

Subspecies	Morphology	Molecular	Biogeography	Certainty	Comments
<i>Neofelis diardi diardi</i>	++	++	++		
<i>Neofelis diardi borneensis</i>	+	++	++		Skulls distinguishable between subspecies, but pelage variation poorly known

Genus *Panthera* Oken, 1816; 1052.

This genus contains five species, including the largest known felid species.

Panthera tigris

E: Tiger; F: Tigre; G: Tiger; Sp: Tigre.

Few species have received so much scientific attention regarding subspecific taxonomy as the tiger. Wozencraft (2005) recognised eight subspecies:

Panthera tigris tigris (Linnaeus, 1758; 41).

Locality from where the species was first described: Asia; restricted by Thomas (1911) to Bengal [India].

Holotype: None designated.

Distribution: India, Pakistan, Bangladesh, Bhutan, Nepal.

Panthera tigris virgata (Illiger, 1815; 90, 98).

Locality from where the subspecies was first described: in Persien und am Kaspischen Meere [in Persia and the Caspian Sea]; restricted by Harper (1940) to the Province of Mazanderan, northern Persia [= Iran].

Type: None designated.

Distribution: Caspian region (Turkmenistan, south Azerbaijan, northern Iran), Uzbekistan, Tadjikistan, Afghanistan, China (Tarim Basin, Lobnor). Extinct.

Panthera tigris altaica (Temminck, 1844; 43).

Type locality: la Corée (Korai) [= Korea].

Holotype: RMNH.MAM f or 13.

Distribution: Russian Far East, NE China, Korea.

Panthera tigris sondaica (Temminck, 1844; 43).

Type locality: Java.

Lectotype: RMNH.MAM c or 39216 female mounted skin.

Distribution: Java (extinct).

Panthera tigris amoyensis (Hilzhemier, 1905; 598).

Type locality: Hankau in China [= Hankou, China].

Syntypes: MZS Mam03305, Mam03306, Mam03307, Mam03308, Mam0311 five skulls.

Distribution: China (extinct in wild).

Panthera tigris balica (Schwarz, 1912; 325).

Type locality: Bali.

Holotype: SMF 2576 female skull and skin.

Distribution: Bali (extinct).



© A. Sliwa

Panthera tigris sumatrae Pocock, 1929; 535, pl. H (live animal), pls. 1C and 1D (skull).

Type locality: Deli in Sumatra.

Holotype: BMNH 1912.11.10.1 male skin and skull.

Distribution: Sumatra.

Panthera tigris corbetti Mazák, 1968; 105.

Type locality: Quang-Tri, Annam [= Vietnam].

Holotype: BMNH 1933.4.1.203 male skin and skull.

Distribution: Indochina, S China.

A further molecular study, based on 4kb of mtDNA sequences and 30 nuclear microsatellites markers, apparently distinguished a further subspecies from the Malay Peninsula (Luo et al. 2004), which was named:

Panthera tigris jacksoni Luo et al., 2004; 2275.

Type locality: Melaka, Malaysia.

Holotype: Zoo Melaka #12 live male.

However, there is no description or definition (genetic or morphological distinction) of the subspecies *Panthera tigris* "jacksoni" that makes the name available (Article 13 of the International Code of Zoological Nomenclature) and, indeed, the authors state "the taxonomic diagnosis will be described elsewhere".

Under the Code, a holotype or syntypes must be fixed for a new name to be available (Article 72.3). However, it is not absolutely necessary for there to be (an) existing specimen(s) (Article 73.1.4). Thus, a live animal would be acceptable as the type.

Therefore, this subspecies has not been named in accordance with the rules of the ICZN and is a *nomen nudum*.

