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PLEISTOCENE REMAINS OF *PANTHERA TIGRIS* (LINNAEUS) SUBSPECIES FROM WANHSIEN, SZECHWAN, CHINA, COMPARED WITH FOSSIL AND RECENT TIGERS FROM OTHER LOCALITIES

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INTRODUCTION

The remains of the tiger dealt with in the present paper form part of a collection of fossil mammals secured for the American Museum of Natural History by the late Dr. Walter Granger during the winters of 1921–1922, 1922–1923, and 1925–1926. The exact locality is Yen Ching Kao, Wanhsien, eastern Szechwan. A preliminary description of part of the collection has been given by Matthew and Granger (1923), who then considered the fauna to be probably upper Pliocene. In this paper the specimens were mentioned under the head *Felis* aff. *tigris* Linnaeus. They were sent to the Leiden Museum of Natural History in 1937 at the request of Dr. L. D. Brongersma who had made a study of the fossil cats from Java in the Dubois collection (Brongersma, 1935). The feline fossils fortunately survived the war.[2] They consist of cranial remains, including an almost complete but crushed skull (figured by Matthew and Granger, 1923, p. 585, fig. 16), and of limb and foot bones: a humerus, two metacarpals, a tibia, an astragalus, two calcanea, and five metatarsals.

For comparison I used a series of recent tiger and lion skulls and skeletons, and the fossil tiger remains from Java collected by Eugène Dubois, now in the Leiden Museum.

The age of the Chinese specimens is now regarded as lower Pleistocene. As Dr. G. G. Simpson kindly wrote me, the circumstances of occurrence and of collecting do not guarantee that the Yen Ching Kao fauna is absolutely unified as to age. He is inclined to think that the bulk of the fauna is Pleistocene, although it is possible that a few Pliocene elements (*Stegodon*, *Chalicotherium*) are included.

Brongersma's paper assembles previous records of fossil tigers. Matthew and Granger's paper, however, is mentioned as the sole reference to the fossil tiger of China. Its synonymy is[3]:

Panthera tigris (Linnaeus) subspecies

? *Felis*, KOKEN, 1885, Palaeont. Abhandl., Berlin, vol. 3, pt. 2, p. 106, pl. 6, fig. 3 (?Y, ?A).

Felis aff. *tigris*, MATTHEW AND GRANGER, 1923, Bull. Amer. Mus. Nat. Hist., vol. 48, p. 584, fig. 16 (W); YOUNG, 1932, Bull. Geol. Soc. China, vol. 11, no. 4, p. 388 (W); YOUNG, 1939, *ibid.*, vol. 19, no. 2, p. 320 (W).

F[*elis*] aff. *tigris*, PEI, 1934, Palaeont. Sinica, ser. C, vol. 8, pt. 1, p. 132 (W).

Felis acutidens, ZDANSKY (*partim*), 1928, Palaeont. Sinica, ser. C, vol. 5, pt. 4, p. 48, pl. 4, figs. 6–11 (C).

Felis acutidens, YOUNG, 1932, Bull. Geol. Soc. China, vol. 11, no. 4, p. 388 (C).

Felis sp., YOUNG, 1932, Bull. Geol. Soc. China, vol. 11, no. 4, p. 387, fig. 5 (Y).

Felis cf. *tigris*, PEI, 1934, Palaeont. Sinica, ser. C, vol. 8, pt. 1, p. 130, pl. 23, fig. 3, pl. 24, figs. 1, 6, text figs. 40A, 41A, 42 (C); TEILHARD DE CHARDIN, 1936, Palaeont. Sinica, ser. C, vol. 7, pt. 4, p. 15 (C).

F[*elis*] *tigris*, PEI, 1934, Palaeont. Sinica, ser. C, vol. 8, pt. 1, p. 132 (A).

Felis tigris, PEI, 1936, Palaeont. Sinica, ser. C, vol. 7, pt. 5, p. 52 (C); TEILHARD DE CHARDIN AND YOUNG, 1936, Palaeont. Sinica, ser. C, vol. 12, pt. 1, p. 9, pl. 1, figs. 1–2, pl. 2, figs. 1–2, text figs. 1–2 (A).

[1] Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands.

[2] During an air raid in December, 1944, some bombs hit the building in Leiden where the main part of the Dubois collection was stored. Many specimens, especially of proboscideans and deer, were lost; *Pithecanthropus* was saved.

[3] A, Anyang; C, Chou Kou Tien; W, Wanhsien; Y, Yunnan.

? *Felis youngi*, PEI, 1934, Palaeont. Sinica, ser. C, vol. 8, pt. 1, p. 133, pl. 23, figs. 1, 4, text fig. 40B (C).

Loukashkin (1936, 1937) records *Panthera tigris longipilis* (Fitzinger) from the Pleistocene of northern Manchuria, but unfortunately neither describes nor figures his specimens.

The skull in the Wanhsien collection of the American Museum of Natural History (A.M.N.H. No. 18624, fig. 1) was found with the lower jaw *in situ*. The specimen had been subjected to a crushing force which acted especially in the middle of the skull. The right nasal and maxillary are placed on a higher level than the left, both zygomatic arches are fractured and displaced, the brain case is distorted, and the right bulla is missing. The right mandibular ramus is fractured posteriorly and displaced inward and upward.

It is impossible to reconstruct the exact shape of the anterior narial orifice and to establish whether the nasals are wedged in between the frontals posteriorly beyond the maxillaries or not, but there remain other characters which show that the specimen is a tiger. The interval between the bulla and the postglenoid process is greater than in a lion's skull (cf. Haltenorth, 1936, p. 53, figs. 36, 71), and the orbital margin of the malar is more concave (*ibid.*, figs. 38, 63). I do not agree with Haltenorth as to the validity of the shape of the malar-maxillary suture as a specific character, although the shape of that suture in the Wanhsien skull is perfectly in accord with that given by Haltenorth as typically tiger-like.

The shape of the lower edge of the mandibular ramus is fully consistent with that of the tiger, being slightly concave between the symphysis and the angular process. This is well shown on the right side; the swelling on the left ramus below the carnassial shown in Matthew and Granger's figure (1923, p. 585[1]) is the result of crushing.

