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Locating specimens of extinct tiger (*Panthera tigris*) subspecies: Javan tiger (*P. t. sondaica*), Balinese tiger (*P. t. balica*), and Caspian tiger (*P. t. virgata*), including previously unpublished specimens

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Abstract. Recent advances in multivariate statistics, and in ancient DNA techniques, have greatly increased understanding of tiger phylogeography. However, regardless of advances in analytical methodology, researchers will continue to need access to specimens for morphological measurements and sampling for genetic analysis. The tiger has become increasingly endangered, and out of the nine putative tiger subspecies, three (Javan, Balinese, and Caspian) have become extinct in the last 100 years, leaving the specimens kept in natural history collections as the only materials available for research. Frustratingly little information is widely available concerning the specimens of these extinct tiger subspecies. We conducted an extensive search for specimens of extinct tiger subspecies, and also developed a simple on-site method to assign unprovenanced and probable Indonesian specimens to either Javan/Balinese or Sumatran subspecies. We located a total of 88 Javan, 11 Balinese, and 46 Caspian tigers, including seven new Javan tigers, and three Balinese tigers that were not widely known previously. These specimens are critical for research in order to understand the intraspecific phylogeny and evolutionary history of the tiger.

Key words: Central Asia, conservation, Indonesia, museum, Sunda Islands.

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The tiger *Panthera tigris* (Linnaeus, 1758) is a charismatic large felid whose "Endangered" status has also made it one of the most recognisable conservation icons (Nowell and Jackson 1996; IUCN 2012). As a result the tiger has attracted a very wide variety of research, which has contributed to a better understanding of conservation and evolutionary biology of the tiger, but also other felids, particularly with respect to biogeography, morphology, and genetics (Pocock 1929; V. Mazák (Vratislav Mazák of the National Museum, Prague, former Czechoslovakia) 1968, 1981; Hemmer 1987; Kitchener 1999; Luo et al. 2004, 2008; J. Mazák (Ji Mazák of Shanghai Science and Technology Museum, Shanghai, China) and Groves 2006; Driscoll et al. 2009; Kitchener and Yamaguchi, 2010; J. Mazák 2010). However, the tiger has become increasingly endangered, making it difficult for researchers to access and/or secure appropriate sample sizes for all major populations or commonly-recognised subspecies. Furthermore, out of the nine putative tiger subspecies (Luo et al. 2008), three (Caspian tiger, *P. t. virgata* (Illiger, 1815), Javan tiger, *P. t. sondaica* (Temminck, 1844), and Balinese tiger, *P. t. balica* (Schwarz, 1912)) have become extinct in the last 100 years (Nowell and Jackson 1996), leaving the specimens kept in natural history collections as the only materials available for research. An old and large natural history collection always includes specimens whose provenances are not recorded or unclear. We expected that there would be some "undiscovered" specimens of extinct tiger subspecies in such collections, which are scientifically priceless "new" specimens for researchers to study tiger biology.

Recent advances in the user-friendliness and availability of multivariate statistics, and in ancient DNA (aDNA) techniques have already started to help researchers to tease out the phylogeography of the extinct tiger subspecies, both morphologically (J. Mazák and Groves 2006; J. Mazák 2010) and genetically (Driscoll et al. 2009), and will surely contribute to a better understanding of the subject in the future. Furthermore, recent research using aDNA techniques highlights that understanding the phylogeography of extinct populations is providing academically interesting and practically important perspectives on the conservation of endangered charismatic carnivorans, including the tiger (Driscoll et al. 2009), the lion (Barnett et al. 2006), and the cheetah (Charruau et al. 2011). However, regardless of advances in analytical methodologies, researchers will continue to need access to physical specimens for morphological examination and (if appropriate) sampling for genetic and other analyses. In this context, it is frustrating that there has been no widely accessible information (e.g., location, origin, and date of collection) concerning the existing specimens of the extinct tiger subspecies.

In this paper we investigate and report on newly discovered specimens, as well as all the traceable specimens, of the extinct tiger subspecies. This will greatly benefit not only contemporary research into the conservation and evolutionary biology of the tiger, but also (and perhaps more importantly) future research as new methods become available.

Methods

Locating specimens

We have investigated the presence of specimens of the three extinct tiger subspecies in natural history collections in Asia, Europe, and North America on the basis of (1) published references, (2) electronic catalogues/lists of specimens made available by museums (either publicly or through personal communications to any of the authors), and (3) other information known to any of the authors, including unpublished records by the late Vratislav Mazák that are now held by one of the authors (Colin Groves). Special attention has been paid to collections associated with the former distribution of the Caspian tiger (e.g., collections in the former Soviet Union), and Javan and Balinese tigers (e.g., collections in the Netherlands). Although there were few unprovenanced specimens that we suspected as Caspian tigers, there were a handful of interesting specimens kept in the National Museum of Natural History, Leiden and the Zoological Museum, Amsterdam University, Amsterdam, the Netherlands (the Amsterdam collection was transferred to Leiden in 2010). They originated, or were likely to have originated, in the former Dutch East Indies (currently Indonesia, which until 1945 was under Dutch colonial administration), but any further details were unknown.

