

The evolution of the tiger by Andrew C. Kitchener

Excerpted and reprinted with permission of Cambridge University Press and the author from "Tiger distribution, phenotypic variation and conservation issues." 1999. Pages 20-21 and Table A2.1 in *Riding the Tiger: Tiger Conservation in human-dominated landscapes*. Eds. Seidensticker, J., Christie, S. and Jackson. P., Cambridge University Press.

Evidence for the evolution of the tiger comes from fossil remains and molecular phylogenies (Brongersma 1935; Hooijer 1947; Hemmer 1967, 1987; Wayne *et al.* 1989; J. Wentzel *et al.* this volume). Cats of the genus *Panthera* probably evolved within the last five million years or so (Hemmer 1976; Collier & O'Brien 1985; Wayne *et al.* 1989). On the basis of a cladistical analysis of various skeletal and anatomical characters, fossil remains and biogeography, Hemmer (1981) suggested that the original pantherine radiation occurred in eastern Asia, although there is fossil evidence to support an African origin for the lion and leopard (Hemmer 1976). However, the tiger is thought to have an eastern Asian origin (Hemmer 1981, 1987; Herrington 1987; Mazak 1981, 1996).

Reconstructing the fossil history of tigers is difficult owing to the existence of mainly fragmentary remains, risk of confusion with closely related species, and uncertain dating of finds. The oldest fossils are from northern China and Java (Hemmer 1971, 1976, 1987). Originally described as *Felis palaeosinensis* (Zdansky 1924), a small fossil tiger from Henan (formerly Honan), northern China is thought to date from the end of the Pliocene and the beginning of the Pleistocene and so may be up to two million years old (Hemmer 1967, 1987). However, it should be noted that these tigers were intermediate in size between modern Indian leopards and Sunda Island tigers, and may actually represent a large form of leopard or an ancestor of two or more of today's *Panthera* cats. Clearly the taxonomic status of *Felis palaeosinensis* would benefit from further investigation.

Early tiger fossils have also been recorded from the Jetis Beds of Java, which have recently been dated to between 1.66 and 1.81 million years old (Dubois 1908; Brongersma 1935; Hemmer 1971, 1987; Swisher *et al.* 1994). Therefore, by the beginning of the Pleistocene and possibly as long as two million years ago, the tiger already had a wide distribution in eastern Asia. It is commonly stated that the centre of evolution for tigers was northern China (e.g. Mazak 1981; Hemmer 1987; Herrington 1987), but the fossil evidence is equivocal given the wide distribution of the species at the beginning of the Pleistocene. It is also unnecessary to require or even envisage such a restricted locality for the tiger's evolution, since all that is required is sufficient temporal separation of a population to allow its genetic and morphological divergence from a sister or ancestral species, which could have occurred over a wide area of eastern Asia.

Abundant tiger fossils dated approximately from the early middle to late Pleistocene are known from China, Sumatra and Java (Appendix 2), but tiger fossils only appeared in India, the Altai, northern Russia and elsewhere in the late Pleistocene (Brandt 1871; Lydekker 1886; Tscherski 1892; Dubois 1908; Zdansky 1928; Brongersma 1935; Loukashkin 1937; Hooijer 1947; Hemmer 1971, 1976, 1987). Recently, Herrington (1987) identified some fossil big cats from eastern Beringia as tigers, but so far none has been recorded from North America. Small tigers are also known from the late Pleistocene of Japan (Hemmer 1967).

Hooijer (1947) documented a decline in size of tigers during the Pleistocene until the present day, excluding those from the Russian Far East, which have stayed about the same size. This is not unusual in Pleistocene mammals (Guthrie 1984; Kurten 1967) and probably reflects a decline in the seasonal productivity of the environment (Geist 1987a, b), and/or a decline in average prey size.

Holocene remains of the tiger have been recorded from Java and Borneo ([Appendix 2](#); Hooijer, 1947, 1963). The tiger is apparently now extinct on Borneo and the significance of this will be discussed later.