The incisor dentition is complete, but the tips of the left canines have been broken off. P^2 is missing on both sides, and P^3 is damaged. The upper carnassial is beveled away on the inner side. The lower teeth are complete. Notes on the dentition of this and the following specimens are given below.

The second specimen (A.M.N.H. No. 18737) is the anterior portion of a skull with the lower jaw *in situ*. That this, too, is a tiger is evident from the shape of the anterior narial orifice (fig. 2) which is narrowed below instead of being regularly curved from side to side (cf. Boule, 1906, p. 71, figs. 3–4). Of this specimen only the right P^4 is completely preserved. The canines are larger than in the foregoing skull.

A.M.N.H. No. 18741 comprises a fragment of the left maxillary with P^3, P^4, and the alveolus of M^1. The carnassial is tiger-like; the protocone is well developed. There is also a portion of the left ramus of a mandible with P_3–M_1. The lower border is straight.

A.M.N.H. No. 18740 is the left ramus of a lower jaw with the alveoli of the incisors, the entire canine, and the full set of permanent teeth. Only the lower portion of the masseteric fossa is preserved. The lower edge of the ramus shows a slight bulging below M_1. Recent tigers may show the same peculiarity (Leiden Museum, Reg. No. 315, two specimens). A mandible from Chou Kou Tien was described by Pei (1934, p. 133) as a new species, *Felis youngi*, on account of the gently convex lower border and the longer symphysis and larger size as compared to *Panthera tigris* (Linnaeus). In the present specimen the symphysis is even longer than in Pei's type specimen (74 mm. against 71.4 mm. in the Chou Kou Tien jaw), and the convexity of the lower edge of the ramus, although more anterior and more strongly marked than in our specimen, is occasionally found in the tiger, too (Haltenorth, 1936, p. 54). I shall return to the question of size below.

A.M.N.H. No. 18738 includes five specimens, all of young individuals:

1. Fragment of left maxillary with dc, C erupting, alveolus of P^2, dm^3, and erupting P^4.

[1] I removed the piece of bone adhering to the mandible below the anterior portion of the masseteric fossa, as not belonging to the skull.

2. Similar fragment, but of the right side, and without dc.
3. Small fragment of right maxillary with dc, C erupting, and P^2.
4. Right ramus of mandible with central incisors just in place, I_3, C, and erupting M_1.
5. Small anterior fragment of right lower jaw with C in alveolus, dm_3, dm_4, and the germ of the carnassial.

The incisors in the two skulls have not been freed of matrix behind, and offer no interesting points for description. In fact, since Koken's (1885) figure of an incisor of uncertain origin which Schlosser (1903, p. 39) determined as an I^3, no attention has been paid to the incisors of Chinese tigers.

The upper canines possess two longitudinal grooves on the outer surface. Posteriorly they present a longitudinal ridge on the enamel. Of the two outer grooves the anterior is stronger than the other. The grooves do not extend upward to the margin of the enamel, but the posterior ridge does. This is exactly what we find in *Panthera tigris* (Linnaeus). Zdansky (1928, p. 48) observed a posterior ridge on an upper C which he identified as "*Felis acutidens* sp. n.," and states that among recent felines this ridge is to be found only in *Neofelis nebulosa* (Griffith).

The lower canines also are indistinguishable in shape from those of the recent tiger, having an outer and an inner longitudinal groove and a medio-posterior longitudinal ridge.

P^2 has not previously been described from China. It can be studied only in the juvenile specimen (A.M.N.H. No. 18738, 3 of the preceding list). The basal plane is subtriangular, the angle between the inner and posterior sides is approximately a right angle, and the posterior side is about three-fourths as long as the inner. The paracone is low and elongated. The metacone is merely a ridge behind it and descending less steeply than the protocone. The cingulum is present only along the inner and posterior inner margins.

In recent specimens P^2, if present, has exactly the same shape. Variations, however, are often found in this functionless tooth: e.g., the base may be oval-shaped (Leiden Museum, Reg. No. 3319), and the difference between length and width may be less than in the fossil specimen. The latter is larger, as a whole, than its recent homologues examined by me, but it is smaller than the P^2 from Java which von Koenigswald (1933, p. 9) refers to *Feliopsis palaeojavanica* Stremme, a species which has been placed by Brongersma (1935, p. 59) in the synonymy of *Panthera tigris* (Linnaeus).

P^3 presents a fair amount of variation in the development of the metacone, which is incipient in the complete Wanhsien skull and distinctly developed in A.M.N.H. No. 18741. This is, however, of no importance, because I have found similar variations in the recent teeth. The upper carnassial is noticeable for the same variability in size of the paracone. P^4 is also preserved in the partial skull (A.M.N.H. No. 18737), and in this specimen the paracone is of intermediate development. None of the teeth has a definite parastyle. The tiny M^1 is lost or too much damaged for study in our specimens.

Of the lower premolars, P_3 is proportionally longer in A.M.N.H. No. 18741 than in No. 18740, and the same holds for P_4. M_1, however, is shorter in the former than in the latter specimen. It is especially large in a young jaw (the fourth specimen under A.M.N.H. No. 18738). Study of variation in recent lower teeth of *Panthera tigris* (Linnaeus) convinces me that these variations are now exceptional. The only further point worthy of mention with respect to the teeth is their size.

Of the milk dentition there are two specimens, both with dc, dm_3, and dm_4, and a dm^3. The latter tooth (first and second specimens under A.M.N.H. No. 18738) has a strong inner root, parastyle and paracone of equal development, pointed metacone, and elongated metastyle. The inner surface of the crown is convex anteroposteriorly, the outer approximately straight with a slight bulging below the metacone. The upper dc's have an antero-internal longitudinal ridge, which is not shown to such an extent in the permanent canines. The lower milk molars are built on the same general plan as the dm^3 but reversed:

the outer surface convex and the paraconid elongated. Behind the main cusp or protoconid there are two cusps, of which the metaconid is stronger than the talonid. These milk teeth are identical in shape with those in living specimens. I have two young skulls for comparison, of which one (Leiden Museum, Reg. No. 1034), a female, is of unknown origin, and the other (Leiden Museum, Reg. No. 1120) is a hybrid between male *Panthera tigris sondaica* (Temminck) and female *Panthera tigris sumatrae* Pocock. Measurements are given in table 1.

