### Subspecies Comparison

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<tbody>
<tr>
<td><em>Neofelis diardi diardi</em></td>
<td>++</td>
<td>++</td>
<td>++</td>
<td></td>
<td>Skulls distinguishable between subspecies, but pelage variation poorly known</td>
</tr>
<tr>
<td><em>Neofelis diardi borneensis</em></td>
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**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).
  - Localities 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).
  - Localities from where the subspecies was first described: in Persien und am Kasipischen 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, Afganistan, 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** (Hilzheimer, 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).

- **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 & Goves 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 conspecific.

Luo et al. (2010) provide a comprehensive review of tiger phylogeny, but there were no data available for the extinct Javan and Balinese tigers, although it seems likely that based on skull and pelage morphologies these are conspecific (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 by introgression. 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 conspecific. 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 Woyncraft (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 distinct 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 & Goves (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


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.


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<td>Panthera tigris tigris</td>
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<tr>
<td>Panthera tigris virgata</td>
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<td>Genetically closely related to altaica</td>
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<td>Panthera tigris altaica</td>
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<td>-</td>
<td>+</td>
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<td>Genetically closely related to virgata</td>
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<tr>
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<td></td>
<td>Genetically closely related to sumatrae and balica</td>
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<td>Panthera tigris amoyensis</td>
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<td>Unique mtDNA haplotype</td>
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<td>-</td>
<td>++</td>
<td></td>
<td>Included in sondaica</td>
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<tr>
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<td>Included in sondaica</td>
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<tr>
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<tr>
<td>Panthera tigris ‘jacksoni’</td>
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<td></td>
<td>Diphyletic</td>
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