those of males.
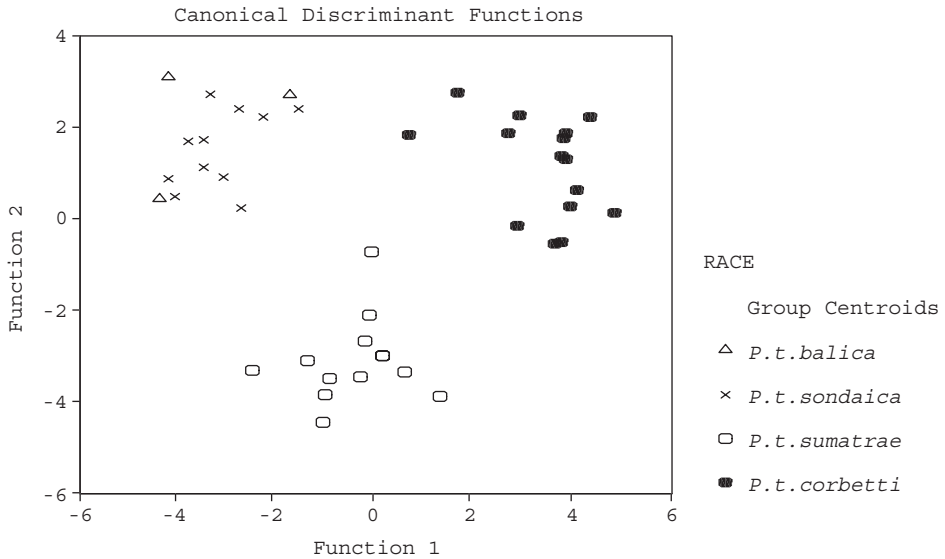
Sexes combined

We also ran a discriminant analysis for both sexes combined using the following set of variables: GLS, CBL, RB, BZB, SOB, OH, GLN and P4L. Figure 6 shows that although there is some overlap between *corbetti*, *sumatrae* and *sondaica/balica*, the three clusters are still clearly distinguishable. The DFA correctly identified 88.9% of specimens, with 89.7% classification accuracy for *corbetti*, 95.2% for *sumatrae*, 80% for *sondaica*

Fig. 5. Plot of discriminant function analysis of female Southeast Asian tigers.

Table 4. Loadings of variables on DF 1 and 2 from DFA analysis for combined-sexes group

Craniometric variable	Function 1	Function 2
GLS	−2.359	−0.455
CBL	0.214	−1.446
RB	−0.994	−0.843
BZB	−0.302	0.241
SOB	1.408	−0.577
OH	1.002	1.024
GLN	0.926	1.993
P4L	0.767	0.389
% Variance Explained	67.6	25.5

and 100% for *balica*. There was much overlap between *sondaica* and *balica*. Functions 1 and 2 explain 67.6% and 25.5% of the total variance, respectively. In Function 1, SOB and OH are the main contributors to the separation; those higher on DF1 have a broader and higher occiput. GLN and OH are the predominant causes for separation on Function 2; those higher on DF2 have relatively longer nasals and again a higher occipital bone.

Allometric analysis

All important allometric parameters (coefficient of correlation, regression coefficient, value of allometric coefficient and its 95% confidence intervals) are shown with the bivariate diagrams in figures 7 and 8. The results indicate that in the relationship between GLN and CBL, most putative subspecies tend to show positive allometry (i.e. nasal increases at a relatively greater rate than skull length), while in the Sumatran tiger, they show clear negative allometry. The coefficient of allometry is generally similar in Indochinese, Java and Bali tigers, but they differ from the Sumatran one. Although in SOB (supraoccipital breadth) all subspecies show a clearly negative allometry in relation with OH (occiput height), this is most extreme in Java and Bali tigers. The Sumatran tiger has the highest *b* value compared with other geographic groups. There is some minor overlap in 95% confidence intervals of *b* values between Indochinese, Sumatran and Java tigers, and much more overlap between Java and Bali (Figs. 7 and 8).
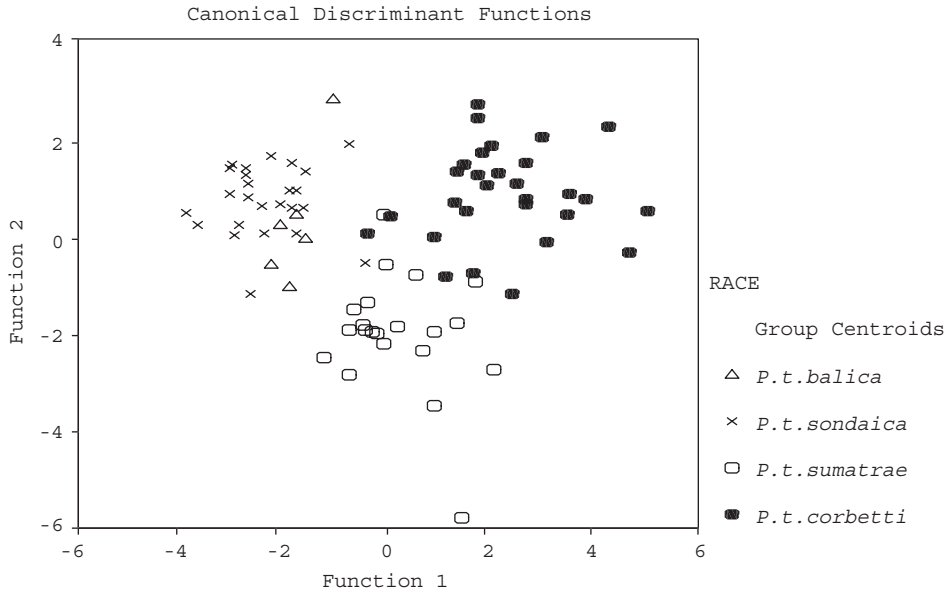
Fig. 6. Plot of discriminant function analysis for combined-sexes of Southeast Asian tigers.

