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Panthera tigris.

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Panthera Oken, 1816

Panthera Oken, 1816:1052, see Remarks. Type species *Felis pardus* Linnaeus, 1758.
Tigris Oken, 1816:1066. Type species *Felis tigris* Linnaeus, 1758.
Leo Oken, 1816:1070. Type species *Felis leo* Linnaeus, 1758.
Leo Brehm, 1829:637. Type species *Felis leo* Linnaeus, 1758.
Jaguarius Severtzow, 1858:386. Type species *Felis onca* Linnaeus, 1858.
Pardus Fitzinger, 1868:459. Type species *Felis pardus* Linnaeus, 1758.

CONTEXT AND CONTENT. Order Carnivora, Family Felidae, Subfamily Pantherinae. The genus *Panthera* includes four living species, *Panthera pardus*, *Panthera onca*, *Panthera leo*, and *Panthera tigris*, and several fossil species. Two subgenera may be recognized: *Panthera* Oken, 1816, for the first three of the above mentioned species, and *Tigris* Oken, 1816, for the fourth species (Hemmer, 1966, 1978*a*).

For a key to species of the genus *Panthera* see Hemmer (1966).

Panthera tigris (Linnaeus, 1758)

Tiger

Felis tigris Linnaeus, 1758:41. Type locality "Bengal" (Thomas, 1911).
Tigris striatus Severtzov, 1858:386. Renaming of *Felis tigris* Linnaeus, 1758.
Tigris regalis Gray, 1867:263. Renaming of *Felis tigris* Linnaeus, 1758.

CONTEXT AND CONTENT. Context given above. Eight living subspecies have been recognized by the latest reviser (Mazák, 1979; see also Mazák, 1965, 1967, 1968, 1976), as follows:

P. t. tigris (Linnaeus, 1758:41), see above (*striatus* Severtzov, *regalis* Gray, *montanus* Sterndale, and *fluviatilis* Sterndale are synonyms).
P. t. virgata (Illiger, 1815:98). Type locality Mazanderan, northern Iran (Harper, 1940) (*septentrionalis* Satunin, *lecoqi* Schwarz, *trabata* Schwarz, and probably *sudanensis* Deraniyagala, are synonyms).
P. t. altaica (Temminck, 1844:43). Type locality Korea or more exactly Pisihan Mountains in northernmost Korea (*longipilis* Fitzinger, *amurensis* Dode, *coreensis* Brass, *mikadoi* Satunin, and *mandshurica* Bajkov are synonyms).
P. t. sondaica (Temminck, 1844:43). Type locality Java (*sondaicus* Fitzinger is a synonym).
P. t. amoyensis (Hilzheimer, 1905:598). Type locality near Hankau (=Hankow), Hupeh, China (*styani* Pocock, is a synonym).
P. t. balica (Schwarz, 1912:325). Type locality Denpasar, South Bali (Schwarz, 1913).
P. t. sumatrae Pocock, 1929:535. Type locality Deli, Sumatra.
P. t. corbetti Mazák, 1968:105. Type locality Quang-Tri, Annam (=Vietnam).

DIAGNOSIS. The tiger is the largest species of Felidae. Ground coloration is reddish orange to reddish ochre, with dark stripes that are generally vertical (Fig. 1). Underparts are white or whitish. The skull is large, rivalled in the existing Felidae only by that of the lion, *Panthera leo*. The tiger skull (Fig. 2), when compared to that of the lion, is more vaulted and thus more catlike, with shorter and relatively broader rostrum and a more convex frontal region. Skulls of large males are as massive as those of lions. The total skull length is more than 255 mm, and usually between 285 and 360 mm. The skull is robust, relatively short, broad in its facial and rostral parts, and very wide in the zygomatic arches (Fig. 2). Sagittal and temporal crests, especially in large males of the subspecies *altaica* and *virgata*, are very strong and prominent. Nasal bones are elongated, projecting always beyond the frontal processes of maxillae. The frontal area is elevated in the region of postorbital processes. The anterior nasal aperture is rather narrow and heart-shaped. The lower edge of the mandible is slightly concave or, very rarely, straight in the middle; mental apophysis is generally prominent; frontal part of mandibular symphysis is flat and more or less concave. (Compiled from data in Pocock, 1929, 1939; and my observations.)

Dental formula is i 3/3, c 1/1, p 3/2, m 1/1, total 30. The monotypic subgenus *Tigris* differs from other Pantherinae in the following dental characters: P4 with a strong and well-developed ectoparastyl; m1 with a more or less distinct hypoconid (absent in other species of Pantherinae); p4 with a strongly developed hypoconid that is generally larger than paraconid; p3 with both hypoconid and paraconid small and almost indistinct (Hemmer, 1966).

GENERAL CHARACTERS. The body structure corresponds to the general form of the Felidae. Tigers are muscular, with powerful forequarters and, especially in males, with a relatively large head (Fig. 1). Total length of adults generally ranges between 2200 and 3000 mm; females are somewhat smaller. The length of tail usually does not exceed one half of the head-and-body length. Hair length varies geographically. The hairs are short (7 to 20 mm on the back and 15 to 35 mm on the belly) in the southern subspecies *P. t. tigris*, *P. t. corbetti*, *P. t. sumatrae*, *P. t. sondaica* and *P. t. balica*, and long, especially in winter (40 to 60 mm on the back and 70 to 105 mm on the belly), in the northern subspecies *P. t. virgata* and, particularly, *P. t. altaica*. The face is framed by long hairs which form whiskers; these are generally more conspicuous in males. The ears are rounded and rather small, and are black on their dorsal side, with a conspicuous central white spot.

Ground coloration varies between Tawny and Xanthine Orange or Cinnamon Brown in the southernmost populations to between Ochraceous-Orange or Zinc Orange and Capucine Orange in the northernmost populations (capitalized terms from Ridgway, 1912). The ventral parts are usually White, but in some southern populations a more or less intensive tinge of the ground coloration is present. The whole body is marked with dark stripes of various lengths, breadths, and/or forms. The color of stripes is generally Black or Chaetura Black. In the subspecies *virgata* and *altaica* the stripe color, especially on flanks, thighs, and proximal half of the tail, is usually Fuscous, Hair Brown, Mikado Brown, or Benzo Brown. Black may then be found only on the head, back, belly, and on the distal half of the tail. In some individuals stripes may be reduced on forelegs, shoulders, and on the sides of thorax.