TABLE 1

MEASUREMENTS IN MILLIMETERS OF MILK TEETH OF RECENT AND FOSSIL TIGERS

	Panthera tigris (Linnaeus)				
	Leiden Museum No. 1034	Leiden Museum No. 1120	A.M.N.H. No. 18738		
Upper dc					
Length	9.7	11.1	11.3	12.3	—
Width	6.0	6.2	7.6	7.1	—
dm^3					
Length	22.4	21.3	24.6	—	—
Width	6.7	6.1	7.4	—	—
dm_3					
Length	12.2	12.2	—	14.0	14.3
Width	6.6	5.2	—	6.5	6.7
dm_4					
Length	16.7	16.5	—	19.3	20.4
Width	6.7	5.8	—	7.0	7.5

the difference is so great as to induce one to distinguish different species. The latter example brings us to another point, viz., the alleged insular nanism.

The belief is widespread that the small size of so many insular species or races has something to do with restricted habitat, inbreeding, scarcity of food, etc. This explanation has been offered, e.g., for the existence of dwarf elephants and hippopotamuses on the Mediterranean islands, the Shetland pony, the Balinese tiger, Kuhl's deer of Bawean, the buffalo of Mindoro, the Sika deer of Japan. In opposition to this view stands the evidence of the existence of, e.g., the giant asses of Malta and Cyprus, and the tall Polynesians in contrast to the Pygmies of the Congo forests, southern India, and New Guinea, the largest but one of the islands of the world. Among other vertebrates one might recall the Galápagos turtles, the "elephant birds" of Madagascar, and the giant moas of New Zealand. Moreover, small races of species may also be found on continents: e.g., races of the African elephant and of the mammoth.

It is not surprising that the Pleistocene teeth are larger than the recent. During my studies on recent and fossil mammals I have repeatedly found fossil and subfossil teeth and bones referable to living species to be slightly larger than the corresponding recent material. To quote a few examples from published papers, I may mention that the Pleistocene European hippopotamus, deer, bovids, and various Carnivora (Reynolds, 1902–1939, and others), the North American pumas and jaguars (Simpson, 1941), the Asiatic Przewalski's horse (Zdansky, 1935), chigetai (Boule and Teilhard, 1928), orang utan (Pei, 1935), and prehistoric tapir (Teilhard and Young, 1936) often have greater dimensions than their recent representatives. Sometimes, e.g., in the case of the urus, and in that of *Bubalus palaeokerabau* Dubois from Java,

The preceding digression is introductory to discussion of the dimensions of the permanent teeth, given in tables 2 and 3.

The 10 columns of table 3 give the observed range of variation of the measurements of:

1. *Panthera tigris sondaica* (Temminck),

Leiden Museum, Cat. a, d, h, j, Coll. Van Lidth de Jeude Nos. 314 and 319, Reg. Nos. 1929 and 4695.

2. *Panthera tigris sumatrae* Pocock, Leiden Museum, Cat. a, g, i, Reg. Nos. 315 (two skulls), 872, 2171, 2202, 3319, 4694, 4696–4698.

3. *Panthera tigris* (Linnaeus) subsp. from Java, as given by Stremme (1911), von Koenigswald (1933), and Brongersma (1935) from various Pleistocene localities.

4. *Panthera tigris* (Linnaeus) subsp. from prehistoric caves in the Padang highlands, Sumatra; teeth that were cursorily referred to by Brongersma (1937, p. 1862).

5. *Panthera tigris tigris* (Linnaeus) from India, as given by Hilzheimer (1905).

6. *Panthera tigris amoyensis* (Hilzheimer, 1905), based on five skulls secured at Hankow, and originating from southern China.

7. *Panthera tigris* (Linnaeus) subsp. from the Pleistocene of Wanhsien, Szechwan, China, as described by Young (1932, upper C; 1939, M_1), Pei (1934, P4, M1), and by the present author.

8. *Panthera tigris* (Linnaeus) subsp. from the Pleistocene of Chou Kou Tien, the *Sinanthropus* locality, as described by Zdansky (1928) and Pei (1934, 1936).

9. *Panthera tigris* (Linnaeus) subsp. from the archaeological site of Anyang, Honan, China, as described by Pei (1934) and Teilhard de Chardin and Young (1936).

10. *Panthera tigris altaica* (Temminck), from the Leiden Museum specimen (Cat. n).

From this table is seen that, although the different ranges of variation overlap to some extent, the Wanhsien, Chou Kou Tien, and Javan fossil tigers are larger than the recent tigers from the Greater Sunda Islands. The Indian tiger has the biggest jaws, but its teeth do not seem to be especially large; Pocock (1929, p. 517), however, gives 38 and 29 mm. for the maximum lengths of the upper and the lower carnassial, respectively. These figures are found only in fossil or subfossil but not in recent teeth from Java and Sumatra. The Manchurian tiger, as judged by Busk's (1874) figures (P^4 length, 36.8 mm.; M_1 length, 26.7 mm.) is only slightly inferior in size to the Indian form. The southern tiger from China is smaller than the Indian, but not so small as the insular subspecies. The Bali tiger is known to be the smallest of all races.

It is evident that the tiger has undergone a diminution in size in the course of time. The fossils prove this beyond doubt. Once there were living tigers in China and the Malay Archipelago which were as large as, if not even larger than, the largest of all surviving races. No doubt the species is now on its way to extinction; six of the nine subspecies were placed among the "Extinct and vanishing mammals of the Old World" by Harper (1945). I shall return to the size problem at the end of this paper.