Assignment of unprovenanced specimens from the Sunda Islands

Several morphological characteristics, including a narrower occipital plane with its lateral margins parallel and its upper margin forming an isosceles triangle, and proportionally longer and narrower nasals (Fig. 1), have been suggested to diagnose Javan and Balinese tigers, although they do not occur exclusively in those subspe-

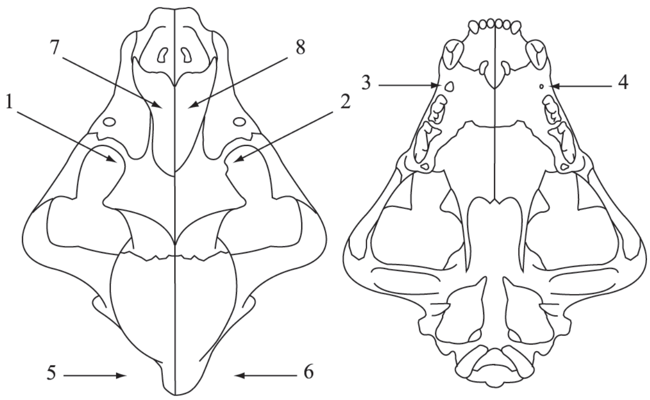

Fig. 1. Skull characteristics potentially useful for distinguishing Javan/Balinese tiger skulls from those of Sumatran tigers. Absence (1) or presence (2) of small ramps towards the upper anterior edges of the orbits where the inter-orbital width is narrowest. The size of P^2s based on size category; normal (3) or small (4). The typical occiput of the Javan/Balinese tiger skull (5), and the wider, rounder one of the Sumatran tiger (6). The proportionally narrower and longer nasal of Javan/Balinese tiger (7), and the wider and shorter one of the Sumatran tiger (8).

cies (Pocock 1929; Hemmer 1969; V. Mazák et al. 1978; Kitchener 1999; J. Mazák and Groves 2006). Recently, multivariate statistics have been also used to analyse skull morphology to distinguish the putative Sunda Islands tiger subspecies (J. Mazák and Groves 2006). A combination of multivariate statistics, based on large sample sizes and molecular analyses, which will become available in the future, is recommended to assign the likely geographical origins of unprovenanced specimens. However, for researchers working in a museum collection, examining as many specimens as possible within the shortest possible period, a quick "on site" assignment is crucial for deciding whether the specimens in question should be measured or/and included in an analysis—a similar problem was emphasised by Macdonald et al. (2010) concerning the crucial importance of on site identification of wildcats (*Felis silvestris*), even if such methods are not as accurate as more time-consuming methods. In addition to the characters that have been discussed above, we examined the following three morphological characteristics that were easy to score on site and which we considered were potentially useful in distinguishing Javan and Balinese tiger skulls from those of Sumatran tigers based on the frequency distribution and *k*-means cluster analysis.

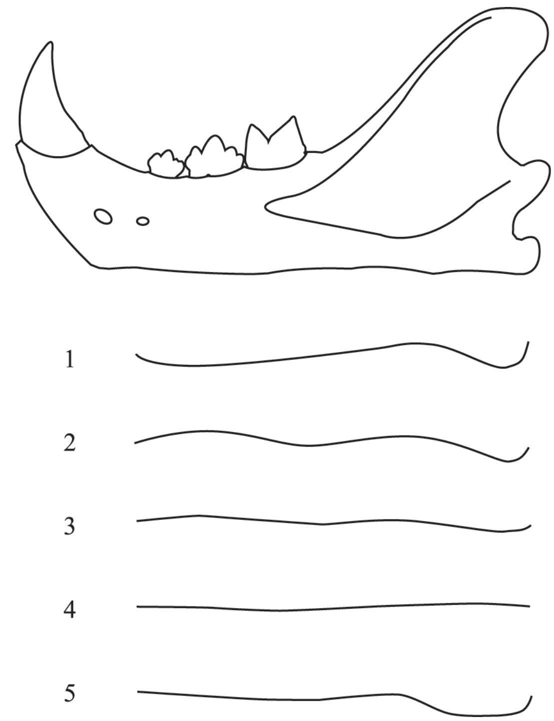

Fig. 2. Five types of ventral profile of the mandible of the tiger. The strongly concave profiles (1 and 2) are more common in the Javan/Balinese tiger mandibles in comparison to those of Sumatran tigers, many of which possess profile 5.

1) Orbit: small ramps towards the upper anterior edges of the orbits near where the inter-orbital width is narrowest (Fig. 1). If they are present, the skull is very unlikely to belong to either Javan or Balinese tigers.
2) P^2: the size of P^2s (Fig. 1). V. Mazák et al. (1978) reported that Balinese tiger skulls often lack (or have very small) P^2s. This characteristic also occurs in the Javan tiger.
3) Mandible: the ventral profile of the mandible around the angular process (Fig. 2). It is more concave in Javan and Balinese tigers in comparison to that in Sumatran tigers. Amongst the five profiles shown in Fig. 2, which are often found in the tiger, profiles 1 and 2 were classified as strongly concave in comparison to profiles 3, 4 and 5.

