

Ailurus fulgens. By Miles S. Roberts and John L. Gittleman

Published 14 November 1984 by The American Society of Mammalogists

***Ailurus* F. Cuvier, 1825**

Ailurus F. Cuvier 1825:3. Type species *Ailurus fulgens* by monotypy.

Arctaelurus Gloger 1841:28. Renaming of *Ailurus* F. Cuvier 1825.

CONTEXT AND CONTENT. Order Carnivora, Superfamily Canoidea, Family Ailuridae (placed by some in Procyonidae; see REMARKS). The genus *Ailurus* includes only one species. Classification below the subordinal level follows Pocock (1941).

***Ailurus fulgens* F. Cuvier, 1825**

Red Panda

Ailurus fulgens F. Cuvier 1825. Type locality designated as "East Indies."

Ailurus ochraceus Hodgson 1847:1118. Type locality "sub-Himalayas." *Nomen nudum.*

Ailurus refulgens Milne-Edwards 1874. Type locality unknown.

Ailurus styani Thomas 1902:251. Type locality "Yang-liu-pa, NW Sze-chuen."

CONTEXT AND CONTENT. Context noted above under genus *Ailurus*. Two subspecies of *Ailurus* currently are recognized.

A. f. fulgens F. Cuvier 1825:3, see above. (*ochraceus* Hodgson and perhaps *refulgens* Milne-Edwards are synonyms.)

A. f. styani Pocock 1941:258, see above.

DIAGNOSIS. The genus *Ailurus* includes one living species; thus the following characters (Pocock, 1921, 1941; Thomas, 1902) apply to both genus and species. Readily distinguishable from other Carnivora in coat color: face predominantly white with reddish-brown "tear" marks extending from the inferior region of the orbit to the corner of the mouth (Fig. 1); post-cranial dorsal pelage reddish- or orange-brown and ventral pelage glossy black; legs are black and the soles of the feet are covered with dense, white hair. This is the only Asian carnivore in which the plantar surface of the foot is completely covered with hair. The skull (Fig. 2) is robust (110-120 mm condylobasal length). The sagittal crest is poorly developed and the zygomatic arches widely flared and highly arched. The postorbital process is poorly developed. The palatines extend beyond the level of the most posterior molar, the mesopterygoid fossa is constricted anteriorly, the auditory bulla is small and medially inflated and the postglenoid process is robust and anteriorly recurved. The alisphenoid canal is present. The mandible is robust but relatively short in relation to the height of the ramus. The mandibular symphysis is constricted. The coronoid process is strongly hooked posteriorly and the mandibular condyles are large.

Ailurus possesses extremely robust dentition in contrast with that of the procyonids with which it is compared frequently. The P4, M1, and M2 are wider than they are long and bear accessory cusplets (Fig. 3). Each upper premolar possesses more than one cusp and P3 has a well developed paracone and hypocone; P1 is absent and the p1 is minute or absent.

GENERAL CHARACTERS. Mean mass of captive adult males is 5.0 kg (range, 3.7 to 6.2 kg) and is 4.9 kg (range, 4.2 to 6.0 kg) for females (Roberts and Kessler, 1979). Length of head and body is 560 to 625 mm and length of tail 370 to 472 mm (Pocock, 1941; Roberts, 1975). The head is rounded, rostrum shortened, and ears large, erect, and pointed. The tail is comparatively long and marked with about 12 alternating red and buff rings (Fig. 1). There is no sexual dimorphism in size or color (Roberts, 1981). Long, coarse guard hairs cover the entire body and there is a soft, dense, woolly undercoat. Specimens collected from the eastern sector of the range of the species may be somewhat larger and

darker in color than those from western areas (Pocock, 1921; Thomas, 1902).

DISTRIBUTION. The red panda is found between 2,200 and 4,800 m in temperate forests of the Himalayas and high mountains of northern Burma and western Sichuan and Yunnan (Fig. 4). The distribution is associated closely with temperate forests having bamboo-thicket understories (Allen 1938; Anon., 1978; Feng et al., 1981; Jackson, 1978; Mierow and Shrestha, 1978; Roberts, 1982a; Sowerby, 1932; Stainton, 1972).

The confirmed western-most range of *Ailurus* seems to be the Namlung Valley in Mugu District and the Lake Rara region of northwestern Nepal (Jackson, 1978). The southern limit is the Liankiang Range of western Yunnan and the northern and eastern limit is the upper Min Valley of western Sichuan. The existence of *Ailurus* in southwestern Tibet and northern Arunachal Pradesh is strongly suspected but has not been documented. A specimen exhibited in the Srinagar Museum in Kashmir reportedly was taken in Ladakh, eastern Kashmir; although this could not be confirmed, it would represent a substantial western expansion of the range (Roberts, 1982c).

The red panda seems to be more common in the eastern part of its range, especially along the Burma-Yunnan border, but it cannot be considered a common species (Allen, 1938; Pousargues, 1896).

The current distribution of *Ailurus* suggests a radiation outward from a central core in the Burma-Yunnan-Sichuan highlands along regions of recent orogenic activity, most notably the Himalayas (Gansser, 1964; Manadhar, 1978). The zone of highest density includes a region in western China proposed as a Pleistocene refugium for a variety of endemics (Pei, 1974; Pen, 1962). The extensive mountain ranges uplifted during the Pleistocene created substantial new habitat for *Ailurus* and a variety of other species of Indochinese origin (Cronin, 1979; Rau, 1974). Erosive activity by rivers originating in the Tibetan plateau caused the partitioning of the Himalayan Mountain system into a series of blocks separated by deep gorges that pose physical and ecological barriers to transmigration. For this reason, the distribution of *Ailurus* should be considered as a series of disjunct, physically isolated populations rather than a continuous, interbreeding one.

FOSSIL RECORD. No fossil congeners of *Ailurus fulgens* are known. A variety of Old World and New World fossils intimately link *Ailurus* with the Procyonidae. McGrew (1938) described the similarity of the molar patterns of the early procyonid, cynarctine genera *Cynarctis* (Middle Miocene to Lower Pliocene of North America) and *Cynarctoides* (Lower Miocene of North America) with that of *Ailurus*. He concluded that cynarctine affinities were closer



FIGURE 1. Captive male adult red panda. Photo by Miles S. Roberts.