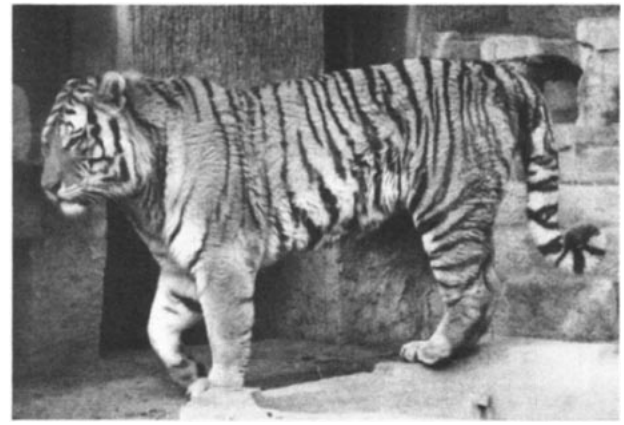

FIGURE 1. Male Ussurian tiger, *Panthera tigris altaica*, wild-caught in the Ussuri Region of the Soviet Far East, and held in the Prague Zoo. At his death the male measured 3190 mm in total length. Photo by V. Mazák in 1960.

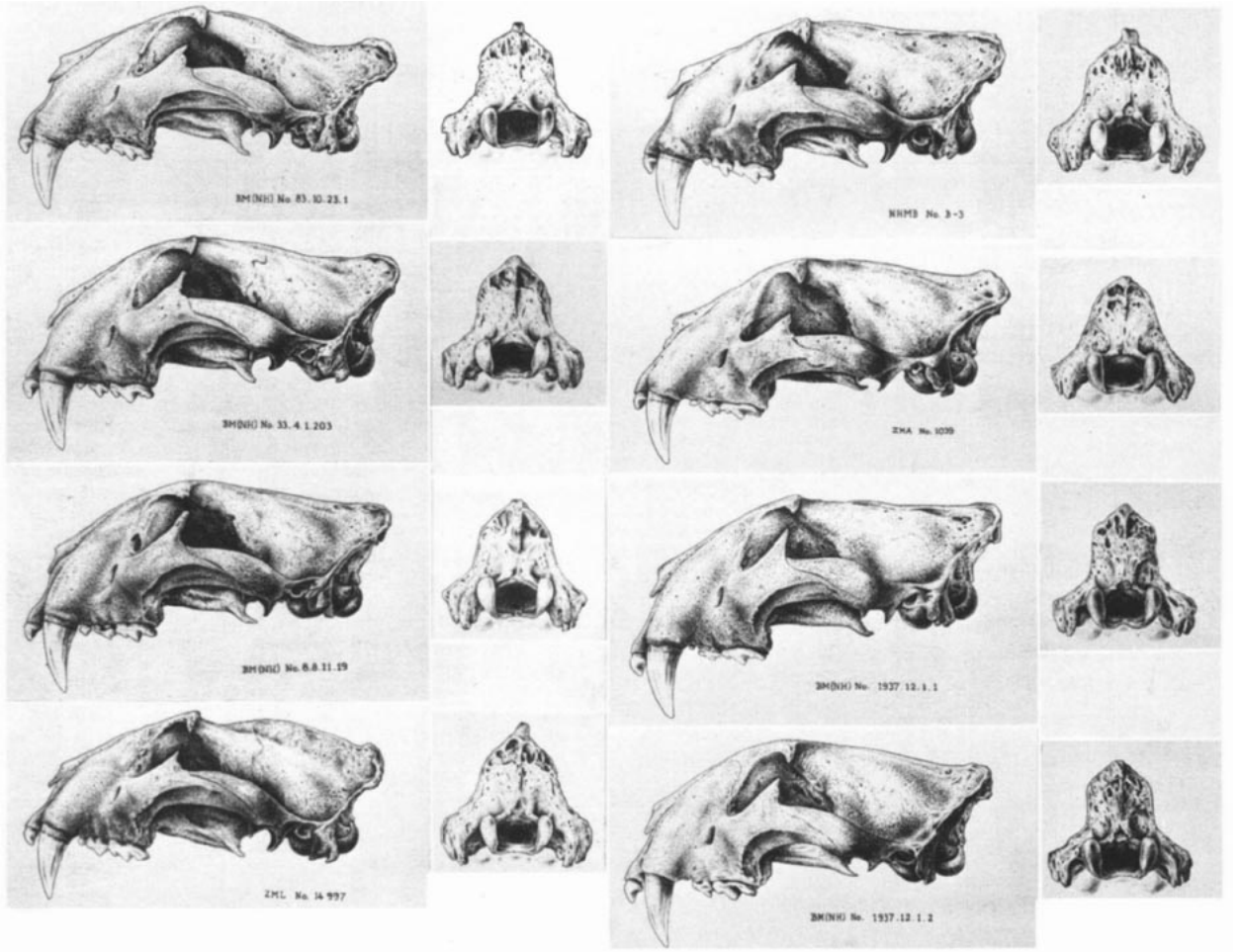

FIGURE 2. Left lateral view of skull and view of occipital region of adult males of individual subspecies of *Panthera tigris*. Left column, from top to bottom: *P. t. tigris*, from Nepal Terai, BM 83.10.23.1, greatest length 364 mm; *P. t. corbetti*, holotype, from Quang-Tri in Vietnam, greatest length 322.6 mm, BM 33.4.1.203; *P. t. amoyensis*, from north-eastern Central China, BM 8.8.11.19, greatest length 335 mm; *P. t. virgata*, from Turkmenia, ZML 14997, greatest length 338.2 mm. Right column, from top to bottom: *P. t. altaica*, from northernmost Manchuria, NHMB B-3, greatest length 383 mm; *P. t. sumatrae*, from Palembang in Sumatra, ZMA 1039, greatest length 331.5 mm; *P. t. sondaica*, from Popoh Blitar in Java, BM 1937.12.1.1, greatest length 332 mm; *P. t. balica*, from Sendang in Bali, BM 1937.12.1.2, greatest length 297.6 mm. Note the typical elongated shape of the occiput in *sondaica* and *balica*. Drawings by V. Mazák.

In southern forms, especially in *sumatrae*, *sondaica* and *balica*, the stripes tend to disintegrate into spots near their ends, and lines of small dark specks between regular stripes may be found on the back, flanks and hind legs.