Skulls of Javan and Balinese tigers are not clearly distinguished based on multivariate statistics, and major morphological differences are probably related to size differences (Hemmer 1969; J. Mazák and Groves 2006; J. Mazák 2010). If a skull was assigned as Javan/Balinese tiger, we tried to further classify it as either Javan or Balinese based on its size. Figure 3 suggests that there is overlap in the greatest length of skull between the two subspecies, although it may be very small. Considering known Balinese tiger specimens are much rarer than those of Javan tiger by approximately 1

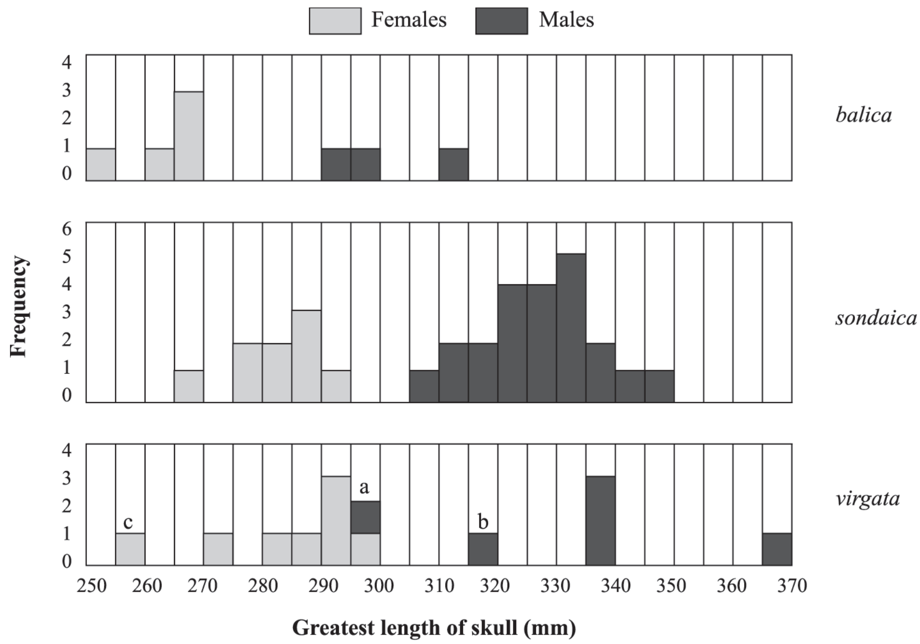

Fig. 3. Sexual size dimorphism in greatest length of skull in adult Caspian, Javan and Balinese tigers. Letters indicate captive Caspian tigers that show skull deformation: a (Berlin 12057, labelled male), b (Berlin 15683, labelled male) and c (Berlin 12413, labelled female).

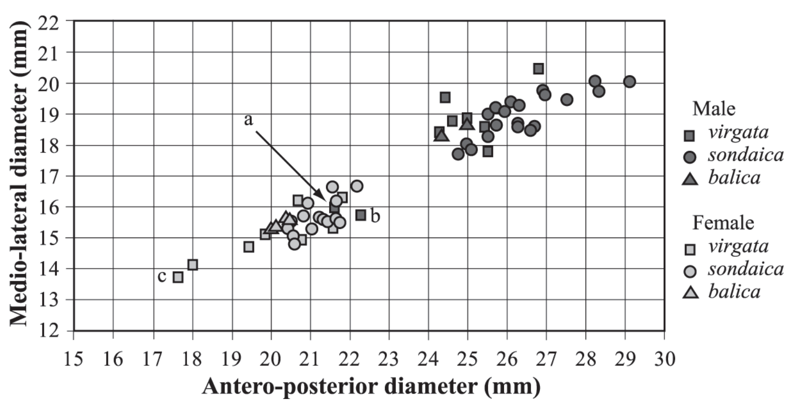

Fig. 4. Sexual size dimorphism in upper canine diameter in Caspian, Javan and Balinese tigers. Letters indicate the captive Caspian tigers that show skull deformation: a (Berlin 12057, labelled male), b (Berlin 15683, labelled male) and c (Berlin 12413, labelled female).

to 8, an unknown adult specimen was classified as a possible Balinese only when its greatest skull length was smaller than "standard deviation × 3" distance from the average size of adult Javan tiger of each sex—the threshold size was 295.90 mm for males, and 259.79 mm for females.

Age and sex of the specimens

A specimen was classified as juvenile, if the cemento-enamel junction of any permanent canine was not clearly visible above its alveolus. If these junctions were visible and yet the basioccipital-basisphenoid suture and/or frontal suture were still open, a skull was classified as subadult. If these sutures were closed (even if clearly visible), a skull was classified as adult. The sex of a specimen followed that recorded on its label or other documentation, or as assigned previously. If no information was available, the sex of a specimen was assigned based on sexual size dimorphism. Canine size dimorphism is a most useful parameter for distinguishing sexes in felids (Gittleman and Van Valkenburgh 1997). However, Gittleman and Van Valkenburgh (1997) found that sexual dimorphism in tiger canines is not as evident as it is in some other felid species. Fortunately, by focusing on the same subspecies, we found a clear sexual dimorphism in the canine size in tigers (Fig. 4). Also, previous

Table 1. Frequencies (upper right) and percentages (lower left) of all dyads of the four skull characters (occiput, orbits, P^2, and mandible (see the text for the details)) amongst the known-originspecimens. The shaded cells indicate character combinations found exclusively in Javan (J)/Balinese (B) tiger skulls and not in those of Sumatran tigers (S)