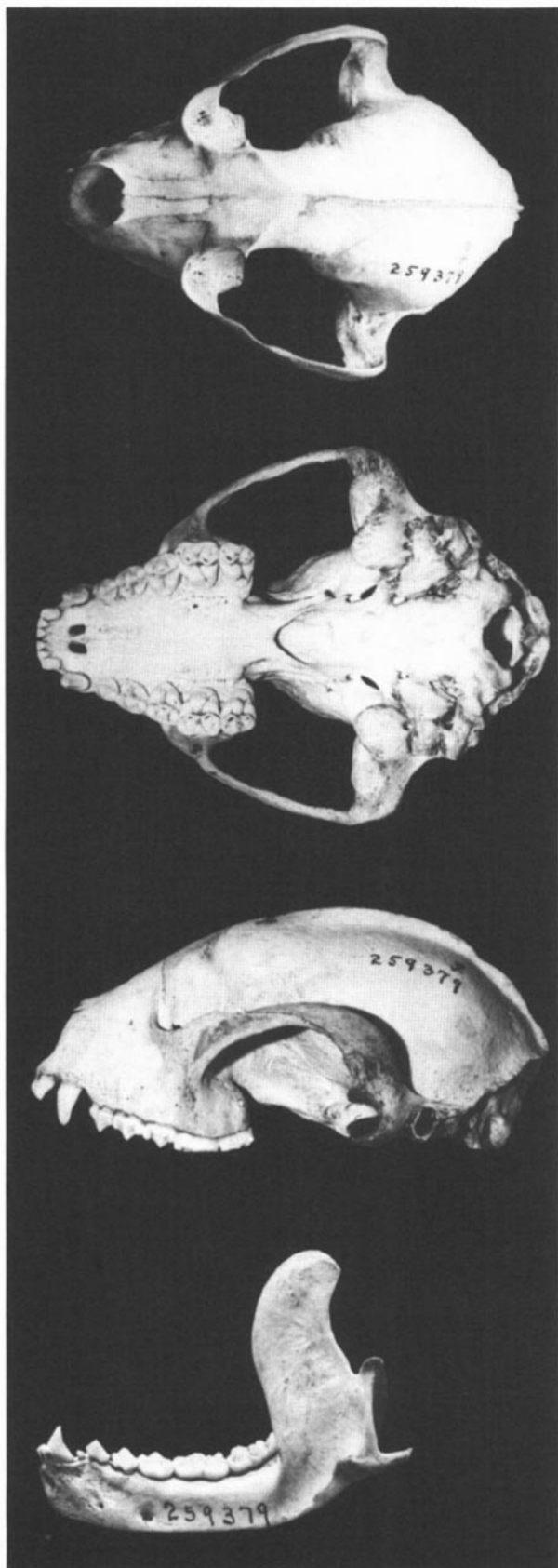


FIGURE 2. Skull of *Ailurus fulgens* (USNM 259379) collected at Wen Chuan, Sichuan, China (D. C. Graham, collector). Condylobasal length is 105.5 mm. Photos by Miles S. Roberts.



FIGURE 3. Occlusal surface of right maxillary premolars and molars of USNM 259379 demonstrating wear pattern and pattern of cusps and accessory cusplets. Photo by Miles S. Roberts.

to Ailurinae than to Procyoninae. *Phlaocyon* (Lower-Middle Miocene of North America) and *Aletocyon* (Lower Miocene of North America) also bear substantial similarities to *Ailurus* on the basis of molar patterns and the structure of carnassials and auditory regions (McGrew, 1938; Romer and Sutton, 1927). However, Wortman and Matthew (1899) suggested that *Phlaocyon* was more intermediate between *Cynodictis* and *Procyon*. Simpson (1945) agreed with this view and applied the same line of argument to *Aletocyon*, placing both genera in the subfamily Procyoninae and indicating that they were more likely precursors of the New World procyonid radiation than that of the Old World.

Sivanasua of the Upper Miocene of Europe and Lower Pliocene of Asia seems to be the earliest indisputable ailurine and exhibits cranial and dental structures ancestral to and possibly contemporaneous with *Ailurus* (Pilgrim, 1932; Schlosser, 1899). *Parailurus* from the Lower Pliocene of England, Europe, and North America seems closest to *Ailurus* in general cranial and dental morphology (Dawkins, 1888; Tedford and Gustavson, 1977). The available *Parailurus* material suggests that there were possibly as many as three different species (Kurtén and Anderson, 1980; Tedford and Gustavson, 1977), all larger and more robust than *Ailurus* in dental and cranial characters. The approximate biochron for *Parailurus* is 3–4 m.y.b.p. The *Parailurus* findings indicate an European-Asian origin for the Ailurinae with a subsequent trans-Beringian radiation (Kurtén and Anderson, 1980; Tedford and Gustavson, 1977).

Intermediate forms between *Parailurus* and *Ailurus* are not known. The smaller size and diminished range of *Ailurus* suggests that it may represent a specialized offshoot of the early ailurine lineage (and possibly even of an Asian form of *Parailurus*) that survived the Pleistocene glaciations in the mountain refugia of southern China (Pen, 1962).

FORM AND FUNCTION. The reddish-orange pelage appears cryptic against the canopy of fir (*Abies*) trees where branches are covered with clumps of reddish-brown moss (Order Bryales) and white lichens (*Usnea*) (Roberts, 1982a). Tufts of facial vibrissae, situated low down on the cheek, are present. A series of small pores from which appear small amounts of clear, colorless, and odorless fluid occurs on the plantar surface of the feet (Roberts, 1981). The pores are contained in slightly raised areas between the plantar pads, and are associated with small, slightly elongated, and thickened hairs. These pores may secrete substances that are used in depositing scent trails (Roberts, 1981). Urine and secretions originating from the anogenital region may be other sources of scent. Adults of both sexes possess paired anal glands each approximately 2 cm long and 1 cm in diameter located bilaterally adjacent to the anal opening (Flower, 1870; Pocock, 1921; Roberts, 1981). Short ducts lead from the glands and empty into the distal portion of the rectum about 2 cm from the anal opening or anal sphincter. The content of the glands is a dark green-black, iridescent, oily fluid with a very pungent odor.

The number of mammae in females is eight, arranged in two rows of four each (Sokolowsky, 1918).

The dental formula is $i\ 3/3, c\ 1/1, p\ 3/3-4, m\ 2/2$, total 36–38. The fourth upper premolar, a principal discerning dental character in Carnivora, is large with five cusps as in *Procyon* and *Ailuropoda* (Davis, 1964; McGrew, 1938). By contrast, in the Ursidae P4 has only three cusps which are degenerate. The second

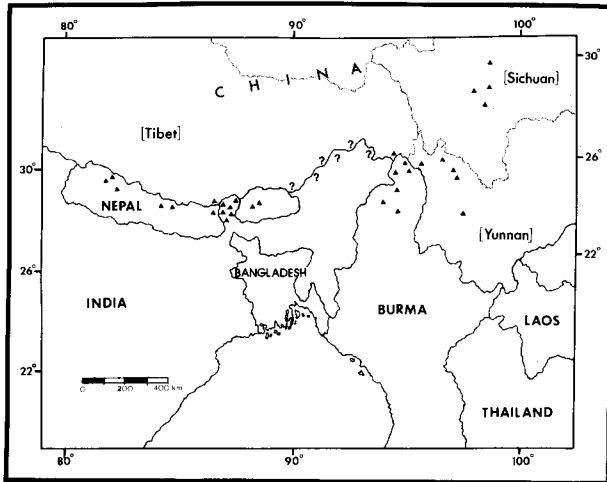


FIGURE 4. Distribution of *Ailurus fulgens* based on Pocock (1941), Roberts (1982c), and Thomas (1902, 1922). Collection localities are indicated by closed triangles. Areas where the species is reported but for which confirming specimens are lacking are indicated by (?).

and third upper and lower premolars are large and robust. The large cheektooth surface promotes mediolateral movement for a grinding action and correlates with a highly specialized diet of bamboo and fibrous plant material (Gregory, 1936; Hodgson, 1848; Scapino, 1981). The symphysis menti is relatively flexible with a moderate degree of independent movement of the hemimandibles (Scapino, 1981).

In general, skull size is large compared with that of carnivores of similar body size such as Procyonidae. Greater depth of skull may improve bite pressure at the level of the cheekteeth; particularly high values are found for zygomatic arch width, occipital height, condyle to m1 length and jaw cross-section area (Gregory, 1936; Radinsky, 1981). Relative brain size, measured from cranial capacity, is comparable with that of Procyonidae (Gittleman, 1983). The auditory bulla is relatively small as indicated by the reduced caudal entotympanic elements, and may be correlated with reduced auditory sensitivity (Hunt, 1974). In both juvenile and adult forms the bulla is formed almost entirely by the tympanic as in ursids, and lutrinae and mephitinae mustelids. Rostral and caudal entotympanics form a small part of the medial wall of the bulla as in Ursidae but in contrast with that in *Procyon*, which possesses a swollen caudal entotympanic (Hunt, 1974).