Forefeet have five toes; the pollex is raised above the others and does not touch the ground. The hind feet have only four toes, the hallux being absent. All toes bear large, curved, and compressed claws of up to 80 to 100 mm long, measured over their curve. Claws are normally drawn back into their sheaths and are bared only for catching prey or in defense.

Teeth of tigers are exceptionally stout. Canines are long and slightly curved; they are the longest among living felids. The height of crown of the upper canine is as much as 74.5 mm in *P. t. altaica* (Mazak, 1979) or even 90 mm (Gewalt, in litt.). The second upper premolar and the single upper molar (M1) are small and have little function; either or both of these teeth may occasionally be absent. The carnassials (P4 and m1) are as large as 39 mm and 28 mm, respectively.

The subspecies *P. t. tigris*, *P. t. virgata*, and *P. t. altaica* represent the largest living felids, and rank among the biggest felids that ever existed. The smallest subspecies, *P. t. sumatrae*, *P. t. sondaica*, and *P. t. balica*, are about the size of big leopards (*P. pardus*) and jaguars (*P. onca*). Of the data on size (Table 1), those on the greatest length of skull are most reliable (being based on my measurements from 227 skulls). Data on body length and weight are based on both my data and those from the literature. No "shooting sport" sources, including R. Ward's Records of Big Game, were included.

The largest Indian tiger (*P. t. tigris*) known was the "Bachelor of Powalgarh," shot in 1930 in Kumaon; it measured 3228 mm (10 ft 7 in) "over curves" which equals about 3070 to 3100 mm measured "between pegs" (Corbett, 1961). The biggest Ussurian tiger (*P. t. altaica*) with reliable measurements was a male shot in the basin of the upper course of the Sungari River in Manchuria, in 1943. The total length of the animal was 3507 mm (11 ft 6 in) measured "over curves" (Jankovskij, in litt.); thus the tiger would be about 3300 to 3350 mm if measured "between pegs."

The heaviest Indian tiger weighed 258.2 kg (Hewett, 1938), while the heaviest Ussurian male weighed 306.5 kg (Baudy, 1968; Bouglione, in litt.). The weight of the mentioned male from the Sungari River in Manchuria was "certainly not less than about 300 kg" (Jankovskij, in litt.; for details see Mazák, 1979).

The largest skull measured by me was that of an Ussurian male, shot in northern Manchuria, and housed in the Berlin Natural History Museum. Its measurements (in mm) were as follows: greatest length, 383; condylobasal length, 342; rostral breadth, 113; interorbital breadth, 83; bizygomatic breadth, 268; mastoid breadth, 148.5; length of mandible, 260; P4 length, 37.8; greatest height of sagittal crest, 50.

DISTRIBUTION. The distribution of tigers (Fig. 3) once extended from easternmost Turkey, Transcaucasia, and northernmost Iran through Soviet Central Asia and northern Afghanistan, and from upper Sind, Kumaon, and Punjab, through the Indian Peninsula, Indochina, the Malayan Peninsula, to Sumatra,

Java, and Bali. From Indochina, tigers once ranged through large areas of eastern China, where they penetrated along the great rivers deep into central China. Further north the tiger was found in Manchuria, Korea, and in southeastern Siberia, where it reached the northernmost limits of its distribution. Tigers never inhabited the Tibetan plateau, Iran south of the Elburz Mountains, southern Afghanistan, western and southwestern Baluchistan (Pakistan), lower Sind and Cutch, Sri Lanka, or other islands of the Malayan Archipelago (except Sumatra, Java and Bali, as mentioned above).

Occasionally, tigers wander far from the area of their regular occurrence. In 1905, a tiger was shot as far north as some 80 km north of Ust'-Maja on the river Aldan (about 60°40′ north latitude) in eastern Siberia. In the last century in western Siberia, tigers were rather frequently reported from the vicinity of Barnaul, Bijsk, Zmeinogorsk, and about 180 km northeast of Atbasar; they were also known to cross the frozen Tatar Strait and visit Sakhalin Island (Ognev, 1935; Sludskij, 1953, 1966).

Presently, tigers are extremely rare in many places, and have been exterminated from most of their former geographic range. I estimate that the whole contemporary population numbers not more than some 3,500 tigers. India, Nepal, and possibly Malaya have the largest extant populations, all together numbering about 2,800. Much smaller tiger populations live in the Soviet Far East (Ussuri and Amur regions), where some 100 or 120 still survive, and perhaps in northern China. Possibly a few tigers remain in southeastern Turkey and northern Afghanistan. Tigers still exist on Sumatra, but this population is in a rapid decline; the Balinese population is definitely extinct, and it seems that the same is true (or will be true very soon) for the Javan population. (For details on the distribution of tigers and their decline see Abramov and Pikunov, 1976; Baytop, 1974; Brass, 1911; Brongersma, 1935; Geptner and Sludskij, 1972; Guggisberg, 1975; Harper, 1945; Kumerloeve, 1974, 1975; Mazák, 1965, 1967, 1968, 1976, 1979; Ognev, 1935; Pocock, 1929, 1939; Shou Chen-Huang, 1962; and Sludskij, 1966.)

FOSSIL RECORD. *Panthera tigris* probably differentiated in the early Pleistocene in northcentral and northeastern China (see Mazák, 1979). The earliest forms averaged smaller than those of later Pleistocene times. It thus seems that the species has reached its maximum size in the living subspecies *P. t. altaica*. The early Pleistocene species *Panthera palaeosinensis* (Zdansky, 1924), from northern China, appears to represent an early tiger or a form ancestral to the tiger (Hemmer, 1967).

Fossil remains, definitely identified as *P. tigris*, are of lower to upper Pleistocene age and originate from the Altai caves in central Asia (Brandt, 1871; Tscherski, 1892), eastern and northern China, including Choukoutien localities (Hooijer, 1947; Loukashkin, 1938; Teilhard de Chardin and Young, 1936; Zdansky, 1928), Japan (Hemmer, 1968*a*), Jana River in northern Siberia, the Ljachov Island situated off the northern coast of Siberia (Tscherski, 1892), and from Sumatra (Brongersma, 1937) and Java (Brongersma, 1935). In addition, several sub-Recent tiger remains were found in Caucasus region (Vereshchagin, 1959), India (Lydekker, 1886), and Borneo (Medway, 1964). It is not clear whether the material from Borneo represents a member of the native late Pleistocene fauna or a later introduction by humans (there is no reliable evidence of tigers on Borneo within historic times).