		Occiput		Orbit		P^2		Mandible	
		Yes	No	Yes	No	Yes	No	Yes	No
Occiput	Yes			J 25 S 0 B 5	J 2 S 0 B 0	J 26 S 0 B 9	J 10 S 1 B 0	J 26 S 1 B 5	J 11 S 0 B 2
	No			J 1 S 2 B 0	J 0 S 32 B 1	J 10 S 1 B 0	J 1 S 33 B 1	J 11 S 0 B 2	J 1 S 31 B 1
Orbit	Yes	J 89 S 0 B 83	J 4 S 6 B 0			J 20 S 0 B 5	J 11 S 2 B 0	J 20 S 0 B 4	J 10 S 2 B 1
	No	J 7 S 0 B 0	J 0 S 94 B 17			J 0 S 2 B 0	J 2 S 30 B 1	J 0 S 2 B 0	J 2 S 29 B 1
P^2	Yes	J 55 S 0 B 90	J 21 S 3 B 0	J 61 S 0 B 83	J 0 S 6 B 0			J 21 S 0 B 5	J 5 S 2 B 2
	No	J 21 S 3 B 0	J 3 S 94 B 10	J 33 S 6 B 0	J 6 S 88 B 17			J 6 S 3 B 0	J 8 S 29 B 1
Mandible	Yes	J 53 S 3 B 50	J 22 S 0 B 20	J 63 S 0 B 68	J 0 S 6 B 0	J 52 S 0 B 63	J 15 S 9 B 0		
	No	J 22 S 0 B 20	J 3 S 97 B 10	J 31 S 6 B 16	J 6 S 88 B 16	J 13 S 6 B 25	J 20 S 85 B 12		

studies strongly suggested clear sexual dimorphism in tiger skull size (Kitchener 1999; J. Mazák 2004, also see Fig. 3). We assigned the sex of previously unsexed specimens using discriminant function analyses based on skull size and/or canine sizes.

Statistical analysis

All statistical tests were carried out using SPSS (IBM, New York, USA). The *k*-means cluster analysis was based on four categorical variables: occiput, orbits, P^2, and mandible, and a character state associated with Javan/Balinese tiger was given a score of “yes” or 1 whilst that with Sumatran tiger was given “no” or 0.

Table 2. Classification by *k*-means cluster analysis, based on occiput, orbits, P^2, and mandible (see the text for the details), with the number of clusters set for two (i.e. either Javan/Balinese or Sumatran). Unknown individuals are those that had Javan/Balinese characteristics at least in two of the three characters: orbits, P^2, and mandible. Only skulls on which all four characters were assessed were included in the analysis

	Predicted group membership		Total
	Javan/Balinese	Sumatran	
Original group membership			
Javan/Balinese	31 (88.6%)	4 (11.4%)	35
Sumatran	0 (0%)	33 (100%)	33
Unknown	5 (100%)	0 (0%)	5

Results

Highly significant differences were detected between Javan/Balinese and Sumatran tiger skulls using G-tests (two tailed) for orbit ($n = 73$, $df = 1$, likelihood ratio $\chi^2 = 64.7$, $P < 0.001$), P^2 ($n = 88$, $df = 1$, likelihood ratio $\chi^2 = 42.9$, $P < 0.001$), and mandible ($n = 99$, $df = 1$, likelihood ratio $\chi^2 = 34.3$, $P < 0.001$). Also, amongst known-origin specimens, if at least two of the three discriminating skull characters showed the Javan/Balinese characteristic in an individual skull, it always belonged to either Javan or Balinese tiger (Table 1). This was consistent with the result obtained using a *k*-means cluster analysis (Table 2). Therefore, if a skull with an unknown origin had at

Table 3. Specimens of the extinct Javan tiger. The dates indicate either when the specimens were collected (e.g., collected in the field, presented to zoos, or died in zoos), or when the specimens were brought to the collections. The geographical origins were located and described using the original names only for obvious cases. When the original records alone did not clearly identify the locations, further information is provided using the current common English names (e.g., "Oedjoeng Koelon" = Ujung Kulon, W. Java). Abbreviations and the details of the collections are as follows: m (male), f (female), a (adult), sa (subadult), j (juvenile), s (skin both complete and damaged, including mounted skin), c (skull, including complete, damaged, and pieces of cranium and/or mandibles), and b (any postcranial skeletal specimens)