There are 6 lumbar vertebrae and 14 thoracics (Davis, 1964). The cervical region is short. Relative proportions of the vertebral column are: cervical (22%), thoracic (47%), and lumbar (31%). Forelimbs and hindlimbs are of roughly equal length (Davis, 1964). The five digits on each foot are in a strongly curved line and terminate with curved semiretractile claws, used effectively in climbing. The radial sesamoid bone of the wrist articulates primarily with the radial carpal bone, and is greatly enlarged but relatively less so than the sesamoid of the giant panda, *Ailuropoda* (Davis, 1964). Forepaws are frequently used to pick, manipulate, and pull apart food, particularly bamboo leaves and stalks (Roberts, 1981; Sokolowsky, 1918). The postscapular fossa is moderately large and may be indicative of its arboreality where the forelimbs are more supportive while climbing than the hindlimbs (Davis, 1949).

The left lung is divided into two lobes (Goppert, 1937) similar to Procyonidae, Mustelidae, and Ursidae but contrasting with the remaining carnivore families that have three lobes. Reduction of lobes seems to be associated with a broadening of the thorax (Marcus, 1937), whose functional change is unknown. The right lung is divided into four lobes as in all fissioned carnivores.

The salivary glands are relatively large as in most omnivorous carnivores (Carlsson, 1925). The tongue is similar to *Ursus*, being of moderate length and having numerous foliate papillae (Davis, 1964; Sonntag, 1923). The stomach is simple, as in all fissioned carnivores, with a spherical fundus, no caecum, and a cylindrical, thick-walled pylorus (Hodgson, 1848). The intestinal tract is simple and comparatively short (4.2 times body length). This characteristic

is unusual considering the common association between herbivory and an extended gut in mammals.

Males possess a comparatively short penis, the prepuce closer to the scrotum than in Procyonidae (Flower, 1870; Pocock, 1921). The baculum is comparatively short, only about 2 cm long (Davis, 1964; Pocock, 1921).

ONTOGENY AND REPRODUCTION. The mean of 17 reported gestations in captivity was 134.2 days ($SD = 14.7$ days; range, 112 to 158 days; Dittoe, 1944; Erken and Jacobi, 1972; Mottershead, 1958; Roberts, 1981; Roberts and Kessler, 1979). Pocock (1941) reported a gestation of 90 days provided by Dr. Vevers of the Zoological Society of London. However, the derivation of this measurement was not stated; therefore, it likely was erroneous. The exceptional length and range of gestations suggests that delayed implantation may occur although this has not been demonstrated.

In captivity, pregnant females become noticeably heavy and lethargic about 6 weeks before parturition (Roberts, 1980, 1981). Several days before parturition a pregnant female begins to carry nest materials such as sticks, grasses, and leaves into suitable nest sites. Nest building may continue after the young are born but the behavior is highly variable among females (Mottershead, 1958; Roberts, 1981). In the wild, animals may use hollow trees or rock crevices as nest sites (Hodgson, 1847; Pocock, 1941) but in captivity females readily adopt nest boxes placed on the ground, hollow logs, or other artificial dens (Keller, 1977; Roberts, 1975, 1980). Within 24 h of parturition, females become more active and move about aimlessly, pausing occasionally to lick the anogenital region or to prop the hindquarters against a vertical object as if to strain during abdominal contractions (Roberts, 1981). All known births occurred between 1600 and 0900 h, the period of highest activity. Parturition occurs rapidly, with females quickly cleaning the cubs and remaining with them for 60 to 90% of the time during the first few days after birth (Erken and Jacobi, 1972; Keller, 1977; Mottershead, 1958; Roberts, 1975, 1981; Wall, 1908). Females may recognize their young by olfactory cues established shortly after birth. After the cubs are about 1 week old, females gradually spend more time away from them, returning every few hours to nurse and groom them (Roberts, 1975, 1981). Mothers move young frequently, presumably in response to nest disturbance; all active nest sites are kept clean by the mother. Lactating females increase food consumption within 24 h of parturition and continue to do so until weaning. Young are nest-bound for approximately 90 days, after which they make their first excursions from the nest at night. At first, mothers attempt to restrain cubs from emerging but cubs soon become too active to monitor closely. Initial excursions from the nest coincide with the first evidence of the young eating solid food (Roberts, 1975, 1981). By 120 days of age, young consistently rest away from the nest area with their mother. Mother-young proximity continues to be close until the onset of the next breeding season when mild aggression between the mother and young may occur (Roberts, 1975, 1980). Young attain adult size at approximately 12 months and are sexually mature at approximately 18 months (Roberts, 1975, 1980, 1981).

In captivity, mating is strictly seasonal with onset in the early winter, usually between early January and mid-March (Dittoe, 1944; Erken and Jacobi, 1972; Keller, 1980; Mottershead, 1958, 1963; Roberts, 1980, 1981; Roberts and Kessler, 1979; Zuckerman, 1953). The onset of sexual activity coincides closely with increasing photoperiod following the winter solstice (Roberts, 1981). The mating season for individuals in captivity in the northern hemisphere seems not to differ substantially from that in the wild although there may be a tendency for prolongation of the mating season in captive colonies (Roberts, 1981). Captive individuals in the southern hemisphere mate in the austral winter, generally in July and August. Roberts (1981) reported that a hierarchy of environmental cues triggered reproduction in captivity; photoperiod is a general cue and lunar periodicity is a more specific cue, with copulations tending to cluster during the 'new moon' phase of the lunar cycle. In the wild, births occur in spring and summer, but mainly in June (Hodgson, 1847; Pocock, 1941; Wall, 1908). In captivity in the northern hemisphere, 3.5% of 199 litters were born in May, 79% in June, 16% in July, and 1.5% in August. Of 11 litters born in the southern hemisphere 8 were in December, 2 in January, and 1 in March (Glatston, 1980, 1982). In captivity, no synchrony of mating or birth dates is evident among females housed in the same or nearby

enclosures. The time of mating and birth also is not affected by latitude (within a hemisphere) or by altitude. Females tend to give birth within 10 days of the date of parturition the previous year (Roberts, 1981).

In captivity, litter size ranges from one to four with a mode of two (Erken and Jacobi, 1972; Glatston, 1980, 1982; Hodgson, 1847; Pocock, 1941; Roberts, 1975, 1980, 1981; Roberts and Kessler, 1979; Wall, 1908; Zuckerman, 1953). Litter size does not affect gestation length (Roberts, 1981). The sex ratio in a sample of 100 infants born in 78 litters was 48 males to 52 females (Roberts, 1981). The mortality schedule is similar to that of other mammals being highest in the youngest (0 to 1 year) and oldest (7 to 12 years) age classes with a decline during middle age (1 to 7 years). Litters of two and three young have the lowest juvenile mortality. Survivorship of the young is independent of maternal age and experience. Generally mortality is higher in males and increases significantly with higher inbreeding coefficients (Roberts, 1981, 1982b).

Neonates weigh 110 to 130 g and grow at a rate of 7 to 20 g/day until they begin to eat solid food at approximately 90 days (Brahm and Bartmann, 1976; Conway, 1981; Roberts, 1975; Roberts and Kessler, 1979; Watson and Barfield, 1982). At birth, eyes and ears are closed, and head, body, and tail are covered with thick, woolly, gray-buff fur approximately 25 mm long (Roberts, 1975). Total length is about 280 mm. The tail is proportionately shorter in young than in adults, averaging about 70 mm or 25% of the total length in contrast to about 40% of the total length in adults. At birth, the skin is pink, plantar surfaces of the feet are unfurred, mystacial vibrissae are about 20 mm long, and the pelage lacks adult coloration and markings. By day 14, long reddish guard hairs appear giving a slightly reddish tinge. Eyes and ears open by day 18. Adult coloration and coat pattern are discernable at about day 50; the tail is ringed, the face white with a dark track from the eye to the corner of the mouth, and the soles of the feet are fully furred. Adult coloration and patterning essentially are complete by day 70 (Roberts, 1975). Adult size and mass are attained by 12 months of age. Premolars, both upper and lower, first appear about 30 days and complete dentition appears by 6 months (Brahm and Bartmann, 1976; Conway, 1981; Erken and Jacobi, 1972; Gray, 1970; Munro, 1969; Roberts, 1975, 1981; Roberts and Kessler, 1979; Wall, 1908).