Molecular phylogenies based on a variety of methods confirm the close relationship between members of the genus *Panthera* and show that the tiger diverged more than two million years ago and before the divergence of the lion, leopard and jaguar (Collier & O'Brien 1985; Wayne *et al.* 1989; J. Wentzel *et al.* this volume). Therefore, the fossil and molecular histories of the tiger are broadly in agreement.

Although it is unclear where the tiger first diverged from other *Panthera* cats in eastern Asia, it is presumed to have spread north into northeast Asia, and south into the Sunda Islands and the Indian subcontinent (Hemmer 1987). The late arrival of the tiger in India is apparently supported by its absence from Sri Lanka (unless it became extinct there subsequently), which was cut off by rising sea levels at the beginning of the Holocene. There is some uncertainty over the origin of tigers in southwest Asia. Heptner & Sludskii (1992a) proposed that tigers colonised this area from northwest India, but Hemmer (1987) and Mazak (1981, 1996) suggested a route from northeast Asia via central Asia.

Although absent today, on zoogeographical grounds the tiger should be an inhabitant of Borneo, but the evidence is equivocal and includes a skull, skins, teeth, wall paintings and photographs, which are usually assumed to be of external origin or influence (Hose & McDougall 1912; Pocock 1929; Peranio 1960; Gersi 1975; Medway 1977; Yasuma 1994). However, members of the Bisaya tribe claimed that the teeth in their possession were from indigenous tigers, although they had been inherited through four to seven generations (Peranio 1960). This suggests that the tiger may have been an indigenous species until 200 or so years ago, but is probably now extinct. The best evidence for the former existence of the tiger on Borneo is the tip of an unerupted upper canine that was found in the Niah Cave, Sarawak in deposits thought to date to the Neolithic of Borneo (Hooijer 1963; Medway 1977).

References

- Brandt, F. 1871. Neue Untersuchungen über die in den altaischen Höhlen aufgefunden Säyugethierreste, ein Beitrag zur quaternären Fauna des Russischen Reiches. Bulletin de l'Académie Impéiale de St. Petersbourg, 15:147-202.
- Brongersma, L. D. 1935. Notes on some recent and fossil cats, chiefly from the Malay Archipelago. Zoologische Mededeelingen. 18:1-89.
- Collier, G. E., and O'Brien, S. J. 1985. A molecular phylogeny of the Felidae immunological distance. Evolution. 39:473-487.
- Dubois, E. 1908. Das geologische Alter der Kendengoder Trinil-Fauna. Tijdschrift van het Koninklijke Nederlandsch Aardrijkskundig Genootschap. 2 Series 24:1235-1271.
- Geist, V. 1987a. Bergmann's Rule is invalid. Canadian Journal of Zoology. 65:1035-1038.
- Geist, V. 1987b. On the evolution and adaptations of *Alces*. Swedish Wildlife Research Supplement. 1:11-23.
- Gersi 1975; Gersi, D. 1975. Dans le Jungle de Borneo. Paris, Editions GP.
- Guthrie 1984; Guthrie, R. D. 1984. Mosaics, allelochemicals and nutrients. In *Pleistocene Extinctions*, ed. P. S. Martin and R. G. Klein. Pp. 259-298. Tucson, Arizona, University of Arizona Press.
- Hemmer 1967, 1971, 1976, 1981, 1987; HemmerH. 1967. Wohin gehört '*Felis*' *palaeosinensis* (Zdansky 1924) in systematischer Hinsicht? Neues Jahrbuch für Geologie und Paläontologie. Stuttgart. Abhandlungen 129:83-96.
- Hemmer. H. 1971. fossil mammals of Java. II . Zur Fossilgeschichte des Tigers (*Panthera tigris* (L.)) in Java. Koninklijke Nederlandse Akademie van Wetenschappen, Series B. 74:35-52.