collection (register no)	sex/age	date	specimen	origin	comments
Panthera tigris sondaica (Temminck, 1844) Javan tiger Distribution: Java					
London (1867.4.12.185)[b]			c	Java	"114R" recorded by V. Mazák before 1980?
London (1867.4.12.192)	m/a		c	Java	
London (1867.4.12.194)	m/a		c	Java	
London (1867.4.12.198)	m/a		c	Java	
London (1867.4.12.199)	m/sa		c	Java	
London (1867.4.12.200)	f/sa		c	Java	
London (1867.4.12.201)	f/a		c	Java	
London (1920.11.14.2)	m/a		c	Probolingo, Java	
London (1937.12.1.1)	m/a	1937	s/c	Popoh, Blitar, E. Java	
London (1939.1643a)	f/a		c	Java	
London (1978.2459)	j		c	Java?	
London (1978.2460)			c/b	Java?	(*P. t. sondaica*? *P. t. regalis*?), presence unconfirmed
Edinburgh (Z.1995.291.1)	m	1924	c	Banjuwangi, E. Java	
Edinburgh (Z.1995.291.2)	m/sa	1930	c	Blitar, W. Java	
Paris (A1872)	f/a	1837	c	Java	other ID: I1466
Paris (A1877)	f/a	1826	c	Java	1836?, other ID: I1465
Paris (A1878)	f/a		c	Java	c. 1830, other ID: I1464
Paris (A1888)	m/a	1837	c	Java	other ID: I1462
Paris (1962.2869)	f/a		c	Java	c. 1830
Leiden (264)	m/sa	1912	c	Java	
Leiden (314)			c	Java	
Leiden (514)	f/a		c	Java	"*Panthera tigris sondaica*"
Leiden (1929)	m/a	1929	c	Java	"*Panthera tigris sondaica*?", captive animal (looks like a Sumatran tiger)
Leiden (4695)	f/sa	1941	c	Toeloeng Agoeng (Tulungagung), E. Java	"*Felis tigris sondaica?*"
Leiden (15755)	f/a	1934	c	Tieuri, Indonesie (Cieuri, Jampang Kulon, W. Java)	"*Panthera tigris sondaica*," other ID: 806
Leiden (23088)	m/a	1939	c	Zuid-Banjoewangi (S. Banyuwangi), Kesilir, E. Java	
Leiden (39216)[a]	f	1821–1824	s	W. Java	mounted skin (lectotype: *F. t. sondaica* (Temminck, 1845) by Jentink 1892)
Leiden (43493)			b	Java	
Leiden (45096)	m/a	1938	c	Oedjoeng Koelon (Ujung Kulon), W. Java	
Leiden (45098)	m/a	1933	c	Oedjoeng Koelon (Ujung Kulon), W. Java	
Leiden (45099)	m/sa		c	Java	
Leiden (45100)	f/a		c	Java	
Leiden (45101)	f/a		c	Java	
Leiden (45105)			c	Java	
Leiden (45107)			c	Java	other ID: 314
Leiden (45106)	f/a	1863	c	Java?	
Leiden (4699)	f/a	1890–1900	c		assigned to Java in this study
Leiden (45095)	m/sa	1860	c		assigned to Java in this study
Leiden (45097)	f/a	1886	c		assigned to Java in this study
Leiden (45102)	f/a		c		assigned to Java in this study
Leiden (45103)	f/a		c		assigned to Java in this study
Amsterdam (2231)			c	Java	"*sondaica*", captive animal
Amsterdam (2232)			c	Java	"*sondaica*"
Amsterdam (9174)		1853/1854	s	Java	"*sondaica*", captive animal?, mounted skin
Amsterdam (9179)	f/sa	1888	c	Preanger Regencies, W. Java	other ID: 283
Amsterdam (13542)	m/a	1892	c	Theeland Sinagar (Sinagar-Tjirohani), Cirohani, Mt Pangarango, W. Java	
Amsterdam (560)	m/a		c	Java "Azië"	assigned by V. Mazák before 1980
Amsterdam (562)	m/a		c	Java "Azië"	assigned by V. Mazák before 1980

Table 3. continued

collection (register no)	sex/age	date	specimen	origin	comments
Amsterdam (1428)	m/a		c	Java	assigned by V. Mazák before 1980, other ID: 9178
Amsterdam (1827)	f/a		c	Java "Netherl. Indië"	assigned by V. Mazák before 1980
Amsterdam (1829)	m/a	<1957	c	Java "Netherl. Indië"	assigned by V. Mazák before 1980
Amsterdam (9183)	f/a	<1957	c	Java "Netherl. Indië"	assigned by V. Mazák before 1980
Amsterdam (563)	f/a		c		assigned to Java in this study
Amsterdam (9201)	f/a		c		assigned to Java in this study
Brussels (9323/907e)[b]	m/a		c	Java	recorded by V. Mazák before 1980, ID 9323/9079?
Brussels (9323/9078)[b]	f/a		c	Java "Iles de la Sonde"	recorded and assigned by V. Mazák before 1980
Berlin (3387)	f/		s/b	Java	
Berlin (7620)	f/a		c	Java	
Berlin (14365)	m/j		c	Java	63 (1863?)
Berlin (14366)	f/sa		c	Java	
Berlin (14367)	f/a		c	Java	63 (1863?)
Berlin (14369)	f/sa		c	Java	
Berlin (19659)	m/		b	Java	
Berlin (28793)	m/a		c	Java	
Berlin (28794)	m/a		c	Java	
Berlin (56039)	m/sa		s/c/b	Java	
Berlin (56040)	m/a		c	Djokia (Yogyakarta), Central Java	
Berlin (56042)	/j		c	Java	
Berlin (56045)	f/a		c	Java	
Frankfurt (952)	m/sa		c	Java	"*sondaica*"
Frankfurt (15737)	f/a	1840	s/c	Java	
Frankfurt (16261)	f/a	1836	c	Java	
Frankfurt (16263)	m/a	1836	c	Java	
Frankfurt (16264)	m/a	1843	c	Java	
Frankfurt (38472)		1837	c	Java	
Frankfurt (60053)		1933	s/c	Udjung Kulon (Ujung Kulon), W. Java	
Stuttgart (7628)	m/a	1879	c/b	Java	captive animal, other ID: 2481
Stuttgart (31901)	m/a	1859	c	Java	other ID: 945
Munich (1904/084)			s	Menes, W. Java	
Budapest (65.111.1)	f/a		s/c	Java?	captive animal
Budapest (65.130.1)	m/a		s/c	Java?	captive animal
Budapest (77.8.1)	m/a		s/c	Java?	captive animal, dam (65.111.1) sire (65.130.1)
Stockholm (A61.9586)	/a	1918	s/c/b	Java	captive animal
Stockholm (A60.8550)		1829	s/c/b	Java	s and c/b may come from different animals
SPb (5737)	m/a	1800s	c	Java	skin ID: 568
Bogor (2428)[b]	f/sa		c	E. Java	Recorded by V. Mazák before 1980
Bogor (6836)[b]	m/a	1937	c	Tamanjaya, W. Java	Recorded by V. Mazák before 1980
Ito (no ID)			c	Java	
Either Javan or Balinese tiger					
Leiden (45104)	/j	1876	c/b		assigned in this study

[a] C. Smeenk (personal communication): Lectotype, RMNH 39216 (Jentink, 1892: 96 c), female, mounted skin. West Java, Indonesia, [1821–1824]. Leg. J. van Raalten. Paralectotype, RMNH 17655 (Jentink, 1887: 82 i; 1892: 96 d), female, mounted skin and skull. Padang, Sumatra, Indonesia, [1833–1835]. Leg. S. Müller. The lectotype was effectively designated by Brongersma (1935: 65–66), since he erroneously regarded the Javan skin as the "type" and restricted the type locality to Java. However, Temminck (1844: 54) clearly includes the other islands of the Indian Archipelago in this form, and the specimen from Sumatra was then present in the Leiden collection and so belongs in Temminck's type series. The catalogues by Jentink list the specimens by letters (1887: catalogue of osteological material; 1892: first part of catalogue of skins).