Phenetic analysis

Results of surveys of six polymorphic cranial characters are given in table 5. They are in broad agreement with our previous understanding. The supraoccipital bone of Indochinese and Sumatran tiger is much broader than that of the Java and Bali forms, and they display a similarly obtuse triangular shape although they still differ in some details: the supraoccipital bone of *corbetti* seems moderately broadened (in most of the examined specimens they show an intermediate state, especially in males) but it is more extremely wide in *sumatrae*; its upper margin appears much more rounded in *corbetti* (especially in the type specimen of this subspecies), whereas in *sumatrae* a somewhat isosceles triangle is more frequently present. The form of the occipital plane is similar in the Java and Bali races; they show an acute triangular shape in a general overview, with a remarkably narrow supraoccipital bone, with its upper margin forming an isosceles triangle and its lateral margins being strongly concave in the middle. The nasals are narrow and

longer in *corbetti*, *sondaica* and *balica* but are always notably wide and short in *sumatrae*. The shape of the sagittal crest is generally similar in all of these subspecies and it thus seems of no value in distinguishing them (Figs. 9 and 10).

Table 6 gives the scores of proportional difference within and between each geographic group (means, SD). It is conspicuous that the differences in these craniological characters between geographically neighbouring subspecies is much greater than within them, except between Java and Bali. This is also confirmed by an independent-sample *T* test (Tab. 7). Table 8 shows the matrix of dissimilarity coefficients based on Euclidean distances. A framework of phylogenetic relationships between these geographic forms is reflected by a Neighbour-joining dendrogram and a UPGMA tree (Figs. 11 and 12). Clearly, these putative subspecies can be divided into two clusters: one contains the Indochinese and Sumatran tiger, the other the Javan and Balinese tiger. The Sumatran tiger, in this light, is undoubtedly of mainland origin.
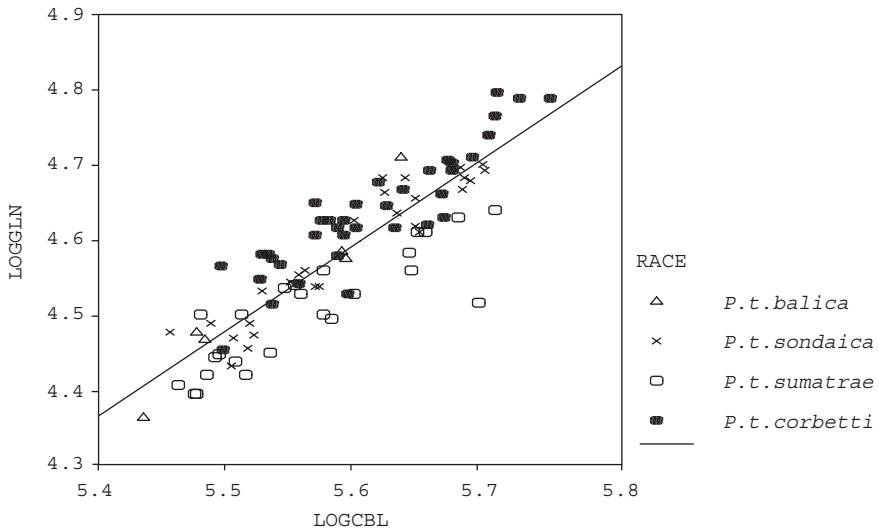
	r	a	b	CI (L)	CI (U)
Corbetti	0.927 ± 0.03	- 1.754 ± 0.5	1.14 ± 0.09	0.96	1.32
Sumatrae	0.872 ± 0.04	- 0.331 ± 0.62	0.87 ± 0.11	0.64	1.10
Sondaica	0.940 ± 0.03	- 1.704 ± 0.47	1.13 ± 0.09	0.95	1.30
Balica	0.97 ± 0.04	- 3.64 ± 1.10	1.48 ± 0.20	0.93	2.03

Fig. 7. Allometric bivariate diagram in relationship of log GLN/log CBL with parameters of Southeast Asian tigers (sexes combined), *r* (coefficient of correlation), *a* (regression coefficient), *b* (value of allometric coefficient), CI (95% confidence interval of allometric coefficient).

Discussion

The relationships of each of these Southeast Asian tiger forms will now be discussed.

Sumatran tiger

It was Schwarz (1912) who first separated the tigers of Sumatra, Java and Bali into three distinguishable subspecies based on 10 skulls and flat skins from the collections of the Senckenberg Museum, Frankfurt; he never gave the Sumatran tiger a formal subspecific name but retained it simply as ''*Felis tigris* subsp''. Pocock (1929) placed the Sumatran tiger in the same subspecies as that of the Malay Peninsula. It was Pocock (1929) who, in his classic study on tiger taxonomy, proposed the name *P.t.sumatrae* for Suma-

tran tiger, describing several skull, pelage and striping features in which it is distinct from the Indian and Javan tigers and confirming it as a valid subspecies. This view was accepted widely by later investigators (Brongersma 1935; Hemmer 1969; Kirk 1994; Kock 1995; 1979, 1981; Sody 1932, 1949).