FORM AND FUNCTION. See General Characters for discussion of hair length and normal coloration. Density of hair depends on season and geographical factors. In *P. t. tigris* there are about 1,700 to 2,000 hairs per cm² on the back, while in *P. t. altaica*, in its winter coat, there are as many as 3,000 to 3,300 hairs per cm² (Cerevitinov, *in* Geptner and Sludskij, 1972; and unpubl. data). The pupil of the eye is circular and the iris is normally yellow. As in other species of Pantherinae (i.e., *Panthera* and *Uncia*), the short hairs of the nose grow almost to its anterior margin, so that in dorsal view none or only a very narrow part of the hairless rhinarium is visible (Pocock, 1917*a*, 1917*b*; Hemmer, 1966). The shape of rhinarium is typical for the subfamily Pantherinae, differing from those of representatives of the subfamilies Felinae and Acinonychinae (Pocock, 1917*a*; Hemmer, 1966). The cervical whorl of hair (Mähnenwirbel) is located on the sides of neck or at the base of the shoulder, rather than immediately below the back of the ears, as in *Uncia* and members of the subfamily Felinae. It is generally not so far posterior as in the subgenus *Panthera* (Leyhausen, 1950; Hemmer, 1966). There are two pairs of mammae situated in abdominal position.

Detailed and comparative descriptions of skull characters and their functional interpretations were summarized by Haltenorth (1936, 1937), Hemmer (1966), and Leyhausen (1950). Dentition was described in detail and functionally interpreted by Kabitzsch (1960). The spinal column consists of 7 cervical, 13 thoracic, 7 lumbar, 3 sacral, and 25 to 26 caudal vertebrae. The clavicle is very small, curved, and functionless. The thorax is built of 13 pairs of ribs. The structure of hyoid apparatus is typical

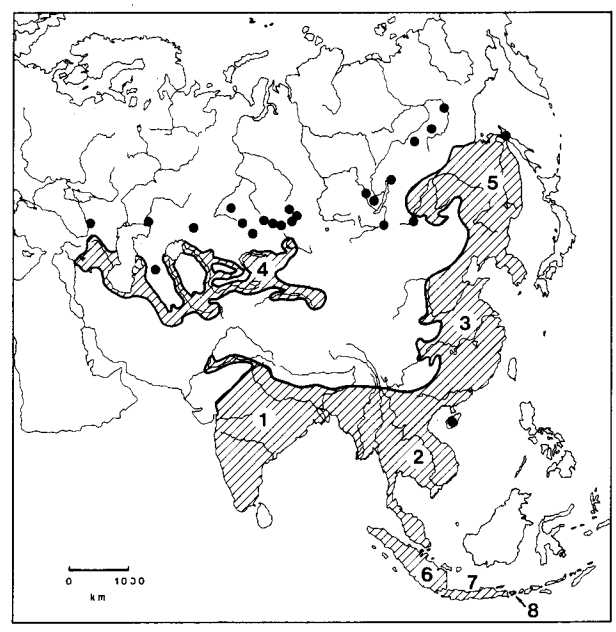

FIGURE 3. Geographic distribution (shaded area) of the tiger, *Panthera tigris*, as it was known in the second half of the 19th century. Black dots outside of shaded area show the occasional occurrences of tigers (stragglers). At present, the tiger is extinct within most of the indicated area (see text). Subspecies are: 1, *P. t. tigris*; 2, *P. t. corbetti*; 3, *P. t. amoyensis*; 4, *P. t. virgata*; 5, *P. t. altaica*; 6, *P. t. sumatrae*; 7, *P. t. sondaica*; 8, *P. t. balica*.

TABLE 1. Size variation in subspecies of *Panthera tigris* (adult specimens).

Subspecies	Total length (mm) ("between pegs")		Weight (kg)		Greatest length of skull (mm)	
	♂	♀	♂	♀	♂	♀
tigris	2700–3100	2400–2650	180–258	100–160	329–378	275–311
corbetti	2550–2850	2300–2550	150–195	100–130	319–365	279–302
amoyensis	2300–2650	2200–2400	130–175	100–115	318–343	273–301
virgata	2700–2950	2400–2600	170–240	85–135	316–369	268–305
altaica	2700–3300	2400–2750	180–306	100–167	341–383	279–318
sumatrae	2200–2550	2150–2300	100–140	75–110	295–335	263–294
sondaica	2480	—	100–141	75–115	306–349	270–292
balica	2200–2300	1900–2100	90–100	65–80	295–298	263–269

for the genus, and subfamily (Pocock, 1916, 1917*b*, 1939), showing a long elastic ligament interposed between the ceratohyal and upper bones of the hyoid suspensorium. The basihyal of the tiger (subgenus *Tigris*) seems to be more rounded than that of the members of the subgenus *Panthera* (Diekmann, 1932).

Weights and measurements of some internal organs of three females and one male with lengths of head and body of 1720, 1650, 1650, and 1980 mm, and weights of 145, 135, 97, and 170 kg, respectively, were as follows: weight of heart, 770, 570, 970, 1090 g; weight of lungs, 850, 1480, 2070, — g; weight of liver, 1720, 1955, 2170, 2390 g; weight of spleen, 265, 290, 250, — g; weight of stomach, —, 795, 910, 1150 g; weight of kidneys, —, 990, 1160, 1210 g; total length of intestinal tract, 7420, 6400, 7100, 7840 mm; length of small intestine, 6420, 5500, 6600, 6770 mm; length of caecum, 60, 50, 105, 95 mm; greatest width and length of heart, 118/132, —/—, —/—, 126/147 mm (Geptner and Sludskij, 1972; Tschernyshev, 1958; unpubl. data). The diameter of the eye ranges from about 35 to 40 mm (unpubl. data). The capacity of the braincase, which is similar to the weight of brain in grams, varies from 264 to 305 cm^3 in males and from 251 to 285 cm^3 in females (unpubl. data from one *P. t. sondaica*, four *P. t. altaica*, and four *P. t. tigris*).

Body size of different populations of tigers seems to be correlated with climate (the so-called Bergmann's Rule), and can be explained from the point of view of thermoregulation. The correlation between the shade and intensity of coloration and the length of hair, especially in winter, and average environmental temperature is evident (the so-called Gloger's and Rensch's Rules, respectively), and needs no special explanation. Molt occurs twice a year, in spring and autumn; the cycles of hair shedding and growth are most regular and conspicuous in northern populations of tigers (Mazák, 1965, 1979).