[b] Existence was not confirmed by this study.

Collections are London (Natural History Museum, London, UK), Edinburgh (National Museums Scotland, Edinburgh, UK), Paris (National Museum of Natural History, Paris, France), Leiden (National Natural History Museum, Leiden, the Netherlands), Amsterdam (Zoological Museum, Amsterdam University, Amsterdam, the Netherlands), Brussels (Royal Belgian Institute of Natural Sciences, Brussels, Belgium), Stockholm (Swedish Museum of Natural History, Stockholm, Sweden), Berlin (Museum of Natural History, Berlin, Germany), Frankfurt (Senckenberg Research Institute and Natural History Museum, Frankfurt am Main, Germany), Stuttgart (State Museum of Natural History, Stuttgart, Germany), Munich (Museum of Natural History, Munich, Germany), Budapest (Hungarian Natural History Museum, Budapest, Hungary), SPb (Zoological Institute, Russian Academy of Sciences, St Petersburg, Russia), Bogor (Zoological Museum, Bogor (now relocated to Cibinong), Indonesia), and Ito (Cat Museum, Ito, Japan).

Table 4. Specimens of the extinct Balinese tiger. All abbreviations and details are the same as those presented in Table 3

collection (register no)	sex/age	date	specimen	origin	comments
Panthera tigris balica (Schwarz, 1912) Balinese tiger Distribution: Bali					
London (1937.12.1.2)	m/a	1937	s/c	Sendang, N. W. Bali	
London (1938.3.14.5)	m/a	<1938	s/c	Bali	
London (1938.3.14.6)	f/a	1937	c	Propat, Agoeng, W. Bali	Prapat Agung?
Oxford (21424)	m	c. 1916	s/c	Bali	Fig. 6
Leiden (26135)	f/a	<1931	s/c/b	Sendang, N. W. Bali	
Frankfurt (2576)	f/a	1909	s/c	Den Pasar, S. Bali	holotype: *F. t. balica* (Schwarz, 1912), classified as subadult in V. Mazák et al. (1978), but adult based on our definition
Stuttgart (18922)	f/a	1926	c	Poeloekan (Pulukan), Bali	
Stuttgart (18923)	f/a	1924	c	Medewi, Bali	
Budapest (4250.17)	m/a	1911	c	Gunung (or Tanjung) Gondol, N.W. Bali	
Bogor (6834)[b]	f/a	1937	s/c	Sumber Kima, W. Bali	source: V. Mazák et al. (1978)
Izu (no ID)	f/a	1933	c	W. Bali	examination was carried out on the replica kept in Amsterdam (ID: 25208)

[b] Existence was not confirmed by this study.
Oxford: Natural History Museum, University of Oxford, Oxford, UK.

least two of the three characters associated with Javan/Balinese characteristics, we assigned it as Javan/Balinese, and identified eight previously unrecorded Javan/Balinese skulls. The results are summarised in Tables 3–5, which also includes all the specimens of the extinct tiger subspecies that we have been able to trace.

We report three Balinese tiger specimens that were not previously widely known. For example, there are no data for the original Izu specimen (Table 4). However, according to the records of the cast kept in the Leiden (Amsterdam 25208: see Table 4), it originated from West Bali in March 1933. It was sexed as an adult female. The Leiden specimen (26135: see Table 4) consists of an undamaged skull, skin and four limb bones, and is sexed as an adult female. The Oxford specimen (21424: see Table 4 and Fig. 5) was recorded as a male. The age of the specimen cannot be determined, as the skull, which is mounted inside the skin, could not be examined. However, it is likely to be an adult. The specimen was shot by Cecil H. H. Heaps in c. 1916 in central Bali, reportedly after having killed some villagers and children. The specimen was presented to the Oxford Natural History Museum in 1996 by his daughter, Marjorie Paterson.

Discussion

Javan and Balinese tigers

The results suggest that the Javan tiger specimens we located originate from the entire range of the subspecies, from Java's westernmost tip at Ujung Kulon to the eastern part of East Java at Kesilir. It is perhaps surprising that as many as 87 Javan tiger specimens were located, including the seven newly discovered specimens. This number is greater than those of extant Amur (*Panthera tigris altaica*), South China (*P. t. amoyensis*), Indochinese (*P. t. corbetti*), or Malayan (*P. t. jacksoni*) tigers kept in the natural history collections that we investigated (Yamaguchi, unpublished). The specimens include a relatively large number of less damaged adult skulls (Fig. 3), which are important for morphological investigations of these extinct subspecies, because the skull appears to have been used for morphological analysis more often than any other materials. It should also be noted that researchers are able to access the majority of existing Javan tiger specimens by travelling to a few natural history collections in Europe, thus potentially providing cost-effective research opportunities. Furthermore, Javan tiger specimens were collected over a period of at least c. 120 years (between 1821 and 1941),