In its systematic affinities it is generally considered that the Sumatran form is closely allied with the Indochinese or Corbetti's tiger, and originated from mainland populations that colonized Sumatra at a time of low sea-levels during the last Ice Age (Hemmer 1969; Mazák 1979; Kitchener 1999). Hemmer (1967, 1969) indicated that, in the index M1 length/p4 length (which he found significant in distinguishing different geographic forms of tiger), the value of the Sumatran tiger is 108, which is similar to that of mainland
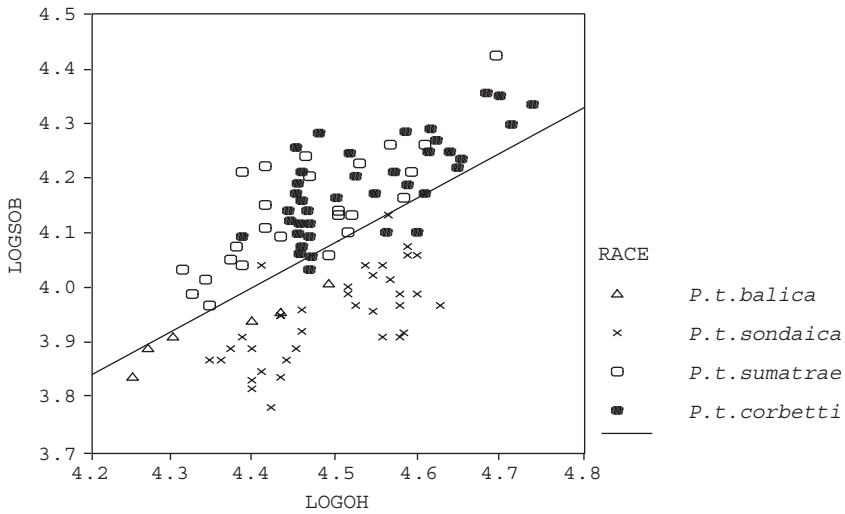
	r	a	b	CI (L)	CI (U)
Corbetti	0.715 ± 0.07	1.08 ± 0.59	0.68 ± 0.13	0.42	0.95
Sumatrae	0.872 ± 0.04	0.47 ± 0.63	0.82 ± 0.14	0.53	1.12
Sondaica	0.629 ± 0.06	1.50 ± 0.62	0.55 ± 0.14	0.26	0.84
Balica	0.947 ± 0.02	1.70 ± 0.38	0.51 ± 0.09	0.27	0.75

Fig. 8. Allometric bivariate diagram in relationship of log SOB/log OH with parameters of Southeast Asian tigers (sexes combined), *r* (coefficient of correlation), *a* (regression coefficient), *b* (value of allometric coefficient), CI (95% confidence interval of allometric coefficient).

tigers. The shape of the occipital plane of the Sumatran tiger also shows all the features of the mainland forms (Hemmer 1969; Mazák 1979; Schwarz 1912). Our present finding confirms this.

Cracraft et al. (1998) found that in variable sites of the mitochondrial cytochrome *b* gene there are three diagnostic markers of the Sumatran tiger which can be used to separate it from its mainland relatives. Luo et al. (2004) also supported the distinction of the Sumatran tiger from other mainland forms by multiple unique microsatellite alleles. Our craniometric analysis likewise shows that specimens of Sumatran tiger, at least when sex is taken into account, are clearly separated from both Indochinese and Javan tigers with 100% accuracy.

Further investigation indicates that the short nasal of the Sumatran tiger probably depends on negative allometry, while in other tigers nasal length is positively allometric to CBL. As has been previously documented (Mazák 2004), the Sumatran tiger also appears to show more pronounced sexual dimorphism than do Indochinese or Javan tigers.

