Ailuropoda melanolueca. By John Chorn and Robert S. Hoffmann

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**Ailuropoda Milne-Edwards, 1870**

*Ailuropoda* Milne-Edwards, 1870:1. Type species *Ursus melanoleucus* David, 1869, by monotypy.


**Ailuropoda melanoleuca (David, 1869)**

Giant Panda, Great Panda, Parti-colored Bear, Beishung, Bamboo Bear, White Bear, Panda Bear

*Ursus melanoleucus* David, 1869-13. Type locality vicinity of Mouping (Poo-hsing), Schzechuan Province, China.

**CONTEXT AND CONTENT.** Content noted in generic summary above. The genus *Ailuropoda* is now monotypic.

**DIAGNOSIS.** The following diagnosis (from Davis, 1964 and Henley, 1972) applies to both the genus and the species. Recognizes other living bears in general body shape and proportions, but differs from them in distinctive coat color (figure 1), white with black eye patches, ears, fore and hind legs, stripe across shoulders, and sometimes tip of tail. Skull and mandible are robust (figure 2), sagittal crest is well developed, and zygomatic arches are expanded laterally and dorsosvertically relative to other arctoid carnivores (dogs, bears, raccoons and relatives). In contrast to characters of other living bears, the orbital fissure is confluent with the foramen rotundum, postorbital processes are reduced, alisphenoid canal is lacking; P4 is large, with prominent protocone and parasial; M1 is roughly square, internal cingulum and multiple cusplets are present on M1 and M2; and M2 is elongated. An entepicondylar foramen is present, a primitive character shared, among living bears, only with *Tremarctos*.

**GENERAL CHARACTERS.** Head-body length is 1.2 to 1.5 m; tail approximately 127 mm; weight 75 to 160 kg. Coat is thick and woolly, color black (sometimes with brownish tinge) and white (sometimes reddish). Hind feet are not fully plantigrade—no heel pad; as in other bears the humerus is held firmly in place by a well-developed postscapular fossa. Dental formula is 1:3, c:1, p 4:4, m 2:5, total 42; first premolar is degenerate in both jaws and may be absent from the upper jaw; in contrast to those of other bears, second and third premolars are well developed; molars, particularly upper molars, are large relative to the skull, secondary cusps and tubercles (as in the European caviar and *Ursus spelaeus*) are present on all molars. Muscles associated with mastication are large and both origins and insertions of jaw muscles are expanded. Vision is said to be poor and olfaction acute (Peking Zoo, 1974a). See especially Walker et al. (1964), Davis (1964), and Evera (1973).

Davis (1964) provided an exhaustive and well-illustrated account of all aspects of the morphology of the giant panda. Goodwin et al. (1976) supplemented this monograph with studies of blood, alimentary tract, nervous system, eye, cranial arteries, vitamin D transport, mammary gland secretion, visual pigment (see also Dartnell, 1973), neurochemistry, cytochrome C, and transferrin. Cave (1974, 1975) published on the *sarcocys epiphyseum* and the thyroid and parathryoid glands in this species. Discussion of pathology and diseases of the giant panda can be found in several papers in Goodwin et al. (1976) and, also that of the Peking Zoo (1974a), which includes symptoms and treatment of gastroenteritis, roundworm (*Ascari* = *Beylisascaris sroederi*) (see also Sprent, 1968, and Giant Panda Expedition, 1974), respiratory tract infection, epilepsy, inflamed uterus, conjunctivitis, and inflamed bone marrow. Gastroenteritis and roundworm are the most common diseases of these animals.

