What is a Snow Leopard? Taxonomy, Morphology, and Phylogeny

Andrew C. Kitchener*,**, Carlos A. Driscoll†, Nobuyuki Yamaguchi‡

*Department of Natural Sciences, National Museums Scotland, Edinburgh, UK
**Institute of Geography, University of Edinburgh, Edinburgh, UK
†WWF Chair in Conservation Genetics, Faculty of Wildlife Sciences, Wildlife Institute of India, Dehradun, Uttarakhand, India
‡Department of Biological and Environmental Sciences, College of Arts and Sciences, Qatar University, Doha, Qatar

INTRODUCTION

The snow leopard is the smallest of the so-called big cats of the genus *Panthera* with a head and body length of 1–1.3 m, tail length 0.8–1.1 m, and a weight of 20–50 kg. The snow leopard is adapted to montane habitats in Central Asia, including principally the Altai, Tian Shan, Kun Lun, Pamir, Hindu Kush, Karakorum, and Himalayan mountain ranges, where it preys on ungulates, particularly blue sheep (*Pseudois* spp.), goats and ibex (*Capra* spp.), marmots (*Marmota* spp.), and lagomorphs. In order to survive in this often hostile environment, the snow leopard has evolved a suite of adaptations for combating low temperatures and hunting on steep heterogeneous slopes at high altitude. These adaptations have resulted in the snow leopard being treated as taxonomically and phylogenetically distinct from other big cats (*Panthera* spp.) in the past, but recent molecular data have confirmed its inclusion within *Panthera* as a sister species to the tiger (*P. tigris*). In this chapter we explore the morphological characteristics of the snow leopard and its adaptations in relation to its montane habitats, and we also explain its taxonomic and phylogenetic history to provide a clearer understanding of its position within the Felidae.

TAXONOMIC HISTORY AND GEOGRAPHICAL VARIATION

The snow leopard was first described by Buffon (1761) as l'Once. The snow leopard was initially described as either a felid related to the lynx or a small panther, with long hairs and long tail, occurring from North Africa through Arabia to southern Asia (Buffon, 1761). Clearly there was considerable confusion with leopards and lynxes. Schreber (1775) copied Buffon's figure of l'Once, but gave it a scientific name, *Felis uncia*. The type locality was subsequently fixed by Pocock (1930) as the Altai Mountains, although Ognev (1962) stated that it was the southern slope of the Kopet Dagh Mountains. However, this mountain range is outside the geographical distribution of the snow leopard, so that the Altai Mountains are regarded as the type locality.

The snow leopard was at first placed in *Felis* with all other cats, but Pocock (1916b) followed Gray (1854) and placed it in the genus *Uncia*, which Gray had created for *Felis irbis*, a junior synonym of *F. uncia*. However, more recently based on phylogenetic data, the snow leopard has been placed in the genus *Panthera* (see below). Few other scientific names have been proposed for the snow leopard; Ehrenberg (1830) described *F. irbis* from the Altai Mountains, but this is synonymous with *P. uncia*, while Horsfield (1855) described *F. uncioides* from Nepal, which was recognized as a subspecies, *F. uncia uncioides* by Stroganov (1962) on the basis of apparent differences in pelage, including lighter coloration and a reduction of spots compared with snow leopards from Central Asia. Hemmer (1972) found that these differences were inconsistent and considered that the snow leopard is monotypic. However, there have been no detailed molecular or craniometric analyses to investigate geographical variation.

More recently Zukowsky (1950) described *Uncia uncia schneideri* from Sikkim based on an aberrant individual, while Medvedev (2000)

described *Panthera baikalensis-romanii* from the spurs of the Malkhan range in the Petrovsk-Zabaikal region, Chita Region of the River Ungo, which is said to be darker and browner and lacking rosettes, except in the lumbar region, compared with Central Asian snow leopards. However, Wozencraft (2005) included it within the synonymy of *P. uncia* without comment.