Tiger fossils have been recorded from the Early Pleistocene of Sangiran in Java and from the Late Pleistocene of Ngandong in Java and the Padang Highlands of Sumatra (Brongersma 1935, 1937; Hemmer 1971). This may suggest that during Middle to Late Pleistocene the mainland tiger had already colonized Sumatra. Hemmer (1971) noted the possibility that at times of glacial marine regression there could be genetic exchanges between the populations of mainland Southeast Asia and Java, when Java, Sumatra and the Asian continent were connected. These observations led Kitchener (1999) to propose
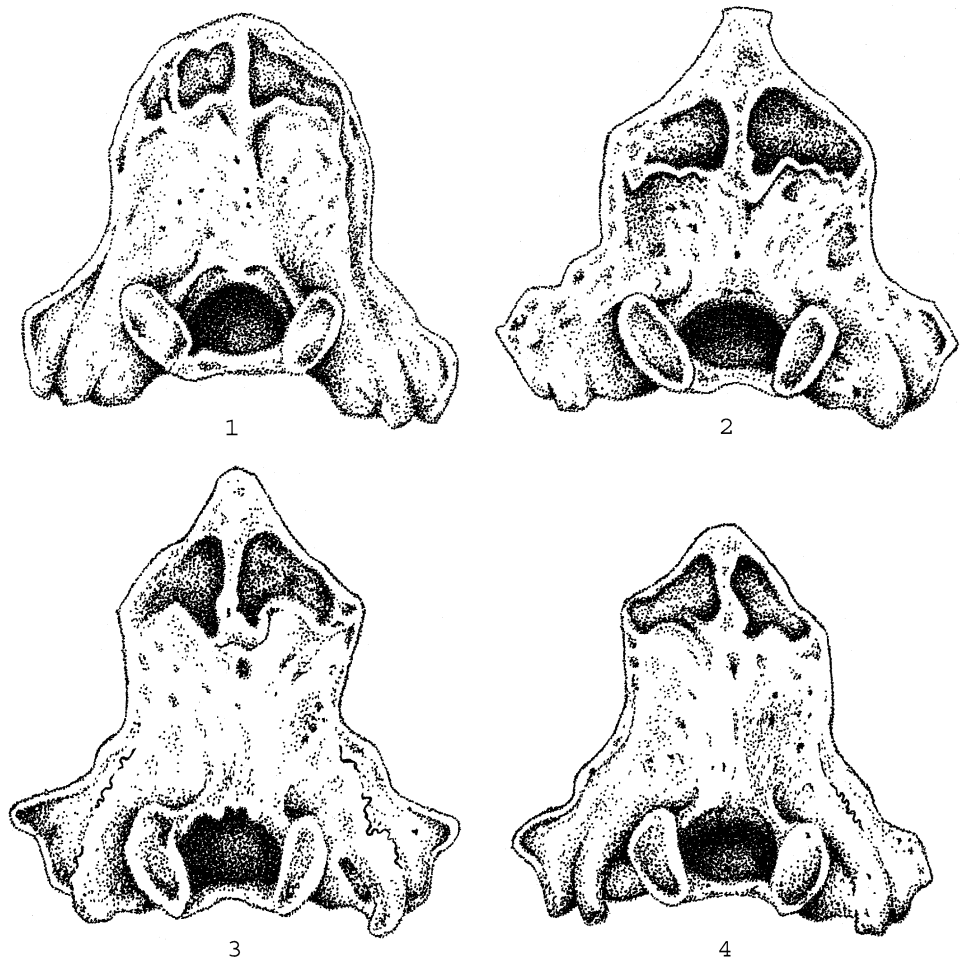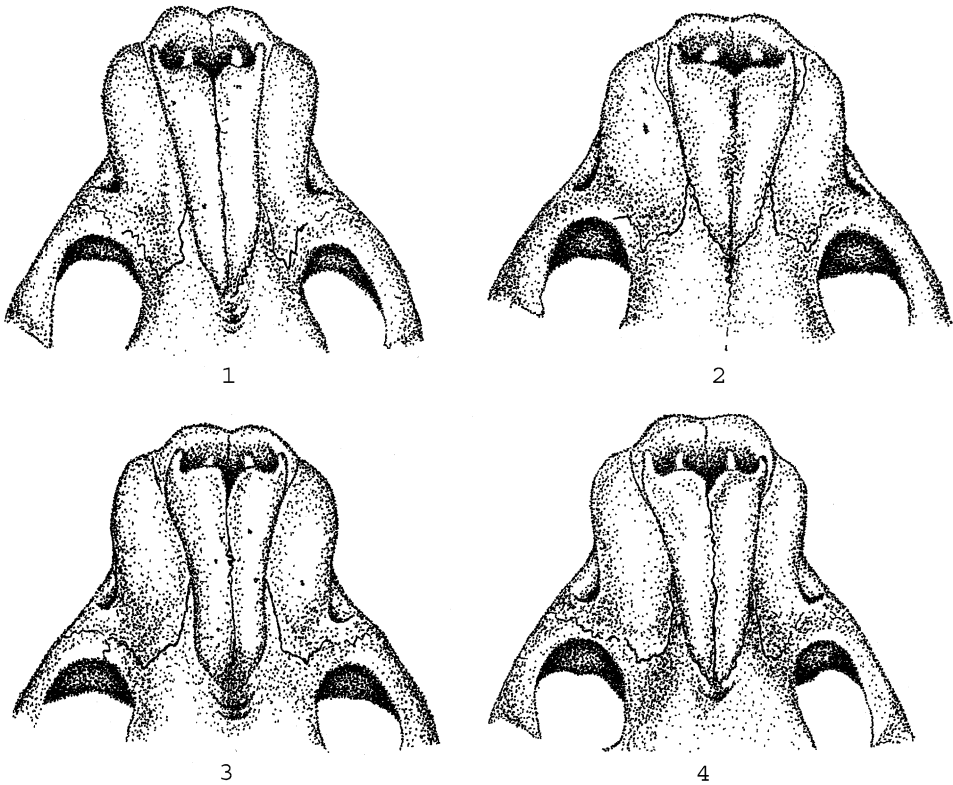
Fig. 9. View of occipital region of adult males of Southeast Asian tigers: (1) Indochinese tiger *P.t.corbetti*, holotype (BM 33.4.1.203); (2) Sumatran tiger *P.sumatrae*, holotype (BM 1912.11.10.1), from "Deli" in Sumatra; both showing a clearly acute triangular occipital plane and a broad supraoccipital bone, the upper margin of supraoccipital bone in *P.t.corbetti* is nearly rounded but in *P.sumatrae* a somewhat isosceles triangle is more frequently present; (3) Javanese tiger *P.sondaica*, (BM 67.4.12.194); (4) Bali tiger *P.s.balica* (BM 37.12.1.2); occiputs of Java and Bali tiger are broadly similar, showing a obtuse triangular in a general overview, its lateral margins being concave deeply, with a narrow supraoccipital bone and its upper margin forming an isosceles triangle.

that the Sumatran tiger might be of hybrid origin (mainland × Java). Considering that it has (mainly cranial) characters recalling mainland tigers as well as (mainly pelage) features resembling the Javan tiger, this must be regarded as a plausible hypothesis. Subsequently the Sumatran tiger evolved a series of unique cranial and molecular genetic features after isolation. This hypothesis would be testable if Y chromosome and mtDNA could be extracted from preserved remains of the Javan tiger and compared with corresponding sequences of larger series of both *sumatrae* and *corbetti*.

Given the evidence that Sumatran tigers are cranially 100% distinct from both Javan

Fig. 10. Dorsal view of nasal of adult males of Southeast Asian tigers: (1) Indochinese tiger *P.t.corbetti*, holotype (BM 33.4.1.203); (2) Sumatran tiger *P.sumatrae*, holotype (BM 1912.11.10.1); (3) Javanese tiger *P.sondaica*, (BM 67.4.12.194); (4) Bali tiger *P.s.balica* (BM 38.3.14.5); note that the nasal bone in Sumatran tiger is obviously shorter and broader, while in other forms is long and narrow.

tigers and the neighbouring mainland subspecies (*corbetti*), we propose that the Sumatran tiger should be recognized as a separate species, *Panthera sumatrae*, under the Phylogenetic Species Concept (PSC), in accord with Cracraft et al. (1998).