TABLE 2

MEASUREMENTS IN MILLIMETERS OF TEETH OF *Panthera tigris* (LINNAEUS) SUBSPECIES, FOSSILS FROM WANHSIEN

	P^3		P^4		P_3		P_4		M_1	
A.M.N.H. Nos.	Length	Width	Length	Width	Length	Width	Length	Width	Length	Width
18624	19.3	10.5	33.3	—	14.9	—	22.8	—	—	—
18737	—	—	36.8	—	—	—	—	—	—	—
18741	24.5	13.0	38.1	19.9	18.0	10.0	25.7	13.0	27.6	14.7
18740	—	—	—	—	16.7	10.0	24.5	12.9	28.0	14.3
18738.4	—	—	—	—	—	—	—	—	31.2	15.4
18738.5	—	—	—	—	—	—	—	—	28.0	13.7

The limb and foot bones in the Wanhsien collection have been compared with those of the living tiger and lion, of which I examined the following skeletons:

Panthera leo (Linnaeus)

1. Leiden Museum, Cat. d. Female, locality unknown. From the Rotterdam Zoo, April 1865.

2. Leiden Museum, Cat. e. Male, incomplete

TABLE 3

OBSERVED RANGES OF VARIATION OF MEASUREMENTS OF DENTITIONS OF RECENT AND FOSSIL TIGERS

(Specifications of the 10 samples are given in the text.)

	1. Java, Recent	2. Sumatra, Recent	3. Java, Fossil	4. Sumatra, Subfossil	5. India, Recent	6. Southern China, Recent	7. Wanhsien, Fossil	8. Chou Kou Tien, Fossil	9. Anyang, Subfossil	10. Vladivostok, Recent
Length of upper jaw	110–131	110–136	121.3	—	140–151	122–143	130–146	—	—	130
Upper C, length	20.5–25.0	20.0–28.0	25.1–31.6	—	—	—	23.5–31.0	27.0	—	25.4
Upper C, width	15.0–18.2	15.0–19.7	23.2	—	—	—	22–23.5	19.0	—	18.4
P^2, length	7.6– 7.7	7.2– 9.4	6.3–10	—	—	—	9.2	—	—	—
P^2, width	5.7– 6.2	4.9– 6.6	6.0– 7	—	—	—	6.4	—	—	—
P^3, length	18.8–22.5	19.1–22.5	19.7–25.3	—	21.8–22.8	20 –23.8	19.3–24.5	22.3–24.0	22.0	22.0
P^3, width	9.8–11.0	9.6–12.4	8.6–13.4	—	11.5–12.5	10.5–12.5	10.5–13.0	13.1–13.8	11.4	11.6
P^4, length	30.0–33.7	30.3–34.6	29.1–38.8	21.2–37.6	35 –36.3	31 –36	33.3–38.1	33.0–35.0	33.5	30.5
P^4, width	15.4–17.7	15.0–18.0	16.6–20.1	20.0–20.1	17 –19	15 –18	19.2–19.9	17.2–18.8	17.2	15.4
M^1, length	5.7– 6.0	5.8– 6.8	5.4	—	—	—	7.5	7.6	4.6	—
M^1, width	9.8–11.0	10.0–12.0	8.2	—	—	—	11.7	10.1	7.4	—
Length of lower jaw	173–210	175–219	195–222	—	203–225	184–219	*ca.* 215	—	194	218
Lower C, length	18.2–23.0	18.8–25.0	23.4–26	—	—	—	—	24.4	—	25.0
Lower C, width	13.1–15.8	13.0–17.0	—	—	—	—	—	17.3	—	15.7
P_3, length	13.5–16.3	13.1–16.0	15–19	15.7	16 –17	15 –17.3	14.9–18.0	15.5–20.3	15.6	15.9
P_3, width	7.0– 8.0	7.0– 8.0	7.3–10	8.2	7.8– 8	8 – 9	10.0	8.2– 9.7	8.0	8.9
P_4, length	19.7–22.9	20.4–23.5	22.0–28.5	22.0	23 –24	21 –24.3	22.8–25.7	22.2–25.5	22.4	22.8
P_4, width	10.0–10.5	9.1–11.8	10.8–14	11.6	11.8–12	10.5–12.5	12.9–13.0	13.0–14.2	11.2	10.0
M_1, length	22.1–25.3	22.2–26.0	23.8–30	26.3	26 –27.8	23 –26.5	25 –31.2	24.0–28.4	25.5–26	24.5
M_1, width	11.8–13.0	12.0–13.7	12.1–16	13.5	13 –14	11 –14	13 –15.4	13.4–15.6	13.4–13.5	12.2

skeleton of an individual that lived in the Tower in London, and originated in Africa.

3. Leiden Museum, Cat. f. Female from Africa, don. Van Aken.

4. Leiden Museum, Reg. No. 1751. Female, originating from Rhodesia, Rotterdam Zoo, May 17, 1929.

5. Leiden Museum, Reg. No. 2352. Male, locality unknown, from the Rotterdam Zoo, July 30, 1935.

Panthera tigris sondaica (Temminck)

1. Leiden Museum, Cat. a. Sex not recorded. Java, leg. Kuhl and Van Hasselt.

2. Leiden Museum, Reg. No. 1929. Male, Java, from the Rotterdam Zoo, February 13, 1931.

Panthera tigris sumatrae Pocock

3. Leiden Museum, Reg. No. 925. Male, Soengei Bras, Deli, Sumatra, from the Rotterdam Zoo, July 14, 1919.

4. Leiden Museum, Reg. No. 2171. Female, Sumatra, from the Rotterdam Zoo, June 6, 1933.

5. Leiden Museum, Reg. No. 2174. Male, Deli, Sumatra, from the Rotterdam Zoo, June 14, 1933.

6. Leiden Museum, Reg. No. 2202. Female, Palembang, S. Sumatra, 14 years old. From the Rotterdam Zoo, November 17, 1933.

Panthera tigris (Linnaeus) subsp.

7. Leiden Museum, Reg. No. 3075. Female, locality unknown, from the Rotterdam Zoo, May 20, 1937.

8. Leiden Museum, catalogued as *Felis leo* Linnaeus, Cat. a, by Jentink, 1887, p. 81. There is no record for the exact locality.

Panthera tigris altaica (Temminck)

9. Leiden Museum, Cat. n. Male, Vladivostok, Siberia, from the Rotterdam Zoo, November, 1897.

The observed ranges are given in tables 4–8. To avoid endless repetition, it can be said first that the fossil bones from Wanhsien are all larger than those of the recent tiger of Java and Sumatra. The Vladivostok tiger is very near the fossils in dimensions, but the metapodials from Wanhsien are very much more massive. There is one lion skeleton (No. 5) which presents slightly greater dimensions than the Wanhsien tiger; the other lion skeletons are smaller. It is almost impossible to distinguish between the post-cranial skeleton of lion and tiger, but some points of difference will be noticed below.