Fox (1994) highlighted the gap in distribution between the main southern "Tibetan" (i.e., Himalayan) population and the northern population in Russia and Mongolia. He suggested that these two populations may differ from each other. However, snow leopards are able to travel across more than 50 km of open steppes, not an optimal habitat for them, between isolated massifs, which suggests that fragmented populations, seemingly separated by distance and unsuitable habitat, may not be totally disconnected (McCarthy and Chapron, 2003). Further research is clearly required for understanding the intraspecific phylogeny and biogeography of snow leopards.

FOSSIL RECORD

Few fossil snow leopard remains have been found and even fewer have been dated to any degree of accuracy. Fossil remains were reported by Brandt (1871) and Tscherski (1892) from Upper Pleistocene in caves in the Altai. Other fragmentary fossils from locality 3, Choukoutien, China, have been variously identified as leopard, *Panthera pardus* or *P. uncia* (Hemmer, 1972). There is a mandibular ramus from the Siwaliks in the Natural History Museum London (Register no. 16537a), which appears to be from a snow leopard (Dennell et al., 2005). Other putative snow leopard fossils, from locality 1 at Choukoutien, China; Stranská Skála, Russia; and Woldrich, Austria, are misidentifications (Hemmer, 1972).

Dennell et al. (2005) have described a *Panthera* cf. *uncia* dated to 1.2–1.4 Mya from locality 73 in the Pabbi Hills, Pakistan (Upper Siwaliks).

Deng et al. (2011) mention an almost complete skull of an apparently ancestral snow leopard, *Panthera* sp., from the Zanda fauna of Tibet. This skull is dated to ca. 4.4 Mya (but could be as much as 5.95 Mya) and is the oldest known snow-leopard-like fossil, but it is about 10% smaller than today's animals. This specimen has recently been described as a new species, *Panthera blytheae* (Tseng et al., 2014). Although sharing characters with *P. uncia*, such as canines with an almost circular cross-section, a weakly inclined mandibular symphysis, a smooth transition between the mandibular rami and symphysis, the presence of a frontonasal depression, a narrow distance between the anterior edge of the bullae and the glenoid ridge, a sharp-turning ventral premaxilla–maxilla border at the canines, and straight and symmetrical P4 cusp alignment, *P. blytheae* can be distinguished from it and other *Panthera* by uniquely having a small labial cusp on the posterior cingulum of P3 and converging ridges on the labial surface of P4. Phylogenetic analyses of skull characters place *P. blytheae* as a sister species to *P. uncia* in the same clade as the tiger, *P. tigris* (Tseng et al., 2014), although with the information currently available, we cannot reject the possibility that *P. blytheae* is an earlier species of the genus *Panthera* without a close phylogenetic relationship to *P. uncia* in particular.

PHYLOGENY

In the most comprehensive genetic phylogeny to date, Davis et al. (2010) inferred the relationships among *Panthera*, including clouded leopard (*Neofelis nebulosa*), snow leopard, tiger, jaguar (*P. onca*), leopard (*P. pardus*), and lion (*P. leo*), using 39 Y chromosome segments, 3 autosomal genes, and 4 mitochondrial genes in a supermatrix phylogenetic analysis (Fig. 1.1). An independent inference, using the major urinary protein, transthyretin, recapitulated an identical topology. Transthyretin is putatively involved in male scent marking and is speculated to be a speciation protein.
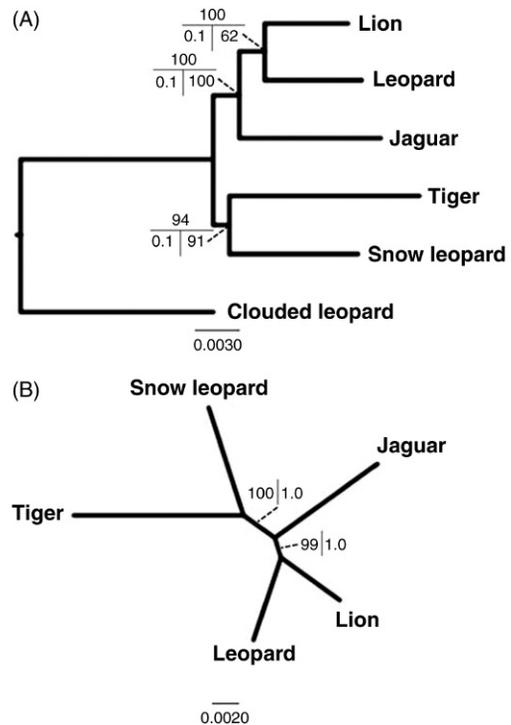