**DISTRIBUTION.** Published data on the geographic range (figure 3) of the giant panda are equivocal and somewhat vague. The most recent reference to the range (Brambell, 1976) placed *Ailuropoda* in three main areas, possibly contiguous: southern Kansu (Min Shan), and northern and central Schzechuan (Ching-Hsia Shan = Chiang-Lai Shan); southern Schzechuan (Ta-Liang Shan); and southern slopes of the Chin Ling (= Ch'ing-ling), or Tapai Shan (= T'ai-pai Shan) of Sowerby (in Hsu, 1973), southern Schensi Province (the Chinese words shan and ling both refer to mountains). Older reports also place the giant panda in the Min Shan south of "Sai-ku" (= Sikou) on the Kansu-Schzechuan border (Buchner and Berezovski, 1891), near Batang (= Pa-lang) (Edgar, 1972, 1930, in Hsu, 1973), "Yunwu Mountain" (not found east of Pa-lang, Pen Hung-Shou, 1962), and at Oring Nor (= Cha-ling Hu), Tsinghai Province (Pen Hung-Shou, 1943). A recent unconfirmed report of four pandas found "in the hills to the north of Sining" (= Hsi-ning) (T'-Iai Shan, Tsinghai Province) also has appeared (Perry, 1969; Edgar, 1966, in Hsu, 1973). Morris and Morris (1966) suggested that the probable range extends from Tsinghai in the northwest to Schensi in the northeast and to Yunnan in the south. However, Wang Sung (Inst. Zool., Acad. Sinica, Peking—letter dated 14 April 1978) states that the occurrence of giant pandas in Tsinghai and Yunnan remains unconfirmed.

According to Wang Sung and Lu Chang-kung (1973), giant pandas range from 2700 to 3900 m above sea level; Brambell (1976) placed them between 2600 and 3500 m, the limits of the subalpine coniferous forest (Giant Panda Expedition, 1974) in which Chinacane bamboo (*Sinarundinaria*), the main food of the giant panda, grows in dense stands. Studies in the Wanglang Natural Reserve (Giant Panda Expedition, 1974) indicated that the distribution of these animals is limited below 2300 m but that they may occasionally descend to approximately 800 m in winter. Signs such as droppings and "claw prints" have been recorded as high as 4040 m.

**FIGURE 1.** Subadult *Ailuropoda melanoleuca* (courtesy National Zoological Park, Washington, D.C.).
Figure 2. Skull (dorsal, lateral, and ventral views), and mandible (lateral) of adult female Ailuropoda melanoleuca, Chengwei, 7000 ft., 25 mi W Wenchwan, Szechwan, China, 17 November 1934 (AMNH 110451).

Fossil Record. According to Wang Sung and Lu Chang-kun (1973) the geographic range of the giant panda extended throughout southern China during the middle and late Pleistocene (see map, fig. 1, in Wang Tsiang-ke, 1974). Fossils are known from Szechwan, Yunnan, Shensi, Hupeh, Chekiang, Kiangsi, Fukien, Kwangsi, and Kwantung provinces (figure 3). Middle Pleistocene material from Szechwan was described as Ailuropus joveuxi (Matthew and Granger, 1933), and Ailuropopopuscule was described (Woodward, 1915) from the Pleistocene of the northern Shan States in Burma. Davis (1964) placed both taxa in the genus Ailuropoda, and Wang Tsiang-ke (1974) further regarded the Burmese material as representing merely a large extinct subspecies, Ailuropoda melanoleuca bicont, as did Colbert and Hoijeer (1953) for A. m. joveuxl. Pei Wen-chung (1962) described a small Ailuropoda from the early Pleistocene of Gigantopithecus Cave, Kwangsi, as A. microto. See Wang Tsiang-ke (1974) for tables of occurrences of fossil giant panda material and extensive specimen measurements.

The closest relatives of Ailuropoda (tribe Ailuropodini) are found in the extinct tribe Agriotherini. Two genera of that tribe, the Pliocene Indarctos and the Pleistocene Agriotherium are allied with Ailuropoda within the subfamily Agriotheriinae. These three taxa are united largely on the basis of dental characters. All display a prominent protcone and a paracone on the P4, and the M1 is roughly square and displays multiple cusplets (Hendey, 1972; see also Erdbrink, 1953). The subfamily includes a third tribe, Tremarctini, whose living representative is the South American spectacled bear, Tremarctos ornatus.

Form. Davis (1964) revealed a close similarity between most of the organ systems in the giant panda and those of other bears. The histology of the bone does differ from that of Ursus due to greater thickness of the compacta in Ailuropoda. This is especially true in the skull and is correlated with the massive structure of the jaws and their use in chewing bamboo (Prayer et al., 1978). Differences between giant panda and bear skulls, such as absence of the alisphenoid canal or of postorbital processes on the frontal bones, Davis ascribed to "expansion of the masticatory apparatus" (see also Chang et al., 1960).