The humerus in the Wanhsien collection (A.M.N.H. No. 18448) is complete except for the lateral tuberosity. It is from the right side. I do not consider as of specific value the difference in shape of the lateral tuberosity in the humerus of a tiger and in

TABLE 4

MEASUREMENTS IN MILLIMETERS AND INDICES OF HUMERI OF FOSSIL AND RECENT TIGERS AND OF RECENT LIONS

	Panthera tigris (Linnaeus) Fossil Wanhsien	*P. leo* (Linnaeus) Recent	*P. tigris* (Linnaeus) Recent			
			Java	Sumatra	Loc.?	Vladivostok
1. Length from caput to middle of trochlea	306	253–329	256–284	257–279	295–296	310
2. Width across caput and posterior part of lateral tuberosity	67	59– 77	56– 62	53– 61	61– 62	68
3. Smallest width of shaft	28	24– 31	25	24– 25	23– 24	25
4. Greatest width of distal epiphysis	82	74– 91	68– 75	67– 77	72– 76	85
5. Width of trochlea	56	48– 61	46– 51	46– 51	50– 53	57
6. Anteroposterior diameter condylus medialis	56	48– 65	47– 51	46– 51	49– 52	57
7. Anteroposterior diameter condylus lateralis	46	39– 53	41– 42	39– 42	42– 44	46
8. Length-width index (meas. 2 × 100)/(meas. 1)	22	21– 27	22	21– 22	21	22
9. Trochlea-epicondyle index (meas. 5 × 100)/(meas. 4)	68	64– 69	68	66– 69	69– 70	67

that of a lion as indicated by Boule (1906, p. 74, figs. 9–10).

The measurements given by von Koenigswald (1933, p. 12) indicate the presence of still larger specimens in the Pleistocene of Java. One humerus is even stated to have a greatest length of 381 mm., others 353 mm., which is about the maximum I found in the lion (No. 5: 352 mm.) and that in a fossil humerus from Chou Kou Tien (Teilhard de Chardin, 1936, p. 15: 355 mm.). In *P. tigris altaica* (Temminck) the maximum length is 328 mm., and in the other recent tiger humeri it is 311 mm. at flexor muscle of the digit is attached (two points of difference noticed by Brongersma, 1935, p. 61, in his description of the fossil tiger tibia from Java) is there a difference from the recent bones. In the length-width index and in the proximal epiphysis index the fossil specimens are seen to be entirely tiger-like.

The astragalus (A.M.N.H. No. 18691) is from the left side. Some substance is lost at the medial surface of the distal projection. Dawkins and Sanford (1866–1872, p. 13) give no differences between the astragalus of the lion and that of the tiger.

TABLE 5

Measurements in Millimeters and Indices of Tibiae of Fossil and Recent Tigers and of Recent Lions

	Panthera tigris (Linnaeus) Fossil		*P. leo* Linnaeus) Recent	*P. tigris* (Linnaeus) Recent			
	Wanhsien	Java		Java	Sumatra	Loc.?	Vladivostok
1. Length from intercondyloid eminence to median ridge of distal surface	297	282	257–309	247–273	249–275	291	314
2. Proximal width	78	68	71– 84	64– 70	63– 73	71– 72	76
3. Proximal anteroposterior diameter	81	70	75– 91	65– 72	62– 73	71– 75	78
4. Smallest width of shaft	25	25	25– 30	23– 25	23– 24	23– 24	27
5. Least anteroposterior diameter of shaft	24	22	21– 27	21	20– 23	20– 22	21
6. Length-width index (meas. 2 × 100)/(meas. 1)	26	24	25– 28	26	25– 27	24– 25	24
7. Proximal epiphysis (meas. 2 × 100)/(meas. 3)	96	97	88– 95	97– 98	99–107	96–100	97

the most. Teilhard de Chardin (1936, p. 15) remarks that in two specimens of the tiger collected in the late Pleistocene "Upper cave" of Chou Kou Tien the humerus does not even reach 300 mm. in length.

The tibia (A.M.N.H. No. 18448) is also from the right side. It lacks a portion of the lateral malleolus. The medial surface is injured distally. The nine tiger tibiae present great variations, and neither in the shape of the tuberosity for the patellar ligament, nor in the obliqueness of the ridges on the posterior surface between which the

My table shows, however, that the length-width index tends to be smaller in the tiger (89–98) than in the lion (95–102), and that the trochlea-caput index averages larger (tiger: 57–63, lion: 55–61). In the latter index the Wanhsien astragalus even surpasses the recent tiger, whereas the former index remains within the limits of the tiger. Tscherski (1892, p. 56, pl. 1, fig. 3) has described a left and a right astragalus from the Pleistocene of Lyakhov Island, off the north coast of Siberia. They are larger and smaller, respectively, than

TABLE 6

MEASUREMENTS IN MILLIMETERS AND INDICES OF ASTRAGALI OF FOSSIL AND RECENT TIGERS AND OF RECENT LIONS

	Panthera tigris (Linnaeus) Fossil			*P. leo* (Linnaeus)		*P. tigris* (Linnaeus) Recent		
	Wanhsien		Lyakhov Isl.	Recent	Java	Sumatra	Loc.?	Vladivostok
1. Medial (greatest) length	61	64	58	45–60	46–50	46–55	50–52	56
2. Lateral length of trochlea	48	52	45	39–49	39–40	36–41	39–42	45
3. Greatest proximal width	57	—	—	44–57	43–49	44–49	47–50	54
4. Greatest distal width	37	41	34	27–33	27–29	25–30	29–30	31
5. Greatest width of collum	30	32	28	22–26	22	22–24	23–25	26
6. Length-width index (meas. 3 × 100)/(meas. 1)	93	—	—	95–102	93–98	89–96	94–96	96
7. Trochlea-caput index (meas. 4 × 100)/(meas. 3)	65	—	—	55–61	59–63	57–61	60–62	57