FIGURE 1.1 **Maximum likelihood (ML) tree based on analysis of the complete supermatrix.** (A) Rooted with clouded leopard as outgroup. 1000 ML bootstrap replicate percentages depicted on the top, Bayesian posterior probabilities (BPP) on the bottom left, and BEST posterior probabilities on the bottom right. (B) Unrooted topology with ML bootstrap percentages on the left and BPP on the right (Davis et al., 2010; reproduced with permission).

Molecular dating, using a Bayesian relaxed clock approach, indicates that the snow leopard and the tiger diverged from each other 2.70–3.70 Mya, which is prior to the divergence of the jaguar (2.56–3.66 Mya) from the lion/leopard ancestor, and of that ancestor into those two species (1.95–3.10 Mya). Thus, in this analysis, the snow leopard is a sister species to the tiger, however distantly related, with the caveat that the tiger is the closest relative among extant taxa used in this analysis (i.e., excluding *P. blytheae*, *P. palaeosinensis*; see Christiansen, 2007). Based on the assumption that *P. blytheae* and *P. uncia* are sister taxa, Tseng et al. (2014) suggest that the

divergence between the snow leopard and tiger lineages took place 4.86–5.13 Mya, making this the oldest divergence date estimated so far.

MORPHOLOGICAL ADAPTATIONS

The snow leopard has a number of morphological adaptations for living and hunting at high elevations in montane habitats. These are reviewed next.

Pelage

The snow leopard has the longest and densest pelage of any *Panthera*, with 4000 hairs per square centimeter, and a ratio of 8 underfur hairs to every guard hair (Heptner and Sludskii, 1992). The dense underfur is long, 43 mm cf. guard hairs 50 mm long. Hemmer (1972) compared summer and winter fur lengths (Table 1.1). The long guard hairs and thick underfur are effective at trapping a layer of air close to the skin for insulation.

The coat pattern of the snow leopard (rosettes) differs from that of the sister taxon, the tiger (stripe), in comparison to the other closely related taxa within the genus *Panthera* (lion – usually juveniles only – jaguar and leopard), all of which have rosettes. This may indicate that the basal primitive coat pattern of the family Felidae is flecks (i.e., dots), from which nearly all other patterns have developed within a relatively short period without involving any nonflecked patterns in between (Allen et al., 2011;

TABLE 1.1   Fur Lengths (Millimeters) in Summer and Winter on Different Parts of the Body of Snow Leopards

Body parts	Summer	Winter
Flanks	25	50
Tail	50	60
Belly	50	120
Back	–	30–55

From Hemmer, H., 1972. Uncia uncia. Mammal. Species 20, 1–5.

Werdelin and Olsson, 1997). The dorsal pelage ranges from pale gray to creamy smoke gray, often tinged with brown or even reddish brown, and is marked with a pattern of solid brownish black spots on the head, neck, and lower limbs, while large rosettes or rings (50–90 mm diameter), often with a few small spots inside, are found on the flanks and tail, but the density of rosettes is lower than in the pelages of leopards and jaguars (Hemmer, 1972). A row of elongated spots and two lateral rows of elongated rings run along the midline of the back to the base of the tail (Hemmer, 1972). The underparts are whitish from the chin to the anus. The basic ground color, coupled with the disruptive effect of the markings, helps match snow leopards to their rocky environment and break up their outline for effective stalking and hunting.