In the auditory bulla and basioccipital region, and the carotid circulation in this area, Ailuropoda resembles Ursus in most respects, and differs markedly from typical procyonids (Segall,
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communication); the external genitalia of the adult male red panda
is well developed, and does not resemble that in giant pandas, as
Davis (1964) thought.

ONTIOGENY AND REPRODUCTION. Estrus takes
place in March, April, and May in the wild and in April and May
in captivity (Peking Zoo, 1974c). The most intense heat occurs in
late April and early May and it is then that mating occurs (Brambell,
1976). Duration of estrus is between four and 14 days but usually
lasts approximately 10 days (Peking Zoo, 1974c). A second
estrus may occur in autumn. Morris and Morris (1966—
see also Walker et al., 1964) speculated that fertilization or im-
plantation may be delayed. Gestation takes approximately five
months; for zoo-born giant pandas, gestation required 122 to 163
days (mean 140.2 ± 8 days—Peking Zoo, 1974c). The shortest
period represents the birth of twins, one of which died, and may
reflect premature birth. Time of birth is usually in September.
Litter size normally is one or two; occasionally three young are
born, but only a single young is ever raised by the mother (Bram-
bell, 1976)—note, however, that Pen Hung-Shou (1943) reported
 sighting a female and two cubs in Tsinghai. Giant pandas are
blind and toothless at birth, weigh between 90 and 151 g (104.2
g average) and are covered with spars white fur (Peking Zoo,
1974c). According to Brambell (1976) the tail is long at birth,
approximately one-third the body length, quite unlike that of oth-
er bears. Black fur begins to appear in the second week—first
around the eyes, and then the nose, ears, feet, underparts, and
muzzle and paws in that order. Adult coloration is attained by
the end of the first month. Eyes open between days 40 and 60 and
coordinated vision is accomplished at approximately the third
month. Independent feeding begins in the third month. By the sixth
month young weigh approximately 13 kg and leave their mothers
at this time. Studies by the Peking Zoo (1974c) reveal that the
limbs of giant pandas are weak at birth and that it is two months before the third limbs support the body. The young can walk and run by the middle of
the fourth month. Teeth begin to erupt by approximately the third
month. The report by the Peking Zoo (1974c) contains tables of body weight increase for the first year. Growth in size of
bears. Sexual maturity varies but is usually attained in six or
seven years (Peking Zoo, 1974c) (five or six years according to
Brambell, 1976). Sheldon (1975) reported that giant pandas have
lived 13 or 14 years in zoos but they probably live longer in the
wild.

ECOLOGY AND BEHAVIOR. Climate of the region in-
habited by the giant panda is generally damp. Summers are cool
in the winters cold; rain, snow, and fog are frequent (Sung and
Lu Chang-kun, 1973; Morris and Morris, 1966). Tempera-
ture and humidity range from approximately —10°C and 90%
r.h. (when air is above freezing) in winter, to 25°C and 60%
in summer (Brambell, 1976). A partial list of the forest, shrub, and
from the Wanglang Reserve, Szechwan, is in the report of
the Giant Panda Expedition (1974). See also Roosevelt and Roosevelt
(1929) and Sheldon (1975) for accounts of climate and habitat.

What giant pandas eat has been confirmed by their discovery by Peter David (Fox, 1949). Several authors have re-
counted statements by natives to the effect that giant pandas eat
fish, pikas (Ochotonas), and rodents. Brambell (1976) reported that
their droppings sometimes contain the remains of bamboo rats
(Rhizomys pruinosus). Bones have also been found in the stomach
of a dead giant panda (Wang Sung and Lu Chang-kun, 1973; Giant
Panda Expedition, 1974) so it seems that there is no longer
primate for believing that this animal will exclusively herbivo-
rous or that it eats only bamboo. It has long been known that
captive giant pandas will eat meat, and they are even said to steal
meat from logging camps in the wild (Giant Panda Expedition,
1974). Bamboo (culms and leaves) is certainly the giant panda’s
chief food (McClure, 1943; Sheldon, 1975) but gentians, irises,
crocuses, Chinese vines (Lycium chinense) and tussah grasses
such as rice-grass and bent-grass are also eaten (Morris and Mor-
ris, 1966; Pen Hung- Shou, 1943). Fir bark is also eaten (Giant
Panda Expedition, 1974) and reports of local natives indicate that
these animals raid bee-hives for honey (Perry, 1969). Sheldon
(1937) estimated that giant pandas may spend 10 to 12 hours a
day feeding.