TABLE 7

MEASUREMENTS IN MILLIMETERS AND INDICES OF CALCANEA OF FOSSIL AND RECENT TIGERS AND OF RECENT LIONS

	Panthera tigris (Linnaeus) Fossil		*P. leo* (Linnaeus) Recent	*P. tigris* (Linnaeus) Recent			
	Wanhsien			Java	Sumatra	Loc.?	Vladivotsok
1. Greatest length	115	114	93–120	93–97	88–100	98–99	110
2. Length from outer part of tuber to base of inner astragaline articular surface (length of corpus)	85	85	67– 88	68–70	62– 74	70–72	82
3. Greatest width	45	45	34– 43	33–36	32– 36	35–37	39
4. Width at tuber calcanei	30	32	25– 34	25	22– 28	26–28	29
5. Greatest anteroposterior diameter	46	46	34– 48	36–38	35– 39	37–38	41
6. Anteroposterior diameter of inner astragaline articular surface	17	19	14– 18	14	12– 15	13	14
7. Transverse diameter of the same	21	21	16– 18	17–18	17– 19	17–18	19
8. Anteroposterior diameter of cuboidal articular surface	23	22	17– 23	17–18	16– 18	17–19	19
9. Transverse diameter of the same	27	27	22– 28	22	20– 23	21	25
10. Length-width index (meas. 3 × 100)/(meas. 1)	39	39	36– 38	35–37	36– 37	36–37	35
11. Corpus length index (meas. 2 × 100)/(meas. 1)	74	74	72– 75	72–73	70– 74	70–73	75
12. Tuber index (meas. 4 × 100)/(meas. 2)	35	38	35– 39	36–37	34– 38	36–40	35
13. Inner astragaline articular surface index (meas. 6 × 100)/(meas. 7)	81	90	88–100	78–82	71– 83	72–76	74
14. Cuboidal articular surface (meas. 8 × 100)/(meas. 9)	85	82	75– 88	77–82	78– 85	81–90	76

our specimen from Wanhsien. Tscherski refers his specimens to the recent tiger.

An astragalus from the Pleistocene of Chou Kou Tien (Pei, 1934, p. 133) seems to be rather small, length and maximum breadth being given as only 51 and 47 mm., respectively, unless the length is measured at the lateral side of the bone and the breadth is taken across the calcaneum facets. If the measurements were taken in this way, they correspond in size with the other tiger bones from this locality, and are slightly larger than our specimen.

Two left calcanea are in the Wanhsien

TABLE 8

Measurements in Millimeters and Indices of Metapodials of Fossil and Recent Tigers and Recent Lions[1]

	Panthera tigris (Linnaeus) Pleistocene			*P. leo* (Linnaeus) Recent	*P. tigris* (Linnaeus) Recent			
	Wanhsien	Java			Java	Sumatra	Loc.?	Vladivostok
Metacarpal II	(A.M.N.H. No. 18692)							
1	104	87+		86–100	81– 92	82– 89	92– 95	104
2	26	21		19– 24	19– 21	17– 20	19– 20	22
3	34	27		24– 29	23– 26	24– 27	23– 27	27
4	17	15		11– 15	11– 12	11– 12	11– 12	12
5	26	22		18– 24	17– 20	18– 20	19	20
6	25	24		21– 24	23	20– 24	20– 21	21
7	33	31		27– 29	28	29– 30	25– 28	26
Metacarpal V	(A.M.N.H. No. 18693)							
1	87			80– 94	73– 78	70– 79	80– 82	90
2	26			21– 26	18– 19	16– 20	19– 20	23
3	26			20– 26	20	19– 22	21– 22	24
4	16			11– 15	11– 12	10– 13	10– 11	12
5	22			16– 23	17– 18	17– 19	17– 18	19
6	30			26– 28	24– 25	23– 26	24	26
7	30			25– 28	26– 27	25– 28	27	27
	Wanhsien	Lyakhov Isl.						
Metatarsal II		(Tscherski)						
1		113		98–121	95–103	93– 99	106–107	116
2		21.5		15– 18	14– 16	13– 17	15– 16	17
3		31		24– 29	24– 26	23– 26	25– 26	26
4		15.5		13– 15	12– 13	11– 12	10– 12	12
5		21		17– 24	18– 19	17– 19	18– 19	20
6		19		14– 16	15– 16	14– 17	14– 15	15
7		28		22– 24	25	25– 26	23– 25	22
Metatarsal III	(A.M.N.H. No. 18698)	(A.M.N.H. No. 18694)	Java					
1	132	119	119	107– 36	108–116	107–114	118–119	130
2	28	25	23	23– 26	21– 23	21– 22	21– 22	25
3	37	35	33	29– 37	28– 30	27– 31	29– 30	31
4	19	17	16	13– 17	14	13– 15	12– 14	14
5	27	—	23	19– 26	20– 22	19– 22	20– 22	24
6	21	21	19	19– 21	19– 20	19– 20	18– 19	19
7	28	29	28	24– 29	26	24– 27	24– 25	24
Metatarsal IV	(A.M.N.H. No. 18696)	(A.M.N.H. No. 18695)	Java					
1	130	128	—	110–136	108–115	108–115	119	130
2	28	28	24	22– 27	21– 22	19– 23	22– 23	22
3	34	33	30	26– 34	26– 27	23– 27	26– 28	28
4	18	17	15	12– 15	12	12– 13	10– 11	12
5	25	24	—	17– 24	18– 19	18– 20	18	21
6	22	22	—	18– 21	19	17– 20	18– 19	16
7	26	26	—	22– 25	23– 25	20– 24	22– 24	22
Metatarsal V	(A.M.N.H. No. 18697)							
1	112			102–125	97–104	95–102	105–106	116
2	27			17– 28	18– 21	18– 21	19– 20	23
4	14			10– 14	10– 11	10– 12	9– 10	11
5	21			15– 18	16– 17	15– 18	16	18
6	24			16– 22	19– 20	18– 21	18– 19	20

[1] In this table the measurements are indicated by numbers: 1, median length; 2, proximal width; 3, proximal anteroposterior diameter; 4, smallest width of shaft; 5, distal width; 6, length-width index (meas. 2×100)/(meas. 1); 7, length-proximal anteroposterior diameter index (meas. 3×100)/(meas. 1).