Table 5. Specimens of the extinct Caspian tiger. All abbreviations and details are the same as those presented in Table 3

collection (register no)	sex/age	date	specimen	origin	comments
Panthera tigris virgate (Illiger, 1815) Caspian tiger Distribution: Central Asia from the northwestern China to Turkey					
London (1882.11.3.1)	f/a		c	Astrabad, N. Persia	
London (1886.10.15.1)	f/a	1885	s/c	Karaol Khama, Afghanistan	
London (1888.8.7.1)	m/a	1887	c	Maruchak, Perjdeh, N. Afghanistan	
London (1907.7.5.1)	f/a		s/c	Elburz Mountains, S. of Caspian Sea, N. Iran	(= 1822.11.3.1?)
London (1980.18)		c. 1927	s	Iran?	mounted skin
Berlin (11568)[b]	m/a		c	Russian Turkestan	recorded by V. Mazák before 1980
Berlin (12057)	m/a	1900	c	Ascabad, N. Persia	captive animal
Berlin (12413)	f/a	1901	c	N. Persia	captive animal
Berlin (13138)	f/a	1905	c	Petrowsk-Surdaya, Turkmenistan	captive animal
Berlin (15683)	m/a	1910	c	Altai, Kazakhstan	captive animal (type: *F. t.trabeata* (Schwartz, 1916))
Berlin (34285)	m/a	1924	c	Mazanderan, S. of Caspian Sea, N. Persia	
Berlin (83388)	/j	1904	c	Amu Darya River – Aral Sea	
Frankfurt (5805)		1914	s	Kurla District, Lop Nur, N.W. China	"*Panthera tigris lecoqi*"
SPb (1407)			s	Amu Darya River, Turkmenistan/Uzbekistan	mtDNA (1)
SPb (1512)	f/a	1878	s/c	Lop Nur, N.W. China	skin ID: 1654, mtDNA (2)
SPb (2087)	m/a	1882	c	Caucasus	
SPb (2258)[b]	f/a	1886	c	Transcaspian territory	recorded by V. Mazák before 1980
SPb (2981)	/a	1877	s	Turkestan (Kyrgyzstan)	1872 in Heptner & Sludskii (1972)
SPb (2982)	/a		s	Turkestan (Kazakhstan/Uzbekistan/Kyrgyzstan)	
SPb (3030)	/j	1877	s	Balkhash Lake, S.E. Kazakhstan	mtDNA (1)
SPb (3032)	/j	1879	s	Kuldzha, N.W. China	mtDNA (1)
SPb (4046)	m/a	1888	c	Kuldzha, N.W. China	mtDNA (1)
SPb (5728)	m/a	1873	c	Tashkent, Uzbekistan	mtDNA (1)
SPb (5730)	f/a		s/c	Kirgiz Steppe, Kazakhstan	skin ID: 3027, Semirechye, E. Kazakhstan in Heptner & Sludskii (1972)
SPb (5734)	f/a		c	Amu Darya River, Turkmenistan/Uzbekistan	
SPb (7862)	f/a	1889	s/c	Lop Nur, N.W. China	skin ID: 2983, mtDNA (1)
SPb (9386)	/j	1885	c	Darkat Isl., Panj River, Tadjikistan	mtDNA (1)
SPb (9387)	m/j	1858	s/c	Kazalinsk, Syr Darya River, Kazakhstan	mounted skin on display ID: 1077, mtDNA (1)
SPb (9391)	m/a	1903	s/c	Fergana Area, Uzbekistan/ Kyrgyzstan	skin ID: 8679, mtDNA (3)
SPb (9392)	f/a	?1905?	s/c	Atrek River, Turkmenistan	skin ID: 8678, mtDNA (1)
SPb (14997)	m/a	1887	c	Turkestan (Kazakhstan/Uzbekistan/Kyrgyzstan)	mtDNA (4), (?1827?)
SPb (17196)	f/a		c	Lenkoran, Azerbaijan	skin ID: 569
SPb (33110)	f/a		c	Neftezavodsk, Chardzhou Province, Turkmenistan	presented in 1989
Moscow (S-33151)		1939	s	Ili River, S.E. Kazakhstan	mtDNA (1)
Moscow (S-38285)	f/a	1942	s/c	N. Persia	captive animal, mtDNA (1)
Moscow (S-52871)		1950	s	Panj River, Pamir Mountains, Tajikistan	mtDNA (1)
Moscow (S-69458)	m/a	1963	c	Central Asia "Bengal"	assigned by V. Mazák before 1980
Nov (7182/2225)	m/sa	1944	c	Kurgan-Tyube Province, S.W. Tajikistan	mtDNA (1)
Nov (7181/2226)	f/a	1951	c	Kurgan-Tyube Province, S.W. Tajikistan	mtDNA (1)
Almaty (1/10973/2)	m/a	1930s	c	Ili River, near Balkhash Lake, S.E. Kazakhstan	
Almaty (2/10974)		1933	s	Kzyl-Orda, Kostam, S. Kazakhstan	inconsistent with Abdukadir & Breitenmoser (2007)
Almaty (4/10995)			s	Semirechye, near Almaty, S.E. Kazakhstan	inconsistent with Abdukadir & Breitenmoser (2007), mtDNA (1)
Baku (no ID)		1936–1942	s	Azerbaijan	mtDNA (1)
Baku (no ID)		1936–1942	s	Azerbaijan	mtDNA (1)
Tehran (no ID)		1946	s	N.E. Iran	
Ashgabat[b]		1954	s/c	Kopet-Dag, S. Turkmenistan	mounted specimen (Heptner & Sludskii 1972)

[b] Existence was not confirmed by this study.
mtDNA: Segments of mitochondrial DNA are successfully extracted and sequenced in Driscoll et al. (2009). The numbers in brackets indicate one of four haplotypes, including the autapomorphic variants.
Collections are Moscow (Zoological Museum, Moscow State University, Moscow, Russia), Nov (Siberian Zoological Museum, Russian Academy of Sciences, Novosibirsk, Russia), Almaty (Institute of Zoology, Almaty, Kazakhstan), Baku (Azerbaijan Medical University, Baku, Azerbaijan), and Tehran (Tehran, Iran).