Discussion

There have been several molecular and morphological studies of tigers, which have come to different conclusions regarding numbers of subspecies, which vary from two to three up to eight or nine (Cracraft et al. 1998, Kitchener 1999, Wentzel et al. 1999, Kitchener & Dugmore 2000, Luo et al. 2004, 2010, Mazák & Groves 2006, Driscoll et al. 2009, Kitchener & Yamaguchi 2010, Mazák 2010, Wilting et al. 2015, Xue et al. 2015). The most significant of these is Driscoll et al. (2009) who demonstrated a 1 bp fixed difference between *virgata* and *altaica* across a total of 1,257 bp of five partially sequenced mtDNA genes, and tentatively suggested that they should be treated as consubspecific.

Luo et al. (2010) provide a comprehensive review of tiger phylogeography, but there were no data available for the extinct Javan and Balinese tigers, although it seems likely that based on skull and pelage morphology that these are consubspecific (Kitchener & Yamaguchi 2010, Mazák 2010). The taxonomic status of tigers in Indochina and the Malay Peninsula is still unclear; "jacksoni" is diphyletic, based on mtDNA, and must have originated very recently from *corbetti*. Subspecies *corbetti* shows further genetic structure which does not appear to have geographical significance (Luo et al. 2004). However, we should be wary of conclusions based only on living tiger populations. Mondol et al. (2013) showed that modern Indian tiger populations show increased population structure compared with historical samples, indicating a loss of mtDNA and microsatellite diversity, owing to local extirpation and genetic drift.

Recently, two studies have elucidated the relationships between Sunda Island tigers. Xue et al. (2015) showed that *balica*, *sondaica* and *sumatrae* share the same genetic clade but found slight differences (similar to the differences between *virgata* and *altaica*) between the islands. A comprehensive study by Wilting et al. (2015) showed that there is no geographical structure amongst these island populations and that they even share haplotypes, and concluded that Sunda Island tigers should be considered consubspecific. Furthermore, Wilting et al. (2015) failed to find support from multiple lines of evidence for mainland subspecies (morphological, molecular and ecological data), but did support the differentiation of Sunda Island tigers. However, owing to the morphological and ecological distinctiveness of northern tigers (formerly *altaica* and *virgata*), which is due to the large gap in the geographical distribution caused by ancient to modern exploitation of tigers by humans, Wilting et al. (2015) retained these as a MU distinct from a southern (mainland) MU. Following this comprehensive study, we revise the subspecific taxonomy of the tiger as follows:

Panthera tigris tigris (Linnaeus, 1758).

Distribution: Mainland Asia, including India, Pakistan, Nepal, Bhutan, Sikkim, China, Russia, Indochina and the Malay Peninsula (includes *virgata*, *altaica*, *amoyensis*, *corbetti* and "jacksoni").

Distinguishing characters: Larger size, paler pelage with fewer stripes.

Panthera tigris sondaica (Temminck, 1844).

Distribution: Sumatra and formerly Java and Bali (includes *balica*, *sumatrae*).

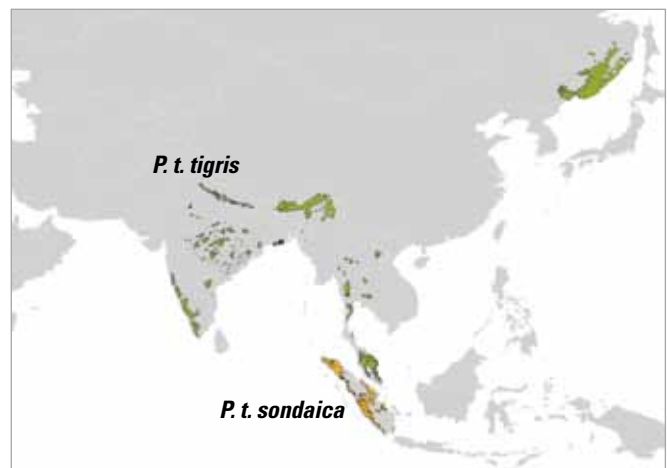
Distinguishing characters: Smaller size, darker pelage with more frequent stripes.