collection (A.M.N.H. Nos. 18689, 18690). There is some variation in the shape of the inner articular surface for the astragalus. I have computed the articular surface indices indicated by Dawkins and Sanford (1866–1872, p. 14) as a character for discrimination between lion and tiger. Of the measurements and indices given in table 7, only few afford distinctive characters. The Wanhsien calcanea are identical in shape with those of the lion and tiger, with the exception that the length-width index (39) is somewhat greater than that in the lion (36–38) or tiger (35–37). There seems to be a small difference in the inner articular surface for the astragalus, the index being 71–83 in the tiger against 88–100 in the lion, but 1 mm. more or less means a difference of 4 to 6 units of the index, and it is seen that, while the first Wanhsien calcaneum is fully consistent with the tiger in this respect, the figure for the index in the second specimen falls within the limits of the lion.

The Chou Kou Tien calcaneum recorded by Pei (1934, p. 133) has a length of 86 mm., which must be the length of the corpus. The maximum breadth (45 mm.) is the same as that in our calcanea from Wanhsien.

The metapodials from Wanhsien (two metacarpals and five metatarsals) are all thicker than in either recent tiger or lion. They are of about the same length as, but much larger transversely and anteroposteriorly than, those of *P. tigris altaica* (Temminck), the Vladivostok specimen in the last column of table 8.

Another fact visible in table 8 is that the metapodials of the tiger are distinguishable from those of the lion by their somewhat more slender shape; consequently the Wanhsien tiger is closer to the lion than to the tiger in this respect.

It is remarkable that the metapodials from the Pleistocene of Java are more slender than those from Wanhsien and thus show a closer approach to the recent form than those of the Wanhsien Pleistocene. The length, however, is the same, at least in the case of the third metatarsal. It can be seen that the Javan fossils fall within the limits of the lion.

The second metacarpal from Java in the Dubois collection is remarkably short, its median length being only 87 mm. as opposed to 81–104 in the recent tiger.[1] This bone, however, consists of two portions (Brongersma, 1935, pl. 9, fig. 2), and the examination of the original specimen convinced me that the fragments do not match precisely and that a small part of the shaft must be lost. The Javan fossil is much smaller transversely and anteroposteriorly than the corresponding bone from Wanhsien, but its shaft is thicker (15 mm.) than in the recent tiger (11–12 mm.). The same thickness of shaft as in the fossil was found as the maximum in the lion.

Of the two third metatarsals from Wanhsien the first is almost equal in length to, but thicker than, that of the Vladivostok tiger, and the other is equal in length to, but thicker than, the third metatarsal from the Pleistocene of Java in the Dubois collection (Brongersma, 1935, pl. 9, fig. 3).

The fourth metatarsal from the Pleistocene of Java (Brongersma, 1935, pl. 9, fig. 1) lacks the distal extremity, and consequently, the length cannot be given. Its proximal part and shaft are again seen to be more slender than in the corresponding bone from Wanhsien. It is, however, thicker again than the recent fourth metatarsal from Vladivostok, as are the other fossil metapodials from Java.

There is another fossil tiger which presents as massive a metapodial as that from Wanhsien. The fossil second metatarsal from Lyakhov Island, off the north coast of Siberia, described and figured by Tscherski (1892, pp. 58–60, pl. 1, fig. 4), is equal in length to the corresponding bone of the Vladivostok tiger, but is greater in the other dimensions, to just the same extent as the Wanhsien bones. It is the only metatarsal which is not represented in the

[1] Von Koenigswald (1933, p. 12) ascribes a second and a fourth metacarpal to the fossil tiger from Java as having lengths of 70.5 and 68 mm., respectively. This is much too short, even for a recent tiger, and I believe the bones to belong to the panther which is also known from the Pleistocene of Java (Brongersma, 1935, p. 71). In two recent skeletons of *Panthera pardus* (Linnaeus) from Java (Leiden Museum, Cat. a and b) the length of the second metacarpal is 54–56 mm., and that of the fourth 61–63 mm. This accords well in size with the humerus from the Javan Pleistocene which von Koenigswald (1933, p. 18) tentatively refers to the panther, which is also longer (228 mm.) than the recent (194–205 mm.).

Wanhsien collection, but, in fact, it might have come from that locality. It has exactly the same disproportional dimensions as compared to the living species and does not fall within the limits of the lion, as the fossil metapodials from Java do. Tscherski (1892, p. 61) does not hesitate to refer the other bones examined by him (a femur from the Jana River system in Siberia, the astragali mentioned above and a phalanx from Lyakhov Island) to *Panthera tigris* (Linnaeus), but is reticent as to the metapodial. Now that we have discovered in Wanhsien a fossil tiger that also presents the greatest deviation from the recent form in its metapodials (no doubt a constant character, as represented in seven bones from different individuals), all doubt is removed about the question as to whether the massive metatarsal belongs to the Siberian tiger or not. And the remarkable fact is disclosed by the direct comparison of the Chinese fossils with those of Java that the Pleistocene Javan tiger had less thick metapodials than the Chinese and Siberian, and thus is nearer to the recent form.

I should not have hesitated to propose a new subspecific name for the Wanhsien tiger were it not that I have found that the Pleistocene Siberian tiger described by Tscherski has exactly the same distinguishing feature. The Pleistocene southern Chinese tiger and the Siberian form are so widely separated in locality that in the recent fauna they certainly would have been shown to represent different geographical races. The Chou Kou Tien tiger is intermediate in locality, and consequently it is highly probable that when some day its metapodials come to light, they will be seen to have also the massive shape which seems typical for the large Pleistocene continental forms. According to the International Rules of Zoological Nomenclature the Pleistocene Chou Kou Tien tiger then has to bear the name *Panthera tigris acutidens* (Zdansky), and the same name would apply to the Wanhsien and the Siberian form. Therefore, pending the question of its racial identity with the Chou Kou Tien tiger, I leave the Wanhsien tiger subspecifically unnamed.