The function of canines and the long and sharp claws seems to be quite clear, yet there has been doubt as to whether the former were used just for grasping and holding the prey, or for the actual killing. Recently, however, it was shown that the primary function of the tiger's long canines is to kill its prey (for details see Schaller, 1967; Mazák, 1979).

ONTOGENY AND REPRODUCTION. Mating may take place at any time of the year; it is most frequent, however, from about the end of November to the first half of April (Corbett, 1961; Geptner and Sludskij, 1972; Kaplanov, 1948; Locke, 1954; Sankhala, 1967, 1978; Stroganov, 1962). A tigress comes into heat at intervals of about 3 to 9 weeks, and is receptive for about 3 to 6 days (Crandall, 1964; Mazák and Volf, 1967). Gestation averages 104 to 106 days, with a range from 96 to 111 days (Mazák, 1979). The usual number of cubs is two or three and typically varies from one to four; in Ussurian tigers, the average of 123 litters was 2.65; in Indian tigers, the average of 16 litters was 2.75; and in Sumatran tigers, the average of 9 litters was 2.44 (Mazák, 1979). Similar results are shown also by other authors (Asdell, 1964; Sankhala, 1967, 1978; Zuckerman, 1953). Quite exceptionally, six cubs may be found in a litter (Sankhala, 1967, 1978). The young are born in a shelter situated in tall grass, in thick bush, under fallen trees, among rocks, or in caves (Abramov, 1962; Corbett, 1961; Geptner and Sludskij, 1972; Pocock, 1939; Smith, 1928; Stroganov, 1962). Sometimes, a tigress makes a covered nest for her cubs with dry leaves, grass, and hair (Abramov, 1962). Cubs are usually born at an interval of 20 to 40 minutes (Sankhala, 1967). In the wild, tigresses produce new litters only after their families have disintegrated, usually two, but sometimes even three or four years after the birth of preceding young.

The newborn tiger cubs weigh from 780 to 1600 g (Crandall, 1964; Mazák, 1965, 1979; Schneider, 1959; Stroganov, 1962); their length of head and body varies from about 315 to 400 mm, and that of tail from 130 to 160 mm (Mazák, 1979; Stroganov, 1962). The fur is thick and wooly and of the same color pattern as in adults, but is somewhat lighter colored. This fur is shed at about 3.5 to 5 months of age. The replacement pelage has a somewhat darker ground color than that of the adults. At the age of 2 to 3 years young tigers attain the general color of adults (unpubl. data). The eyes and ears of newborn cubs are closed; they open 6 to 14 and 9 to 11 days, respectively, after birth (Sludskij, 1953; Stroganov, 1962; Mazák and Volf, 1967; Mazák, 1979). The eruption of milk teeth starts at about week 2 to 3 and is finished at about week 6 to 8 (Mazák and Volf, 1967; Schneider, 1959). The permanent dentition starts to erupt at about age 8.5 to 9.5 months, and is completed at month 12 to 14 (Mazák, 1979; Schneider, 1959). Teeth erupt in the following succession: I1 and i1; I2, I3 and i2, i3; P4 and m1; C and c; P3; P2 and M1; p3 and p4 (Mazák, 1979, and unpubl. data).

Increase in body weight from birth to day 140 averages from 0.1 to 0.25 kg/day; and from 0.30 to 0.55 kg/day from 140 to 180 days of age. One-year-old tigers weigh from about 90 to 130 kg or more (Mazák, 1979). The suckling time lasts 3 to 6 months; the young begin eating small amounts of solid food at about month 2 (Sankhala, 1967, 1978; Geptner and Sludskij, 1972). At about month 2 the young are able to follow their mother on her hunting expeditions; at month 5 or 6 they begin to take part in actual hunting. The tigress teaches them to stalk, attack, and finally to kill the prey (Locke, 1954; Sankhala, 1967, 1978; Schaller, 1967). The young usually separate from their mother at about year 2; some young remain with their mother for three years (Abramov, 1962; Ismail, 1964; Kaplanov, 1948; Schaller, 1967; Sterndale, 1884). In the wild, sexual maturity is reached at year 3 to 4 in females, and year 4 to 5 in males (Mazák, 1965, 1979). In zoos, tigers have lived for 20 to 26 years, which also seems to be their longevity in the wild (Mazák, 1965, 1979).

ECOLOGY. As implied by their original extensive geographic distribution, tigers are tolerant of a variety of environmental conditions, the only apparent requisites for their survival being some form of plant cover, a water supply, and sufficient prey (Schaller, 1967). Tigers were found in tropical Asia in humid rain forest, wet evergreen and semi-evergreen forests, mangrove swamps, moist thorn and dry deciduous forests, thick grass, bamboo thickets, savannahs, and tamarisk shrublands. In western parts of their range tigers lived in hilly country with dense cover of trees and shrubs, while in Soviet Central Asia they preferred dense vegetation fringing riverbanks and floodplains. These strips of vegetation, known as "tugai," consist of tall grass, reeds, shrubs, and trees. The tigers of Manchuria and the Amur-Ussuri region inhabit rocky, mountain slopes and river valleys with forests of the Siberian pine or "cedar" (i.e. *Pinus koraiensis*), mixed pine-oak forests, and/or dense shrubs. In eastern and southeastern China, tigers lived in oak and poplar forests, grass thickets, and jungles; but they were also found in barren, rocky mountains, especially along the coast, opposite the island of Amoy (Abramov, 1962; Geptner and Sludskij, 1972; Locke, 1954; Pocock, 1939; Schaller, 1967; Smith, 1928).

In India and Nepal, tigers occur up to altitudes of 2,000 to 3,000 m (Perry, 1964; Prater, 1965), although they are usually found below about 1,500 to 1,600 m. Similarly, in the Alatau Mountains of Central Asia, tigers were reported from altitudes between 2,500 and 3,000 m (Geptner and Sludskij, 1972). In Sikkim, they were reported from much higher altitudes, namely 3,500, 3,840, and 4,360 m (Bailey, 1939; Battye, 1939). In Amur-Ussuri region and in Manchuria, tigers usually live at altitudes between 600 and 1,600 m (Geptner and Sludskij, 1972), withstanding winters with severe climatic conditions, such as very deep snow cover and temperatures to −30 to −40°C.

Tigers are essentially solitary, except for the short mating season and the time when the young are dependent on their mothers; yet, certain social tendencies may be seen, at least in Indian tigers (Hemmer, 1978*b*; Schaller, 1967).