Javan tiger

Cranially, the Javan tiger is completely separated from both the mainland (*corbetti*) and Sumatran tigers, with 100% accuracy. It is characterized particularly by an obviously narrow occipital plane, long and narrow nasal and relatively long carnassials (Hemmer 1969, 1987; Mazák 1979).
Hemmer (1969, 1971) proposed that the recent Javan tiger evolved from the unspe-

cialized Middle Pleistocene tigers (*Panthera palaeosinensis* Zdansky, 1924) of mainland East and Southeast Asia. This long-term isolation allowed it to become specialized in masticatory structure, with the result that the carnassials tend to be enlarged and the occiput to be narrow. As had been shown already by Hemmer (1967, 1969, 1971), it has a high value of 113 of the index M1 length/p4 length, whilst in mainland and Sumatran tigers, the value is only 108–109.
The evolution of mainland and Javanese tigers was summarized in a diagram by Groves (1992), who argued that the Late Pleistocene ancestor of the modern Javan tiger, *P.t. soloensis*, was completely different from its Early/Middle Pleistocene predeces-

Table 5. Distribution and frequencies (%) of character state on six polymorphic qualitative cranial characters of S.E. Asian tigers. For character and description of character states see Material and methods

	♂♂				♀♀			
	Corbetti N = 12	Sumatrae N = 6	Sondaica N = 11	Balica N = 3	Corbetti N = 9	Sumatrae N = 3	Sondaica N = 3	Balica N = 2
C1								
a	—	—	11	3		—	3	2
	0	0	100	100	0	0	100	100
b	8	—	—	—	4	—	—	—
	66.7	0	0	0	44.4	0	0	0
c	4	6	—	—	5	3	—	—
	33.3	100	0	0	55.6	100	0	0
C2								
a	1	—	11	3	1	—	3	2
	8.3	0	100	100	11.1	0	100	100
b	11	6	—	—	8	3	—	—
	91.7	100	0	0	88.9	100	0	0
C3								
a	12	—	10	3	9	—	—	2
	100	0	90.9	100	100	0	0	100
b	—	6	1	—	—	3	3	—
	0	100	9.1	0	0	100	100	0
C4								
a	1	—	9	2	—	—	2	2
	8.3	0	81.8	66.7	0	0	66.7	100
b	11	6	2	—	9	3	1	—
	91.7	100	18.2	33.3	100	100	11.1	0
C5								
a	2	3	6	3	8	3	3	2
	16.7	50	54.6	100	88.9	100	100	100
b	10	3	5	—	1	—	—	—
	83.3	50	45.5	0	11.1	0	0	0
C6								
a	2	2	10	3	1	2	3	2
	16.7	33.3	90.9	100	11.1	66.7	100	100
b	3	4	—	—	1	1	—	—
	25	66.7	0	0	22.2	11.1	0	0
c	7	—	1	—	6	—	—	—
	58.3	0	9.1	0	66.7	0	0	0

sors (which it presumably replaced), and already had the modern Javan form's high M1 index and narrow occiput.

The evidence indicates that the now extinct Javan tiger must also be assigned to a distinct species, *Panthera sondaica*, and to which the Ngandong tiger also belongs.

Bali tiger

The Bali tiger strongly resembles the Javan, and it cannot be separated from the latter except on average. The occipital height/ supraoccipital breadth index in 15 male Java skulls averages 1.74 (SD = 0.11), while in 3 male Bali skulls it is 1.61 (SD = 0.04, $t = 96.89$, df = 2, $P = 0.000$). A similar result is evident also in female skulls (not shown). The frontals seem more vaulted and the sagittal crests of both sexes are very low and weakly developed. All these features probably relate to the smaller body size and concomitantly more weakly developed masticatory apparatus.
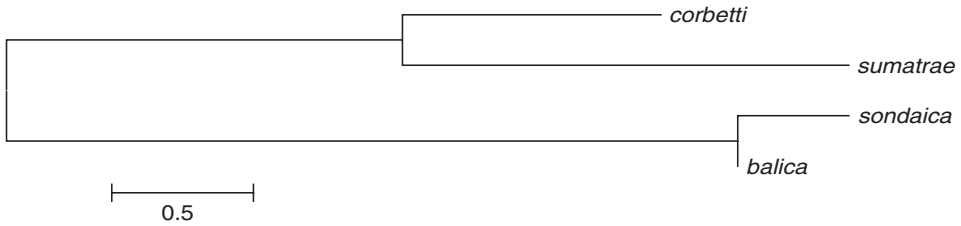
Fig. 11. Neighbour-joining tree for relationships of male Southeast Asian tigers based on six polymorphic qualitative skull characters.
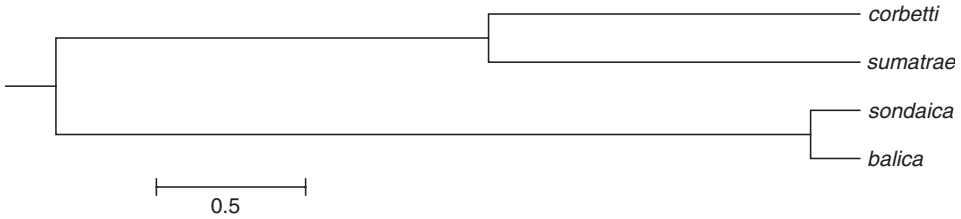
Fig. 12. UPGMA tree for relationships of male Southeast Asian tigers based on six polymorphic qualitative skull characters.