Skull

The snow leopard's skull is typical for cats, with short jaws for a powerful killing bite and a large cranium for the attachment of large temporalis muscles. However, in comparison to other *Panthera* species, the skull of the snow leopard is easily distinguishable (Fig. 1.2) and it is also the smallest; the greatest length of skulls for males is 174.0–196.1 mm in males (*n* = 9) and 175.0–178.8 mm in females (*n* = 6) (Heptner and Sludskii, 1992; NY, unpublished data). The skull is broader, shorter, and more vaulted than in other *Panthera*, and particularly elevated between postorbital processes (Haltenorth, 1937; Pocock, 1916b) because of the inflated nasal cavity and broad nasal bones. The large nasal cavity probably allows for efficient countercurrent warming of inhaled air and cooling of exhaled air when breathing. Schauenberg's index (Schauenberg, 1969; greatest length of skull/cranial volume) suggests that *P. uncia* has a relatively large brain along with the other four *Panthera* species, *Puma concolor, Acinonyx jubatus*, and *Lynx lynx* amongst 38 species of felids that were investigated (Schauenberg, 1971).
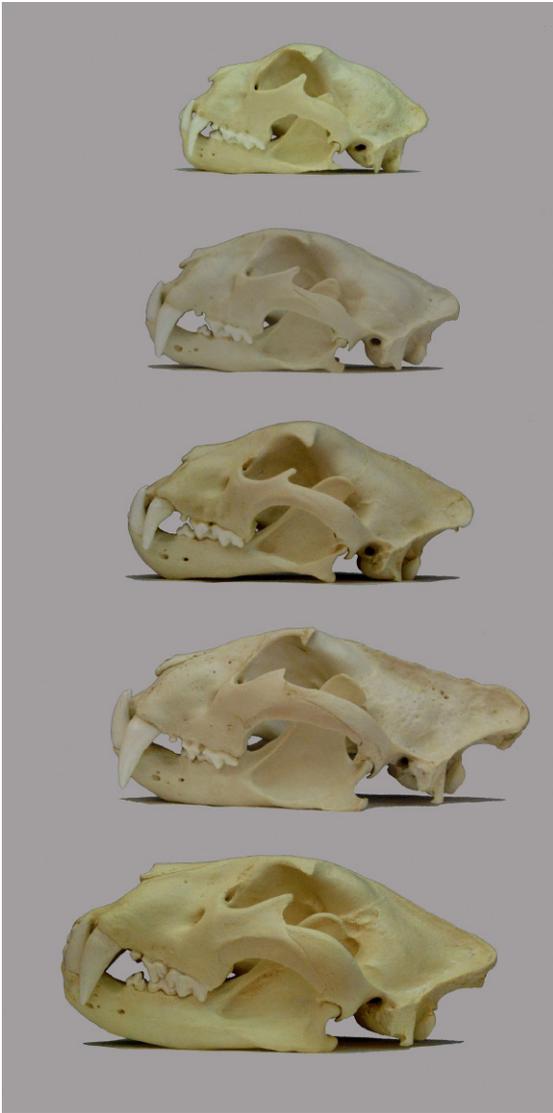
FIGURE 1.2 **A comparison of the skulls of *Panthera* cats, all lateral views, from the top: snow leopard, leopard, jaguar, tiger, lion.** Note the small, highly vaulted skull of the snow leopard (N. Yamaguchi).

In comparison with other cats, excluding the cheetah (*A. jubatus*), the snow leopard has a larger than expected nasal aperture relative to skull length and palate width (Torregrosa et al., 2010), which allows not only for a greater

volume and density of turbinals for warming and humidifying inhaled cold dry air, but also for extracting as much oxygen as possible by increasing the volume of each breath (Hemmer, 1972; Torregrosa et al., 2010). However, in relation to body mass, nasal aperture size is not greater than expected so that skull length and palate width are reduced, or skull width is increased to allow for a larger nasal cavity (Hemmer, 1972; Torregrosa et al., 2010).