The sizes of the territory and home range vary depending on the type of habitat, density of prey, and on the sex and age of the animal (Mazák, 1979). In addition, Schaller (1967) noted that tigers exhibit a wide variety of land tenure patterns—from exclusive use of an area that seems to be defended against others, to peaceful sharing of ranges, to lack of established ranges (depending on the sex, physiological condition, and, perhaps, individual inclinations of the animals involved). The size of territories of Indian tigers usually varies from about 200 to 1,000 km^2, but areas as small as 64 km^2 and as large as 9,252 km^2 have been ascertained (Schaller, 1967; Anderson, 1957). The size of the home range in Malaya was stated to be 380 km^2 (Locke, 1954), and that in Central Asia was about 1,000 km^2 (Sludskij, 1953). In the Amur-Ussuri region and in Manchuria, the size of territories seems to be substantially larger, averaging between about 2,000 and 4,000 km^2, though it may be as large as 10,500 km^2 (Mazák, 1979).

Within its territory, a tiger has one or more dens or lairs, placed in dense cover among rocks or shrubs, a cave, a hollow tree, or a cavity under a fallen tree. Tigers return more or less regularly to their lairs, although some animals do not show any preference for certain resting places (Guggisberg, 1975; Locke, 1954; Mazák, 1979; Schaller, 1967).

Tigers are lone hunters, mainly preying upon larger mammals. These include wild boar (*Sus scrofa*), cheetal (*Axis axis*), hog-deer (*Axis porcinus*), sambar (*Rusa unicolor*), barasingha (*Rucervus duvauceli*), barking-deer or kakar (*Muntiacus muntjak*), bactrian wapiti (*Cervus elaphus bactrianus*), Siberian wapiti (*Cer-*

vus elaphus xanthopygus), Siberian moose (*Alces alces cameloides*), sika deer (*Cervus nippon*), roe deer (*Capreolus capreolus*), muskdeer (*Moschus moschiferus*), nilgai (*Boselaphus tragocamelus*), black buck (*Antilope cervicapra*), gaur (*Bos gaurus*), banteng (*Bos javanicus*), Indian buffalo (*Bubalus arnee*), and a few others (Geptner and Sludskij, 1972; Locke, 1954; Mazák, 1965, 1979; Pocock, 1939; Schaller, 1967). Tigers also attack Indian tapirs (*Tapirus indicus*) and, quite exceptionally, young Indian rhinoceroses (*Rhinoceros unicornis*) and Indian elephants (*Elephas maximus*) (Berg, 1934; Sanderson, 1907; Smythies, 1940). In the Amur-Ussuri region, and also in Manchuria, tigers frequently kill and eat both brown bears (*Ursus arctos beringianus*) and black bears (*Selenarctos thibetanus ussuricus*) (Abramov, 1962; Geptner and Sludskij, 1972; Kaplanov, 1948); in India, tigers occasionally hunt sloth bears (*Melursus ursinus*) (Sanderson, 1907). Rarely, other animals, such as leopards, birds (mainly peacocks and pheasants), crocodiles, turtles, porcupines, rats, frogs, and fish are also eaten (Bajkov, 1925; Flerov, 1935; Pocock, 1939). These latter animals are killed and consumed only when there is a lack of other prey. Tigers attack domestic animals such as cattle, zebus, water buffalo, goats, and dogs (Abramov, 1962; Allen, 1938; Pocock, 1939). Finally, humans are very rarely killed and eaten by certain "specialized" tigers which are the so-called "man-eaters."

Tigers are excellent hunters and killers, yet for each successful kill some 10 to 20 unsuccessful attempts are made (see Guggisberg, 1975; Schaller, 1967). Several different techniques are used by tigers in attacking and killing large mammals; in most cases, the tiger approaches from the side or behind and rushes at the victim from as close a distance as possible, trying to throw it off its feet by the enormous force of the impact. At the same time, it lunges for and grasps the victim's throat with its canines. The hold is retained until the prey dies of strangulation, and usually several minutes afterward. Killing by biting through the back of the neck, which dislocates and breaks the victim's cervical vertebrae, is apparently rarely used to kill large mammals, although the medium-sized and smaller animals are often killed in this way (Schaller, 1967). A tiger generally carries or drags its kill into cover, occasionally over a distance of several hundred meters. A Manchurian tiger, for example, transported a full-grown horse for a distance of about 500 m (Bajkov, 1925), which, despite the fact that the tiger was a large male, illustrates the tremendous strength of tigers. The amount of meat eaten in one meal ranges between about 18 and 40 kg (Bajkov, 1925; Locke, 1954; Schaller, 1967), although in zoos tigers are usually fed 5 to 6 kg of meat per day.

More adult tigers evidently die of having been shot, snared or poisoned by man than of any other cause. Rarely, bears, wild pigs, gaurs, or other large ungulates can mortally wound a tiger (see Mazák, 1979). In addition, a herd of water buffalo or an elephant may kill tigers. There are numerous reports on accidents dealing with porcupines that sometimes lead to severe injuries and death of tigers (Corbett, 1961; Wakefield, *in* Krumbiegel, 1955). It was also reported that a pack of Indian wild dogs or dholes (*Cuon alpinus*) may exceptionally kill adult tigers (Pocock, 1939). Nonetheless, it seems that wild dogs could kill only ill or otherwise weakened tigers. The most important cause of the decline of populations of tigers is the loss of habitat and of the animals the tiger preys on. The tiger cubs face, of course, much more numerous dangers than the adults, including being killed by full-grown male tigers. According to Singh (1973) a 50% survival rate must be regarded as a maximum.

Not much is known of diseases of the free-living tigers. Two cases of rabies were reported from India; otherwise nothing definite has been published (see Mazák, 1979). The following species of parasites were found in wild tigers: Trematoda—*Paragonimus westermani* (eastern Siberia and India); Nematoda—*Toxocara* sp. (India), *Uiteinarta* sp. (eastern Siberia), *Physaloptera praeputiale* (eastern Siberia), *Dirofilaria ursi* (eastern Siberia), *Gnathostoma spinigerum* (Soviet Central Asia); Cestoda—*Diphyllobothrium erinacei* (India), *Taenia bubesei* (Soviet Central Asia), *Taenia pisiformis* (India); Arachnida (Acari)—*Boophilus calcaratus* (Soviet Central Asia), *Dermacentor silvarum* (eastern Siberia), *Hyalomma detritum* (Soviet Central Asia), *Hyalomma kumari* (India), *Hyalomma marginata* (Soviet Central Asia), *Rhipicephalus turanicus* (Soviet Central Asia) (compiled from data in Mazák, 1979, and Schaller, 1967).