Fig. 5. A Balinese tiger (Oxford (21424) in Table 4) shot by Cecil HH Heaps (far right) in Bali around 1916 (by courtesy of his daughter, Ms Marjorie Paterson).

potentially providing a very important sample set for researchers to investigate the possible loss of genetic diversity over the last c. 150 years prior to the extinction of this island carnivoran.

The existence of Balinese tiger specimens has been relatively well investigated, and eight specimens had been identified (Hemmer 1969; V. Mazák et al. 1978; Seidensticker 1987; Buzas and Farkas 1997). Most Balinese specimens originate from the western half of the island, although some specimens without locality data may have come from other areas. We have identified three specimens which have not been included in the previous widely-accessible literature—Izu (no ID), Leiden (26135) and Oxford (21424) (Table 4). Only three photographs of the Balinese tiger appear to have been known previously. Perhaps the most famous and most widespread photograph is of the tiger shot in 1925 (Nowell and Jackson 1996). Another photograph of an animal shot by Zandveld in Bali is published by V. Mazák (1983). Also, there is a photograph of a tiger shot by Baron Oszkár Vojnich of Hungary at Gunung Gondol, northwestern Bali, in November 1911 (Buzas and Farkas 1997). Figure 5 is only the fourth known photograph of the Balinese tiger. It appears that more than 50 Balinese tigers were shot during the early 20th Century (Boomgaard 2001), suggesting that some unknown Balinese tiger specimens may still exist.

Tiger populations in southeast Asia, between the Malay Peninsula and the Sunda Islands, were connected to each other intermittently, owing to sea-level changes associated with past glacial–interglacial oscillations and the effects of the gigantic Toba eruption c. 75,000 years ago (Kitchener and Dugmore 2000; Kitchener and Yamaguchi 2010). Hemmer (1971) suggested that local evolution of the tiger in Java might have been interrupted by colonisations of larger tigers from the mainland during interglacial periods. Such biogeographical events have been influencing the phylogenetic relationships between tiger populations in the region and questions remain today as to how many tiger subspecies used to occur in the region. Based on skull morphology, Hemmer (1969) suggests that Javan and Balinese tigers form a single group, clearly differentiated from the Sumatran tiger. However, V. Mazák appears to have retained the idea of full subspecies status for the Balinese tiger (V. Mazák et al. 1978; V. Mazák 1981, 1983). Recently, J. Mazák and Groves, based on the same data collected by V. Mazák and now held by Groves, supported the grouping of Javan and Balinese tigers together and separate from the Sumatran tiger (J. Mazák and Groves 2006; J. Mazák 2010). Grouping Javan and Balinese tigers together is consistent with a previous analysis of tiger cranial capacity (Yamaguchi et al. 2009). Needless to say, settling these conjectures will require further evidence, including ancient biomolecular research on Balinese and Javan tigers, in order to ascertain the intraspecific phylogeny of the Sunda Islands tigers. The specimens listed in Table 1 will surely contribute to the research necessary to provide further evidence on this issue.

Caspian tiger

Our results also suggest that currently available specimens represent relatively well the former original distribution of the Caspian tiger between northwest China and Azerbaijan (Nowell and Jackson 1996). Because they had not been well studied before their extinction, all tigers inhabiting the vast area from western China to eastern Turkey were treated as a single subspecies, (*Panthera tigris virgata*) without a known designated holotype (V. Mazak 1981; Nowell and Jackson 1996; Kitchener 1999). However, some regional Caspian tiger populations may have formed "discrete taxonomic units" (Hemmer 1987; Kitchener and Dugmore 2000). A recent phylogeographical study based on c. 1,250 bp of mitochondrial DNA showed that only three of out of the 20 specimens that were genotyped carry autapomorphic variants, each of which is a single nucleotide substitution (Driscoll et al. 2009). This suggests that all the tigers that inhabited the vastness of Central Asia form a phylogenetically coherent group, supporting the previous taxonomy, even though it was probably first proposed without clear scientific justification. Also, a recent molecular investigation strongly suggested that the Caspian tiger was practically identical to the Amur tiger (Driscoll et al. 2009). This may result in the merging of these two commonly recognised tiger subspecies into *Panthera tigris virgata* (Illiger, 1815), which predates *P. t. altaica* (Temminck, 1844), following the rule of priority in zoological nomenclature. However, such a merger will likely influence not only taxonomy, but also the course of conservation of the highly endangered tiger, including the possible re-introduction of Amur tigers into Central and southwest Asia (Driscoll et al. 2012). Therefore, a careful evaluation is necessary concerning more detailed genetic and morphological characteristics of these two subspecies before reaching a decision on their possible consubspecificity. The specimens listed in Table 1 will surely contribute to the research necessary to provide further evidence on this issue. In addition, Poland (1892) mentioned that skins of Caspian tigers were imported to the UK "in the rough state through Russia and Leipsic, and fetch from £3 to £25" suggesting that some unknown Caspian tiger specimens may still exist across Europe as antiques.

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