Table 6. Values of proportional difference (M, SD) within and between Southeast Asian tigers

	♂♂	♀♀
	Within group	
Corbetti	1.79 ± 0.5	1.53 ± 0.43
Sumatrae	0.94 ± 0.18	0.44 ± 0.2
Sondaica	1.31 ± 0.94	0.44 ± 0.2
Balica	0.44 ± 0.2	0
	Between groups	
Corbetti–Sumatrae	3.3 ± 0.54	3.04 ± 1.21
Sumatrae–Sondaica	5.96 ± 0.32	5.0 ± 0.58
Sondaica–Balica	1.12 ± 0.97	0.33 ± 0.58

Table 7. Independent-sample *T* test on proportional differences between Southeast Asian tiger

		t	df	P
♂♂	Corbetti–Sumatrae	−7.154	22	0.000
	Sumatrae–Sondaica	−33.574	10	0.000
	Sondaica–Balica	0.461	20	0.86
♀♀	Corbetti-Sumatrae	−3.531	16	0.003
	Sumatrae–Sondaica	−12.952	4	0.000
	Sondaica–Balica	0.312	4	0.77

Externally, the ground coloration and stripe pattern of Bali tiger differ somewhat, on average, from the Javan tiger (Mazák 1976, 1979; Mazák et al. 1978).

The present evidence indicates that the Bali tiger should be classified as a subspecies of the Javan tiger, *Panthera sondaica balica*.

In conclusion, the following species and subspecies of Southeast Asian tigers may be recognized.

Mainland group

Panthera tigris corbetti Mazák, 1968
1868 *Tigris regalis* Fitzinger, SB. AK. Wiss. Wien 58, P.446 (in part).
1929 *Panthera tigris tigris* Pocock, J. Bombay Nat. Hist. Soc. 33, P.519 (in part).
1939 *Panthera tigris tigris* Pocock, Fauna of British India including Ceylon and Burma, Mammalia 1, p.199 (in part).
1968 *Panthera tigris corbetti* Mazák, Mammalia 32, P.105.
2004 *Panthera tigris jacksoni* Luo et al, PLos Biology 2, P. 2290.
Type specimen: Skull and flat skin of an adult male BM(NH) 33.4.1.203. Type locality: "Quang-Tri", Vietnam

Table 8. Matrix of dissimilarity coefficient on six polymorphic qualitative cranial characters of Southeast Asian tigers

♂♂		Corbetti	Sumatrae	Sondaica	Balica
	Corbetti	—	1.46	2.2	2.38
	Sumatrae	1.46	—	2.6	2.67
	Sondaica	2.2	2.6	—	0.52
	Balica	2.38	2.67	0.52	—
♀♀		Corbetti	Sumatrae	Sondaica	Balica
	Corbetti	—	1.65	2.47	2.58
	Sumatrae	1.65	—	2.56	2.67
	Sondaica	2.47	2.56	—	0.33
	Balica	2.58	2.67	0.33	—

Diagnosis: A medium-sized subspecies among the five recognized mainland Asian tiger forms. Frontal well vaulted, but not so much as in Indian tiger. Nasal long and narrow, occiput broad, with its upper margin more or less rounded. Sagittal crest usually low, reaches only 3–4 mm in its middle part, but raised posteriorly, measured as much as 14–15 mm.

Distribution: Mainland Southeast Asia and Malay peninsula.

Notes: Pending a future detailed study, we retain the Southeast Asian mainland tiger as a valid subspecies of *P. tigris*. Luo et al. (2004) proposed the Malayan Peninsula populations as a new subspecies, *P.t.jacksoni*, as they are genetically distinct in mtDNA sequences from those of northern Indochina. There is however no clear difference between them when specimens from the two regions are compared cranially or, as far as we can detect, in pelage; it is not clear that subspecies should be erected on the basis of mtDNA alone, although this may be useful as an adjunct to gross morphological characters. In addition, the naming of this new subspecies does not conform to Art.16.4 of the Fourth Edition of the International Code of Zoological Nomenclature (1999), in that no type specimen was designated.

Island group

Panthera sumatrae Pocock, 1929
1842 *Felis tigris nigra* Lesson, Nouv. Tabl. Régn. Anim., 50. Nomen nudum.

1843 *Felis tigris sumatrana* Blainville, Ostéographie, 2:7. Not of Horsfield, 1821 (a subspecies of *Prionailurus bengalensis*).
1844 *Felis tigris sondaica* Temminck, Fauna Japonica, Mamm., 43
1862 ? *Felis tigris ruber* Ludeking, Geneesk. Tijdschr. Ned. Ind., 9:41. Probably = *Catopuma temminckii* (see Brongersma 1935:64).
1868 *Tigris sondaicus* Fitzinger, SB. AK. Wiss, 58:454 (in part).
1929 *Panthera tigris sumatrae* Pocock, J. Bombay Nat. Hist. Soc. 33:535
1994 *Panthera tigris bintana* Kirk, Säugetierkundliche Mitteilungen, 35:164. Nomen nudum.
Type Specimen: BM(NH) 12.11.10.1, skull of an adult male.
Type locality: "Deli" (= Labuhandeli), Sumatra.
Diagnosis: Frontal vaulted [in the type skull it is however strikingly flat, but this probably due to the abnormalities of captivity, as noted by Pocock (1929)]; nasal short and wide; occiput broad. Cranium relatively narrow across the zygomatic arches, but infraorbital distance wide; carnassials slightly shorter; sexual dimorphism well marked.
Distribution: Sumatra.
Notes: Kirk (1994) gave the name *P.t.bintana* to the tiger of Pulau Bintan, relying on an old record from Dammermann. Kock (1995) noted that Kirk's new subspecies was described in the absence of specimens, and according to the rules of nomenclature the name cannot stand. *P.t.bintana* is probably a synonym of the Sumatran tiger.
Panthera sondaica Temminck, 1844

Synonym etc. given under subspecies headings.