Management of the species in captivity does not present any serious problems, and needs no special emphasis (Crandall, 1964; Mazák, 1979).

BEHAVIOR. Movements are similar to those of other representatives of the Pantherinae. In normal gait, both legs of one side move together or almost so. The length of a step ranges from 500 to 650 mm in females and about 600 to 800 mm in males (Judakov, 1974; Mazák, 1979). Jumping ability is well developed, as indicated by the relatively long hind legs, which average 1.23 times the length of the front legs (unpublished data on five specimens; see also Mazák, 1979). According to various authors (for details see Mazák, 1979) tigers are able to make jumps as long as 8 or even 10 m, though leaps generally do not exceed 5 or 6 m. Tigers usually do not climb trees, although there are several reports of their climbing abilities (Anderson, 1954; Bajkov, 1925; Sanderson, 1907). An adult tiger was observed and photographed climbing a smooth pipal tree trunk; it reached the first branches, which were about 10 m above the ground (Singh, 1961). A dramatic confirmation of the ability of tigers to climb trees was provided during the disastrous cyclone of 1969 in Bangladesh, where most tigers of the Sunderbans escaped the flood by taking refuge in trees (Mountfort, 1973).

Tigers like water and can swim very well, easily crossing rivers and streams as wide as 6 or 8 km, and exceptionally even 29 km (for details see Mazák, 1979).

Postures, in general, are the same as in other Pantherinae and were described in detail by Hemmer (1966, 1968*b*) and Sankhala (1978). Sleeping posture and the posture taken while eating may be explained as functional correlations of the size and body proportions (Hemmer, 1966, 1968*b*, 1972).

Most cats tend to kill their victims by biting through the nape (Leyhausen, 1973). Schaller (1967) supposed that the throat hold, as applied so often in killing of prey by tigers, was a special functional adaptation for dealing with large ungulates. While held by its throat to the ground, the prey is effectively prevented from righting itself and gaining its feet, as well as being unable to use its horns, antlers, and/or hooves in defense. Tigers begin to eat as soon as they move the kill to a suitable place; the buttocks of the prey are generally eaten first. Feeding tigers are usually prone, but they may also crouch, stand, sit, or rest on their elbows with the rump elevated. The forepaws are little used when large prey is consumed, but large bones are sometimes gnawed on while being propped between the pads of the forepaws. Tigers eat steadily but rarely for more than an hour, after which they stop for a few minutes to several hours to rest, drink, or wander around. After resting, they return to their kill and eat some more. When leaving the vicinity of their kill, they often cover it with debris, leaves, grass, and other material (Schaller, 1967).

The white ear spots function in intimidation of prey during the attack (Leyhausen, 1973), but probably also play an important role in intraspecific communication (Schaller, 1967). The long tail was said to be used as a rudder in jumping, but it seems more plausible that the positioning and movements of the tail are more important in intraspecific communication (Guggisberg, 1975; Leyhausen, 1973; Schaller, 1967).

The tiger is essentially solitary, hunting primarily at night when wild ungulates are most active. In India, Schaller (1967) observed tigers hunting or moving a total of 79 times between dawn and dusk; all but 21% of instances were before 0800 and after 1600. Similar activity patterns are also typical for tigers of the Amur and Ussuri regions and of Manchuria, although their daylight activity is slightly greater, especially in winter (Geptner and Sludskij, 1972; Kaplanov, 1948). When moving through its territory, a tiger regularly uses certain routes or beats. A beat is covered once in an interval ranging from several days to several months (Anderson, 1954; Corbett, 1957, 1961; Schaller, 1967), depending on the size of the territory, density of prey, and other factors. When locating their prey, tigers depend much more on hearing and sight than on olfaction (Anderson, 1954; Corbett, 1961; Sankhala, 1978; Schaller, 1967). Tigers searching for prey move considerable distances; in India, they may cover 16 to 30 km in a night (Schaller, 1967). In eastern Siberia and Manchuria, tigers may travel 50 to 60 km in a day (Jankovskij, in litt.; Kaplanov, 1948).

Some special features of behavior are displayed by man-eating tigers. They kill mainly by day, in contrast to man-eating leopards which kill almost exclusively by night. This demonstrates that tigers are able to change their habits according to those of their prey (Corbett, 1957, 1961; Locke, 1954). They also display an unusual understanding of human behavior, which suggests a reasoning and learning ability of rather high order. This is illustrated by the case of a Malayan man-eater which was hunted by five Europeans with all the conceivable stratagems, without ever being shot, although it was continually on the move in the course of the daylight hours (Locke, 1954). There are indications that some man-eating tigers are able to discriminate between an

armed man and a helpless victim (Corbett, 1957, 1961). The technique of attacking and killing men is the same as in stalking normal prey. A man-eater generally tries to surprise its victim from the side or rear and kill it by a bite through the throat or nape. The number of victims killed by a man-eating tiger may reach several hundred. The famous Champawat man-eating tigress killed over 430 people, of which 234 were killed in the course of four years (Corbett, 1961). A characteristic feature of behavior of man-eating tigers is that they operate over a very large area, usually covering several thousand square kilometers (Anderson, 1957; Corbett, 1961). Though man-eaters occasionally appear in the Amur and Ussuri regions, Manchuria, and Korea, they occur much more often in southern countries, mainly in India and Malaya. Tigers probably become man-eaters because they cannot capture and kill their normal prey. This may be because a tiger becomes crippled by a shot-wound or by deep suppurating wounds caused by porcupine quills, because of old age, or because the tiger's normal prey is becoming more and more scarce.

Tigers exhibit a large variety of facial expressions (Hemmer, 1969; Sankhala, 1978; Schaller, 1967), including the so-called "Flehmen" (tongue hangs over the incisors, nose is wrinkled, and upper canines bared). Tigers display the "Flehmen"-grimace after having sniffed urine and scent marks (either their own or those of other tigers), estrous tigresses, and sometimes a cub of their own species (Schaller, 1967; unpubl. data). Similar to the case in lions (Schaller, 1972), it seems that any powerful odor may elicit the "Flehmen"-response. There seems to be no "aggressive threat" facial expression in wild tigers as described by Leyhausen (1973). Schaller (1967) observed a "defense threat" facial expression, performed by pulling the corners of the open mouth back, exposing the canines, flattening the ears, and enlarging the pupils of the eyes. This expression was given even when a tiger was attacking.