For the first 7 to 10 days after birth young remain essentially immobile except when nursing (Roberts, 1975, 1981). The mother remains curled around them when in the nest and, in her absence, the young sleep in a curled or semi-curved position often in contact with one another. Gradually, the young become more active and move about in an uncoordinated fashion. They are able to right themselves when placed on their back by day 12. By day 18, the eyes are open and the young are able to orient toward light. By day 60, siblings are engaging in rough and tumble play in the nest and frequently venture to the entrance of the nest box. Young are able to climb proficiently by the time they emerge from the nest box at about day 90 (Keller, 1977; Roberts, 1975, 1980, 1981).

There are few paternal interactions until the young are weaned (Roberts, 1975, 1981). In captivity, some males were observed to enter nest boxes and even sleep with young for short periods. There is no provisioning of the young, however, by either parent at any time. After young emerge from the nest, males may engage in play with them. Males can be left with females year-around in captivity but females left together in the same enclosure may steal or kill young of others (Mottershead, 1958). Prolonged association of both parents with young and apparent tolerance of mixed-sex groups in captivity has led to speculation that the red panda may be gregarious in nature (Mottershead, 1958; Roberts, 1980, 1981; Roberts and Kessler, 1979).

In captivity, red pandas are polyestrous with an estimated cycle length of between 26 and 44 days (Erken and Jacobi, 1972; Roberts, 1981; Roberts and Kessler, 1979). The duration of estrus reportedly was between 1 and 14 days (Erken and Jacobi, 1972; Keller, 1977, 1980; Kowalska, 1982; Roberts, 1981; Roberts and Kessler, 1979). Sexual behavior is concentrated over 24 h of a single estrous period suggesting (1) an inherently short duration of estrus, (2) induced ovulation, or (3) immediate cessation of estrus following conception (Roberts, 1981). Testis size in captive males undergoes seasonal change, being small and semi-abdominal from April to November and large and scrotal during the pre-mating and mating period (northern hemisphere). Females that lose litters do not undergo a postpartum estrus.

The maximum lifespan of the red panda in captivity is approximately 14 years but generally captive animals do not live beyond 8 to 10 years (Crandall, 1964; Glatston, 1980, 1982). Individuals of both sexes have reproduced up to 12 years of age.

ECOLOGY. Red pandas are found in the temperate forest zone of the Himalayan ecosystem. This zone is characterized by mixed deciduous-coniferous forest dominated by *Abies*, *Tsuga*, *Aesculus*, *Juglans*, *Quercus*, and *Acer* (Mierow and Shrestha, 1978; Seidensticker et al., 1984; Troll, 1969; Vaurie, 1972). Mammals found in association with the red panda include *Presbytis entellus*, *Cuon alpinus*, *Selenarctos thibetanus*, *Martes flavigula*, *Panthera pardus*, *Cervus elaphus*, *Moschus sifanicus*, *Naemorhedus goral*, *Petaurista elegans*, and *Sorex araneus*. Birds include a wide variety of pheasants and partridge (Phasianidae), warblers (Muscicapidae), tits (Aegithalidae), and thrushes (Muscicapidae) (Giant Panda Expedition of the Wanglang Natural Reserve, 1974; Jackson, 1978; Mishra, 1976; Roosevelt and Roosevelt, 1926; Vaurie, 1972). Temperature ranges in red panda habitat are from 10°C to 25°C at elevations from 3,000 to 3,750 m (Allen, 1938; Mani, 1968). In the Himalayan region, there is considerable vertical climatic zonation caused by differences in rainfall and temperature, with the southern area receiving up to 350 cm rainfall annually and the interiors somewhat drier with 130 cm annually (Troll, 1969; Vaurie, 1972). In northern regions, vegetation is dominated by *Tsuga*, *Quercus dilatata*, or *Aesculus*, *Juglans*, and *Acer* forest (Jackson, 1978). In southern, drier regions the dominant species is *Quercus semecarpifolia* (Mierow and Shrestha, 1978; Stainton, 1972). In western China, the mountain chains of Sichuan and Yunnan have a north-south orientation that traps westerly moisture-laden winds to produce abundant rainfall and thick deciduous and evergreen forest composed primarily of *Cyclobalanopsis*, *Fagus*, and *Tsuga* (Allen, 1938; Schaller, 1977; Seidensticker et al., 1984).

In general, all of these vegetational and climatic zones provide moist, well drained soil suitable for bamboo growth (Numata, 1979), the dietary staple of the red panda. The genera of bamboos most likely to form the bulk of the diet are *Phyllostachys*, *Sinarundinaria*, *Thamnocalamus*, *Chimonobambusa*, and *Qiongzhusua* (Numata, 1979; Seidensticker et al., 1984; Sheldon, 1937). In addition to bamboo, red pandas in the wild may eat small mammals, birds, eggs, blossoms, and berries (Hodgson, 1847; Sowerby, 1932). In captivity, animals were observed to eat birds, blossoms, *Acer* and *Morus* leaves, bark and the fruits of *Acer*, *Fagus*, and *Morus* (Bartlett, 1900; Roberts and Collins, 1978; Simpson, 1869; Stott, 1940).

Adults are thought to be solitary outside the breeding season, with territories well posted by scent-marking (Roberts, 1981). There are no data on juvenile dispersal patterns in the wild. In captivity, the young develop slowly and complete independence from maternal care is not established until at least 6 and possibly as much as 12 months of age (Roberts, 1981; Roberts and Kessler, 1979). Home-range size and population density are not known; however, other similar-sized carnivores have relatively small home ranges and high population densities (Gittleman, 1983; Gittleman and Harvey, 1982).

As a result of human encroachment in suitable forest habitat and the unusual biology of bamboos, *A. fulgens* may be near extinction in the western sector of its range, especially in Nepal. Because of its scarcity and unknown habits in the wild an intensive international breeding program was established for the red panda in more than 30 zoos, and an *International Studbook*, edited by A. R. Glatston (1982), documents management techniques, growth in captive populations, and pathology reports. Based on *International Studbook* summaries, numbers of red pandas in captivity increased from 136 in 1980, to 147 in 1981, and to 197 in 1982. Improved longevity and reproduction are effected by larger enclosures, removal from extreme heat and humidity, and a diet high in fiber and bulk, mainly bamboo.

In captivity, animals are maintained most successfully in outdoor enclosures with a natural, grassy substrate, living trees for climbing and perching, and sufficient shade to allow animals to retreat from the heat of summer (Roberts, 1980). The ideal social grouping is a mated pair and their dependent offspring, although a male and two females can be maintained together during the breeding season (Glatston, 1980; Roberts, 1980). A diet high in fiber is essential to prevent gastrointestinal disorders; bamboo and native or cultivated grasses are preferred (Bush and Roberts, 1977; Montali et al., 1984; Roberts, 1980). Orphaned infants have been successfully hand-raised with a variety of carnivore milk-replacers (Con-

way, 1981; Gray, 1970); cross-fostering of infants between females is possible if accomplished when the infants are young (Roberts, 1981). Captive animals are susceptible to canine distemper associated with use of attenuated (modified-live) virus vaccine, dermatophytosis (ringworm), and two types of pulmonary metastrongyles, *Dirofilaria immitis* (heartworms) and *Filaria taxideae*, that cause cutaneous filariasis (Bonney and Schmidt, 1975; Bush and Roberts, 1977; Bush et al., 1976; Conway, 1982; Custer et al., 1978; Frankenhuis and Glatston, 1980, 1982; Gardiner et al., 1983; Itakura et al., 1979; Montali et al., 1984; Parihar and Chakravarty, 1980). High neonatal mortality is associated with congenital malformation in inbred animals (Roberts, 1982a; Montali et al., 1984) and bacterial pneumonia (Montali et al., 1984).