In contrast, Luo & Driscoll (pers. comm.) retain the classification of Wozencraft (2005) for *amoyensis*, *tigris* and *corbetti*, while recognising also "jacksoni" (Luo et al. 2004, 2010) and synonymising *altaica* with

virgata (Driscoll et al. 2009). They maintain the subspecific status of *sumatrae*, *balica* and *sondaica* (Xue et al. 2015), at least provisionally. While Xue et al. (2015) showed that *balica*, *sondaica* and *sumatrae* form a monophyletic clade that is distinctive and equidistant from all other subspecies, the authors found no shared mtDNA haplotype across the three island populations, indicating a lack of detectable gene flow among tigers on these islands, perhaps as a result of prehistoric isolation by rising sea levels. Mazák & Groves (2006) meanwhile suggested separation of the Sunda Islands tigers into two species: *sumatrae* and *sondaica*, including *balica*, based on skull morphology. Subspecies differentiation in the tiger would have resulted from geographical isolation, genetic drift and local adaptation associated with repeated restriction and expansion of habitats in the last 100,000 years. However, Kitchener (1999) and Wilting et al. (2015) showed that skull characters, such as a narrow occipital region, are shared by other putative tiger subspecies and there is complete overlap in skull morphology amongst Sunda tigers.

References

- Cracraft J., Feinstein J., Vaughn J. & Helm-Bychowski K. 1998. Sorting out tigers (*Panthera tigris*): Mitochondrial sequences, nuclear inserts, systematics, and conservation genetics. *Animal Conservation* 1, 139-150.
- Driscoll C. A., Yamaguchi N., Bar-Gal G. K., Roca A. L., Luo S.-J., Macdonald D. W. & O'Brien S. J. 2009. Mitochondrial phylogeography illuminates the origin of the extinct Caspian tiger and its relationship to the Amur tiger. *PLoS One* 4, e4125.
- Harper F. 1940. The nomenclature and type localities of certain Old World mammals. *Journal of Mammalogy* 21, 191-203.
- Hilzheimer H. 1905. Über einiger Tigerschädel aus der Strassburger zoologischen Sammlung. *Zoologischer Anzeiger* 28, 594-599.
- Illiger C. 1815. Ueberblick der Säugethiere nach ihrer Verteilung über die Welttheile. *Abhandlungen der Königlichen Akademie der Wissenschaften in Berlin, 1804-1811*, pp. 39-159.
- Kitchener A. C. 1999. Tiger distribution, phenotypic variation and conservation issues. *In* *Riding the Tiger*. Tiger conservation in human-dominated landscapes. Seidensticker J., Jackson P. & Christie S. (Eds). Cambridge University Press, Cambridge, pp. 19-39.
- Kitchener A. C. & Dugmore A. J. 2000. Biogeographical change in the tiger. *Animal Conservation* 3, 113-124.
- Kitchener A. C. & Yamaguchi N. 2010. What is a tiger? Biogeography, morphology, and taxonomy. *In* *Tigers of the world* (2nd ed.). Tilson R. & Nyhus P. J. (Eds). Academic Press, London, pp. 53-84.



Distribution of subspecies of tiger.