Giant pandas usually feed in a sitting position with the fore-
legs free to manipulate bamboo with the opposable radial sepa-
maid "thumb" (figure 4). In this position the animal grasps the
bamboo stalk in its teeth and strip off the tough outer layers of
the stalk is then fed into the side of the mouth, where a section at
a time is thoroughly masticated. According to Davis (1964) the man-

Figure 4. Wild giant panda in typical sitting position in bamboo thicket, grasping stalk of bamboo on which it feeds (courtesy
nal dexterity of the giant panda is good (see also Giant Panda Expedition, 1974; Collins and Page, 1973, for feeding behavior of Ailuropoda).

Knowledge of giant panda behavior is inadequate and awaits a detailed field study. They are known to bark and hoot. Wang Sung and Lu Chang-kun (1973) stated that their mating call is low and deep. Sound spectrograms of zoo animals were published by Morris and Morris (1966). Activity is mainly crepuscular, but captive giant pandas are also active at night (Kleiman, 1974) and this is probably true of wild giant pandas as well (Giant Panda Expedition, 1974). Captive females are known to mark "territory" with a scented, sticky secretion from the anal region (Morris and Morris, 1966). This is done with either a lateral or circular anogenital rub while in a squatting or quadrupedal stance. A female urinates "while lying flat on the venter with tail raised" (Kleiman and Collins, 1972). Males also mark with a lateral anogenital rub, and in addition they may use a "forward-back" rubbing movement after urinating with the leg cocked. Males also urinate against vertical surfaces while upright on forelimbs in a handstand (Kleiman and Collins, 1972; Kleiman, 1974; see also Collins and Page, 1969). In both males and females, urine and glandular secretions may be rubbed onto the back from a previously marked surface. Food, grass, ice, soil, and other materials often are rubbed onto the ventral surface with the forepaws (Kleiman and Collins, 1972).

Locomotion is similar to that of bears but with a longer stride. Unlike other bears, giant pandas do not gallop, but use a "diagonal walk," moving the limbs on one side forward and backward at the same time (Davis, 1964). They stand erect but never walk in this position. Posture is similar to that of other bears. "Play" behavior in young Ailuropoda is similar for males and females, and includes partial and complete somersaults, lateral rolls, and body twisting (Kleiman and Collins, 1972; see Wilson and Kleiman, 1974, for detailed account). Young giant pandas in the U.S. National Zoo are known to roll on their backs in the dirt while rubbing dirt over the throat and belly with their forepaws (Kleiman, 1975). These giant pandas also take water baths.

Opinion varies as to the climbing ability of the adult giant panda, and ranges from that of Sheldon (1975; see also Collins and Page, 1973) who believed that they seldom climb trees, to that of Chinese workers (Giant Panda Expedition, 1974) and Brambell (1976) who described their climbing ability as excellent (figure 5; also see Giant Panda Expedition, 1974, for photographs of what is probably an adult giant panda descending a large fir tree). Although this response is by no means automatic (Sheldon, 1975), giant pandas sometimes climb trees to escape dogs (Walker et al., 1964; Morris and Morris, 1966; Giant Panda Expedition, 1974).

Other than females with young, giant pandas are solitary except during the breeding season when they may form groups of two or three (Giant Panda Expedition, 1974; Brambell, 1976). Reports of native hunters indicate that the home range of a giant panda is small. It usually lives within an area of 2.5 km, although during the rut it may move from one ravine to another (Giant Panda Expedition, 1974).

Chinese workers have estimated that approximately 200 giant pandas now inhabit the Wanglang Reserve and it is thought that this population is stable (Giant Panda Expedition, 1974). Brambell (1976) estimated that at least 1000 giant pandas survive in the wild, based on a conservative estimate of suitable habitat (6000 km2).

Giant pandas do not hibernate, but they do descend into lower ravines in winter and spring and are active on south-facing slopes. These animals make no permanent dens but take shelter in hollow trees, rock crevices, and caves (Giant Panda Expedition, 1974; Sheldon, 1975). Sheldon noted the occurrence of beds of bamboo, arranged in a circle beneath rock ledges and he suggested that such beds might be used as places to bring forth young.