BEHAVIOR. Captive red pandas are nocturnal and crepuscular and exhibit a polyphasic activity pattern throughout the night. Activity patterns change throughout the year in response to temperature, feeding regimes, and presence of young (Keller, 1977; Roberts, 1981). In the wild, red pandas are reported to be most active at dawn, dusk, and at night (Anon., 1978; Hodgson, 1847). Red pandas are scansorial but forage primarily on the ground. The usual mode of progression on the ground is by a cross-extension gait; faster movement is by trotting or bounding. A similar cross-extension pattern is used to climb tree trunks, and animals descend head first by gripping the tree trunk medially with the hindfeet. Movement on and between small terminal branches is facilitated by a high degree of flexibility of the pectoral and pelvic girdles and limb joints (Keller, 1977; Roberts, 1981). The tail is not prehensile but is used as a support and counterbalance when climbing. In normal progression on the ground, the tail is carried straight out and horizontal to the ground (Roberts, 1981). Red pandas rest and sleep in trees or other elevated surfaces most frequently, and in nature are said to use evergreens as nest sites (Anon., 1978; Hodgson, 1847). Sleeping and resting postures range from prone extension with legs straddling a branch to a tightly curled posture with the head tucked under a hindleg. Temperature and humidity influence the posture adopted, presumably to alter heat conductance. Animals maintain a tightly curled posture during cold weather but stretch their bodies along branches with their legs dangling during hot weather. Adults rarely sleep in contact with one another; however, a mother and her young and nest-bound siblings in the absence of their mother do so frequently. Comfort behaviors include licking the body and limbs, face-washing with one forepaw or hindpaw, and stretching or rubbing the back, abdomen, and flanks against a stationary object. Virtually all comfort behaviors are conducted while in a tree and shortly after awakening or eating. Particular attention is paid to maintenance of the forepaws. Discrete latrine areas are used for defecation but not urination, and these areas generally are located at the periphery of enclosures (Keller, 1977, 1980; Roberts, 1981).

Food items are grasped in a single forepaw and brought to the mouth while sitting, standing, or occasionally lying on the back. Bamboo is grasped by the culm, then bent down to bring the leaves within reach of the mouth. Food grasped in this fashion is inserted in the side of the mouth where it is sheared, then chewed extensively before being swallowed. Small food items such as blossoms, berries, and small leaves are nipped off with the incisors (Keller, 1977; Roberts, 1981).

Visual displays used primarily in intraspecific interactions include arching of the tail and back, a slow raising and lowering of the head while emitting a low intensity puffing, turning of the head while jaw-clapping, shaking the head from side to side, raising a forepaw as an intention movement before striking, and a bipedal posture with forelegs extended above the head before lunging at a playmate or opponent during aggressive interactions. Virtually all of these visual displays occur within close proximity of another animal. "Staring" is another visual display that usually occurs at greater distances between individuals (Keller, 1977, 1980). Interactive social behaviors include a variety of motor patterns that permit olfactory examination of conspecifics including naso-naso, naso-face, naso-torso, naso-flank, and naso-anal contact (Keller, 1977; Roberts, 1981). Approaching, following, sniffing, striking, lunging, biting, and wrestling form a continuum of motor patterns observed in aggressive, play, and social contexts. Adults rarely interact with one another outside of the mating season and aggression is rare. Individuals housed together maintain individual sleeping and resting loci and use a variety of the visual displays in maintaining

individual distances (Keller, 1977, 1982; Roberts, 1981; Roberts and Kessler, 1979).

The vocal repertoire of the red panda is small but there is considerable variability within certain call types (Roberts, 1981). Tonal calls include an infant distress "wheet," which may persist in the adult as a "squeal" under conditions of great duress, and a high-pitched, modulated-frequency "twitter" heard as a contact call in young and adults. A harsh, broad band, polysyllabic "quack-snort" is emitted by young and adults under conditions ranging from mild annoyance to intense aggression. Nonvocal sounds of communicatory function include exhalation of air through the nose and mouth (puffing) while raising and lowering the head during mild threat displays, and jaw-clapping while turning the head towards a nearby individual during a low intensity aggressive encounter. Grunts and snorts also are produced by animals engaged in wrestling or fighting (Roberts, 1981). Structural homologies and functional similarities were found between some vocalizations of the red panda and those of the giant panda, *Ailuropoda*, and Procyonidae (Peters, 1982).

At the onset of the mating season a male and a female rest, move, and eat in close proximity. Scent-marking rates for both sexes increase, most notably in males, and males spend a significantly greater amount of time examining trails and fecal and urine-markings of females. On the day of copulations, female scent-marking increases markedly and the male begins to pursue the female closely. Female precopulatory behavior includes frequent stops during agitated, random movement about the enclosure, tail flicking, and a playful, bounding gait. Copulation occurs on the ground following a mount invitation by the female. The male clasps the female about the abdomen and immediately commences thrusting at a rate approximately 120 thrusts/min. There is no neck bite although the male may lick the neck and shoulders of the female during copulation. There are extravaginal ejaculations and multiple ejaculations per copulation. Copulations last 3 to 39 min; there is no evidence of a copulatory tie and, at the end of copulation, the male and female separate and engage in long bouts of genital autogrooming (Keller, 1977, 1982; Roberts, 1980; Roberts and Kessler, 1979).

Chemical signals are deposited through stereotyped motor patterns associated with the deposition of urine, feces, and secretions from the anal and circumanal glands. Feces deposited in well-defined latrine areas may serve to delineate home ranges or territories. Scent-marking involves applying the anal or circumanal region to slightly raised objects such as sticks or rocks and rubbing these in a lateral and anteroposterior fashion. Urine also may be applied simultaneously. Males mark more frequently and for longer duration than females at all times of the year. Most scent-marking occurs on the ground but it also can occur in trees (Keller, 1982). Habitually used branches may become coated with a layer of slightly sticky material seemingly deposited by the animals as they move about. These scent trails are smelled intensively by animals newly introduced into enclosures. Red pandas have a series of enlarged papillae on the underside of the tip of the tongue that seem to serve a chemocommunication function. Following olfactory inspection the tip of the tongue is applied to certain areas and either vibrated or drawn along the spot being examined. The tongue is withdrawn into the mouth and the process may be repeated (Keller, 1977, 1982; Roberts, 1981).

Most behaviors of the red panda are typically carnivore-like and offer few clues to the taxonomic placement of the species. Certain categories of behaviors, especially scent-marking, some vocalizations, body postures, foraging, and feeding behavior reveal similarities between the red panda and giant panda (Kleiman, 1983).

GENETICS. The diploid (2n) chromosomal complement of *Ailurus* is 36 including 32 metacentrics and submetacentrics and 2 acrocentrics; one marked pair of satellite submetacentrics is on the short arm as in other carnivores (Hsu and Benirschke, 1970; Todd and Pressman, 1968; Wurster, 1969). The typical procyonid karyotype is 2n = 38 and that for Ursidae is 2n = 74. The giant panda has a karyotype of 2n = 42. Albumin and transferrin data indicate early divergence from the procyonid line, with some 41 units of change accumulated subsequent to *Ailurus* divergence (Sarich, 1976).