- Hemmer, H. 1976. Fossil history of the living Felidae. In *The World's Cats*, volume III (2) ed. R. L. Eaton, pp. 1-14. University of Washington, Seattle, The Carnivore Research Institute, Burke Museum.
- Hemmer, H. 1981. Die Evolution der Pantherkatzen Modell zur Überprüfung der Brauchbarkeit der Hennigschen Prinzipien der Phylogenetischen Systematik für wirbeltier Paläontologische Studien. *Paläontologische Zeitschrift* 55:109-116.
- Heptner, V. G. and Slukskii, A. A. 1992a. Mammals of the Soviet Union, volume II, part 2, Carnivores (Feloidea). Leiden, E. J. Brill.
- Herrington, S. 1987. Subspecies and the conservation of *Panthera igris*: Preserving genetic heterogeneity. In *Tigers of the World: The Biology, Biopolitics, Management and Conservation of an Endangered Species*. Ed. R. L. Tilson and U. S. Seal. Pp. 512-60. Park Ridge, New Jersey, Noyes Publications.
- Hooijer, D. A. 1947. Pleistocene remains of *Panthera tigris* (Linnaeus) subspecies from Wanhsien, Szechuan, China, compared with fossil and recent tigers from other localities. *American Museum Novitates*. 1346:1-17.
- Hooijer, D. A. 1963. Further 'Hell' mammals from Niah. *Sarawak Museum Journal* 11:196-200.
- Hose & McDougall 1912; Hose, C. and McDougall, W. 1912. *The Pagan Tribes of Borneo*, volume II. London, Macmillan.
- Kurtén, B. 1967. *The Pleistocene Mammals of Europe*. London, Weidenfeld and Nicolson.
- Loukashkin, A. S. 1937. Some observations on the remains of a Pleistocene fauna and of the Palaeolithic age in northern Manchuria. In *Early Man*, ed. G. G. MacCurdy, pp. 327-340. Freeport, Books for Libraries Press.
- Lydekker, R. 1886. Preliminary notes on the Mammalia of the Karnul Caves. *Records of the Geological Survey of India*. 19:120-122.
- Mazák, V. J. 1981. *Panthera tigris*. *Mammalian Species* 152:1-8.
- Mazák, V. J. 1996. *Der Tiger*. Magdeburg, Westarp Wissenschaften. (Reprint of 1983 edition)
- Medway, Lord 1977. *Mammals of Borneo*. Kuala Lumpur, Malaysian Branch of the Royal Asiatic Society
- Peranio, R. 1960. Animal teeth and oath taking among the Bisaya. *Sarawak Museum Journal* 9:6-13.
- Pocock 1929; Pocock, R. I. 1929. Tigers. *Journal of the Bombay Natural History Society* 33:505-541.
- Swisher III, C. C., Rink, R. J., Anton, S. C., Schwarcz, H. P., Curtis, G. H., Suprijo, A., and Widiasmoro. 1996. Latest *Homo erectus* of Java: Potential contemporaneity with *Homo sapiens* in Southeast Asia. *Science* 274:1870-1872.
- Tscherski, J. D. 1892. Wissenschaftliche Resultate der von der Kaiserliche Akademie der Wissenschaften zur Erforschung des Janalandes und der neusibirischen Inseln in den Jahren 1885 und 1886 ausgesandten Expedition. Abt. IV. Beschreibung der Sammlung posttertiärer Säugetiere. *Mémoires de l'Académie Impériale des Sciences de St.-Petersbourg*, VIIe Série 40:1-511.
- Wayne, R. K., Benveniste, R. E., Janczewski, N., and O'Brien, S. J. 1989. Molecular and biochemical evolution of the Carnivora. In *Carnivore Behaviour, Ecology and Evolution*, ed. J. L. Gittleman, pp. 465-494. London, Chapman and Hall.
- Wentzel, J., Stephens, C., Johnson, W., Menoti-Raymond, M., Pecon-Slattery, J., Yuhki, N., Carrington, M., Quigley, H. B., Miquelle, G. G., Tilson, R., Manansang, J., Brady, G., Zhu, L., Wenshi, P., Shi-Qiang, H., Johnston, L., Sunquist, M., Karanth, K. U., and S. J. O'Brien. 1999. Subspecies of tigers: molecular assessment using 'voucher specimens' of geographically traceable individuals. In *Riding the Tiger: tiger conservation in human-dominated landscapes*, eds. Seidensticker, J., Christie, S., and Jackson, P. Pp. 40-49. Cambridge, Cambridge University Press.
- Yasuma, S. 1994. *An Invitation to the Mammals of East Kalimantan*. PUSREHUT Special Publication 3. Republic of Indonesia, Japan International Cooperation Agency and Directorate General of Higher Education.
- Zdansky, O. 1924. Jungtertiäre Carnivoren. *Palaeontologia Sinica Series C* 2(1):1-145.
- Zdansky, O., 1928. Die Säugetiere der Quartäraufauna von Chou-K'ou-Tien. *Palaeontologia Sinica Series C* 5(4):1-146.