Coat color may be aposematic (Morris and Morris, 1966), cryptic, or thermoregulatory (Lazell, 1974, 1976). Both Morris and Morris (1966) and Wang Sung and Lu Chang-kun (1973) discount the effectiveness of the dhole (Cuon alpinus) and leopard (Panthera pardus) as predators upon the giant panda. Probably only man poses a significant threat to this animal.

The first live Ailuropoda to be transported successfully out of China (Harkness, 1938) was exhibited during 1938-1939 in the Chicago Zoological Park. Since then a number of giant pandas have been exhibited in Western and Chinese zoos (Morris and Morris, 1966; Perry, 1969), but breeding has occurred only in the latter. A detailed account of the management of captive giant pandas is given by the Peking Zoo (1973). Claude (1971) summarized specimens known to have been collected through 1945.

GENETICS. The diploid (2n) number of chromosomes in Ailuropoda is 42; the karyotype includes 32 biarmed and eight acrocentric autosomes, one pair with prominent satellites (Newham and Davidson, 1966). Sex chromosomes were not previously identified, but in the female studied, the X chromosome was probably a medium-sized subtelocentric. Most bears, in contrast, have a 2n = 74 karyotype, with many (60 or more) acrocentrics. The exception is Tremarctos ornatus, the spectacled bear of the South American Andes, which has a 2n = 52, with only 20 acrocentric chromosomes, one pair of which bear prominent satellites as in Ailuropoda (Würster, 1969). These satellites, or "marker," chromosomes resemble those seen in typical procyonids (2n = 38) and Ailurus (2n = 36), but are absent in other ursids.

REMARKS. One of the most interesting aspects of the giant panda is that for over a century it has seemingly defied classification. This is all the more strange considering that the anatomy of Ailuropoda is now well known. Only the domestic dog and cat have been more extensively studied anatomically among the carnivores. Summaries and references pertaining to the classification of the giant panda can be found in Davis (1964), Morris and Morris (1966), and Chu Ching (1974). Prior to the publication of Davis's (1964) anatomical study, British (Mivart, 1885; Lankester, 1901; Lydekker, 1901) and American (Gregory, 1936; Raven, 1936) workers generally supported the theory that Ailuropoda is most closely related to the supposed procyonid Ailurus. These two pandas were thought to be allied by extensive similarities of the dentition and skull structure, viscera, external genitalia, and the opposable sesamoid in the manus. Ewer (1973) also stressed the unbear-like behavior of Ailuropoda.

A second alternative is to separate the giant and lesser pandas from Recent bears and procyonids and place them in their own family(ies) (Ailuridae, Ailuropodidae—Pocock, 1921; Then and Hofer, 1960; Collins and Page, 1973). Todd and Pressman (1960) interpreted the karyotypes of the giant panda (2n = 42) and lesser panda (2n = 36) as possible support for this alternative.
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Another alternative, a viewpoint held by most continental European workers, is that the giant panda is related to the bears. This viewpoint was taken by Davis (1964) to be based on the general morphology of Ailuropoda. Serological studies, beginning with the work of Leone and Wiens (1956) on serum proteins, and Sarich's (1973, 1976) analysis of albumins and transferrins also indicate an affinity between Ailuropoda and Recent bears. Dental characters in particular ally the giant panda with two extinct bears, Agriotherium and Indarctos (Hendey, 1972; see also Bardenfleth, 1913). We believe that the weight of evidence now supports this relationship, and adopt it here. Most of the "specialized characteristics of giant pandas . . . also observed in lesser pandas but not in bears" (Maclintyre and Koopman, 1967), such as the manus and male genitalia, have now been shown to differ in Ailuropoda and Ursidae.

With few exceptions, panda systematics has suffered from the narrow scope of most taxonomic studies of the problem. The question of how closely Ailurus is related to other procyonids (or Ursidae) has received little attention. Assessment of shared derived characters, where these can be determined, based on available knowledge of anatomy, physiology, serology, karyology, behavior, and the fossil record of the pandas and other arctoid carnivores, is now necessary.

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