REMARKS. The higher taxonomic affinity of *Ailurus* has been a subject of almost as much debate as the taxonomic placement of the giant panda (Chorn and Hoffmann, 1978). Since its discovery in the early 1800's, *Ailurus* has, at various times, been placed in the Procyonidae (Gregory, 1936; Hollister, 1915; Honacki et al.,

1982; Sarich, 1976), the Ursidae (Mivart, 1882; Trouessart, 1904), with *Ailuropoda* in Ailuropodidae (Flower, 1870; Lankester, 1901), and in the monotypic family Ailuridae (Pocock, 1941; Eisenberg, 1981). This uncertainty has arisen because of difficulties in determining whether certain characters of *Ailurus* are phylogenetically conservative or are derived and convergent with species of similar ecological habits. Evidence based on the fossil record, serology, karyology, behavior, anatomy, and reproduction reflect closer affinities with Procyonidae than Ursidae. However, ecological and foraging specializations and a distribution distinct from the modern procyonid radiation warrant classification in a separate family (Ailuridae) derivative of the Procyonidae. Subspecific classification of *Ailurus fulgens* also has been somewhat inconclusive and has received little systematic treatment (Roberts, 1982b).

The common name "panda" was applied to *Ailurus* when it first was presented to the western scientific community in 1821 (Hardwicke, 1827). *Ailuropoda* was designated the "giant" panda after its discovery in 1869 because of some affinities to *Ailurus*; subsequently the latter was relegated to "lesser" panda. We prefer the designation "red" panda in view of the chronological seniority of *Ailurus* in the scientific literature and the more accurate description given by this term.

The red panda seems to have little commercial value and is of little economic importance in live animal and fur trades. The species is protected in India, Bhutan, Nepal, and China, and is listed in Appendix II of the Convention on the International Trade in Threatened and Endangered Species. Native names applied to *Ailurus* include lesser panda, fire fox, bear cat, wah, ye, nigalya ponya, thokya, woker, sankam, and wokdonka. The origin of the name "panda" is unknown.

We thank Katherine Ralls, Margaret O'Connell, Richard Thorington, Karl Kranz, and George Schaller for comments and suggestions on drafts of the manuscript. J.L.G. was supported by a Smithsonian Institution postdoctoral fellowship grant.

LITERATURE CITED

- ANON. 1978. Newsletter No. 43, Nature Ann., 2:150-154.
- ALLEN, G. M. 1938. The mammals of China and Mongolia. Nat. Hist. Central Asia, Amer. Mus. Nat. Hist., 11(pt. 1):1-620.
- BARTLETT, A. D. 1900. Life among the wild beasts in the "zoo." Chapman and Hall, Ltd., London, 375 pp.
- BONNEY, C. H., AND R. E. SCHMIDT. 1975. A mixed infection: Chagas' and Tyzzer's disease in a lesser panda. J. Zoo Anim. Med., 6:4-7.
- BRAHM, E., AND W. BARTMANN. 1976. Problemreiche Künstliche aufzucht eines kleinen panda (*Ailurus fulgens*) im Tierpark Dortmund. Verhandlungsbericht des XVIII. Internationalen Symposiums über die Erkrankungen der Zootier, pp. 347-351.
- BUSH, M., R. J. MONTALI, D. BROWNSTEIN, A. E. JAMES, JR., AND M. J. APPEL. 1976. Vaccine induced distemper in a lesser panda. J. Amer. Vet. Med. Assoc., 169:959-960.
- BUSH, M., AND M. ROBERTS. 1977. Distemper in captive red pandas. Internat. Zoo Yearb., 17:194-196.
- CARLSSON, A. 1925. Über *Ailurus fulgens*. Acta Zool., 6:269-305.
- CHORN, J., AND R. HOFFMANN. 1978. *Ailuropoda melanoleuca*. Mamm. Species, 110:1-6.
- CONWAY, K. 1981. Supplemental feeding of maternally reared red pandas *Ailurus fulgens*. Internat. Zoo Yearb., 21:236-239.
- . 1982. Incidence of a parasitic lungworm in red pandas and its management implications. Pp. 45-48, in The red or lesser panda studbook (A. R. Glatston, ed.). The Royal Rotterdam Zoological and Botanical Gardens, Rotterdam, The Netherlands, 2:1-83.
- CRANDALL, L. S. 1964. The management of wild mammals in captivity. Univ. Chicago Press, Chicago, 761 pp.
- CRONIN, E. W. 1979. The Arun. Houghton Mifflin, Boston, 236 pp.
- CUSTER, R. W., M. BUSH, J. M. SMELLER, AND E. E. SMITH. 1978. Clinical experience with dissociative anesthetics in lesser pandas (*Ailurus fulgens*): Hematology and blood chemistry values. J. Zoo Animal Med., 9:22-28.
- CUVIER, F. 1825. Histoire naturelle des Mammifères, avec des figures originales, colorées, dessinées d'après des animaux vivants. Paris, 1824-42, 2:1-3, Plate 203.
- DAVIS, D. D. 1949. The shoulder architecture of bears and other carnivores. Fieldiana-Zool., Chicago Mus. Nat. Hist., 31:285-305.
- . 1964. The giant panda: a morphological study of evolutionary mechanisms. Fieldiana-Zool Mem., 3:1-339.
- DAWKINS, W. B. 1888. On *Ailurus anglicus*, a new carnivore from the Red Crag. Quart. J. Geo. Soc. London, 44:228-231.
- DITTOE, G. 1944. Lesser pandas. Zoonoz, 17:4-5.
- EISENBERG, J. F. 1981. The mammalian radiations. Univ. Chicago Press, Chicago, 620 pp.
- ERKEN, A. H. AND E. F. JACOBI. 1972. Successful breeding of lesser panda (*Ailurus fulgens*, F. Cuvier, 1825) and loss through inoculation. Bijdragen tot die Dierkunde, 42:92-95.
- FENG, Z., C. ZHENG, AND G. CAI. 1981. On mammals from southeastern Xizang. Pp. 1013-1016, in Geological and ecological studies of Qinghai-Xizang Plateau. Proceedings of the Symposium on Qinghai-Xizang (Tibet) Plateau (Beijing, China). Science Press, Beijing and Gordon and Breach, Science Publishers, Inc., New York, 2:1-2138.
- FLOWER, W. H. 1870. On the anatomy of *Ailurus fulgens*. Proc. Zool. Soc. London, 1870:752-769.
- FRANKENHUIS, M. T., AND A. R. GLATSTON. 1980. A review of pathological findings in the red panda. Pp. 31-35, in The red or lesser panda studbook (A. R. Glatston, ed.). The Royal Rotterdam Zoological and Botanical Gardens, Rotterdam, The Netherlands, 2:1-83.
- . 1982. A review of pathological findings in the red panda, 1979-1981. Pp. 37-41, in The red or lesser panda studbook (A. R. Glatston, ed.). The Royal Rotterdam Zoological and Botanical Gardens, Rotterdam, The Netherlands, 2:1-83.
- GANSSER, A. 1964. Geology of the Himalayas. John Wiley, London, 283 pp.
- GARDINIER, C. H., M. R. LOOMIS, J. O. BRITT, JR., AND R. J. MONTALI. 1983. Ulcerative dermatitis in a lesser panda (*Ailurus fulgens*) caused by *Filaria taxidae* (Filarioidea: Filariidae). J. Amer. Vet. Med. Assoc., 183:1285-1287.
- [GIANT PANDA EXPEDITION OF THE WANGLANG NATURAL RESERVE.] 1974. [A survey on the giant panda (*Ailuropoda melanoleuca*) in Wanglang Natural Reserve, Pingwu, Northern Szechwan, China.] Acta Zool. Sinica, 20:162-173 (original in Chinese; translated by Rose W. Chu).
- GITLEMAN, J. L. 1983. The behavioral ecology of carnivores. Unpubl. Ph.D. dissert., Univ. Sussex, England, 372 pp.
- GITLEMAN, J. L., AND P. HARVEY. 1982. Carnivore home range size, metabolic needs and ecology. Behav. Ecol. Sociobiol., 10:57-63.
- GLATSTON, A. R. 1980. Studbook listing of red pandas. Pp. 64-81, in The red or lesser panda studbook (A. R. Glatston, ed.). The Royal Rotterdam Zoological and Botanical Gardens, Rotterdam, The Netherlands, 1:1-88.
- . 1982. Studbook listing of red pandas. Pp. 55-79, in The red or lesser panda studbook (A. R. Glatston, ed.). The Royal Rotterdam Zoological and Botanical Gardens, Rotterdam, The Netherlands, 2:1-83.
- GLOGER, C. W. L. [1841] 1842. Gemeinnütziges Hand- und Hilfsbuch der Naturgeschichte. Für gebildete Leser aller Stände, besonders für die reifere Jugend und ihre Lehrer. Band 1. Verlag von Aug. Schulz and Co., Breslau, 495 pp. (Not seen)
- GOPPERT, E. 1937. Kehlkopf und trachea. Handb. Vergleich. Anat. Wirbeltiere, 3:797-866.
- GRAY, B. J. 1970. Care and development of a hand reared red panda, *Ailurus fulgens*. Internat. Zoo Yearb., 10:139-142.
- GREGORY, W. K. 1936. On the phylogenetic relationships of the giant panda (*Ailuropoda*) to other arctoid Carnivora. Amer. Mus. Novitates, 878:1-29.
- HARDWICKE, MAJ.-GEN. 1827. Description of a new genus of the Class Mammalia, from the Himalaya chain of hills between Nepal [sic] and the snowy mountains. Trans. Linnean Soc. London, 15:161-165.
- HODGSON, B. H. 1847. On the cat-toed subplantigrades of the sub-Himalayas. J. Asiatic Soc., 16:1113-1129.
- . 1848. Addendum on the anatomy of *Ailurus*. J. Asiatic Soc., 17:573-575.
- HOLLISTER, N. 1915. The genera and subgenera of raccoons and their allies. Proc. U.S. Natl. Mus., 49:143-150.
- HONACKI, J. H., K. E. KINMAN, AND J. W. KOEPL (EDS.). 1982.