- Linnaeus C. 1758. Systema Naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis (10th ed.), vol. 1. Laurentii Salvii, Holmiae.
- 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., Karanth U. K., Sunquist M., Smith J. L. D. & O'Brien S. J. 2004. Phylogeography and genetic ancestry of tigers (*Panthera tigris*). PLOS Biology 2, 2275-2293.
- Luo S.-J., Johnson W. E., Smith J. L. D. & O'Brien S. J. 2010. What is a tiger? Genetics and phylogeography. In Tigers of the World. The science, politics and conservation of *Panthera tigris* (2nd ed.). Tilson R. & Nyhus P. J. (Eds). Academic press, London, Burlington and San Diego, pp. 35-51.
- Mazák J. H. 2010. Craniometric variation in the tiger (*Panthera tigris*): Implications for patterns of diversity, taxonomy and conservation. Mammalian Biology 75, 45-68.
- Mazák J. H. & Groves C. P. 2006. A taxonomic revision of the tigers (*Panthera tigris*) of Southeast Asia. Mammalian Biology 71, 268-287.
- Mazák V. 1968. Nouvelle sous-espece de tigre provenant de l'Asie du Sud-Est. Mammalia 32, 104-112.
- Mondol S., Bruford M. W. & Ramakrishnan U. 2013. Demographic loss, genetic structure and the conservation implications for Indian tigers. Proceedings of the Royal Society B: Biological Sciences 280, 20130496.
- Pocock R. I. 1929. Tigers. Journal of the Bombay Natural History Society 33, 505-541, pl. H, pls. 1C and 1D.
- Schwarz E. 1912. Notes on Malay tigers, with description of a new form from Bali. Annals and Magazine of Natural History (8th series) 10, 324-326.
- Temminck C. J. 1844. Aperçu général et spécifique sur les mammifères qui habitent le Japon et les îles qui en dépendent. In Fauna Japonica sive Descriptio animalium, quae in itinere per Japoniam, jussu et auspiciis superiorum, qui summum in India Batava imperium tenent, suscepto, annis 1825 - 1830 collegit, notis, observationibus et adumbrationibus illustravit Ph. Fr. de Siebold. Coniunctis studiis C. J. Temminck et H. Schlegel pro vertebratis atque W. de Haan pro invertebratis elaborata. Siebold Ph.F. von (Ed.). Batavia, Arnz.
- Thomas O. 1911. The mammals of the tenth edition of Linnaeus; an attempt to fix the types of the genera and the exact bases and localities of the species. Proceedings of the Zoological Society of London 81, 120-158.
- Wentzel J., Stephens J. C., Johnson W. E., Menotti-Raymond M., Pecon-Slatery J., Yuhki N., Carrington M., Quigley H. B., Miquelle D. G., Tilson R., Manansang J., Brady G., Zhi L., Wenshi P., Shi-Qiang H., Johnston L., Sunquist M., Karanth K. U. & O'Brien S. J. 1999. Subspecies of tigers: Molecular assessment using "voucher specimens" of geographically traceable individuals. In Riding the Tiger: Tiger conservation in human-dominated landscapes. Seidensticker J., Jackson P. & Christie S. (Eds). Cambridge University Press, Cambridge, pp. 40-49.
- Wilting A., Courtiol A., Christiansen P., Niedballa J., Scharf A. K., Orlando L., Balkenhol N., Hofer H., Kramer-Schadt S., Fickel J. & Kitchener A. C. 2015. Planning tiger recovery: Understanding intraspecific variation for effective conservation. Science Advances 1, e1400175.
- Wozencraft W. C. 2005. Order Carnivora. In Mammal species of the world. A taxonomic and geographic reference (3rd ed.). Wilson D. E. & Reeder D. M. (Eds). Johns Hopkins University Press, Baltimore, pp. 532-628.
- Xue H.-R., Yamaguchi N., Driscoll C. A., Han Y., Bar-Gal G. K., Zhuang Y., Mazak J. H., Macdonald D. W., O'Brien S. J. & Luo S.-J. 2015. Genetic ancestry of the extinct Javan and Bali tigers. Journal of Heredity 106, 247-257.

Subspecies	Morphology	Molecular	Biogeography	Certainty	Comments
<i>Panthera tigris tigris</i>	++	++	++		
<i>Panthera tigris virgata</i>	+	-	++		Genetically closely related to <i>altaica</i>
<i>Panthera tigris altaica</i>	++	-	+		Genetically closely related to <i>virgata</i>
<i>Panthera tigris sondaica</i>	++	++	++		Genetically closely related to <i>sumatrae</i> and <i>balica</i>
<i>Panthera tigris amoyensis</i>	+	?++			Unique mtDNA haplotype
<i>Panthera tigris balica</i>	+	-	++		Included in <i>sondaica</i>
<i>Panthera tigris sumatrae</i>	+	-	++		Included in <i>sondaica</i>
<i>Panthera tigris corbetti</i>	+	-	-		
<i>Panthera tigris 'jacksoni'</i>	+	-	+		Diphyletic