Taking into consideration all the facts concerning fossils gathered above, we can make the following statements:

1. The Pleistocene tiger of Wanhsien, like that of Chou Kou Tien, Java, and Siberia, was as large as the largest of the living subspecies of *Panthera tigris* (Linnaeus).
2. The Siberian form has decreased little, if any, in size since the Pleistocene, but its metapodials have become much more slender.
3. The Chinese form has become smaller than the northern and Indian forms, but not so small as:
4. The Javan form, in which the metapodials were already more slender than those of the continental forms in the Pleistocene, and which must have passed since then through the stages of size today represented by the typical (India), the northern (Manchuria, Siberia), the Chinese, and the Sumatran races, respectively.

The chain of evidence is still far from complete; we badly need fossil tigers from India, Sumatra, and Bali as evidence of what we can now only infer. Is it more than a curious coincidence that the tigers on the smaller islands have become smaller in size than on the larger islands, or is the apparent coincidence related to the fact that the smaller the island, the more peripheral its location in southeastern Asia? I am inclined to the latter view, but I must admit that I do not know what mechanism is responsible for the gradual alteration in size within the species *Panthera tigris* (Linnaeus) from the continent to Bali, as observed at the present day.

Similar clines (Huxley, 1939) have been observed in other southeastern Asiatic mammals. Each of the links has been named as a subspecies, and the fossils throw some light on the early history of the now isolated forms. We now know at least two subspecies of tiger living in the Pleistocene, viz., the large and broad-footed Chinese and Siberian form (for the present inseparable, but probably deserving of distinct subspecific names) and the likewise large, but comparatively slender-footed Javan form which might be called *Panthera tigris groeneveldtii* (Dubois) (see Brongersma, 1935, p. 61). There must have been other races already in existence at that time, and each of them must have come down to the present by gradually changing its characters into those of the subspecies we distinguish today.

In my paper on the fossil and prehistoric rhinoceroses from the Malay Archipelago (Hooijer, 1946) I did not distinguish subspecies, but it is highly probable that, e.g., the prehistoric *Dicerorhinus sumatrensis* (Fischer) from Sumatra is the same as *D. sumatrensis lasiotis* (Sclater) (see Hooijer, 1946, p. 29), and that the Pleistocene *Rhinoceros kendengindicus* Dubois from Java is a subspecies of the recent Indian *R. unicornis* Linnaeus which also dates back to the Pleistocene (Narbada beds). The view is held by Weidenreich (1943, p. 246) that *Pithecanthropus erectus* Dubois and *Sinanthropus pekinensis* Davidson Black are races of one and the same species; the correct names then would be trinomial: *Pithecanthropus erectus erectus* Dubois and *Pithecanthropus erectus pekinensis* (Davidson Black).

I have evidence in other mammals that are represented by the same species in the Pleistocene and (if not extinct) the recent fauna of Java and also in the Pleistocene and/or the recent fauna on the Asiatic continent, that the process of raciation had already begun in the Pleistocene, and that consequently the recent races are the descendants of the racially distinct populations that already existed in the Pleistocene. It is significant that the skull of the Pleistocene tiger of Java already had the narrow occiput that is characteristic of the recent subspecies of that island (Brongersma, 1935, p. 59).

As the external characters which are of paramount importance for the distinction of present day's subspecies leave no record in the skeleton, they probably are lost forever. We can only postulate that the Pleistocene Javan tiger did not have a winter coat. If *Pithecanthropus* and *Sinanthropus* had been trained as systematic zoologists, they doubtless would have found many more characters to distinguish between the northern and the southern forms of the tiger which in their time were of equal size and which we can now distinguish only by the structure of their feet.

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Fig. 1. *Panthera tigris* (Linnaeus) subspecies. A.M.N.H. No. 18624, skull with lower jaw *in situ*. Right lateral view, somewhat ventral because of strong oblique crushing. One-half natural size.

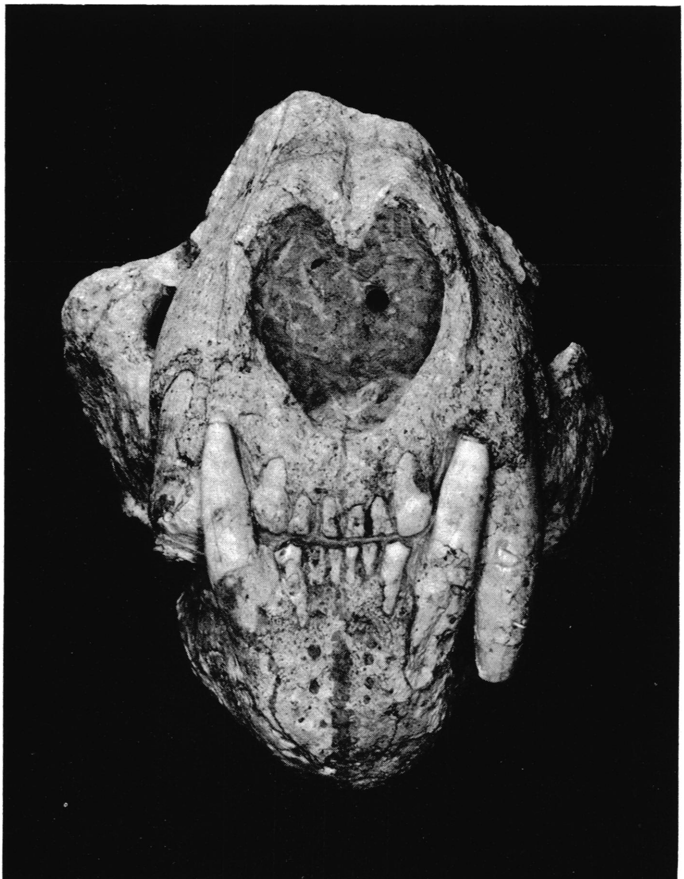

Fig. 2. *Panthera tigris* (Linnaeus) subspecies. A.M.N.H. No. 18737, anterior part of skull with lower jaw *in situ*. Anterior view. One-half natural size.

Fig. 3. *Panthera tigris* (Linnaeus) subspecies. A, A.M.N.H. No. 18698, right third metatarsal B, A.M.N.H. No. 18692, left second metacarpal. Both anterior (dorsal) views. Natural size.