- Mammal species of the world. Allen Press, Inc. and the Association of Systematic Collections, Lawrence, Kansas, 694 pp.
- HSU, T. C. AND K. BENIRSCHKE. 1970. *Ailurus fulgens* (Lesser panda). Atlas of Mammalian Chromosomes, 5(182):1-3.
- HUNT, R. M., JR. 1974. The auditory bulla in Carnivora: an anatomical basis for reappraisal of carnivore evolution. *J. Morphol.*, 143:21-76.
- ITAKURA, C., K. NAKAMURA, K. KAKATSUKA, AND M. GOTO. 1979. Distemper infection in lesser pandas due to administration of a canine distemper live virus vaccine. *Japanese J. Vet. Sci.*, 41:561-566.
- JACKSON, R. 1978. Wildlife in Namlung Valley. *Nature Ann.*, 2: 159-161.
- KELLER, R. 1977. Beitrag zur ethologie des kleinen Pandas (*Ailurus fulgens*, Cuvier, 1825). Unpubl. Ph.D. dissert., Univ. Zurich, Switzerland, 122 pp.
- . 1980. The social behavior of captive lesser pandas (*Ailurus fulgens*) with some management suggestions. Pp. 39-56, in *The red or lesser panda studbook* (A. R. Glatston, ed.). The Royal Rotterdam Zoological and Botanical Gardens, Rotterdam, The Netherlands, 1:1-88.
- . 1982. Das markierungsverhalten des kleinen Pandas (*Ailurus fulgens*, Cuvier, 1825). *Zool. Garten*, 52:369-392.
- KLEIMAN, D. G. 1983. Ethology and reproduction of captive giant pandas (*Ailuropoda melanoleuca*). *Z. Tierpsychol.*, 62:1-46.
- KOWALSKA, Z. 1982. The lesser panda (*Ailurus fulgens*) at Lodz Zoological Gardens. Pp. 25-28, in *The red or lesser panda studbook* (A. R. Glatston, ed.). The Royal Rotterdam Zoological and Botanical Gardens, Rotterdam, The Netherlands, 2: 1-83.
- KURTÉN, B., AND E. ANDERSON. 1980. Pleistocene mammals of North America. Columbia University Press, New York, 443 pp.
- LANKESTER, E. R. 1901. On the affinities of *Aeluropus melanoleucus*, A. Milne-Edwards. *Trans. Linnean Soc. London*, 8: 163-171.
- MANANDHAR, M. S. 1978. Origin of the Himalaya. *Nature Ann.*, 1:1-4.
- MANI, M. 1968. Ecology and biogeography of high altitude insects. W. Junk, The Hague, 527 pp.
- MARCUS, H. 1937. Lungen. *Handb. Vergleich. Anat. Wirbeltiere*, 3:909-988.
- MCGREW, P. O. 1938. Dental morphology of the Procyonidae with a description of *Cynarctoides*, gen. nov. *Field Mus. Nat. Hist., Geol. Ser.*, 6:323-339.
- MIEROW, D., AND T. B. SHRESTHA. 1978. Himalayan flowers and trees. Sahayogi Prakashan Co., Kathmandu, Nepal, 210 pp.
- MILNE-EDWARDS, A. 1874. Recherches pour servir à l'histoire naturelle des mammifères comprenant des considérations sur la classification de ces animaux. G. Masson, Paris, 394 pp.
- MISHRA, H. 1976. Wild animals of Nepal. Ratna Pustak Bhandar, Kathmandu, Nepal, 102 pp.
- MIVART, ST. GEORGE. 1882. On the classification and distribution of the Aeluroidea. *Proc. Zool. Soc. London*, 1882:135-208.
- MONTALI, R. J., M. ROBERTS, R. A. FREEMAN, AND M. BUSH. 1984. Pathology survey of the red panda (*Ailurus fulgens*). Pp. 128-140, in *One medicine* (O. Ryder and M. Byrd, eds.). Springer-Verlag, Berlin, 373 pp.
- MOTTERSHEAD, G. S. 1958. Interesting experiments at the Chester Zoo. *Zool. Garten*, 24:70-73.
- . 1963. The lesser panda at the Chester Zoological Gardens. *Zool. Garten*, 27:300-302.
- MUNRO, G. 1969. Breeding the lesser panda in Bremen Zoo, Germany. *Internat. Zoo News*, 89:281-283.
- NUMATA, M. 1979. The relationship of the limiting factors to the distribution and growth of bamboo. Pp. 258-275, in *Ecology of grasslands and bambuolands in the World* (M. Numata, ed.). Jena, Veb Gustav Fischer Verlag, 352 pp.
- PARIHAR, N. S., AND I. B. CHAKRAVARTY. 1980. Canine distemper-like disease in a lesser panda (*Ailurus fulgens*). *Indian Vet. J.*, 57:198-199.
- PEI, W. 1974. [A brief evolutionary history of the giant panda.] *Acta Zool. Sinica*, 20:188-190 (Original in Chinese; translated by Rose W. Chu).
- PEN, M. 1962. Animals of western Szechuan. *Nature*, 196:14-16.
- PETERS, G. 1982. A note on the vocal behavior of the giant panda, *Ailuropoda melanoleuca* (David, 1869). *Z. Säugetierk.*, 47:236-246.
- PILGRIM, G. E. 1932. The fossil Carnivora of India. *Paleontol. Indica* (new ser.), 18:1-232.
- POCOCK, R. I. 1921. The external characters and classification of the Procyonidae. *Proc. Zool. Soc. London*, 1921:389-422.
- . 1941. The fauna of British India. Mammalia Volume II, Carnivora, suborders Aeluroidea (part) and Arctoidea. Taylor and Francis, Ltd., London, 503 pp.
- POUSARGUES, E. 1896. Sur la collection de mammifères rapportés du Yun-nan [sic] par le Prince Henri d'Orléans. *Bull. Mus. d'Hist. Nat., Paris*, 2:179-182.
- RADINSKY, L. B. 1981. Evolution and skull shape in carnivores. 2. Additional modern carnivores. *Biol. J. Linnean Soc.*, 16: 337-355.
- RAU, M. 1974. Vegetation and phytogeography of the Himalaya. Pp. 247-280, in *Ecology and biogeography in India* (M. Mani, ed.). W. Junk, The Hague, 390 pp.
- ROBERTS, M. S. 1975. Growth and development of mother reared red pandas. *Internat. Zoo Yearb.*, 15:57-63.
- . 1980. Breeding the red panda (*Ailurus fulgens*) at the National Zoological Park. *Zool. Garten*, 50:253-263.
- . 1981. The reproductive biology of the red panda, *Ailurus fulgens*, in captivity. Unpubl. M.S. thesis, Univ. Maryland, 202 pp.
- . 1982a. The fire fox. *Anim. Kingdom*, 85:20-27.
- . 1982b. Demographic trends in a captive population of red pandas (*Ailurus fulgens*). *Zoo Biol.*, 1:119-126.
- . 1982c. On the subspecies of the red panda, *Ailurus fulgens*. Pp. 13-24, in *The red or lesser panda studbook* (A. R. Glatston, ed.). The Royal Rotterdam Zoological and Botanical Gardens, Rotterdam, The Netherlands, 2:1-83.
- ROBERTS, M. S., AND L. COLLINS. 1978. Arboreal folivores in captivity—maintainance of a delicate minority. Pp. 5-12, in *The ecology of arboreal folivores* (G. G. Montgomery, ed.). The Symposia of the National Zoological Park, Smithsonian Institution Press, 574 pp.
- ROBERTS, M. S., AND D. S. KESSLER. 1979. Reproduction in red pandas, *Ailurus fulgens* (Carnivora:Ailuropodidae). *J. Zool.*, 188:235-249.
- ROMER, A. S., AND A. H. SUTTON. 1927. A new arctoid carnivore from the Lower Miocene. *Amer. J. Sci., ser. 5*, 14:459-464.
- ROOSEVELT, T., AND K. ROOSEVELT. 1926. East of the sun and west of the moon. Charles Scribner's Sons, New York, 371 pp.
- SARICH, V. M. 1976. Transferrin. *Trans. Zool. Soc. London*, 33: 165-171.
- SCAPINO, R. 1981. Morphological investigation into function of the jaw symphysis in carnivorans. *J. Morphol.*, 167:339-375.
- SCHALLER, G. B. 1977. Mountain monarchs. Univ. Chicago Press, Chicago, 325 pp.
- SCHLOSSER, M. 1899. *Parailurus anglicus* und *Ursus böckhi* aus den Ligniten von Baróth-Kopecz. *Mitteil. Jah. Königl. Ungar. Geol. Anst.*, 13:1-31.
- SEIDENSTICKER, J. J., J. F. EISENBERG, AND R. SIMONS. 1984. The Tangjiang, Wanglang and Fengtongzuai panda reserves and biological conservation in the People's Republic of China. *Biol. Conserv.*, 28:217-251.
- SHELDON, W. G. 1937. Notes on the giant panda. *J. Mamm.*, 18:13-19.
- SIMPSON, B. 1869. Note on *Ailurus fulgens*. *Proc. Zool. Soc. London*, 1869:507.
- SIMPSON, G. G. 1945. The principles of classification and a classification of mammals. *Bull. Amer. Mus. Nat. Hist.*, 85:1-350.
- SOKOLOWSKY, A. 1918. Zur biologie und stammesgeschichte des Katzenbären (*Ailurus fulgens*, F. Cuv.). *Zool. Anzeiger*, 50: 238-244.
- SONNTAG, C. F. 1923. The comparative anatomy of the tongues of the Mammalia—VIII. Carnivora. *Proc. Zool. Soc. London*, 1923:129-153.
- SOWERBY, A. DE C. 1932. The pandas or cat-bears. China J., 17:296-299.
- STAINTON, J. 1972. Forests of Nepal. John Murray, London, 357 pp.