Social organization, interactions between adults, and behaviors of female and young were described by Schaller (1967). Two of the main points that emerge from Schaller's observations are that a tiger has priority rights to its own meat supply, even in the presence of a larger and stronger animal; and even though they live a solitary existence, tigers seem to be aware of each other's doings. Hemmer (1978*b*) attempted to interpret social behavior in carnivores as a function of relative brain size and environment. He claimed that though the tiger, together with the lion, has the greatest cephalization among felids (the cephalization value being 16 in the lion and 17 in the tiger), and is thus potentially capable of group living, it is still essentially solitary. Hemmer suggested that this habit is probably caused by peculiarities of the habitat of tigers which differ from that of lions and, perhaps, by such features of general behavior that are popularly called "temperament" and are different in the two species.

Schaller (1967) found that tigers primarily use scent and visual signals to mark their territories. These include spraying urine (perhaps mixed with a secretion from the anal glands), leaving their feces in conspicuous piles, and leaving their claw marks on both the ground and trees. Although tigers are rather silent animals, Schaller (1967) lists the following vocalizations: purring; prusten; pooking (the so-called "sambar-call"); grunting; miaowing; woofing; moaning and roaring; growling, snarling and hissing; and a coughing roar. True roaring is accomplished because of the special structure of the hyoid apparatus (see Form and Function), and is produced by expelling the air through the open mouth while progressively closing it. These roars are sometimes repeated three to four times in succession, and are impressive resonant sounds that carry as far as 3 km. Moaning is a more subdued version of roaring, uttered with the mouth either partly opened or closed, and is audible over a distance of up to approximately 400 m. The coughing roar is a short, harsh and very loud sound emitted with the mouth open and the teeth bared. The true roar is generally heard when a tiger has killed a large animal and also during the mating season. Moaning appears to represent a release of tension by vocal means in a variety of circumstances, while the coughing roar is almost exclusively produced when the tiger is attacking (Schaller, 1967).

While mating, tigers are always very excited and noisy. The female rolls on the ground, waves her paws, and finally crouches on her belly. The male, which up to that moment just watches his mate, now stands over her, utters a series of roars, and generally seizes her nape with his canines without piercing the skin (the so-called "Nackenbiss" of Leyhausen, 1973). Copulation lasts 15 to 20 seconds, at the most; when it is over, the male quickly gets out of the way because the female will often jump to her feet and try to hit him with her forepaws. This "love scene" takes place dozens of times a day. At mating time tigers produce grunting, miaowing, growling, and hissing sounds, as well as roars and groans. In the wild, tiger and tigress stay together for about five to seven days. The mates then separate and the male often goes in search of another female (Guggisberg, 1975; Sankhala, 1978; Schaller, 1967; unpubl. data).

GENETICS. There are 38 chromosomes in *Panthera tigris*; the karyotype has 16 pairs of metacentric and submetacentric autosomes and two pairs of acrocentric autosomes. The X chromosome is a medium-sized metacentric and the Y chromosome is a small metacentric. The total number of chromosome arms (fundamental number) is 72 (Hsu and Rearden, 1965). The diploid number of 38 is also found in all the other Felidae of the Old World so far studied, as well as in some American species (Wurster and Benirschke, 1968; see also Hemmer, 1978*a*).

Of the color anomalies, white tigers are best known. True albinos with pinkish eyes and stripes only visible under reflected light are very rare; semi-albinos with blue eyes and stripes of brownish color are more common. The former were reported from Cooch Behar (Narayan, 1924; Pocock, 1939), the latter then from Orissa, Bilaspur, Rewa, Bhagalpoore, North Bengal, Assam and Korea (Gee, 1959; Pocock, 1929, 1939; Thornton et al., 1967; Weigel, 1961). No melanistic specimens have been studied by zoologists, although six cases of allegedly black tigers are recorded in the literature (H. R. Caldwell, 1924; J. C. Caldwell, 1954; Pocock, 1929, 1939; Stonor, 1964).

In zoos, tigers have been successfully crossed with lions many times (the so-called "tigons" and "ligers," according to whether they descend from a male tiger and lioness, or a male lion and tigress). The female hybrids are mostly fertile while the males are sterile (Hemmer, 1966; Leyhausen, 1950).

REMARKS. Tigers are found in most of the larger zoos and they breed without much difficulty. In captivity, they often become quite tame and are frequently trained for circus acts.

Tigers are seriously threatened by extermination over all of their remaining range and they are officially protected in almost all of the countries in which they occur. These protective measures are not always sufficient, however (Mazák, 1970, 1979). All of the subspecies of the tiger have been included in the I.U.C.N. list of endangered species and in the Red Data Book. The Leipzig Zoo (German Democratic Republic) has maintained the International Tiger Studbook since 1973. At the end of 1977, there were 756 individuals of *Panthera tigris altaica* and 142 of *Panthera tigris sumatrae* living in zoos. Compilation of data on other subspecies of the tiger for the studbook is in its preliminary stage; however, there are just several dozens of specimens of pure-bred *Panthera tigris tigris* and only a few specimens of *Panthera tigris amoyensis* and *Panthera tigris corbetti* in zoos. As far as is known to me, no specimen of either *Panthera tigris virgata* or *Panthera tigris sondaica* is kept in a zoo (both subspecies are either extinct or nearly so). There never was a specimen of the extinct *Panthera tigris balica* kept in captivity.

Though Oken's (1816) publication has been ruled to be inconsistently binomial and unavailable for purposes of nomenclature by the International Commission on Zoological Nomenclature, the generic name *Panthera* Oken, 1816, has been very frequently used in the last 60 years in special taxonomic publications and mammalogical as well as general zoological literature and text books. In the interest of reducing confusion and promoting stability the Commission was requested to validate the name *Panthera* Oken, 1816, as allowed by Opinion 417 (for discussion of this problem see Hemmer, Mayr, Morrison-Scott, Mazák, and others *in* Corbet et al., 1974).

Deraniyagala (1951) described a tiger skin that he suggested may have originated in Sudan (sic!), and he proposed the name *Panthera tigris sudanensis* for this "newly discovered" form of tiger. Tigers never inhabited any part of Africa; the skin in question probably came from Iran or eastern Turkey. The name *sudanensis* might thus be a synonym of *P. t. virgata* (for details see Mazák, 1979).

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