Diagnosis: Nasal long and narrow. Occiput remarkably narrow, with its lateral margins being deeply concave in the middle and an isosceles triangle clearly forming in its upper margin. Carnassials relatively long. This species has been extinct since the 1980s.

Panthera sondaica sondaica Temminck, 1844

1844 *Felis tigris sondaicus* Temminck, Fauna Japonica, Mamm., 43

1868 *Tigris sondaicus* Fitzinger, SB. AK. Wiss. Wien, 58:454

Type specimen: A mounted female skin (Jentink's Cat "c"), in Naturalis (formerly Rijksmuseum van Natuurlijke Historie), Leiden.

Type locality: Java.

Diagnosis: Compared to the other subspecies (below), size was larger, frontal relatively flatter, occipital surface more elongated, sagittal crest higher.

Distribution: Java.

Notes: This subspecies became extinct, despite the setting up of a special reserve for it (Meru Betiri) some time during the 1980s.

Panthera sondaica balica Schwarz, 1912

1912 *Felis tigris balica* Schwarz, Ann. Mag. Nat. Hist. (8) 10:325

Type specimen: SMF 2576, skin and skull of a young adult female.

Type locality: Bali.

Diagnosis: Size smaller than nominotypical subspecies; frontal more vaulted; form of the occipital plane similar to the Javan tiger, but not so elongated; sagittal crest very low and poorly developed.

Note: An adult male skull of greatest length as much as 312 mm of Hungarian Natural History Museum, is the biggest specimen so far known to us of this subspecies, and well within the range of the nominotypical (Javan) subspecies.

Acknowledgements

Zusammenfassung

Taxonomische Revision der Tiger (*Panthera tigris*) Südostasiens

Unsere vergleichenden kraniometrischen und kraniologischen Untersuchungen an südostasiatischen Tigern zeigen, dass die Stichproben des Festlands, von Sumatra und von Java/Bali absolut voneinander zu unterscheiden sind. Entsprechend dem phylogenetischen Artkonzept sind drei valide Arten zu benennen: *Panthera tigris*, *P. sumatrae* und *P. sondaica*. Der Balitiger kann als Unterart des Javatigers angesehen werden.

References

Brongersma, L. D. (1935): Notes on some recent and fossil cats, chiefly from the Malay Archipelago. Zoöl. Mededeelingen **18**, 1–89.

Brongersma, L. D. (1937): Notes on fossil and prehistoric remains of the 'Felidae' from Java and Sumatra. Comptes Rendus 12th Congress

Internationale de Zoolologie, Lisbonne. 1935. Pp. 1855–1865.

Cracraft, J. (1983): Species concepts and speciation analysis. Curr. Ornithol. **1,** 159–187.

Cracraft, J. (1997): Species concepts in systematic and conservation biology – an ornithological viewpoint. In: Species the Units of Biodiversity. Ed. by M.F. Claridge, H. A. Dawah and M.R. Wilson. Systematics Association Special Vol. Series 54. London: Chapman and Hall. Pp. 325–339.

Cracraft, J.; Feinstein, J.; Vaughn, J.; Helm-Bychowski, K. (1998): Sorting out tigers (*Panthera tigris*): mitochondrial sequences, nuclear inserts, systematics and conservation genetics. Anim. Conserv. **1,** 139–150.

Goebel, A. M.; Whitmore, D. H. (1987): Use of electrophoretic data in the reevaluation of tiger systematics. In: Tigers of the World: The Biology, Biopolitics, Management, and Conservation of an Endangered Species, Ed. by R. L. Tilson and U. S. Seal. Park Ridge, NJ: Noyes Publications. Pp. 36–50.

Groves, C. P. (1992): How old are subspecies? A tiger's eye view of human evolution. Archaeol. Oceania **27,** 153–160.

Hemmer, H. (1967): Wohin gehört 'Felis' palaeosinensis (Zdansky, 1924) in systematischer Hinsicht ? Neues Jahrb. Geol. Paläontologie **129,** 83–96.

Hemmer, H. (1969): Zur Stellung des Tigers (*Panthera tigris*) der Insel Bali. Z. Säugetierkunde **34,** 216–223.

Hemmer, H. (1971): Fossil mammals of Java. II. Zur Fossilgeschichte des Tigers (*Panthera tigris* (L.)) in Java. Kon. Ned. Akad. Wetenschappen Series B **74,** 35–52.

Hemmer, H. (1987): The phylogeny of the tiger (*Panthera tigris*) In: Tigers of the World: The Biology, Biopolitics, Management, and Conservation of an Endangered Species, Ed. by R. L. Tilson and U. S. Seal. Park Ridge, NJ: Noyes Publications. Pp. 28–35.

Herrington, S. (1987): Subspecies and the conservation of *Panthera tigris*: preserving genetic heterogeneity In: Tigers of the World: The Biology, Biopolitics, Management, and Conservation of an Endangered Species, Ed. by R. L. Tilson and U. S. Seal. Park Ridge, NJ: Noyes Publications. Pp. 51–61.

Kirk, G. (1994): Insel-Tiger *Panthera tigris* (Linnaeus, 1758). Säugetierkundl. Mitt. **35,** 151–176.

Kitchener, A. C. (1999): Tiger distribution, phenotypic variation and conservation issues. In: Riding the Tiger, Tiger Conservation in Human-dominated Landscapes, Ed. by J. Seidensticker, S. Christie and P. Jackson. Cambridge: Cambridge University Press. Pp. 19–39.

Kitchener, A. C.; Dugmore, A. J. (2000): Biogeographical change in the tiger *Panthera tigris*. Anim. Conserv. **3,** 113–124.