- STOTT, K. 1940. Bamboo eaters San Diego Zoonooz, 12:5.
- TEDFORD, R. H., AND E. P. GUSTAVSON. 1977. The first American record of the extinct panda, *Parailurus*. Nature, 265:621-623.
- THOMAS, O. 1902. On the pandas of Sze-chuen [sic]. Ann. Mag. Nat. Hist., ser. 7, 10:251-252.
- . 1922. On mammals from the Yunnan highlands collected by Mr. George Forrest and presented to the British Museum by Col. Stephenson R. Clark, D.S.O. Ann. Mag. Nat. Hist., ser. 9, 10:391-406.
- TODD, N. B., AND S. R. PRESSMAN. 1968. The karyotype of the lesser panda (*Ailurus fulgens*) and general remarks on the phylogeny and affinities of the pandas. Carnivore Genet. Newsl., 5:105-108.
- TROLL, C. 1969. Die klimatische und vegetationsgeographische Gleiderung des Himalaya systems. Khumbu Himal, 1:353-388.
- TROUESSART, E. L. 1904. Catalogue mammalium tam viventium quam fossilium. R. Friedlander und Sohn, Berlin. Suppl., Parts 1 and 2:1-546. (Not seen)
- VAURIE, C. 1972. Tibet and its birds. Witherby, London, 407 pp.
- WALL, F. 1908. Birth of Himalayan cat-bears (*Aelurus* (sic) *fulgens*) in captivity. J. Bombay Nat. Hist. Soc., 18:903-904.
- WORTMAN, J. L., AND W. D. MATTHEW. 1899. The ancestry of certain members of the Canidae, Viverridae and Procyonidae. Bull. Amer. Mus. Nat. Hist., 12:109-138.
- WATSON, J. K., AND V. L. BARFIELD. 1982. Supplemental feeding of infant red pandas at the Knoxville Zoological Park. Pp. 29-35, in The red or lesser panda studbook (A. R. Glatston, ed.). The Royal Rotterdam Zoological and Botanical Gardens, Rotterdam, The Netherlands, 2:1-83.
- WURSTER, D. H. 1969. Cytogenetic and phylogenetic studies in Carnivora. Pp. 310-329, in Comparative mammalian cytogenetics (K. Benirschke, ed.). Springer-Verlag, New York, 473 pp.
- ZUCKERMAN, S. 1953. The breeding seasons of mammals in captivity. Proc. Zool. Soc. London, 122:827-950.
- Editors of this account were B. J. VERTS and SYDNEY ANDERSON. Managing editor was TIMOTHY E. LAWLOR.
- M. S. ROBERTS AND J. L. GITTLEMAN, DEPARTMENT OF ZOOLOGICAL RESEARCH, NATIONAL ZOOLOGICAL PARK, WASHINGTON, D.C. 20008.