The fossil tigers

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Table A2.1. Localities and ages of fossil tigers. Spellings of locality names are as given in original references and may well have changed since date of publication

Geological epoch	Estimated age (millions of years ago, Mya)	Locality	Synonyms	Ref.
Late Pliocene to early Pleistocene	2	China: Anyan, Honan Province Java: 1.3–2.1 1.66	<i>Felis palaeosinensis</i>	1, 4
		Gunung Butak (Jetis Beds); Sangiran; Punung		3, 5
Middle to late Pleistocene		Java:	<i>Felis groeneveldtii</i> , <i>Felis trinilensis</i> , <i>Panthera tigris soloensis</i> , <i>Felis palaeojavanica</i> , <i>Felis oxygnatha</i>	2, 5, 6
	0.7–1.3	Kendeng; Trinil; Kedung Brubus; Bangle; Jeruk; Kebon Duren; Teguan Sumatra: Sangiran; Padang Highlands		
		China:	<i>Felis acutidens</i> <i>Felis youngi</i>	8
	0.23–0.46	Choukoutien; Wanhhsien, Szechuan Province; Chinkiang, W. Hupei Province; Fuminhsien, Yunnan Province; Kweilin, Kwangsi Province;		7, 28, 29, 32
				14
				27
				18
				20
	0.65–0.8	Lantian, Shensi Province; Gongwangling, Shensi Province;		21, 32
				26

Table A2.1. (cont.)

Geological epoch	Estimated age (millions of years ago, Mya)	Locality	Synonyms	Ref.
	0.24	Shihhung, N. Anhwei Province		25, 32
Late Pleistocene	0.27–0.053	Java: Ngangdong China: Shangdong; Harbin Japan: Mikkabi*; Akiyosi, Yamaguti Province; Isa, Yamaguchi Province; Gansuiji Russia: Bolschoj Lyachow I., Siberia; Jana River Basin, Siberia; Tscharisch River, Altai		6, 31
		Caucasus		24
		E. Beringia		16
Holocene		India: Karnul Caves		4
		Java: Sampung		19
		Borneo: Niah Caves, Sarawak		22
				23
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				15

*Also Kuzuu; Tadaki

Table A2.1 References:

1. Zdansky 1924. 2. von Koenigswald 1933. 3. Hemmer 1971, 1976, 1987. 4. Hemmer 1968.
5. Duboi 1908. 6. Brongersma 1935. 7. Pei 1934; Zdansky 1928. 8. Brongersma 1937.
9. Tscherski 1892. 10. Brandt 1871. 11. Lydekker 1886. 12. Vereshchagin 1959 in Herrington 1987. 13. Herrington 1987. 14. Hooijer 1947. 15. Hooijer 1963. 16. Loukashkin 1937, 1938.
17. Young 1939. 18. Young 1932. 19. Shikama & Okafuji 1958. 20. Pei 1935. 21. Minchen 1964.
22. Shikama & Okafuji 1963. 23. Takai & Hasegawa 1966. 24. Zhang Zulu 1994. 25. Young & Chow 1955. 26. Wu *et al.* 1966. 27. Chiu *et al.* 1960. 28. Teilhard de Chardin 1936. 29. Pei 1936.
30. Swisher *et al.* 1994. 31. Swisher *et al.* 1996. 32. Groves 1989.