Kock, D. (1995): Zur Benennung des Tigers *Panthera tigris* L. auf Sunda – Inseln. Säugetierkundl. Mitt. **36,** 123–126.

Luo, S. J.; Kim, J. H.; Johnson, W. E.; van der Walt, J.; Martenson, J.; Yuhki, N.; Miquelle, D. G.; Uphyrkina, O.; Goodrich, J. M.; Quigley, H. B.; Tilson, R.; Brady, G.; Martelli, P.; Subramaniam, V.; McDougal, C.; Hean, S.; Huang, S. Q.; Pan, W. S.; Karanth, U.; Sunquist, M.; Smith, J. L. D.; O'Brien, S. (2004): Phylogeography and genetic ancestry of tigers (*Panthera tigris*). PLoS Biol. **2,** 2275–2293.

Mazák, J. H. (2004): On the sexual dimorphism in the skull of the tiger (*Panthera tigris*). Mamm. biol. **69,** 392–400.

Mazák, V. (1968): Nouvelle sous-espece de tigre provenant de l'Asie due Sud-Est. Mammalia **32,** 104–112.

Mazák, V. (1976): On the Bali tiger, *Panthera tigris balica* (Schwarz, 1912). Vestník Ceskoslovenské Spolecnosti Zoologické **40,** 179–195.

Mazák, V. (1979): Der Tiger *Panthera tigris*. 2nd ed. Neue Brehm Bücherei 356. Wittenberg Lutherstadt: A. Ziemsen Verlag.

Mazák, V. (1981): *Panthera tigris*. Mam. Spec. **152,** 1–8.

Mazák, V.; Groves, C. P.; van Bree, P. J. H. (1978): On a skin and skull of the Bali tiger and a list of preserved specimens of *Panthera tigris balica* (Schwarz, 1912). Z. Säugetierkunde **43,** 108–113.

Newman, A.; Bush, M.; Wildt, D. E.; van Dam, M.; Frankenhuis, M.; Simmons, L.; Phillips, L.; O'Brien, S. J. (1985): Biochemical genetic variation in eight endangered feline species. J. Mammalogy **66,** 256–270.

Nowell, K.; Jackson, P. (1996): Wild Cats: Status Survey and Conservation Action Plan. Gland, Switzerland: IUCN.

O'Brien, S. J.; Mayr, E. (1991): Bureaucratic mischief: Recognizing endangered species and subspecies. Science **251,** 1187–1188.

O'Brien, S. J.; Collier, G.; Benveniste, R.; Nash, W.; Newman, A.; Simonson, J.; Eichelberger, M.; Seal, U.; Janssen, D.; Bush, M.; Wildt, D. (1987): Setting the molecular clock in Felidae: the great cats *Panthera*. In: Tigers of the World: The Biology, Biopolitics, Management, and Conservation of an Endangered Species, Ed.

By R. L. Tilson and U. S. Seal. Park Ridge, NJ: Noyes Publications. Pp. 36–50.

Pocock, R. I. (1929): Tigers. J. Bombay Nat. Hist. Soc. **33,** 505–541.

Schwarz, E. (1912): Notes on Malay tigers, with description of a new form from Bali. Ann. Mag. Nat. Hist. Series 8, **10,** 324–326.

Schwarz, E. (1913): Der Bali-Tiger. Ber. Senckenberg. Naturforsch. Gesellsch. Frankfurt a. M. **44,** 70–73.

Seidensticker, J. (1999): Large carnivores and the consequences of habitat insularization: ecology and conservation of tigers in Indonesia and Bangladesh. In: Cats of the World: Biology, Conservation, and Management. Ed. by S. D. Miller and D. D. Everett. Washington, DC: National Wildlife Federation. Pp. 1–41.

Shepherd, C. R.; Magnus, N. (2004): Nowhere to hide: The trade in Sumatran tiger. Traffic Southeast Asia, Unit 9-3 A, 3rd Floor, Jalan S523/11 Taman SEA, 47400 Petaling Jaya, Selangor, Malaysia.

Sody, H. J. V. (1932): The Balinese tiger, *Panthera tigris balica* (Schwarz). J. Bombay Nat. Hist. Soc. **36,** 233–235.

Sody, H. J. V. (1949): Notes on some Primates, Carnivora, and the Babirusa from the Indo-Malayan and Indo-Australian regions. Treubia, Buitenzorg **20,** 121–190.

Wayne, R. K.; Benveniste, R. E.; Janczewski, N.; O'Brien, S. J. (1989): Molecular and biochemical evolution of the Carnivora. In: Carnivore Behavior, Ecology and Evolution. Ed. by J. L. Gittleman. Ithaca, NY: Comstock Publishing Associates, Cornell University Press. Pp. 465–494.

Wentzel, J.; Stephens, J. C.; Johnson, W.; Menotti-Raymond, M.; Pecon-Slattery, J.; Yuhki, N.; Carrington, M.; Quigley, H. B.; Miquelle, D. G.; Tilson, R.; Manansang, J.; Brady, G.; Lu, Z.; Pan, W. S.; Huang, S. Q.; Johnston, L.; Sunquist, M.; Karanth, K. U.; O'Brien, S. (1999): Subspecies of tigers: molecular assessment using 'voucher specimens' of geographically traceable individuals. In: Riding the Tiger, Tiger conservation in Human-dominated Landscapes. Ed. by J. Seidensticker, S. Christie and P. Jackson. Cambridge: Cambridge University Press. Pp. 40–49.

Authors' addresses:

Corresponding author. Ji H. Mazák, Shanghai Science and Technology Museum (formerly Shanghai Natural History Museum), 260 Yan-an Road (East), Shanghai 200002, PR China
(e-mail: jimazak@citiz.net)

Colin P. Groves, School of Archaeology and Anthropology, Australian National University, Canberra, ACT 0200, Australia.