Teeth and Jaws

The snow leopard has significantly more slender canines along the anteroposterior axis than the other *Panthera* species, except the leopard (Christiansen, 2007). However, its canines are less blade-like, and hence, they have a rounder cross-section along the entire crown, similar to the jaguar's, but the middle of the crown is less rounded compared to that of the lion. Christiansen (2007) estimated average bite forces at the canine tip for various large cats (Fig. 1.3; Table 1.2).

FIGURE 1.3 **Skull of a snow leopard showing dentition (National Museums Scotland).**

TABLE 1.2 Average Estimated Bite Forces at the Canine Tips of Large Cats

Species	*n*	Average bite force (*N*)
Snow leopard	9	363.0
Tiger	14	1234.3
Lion	10	1198.6
Jaguar	9	879.5
Leopard	8	558.6
Clouded leopard	12	344.2
Puma	10	499.6

From Christiansen, P., 2007. Canine morphology in the larger Felidae: implications for feeding ecology. Biol. J. Linn. Soc. 91, 573–592.

The average estimated bite force is the lowest for any *Panthera* and reflects the smaller body size of this species, but its bite force is much lower than the similar-sized puma (*P. concolor*) and equivalent to that of the smaller clouded leopard. The snow leopard's moderate canines are appropriate for killing small to medium-sized prey, although it is not apparent why they should have a more robust circular cross-section, given that a throat bite is typically used for killing larger prey, such as goats and blue sheep (Sunquist and Sunquist, 2002). Circular cross-sections suggest that forces may act from any direction; perhaps the difficulties of dealing with prey on steep heterogeneous slopes means that the direction of forces acting on the canine is more unpredictable than for the killing bites of other *Panthera*.

Compared with other *Panthera* cats, the snow leopard has a jaw gape of more than 70°, only slightly less than the clouded leopard's when measured from their skulls (Christiansen and Adolfsen, 2005), although it is possible that they can achieve an even wider gape than this in life. It is unclear why this is so, but perhaps the relatively large prey of snow leopards (i.e., montane ungulates), which have a wide throat or nape for killing bites, requires the snow leopard to have a wider gape for a throat bite.

Limbs and Vertebral Column

In terms of limb proportions, the snow leopard most resembles the cheetah, which is an open-country pursuit predator (Gonyea, 1976). The humeroradial index (94.6%) is only slightly less than that of the lion (98.3%) and the cheetah (103.3%), while the femorotibial index (105%) matches that of the cheetah, indicating longer lower limbs for a longer stride and potentially higher running speeds. The intermembral index is only 84.7% and falls within values for other large cats. The snow leopard's hunting behavior has been recorded on film in recent years and indicates that from an ambush it can display rapid acceleration and pursuit of bovid prey, with long leaps and sharp turns. The relatively longer tibiae would allow for more effective leaping, which is also supported by the relatively long thoracic (42.4% presacral vertebral length) and lumbar (35.6%) segments of the vertebral column, which ranked second among those of all large felids, thus allowing for more flexibility in leaping and turning.

Rieger (1984) mentioned a muscle, the musculus endopectoralis (= pectoralis major), which runs from the posterior sternum to the distal humerus, and apparently acts as a "spring" when a jumping mammal lands. Among felids the pectoralis major has the highest relative weight, emphasizing its importance in absorbing energy when landing after leaping. Snow leopards have apparently been recorded leaping as far as 15 m across a gorge (Ognev, 1962).

Tail

The snow leopard also has a long tail (75–90% of head-and-body length; Hemmer, 1972; mean 83% in 13 males and mean 82.2% in 15 females, ACK, unpublished data), which acts as a balancing organ (Rieger, 1984), when leaping between rocks and ascending or descending steep slopes, especially while moving rapidly in pursuit of prey. The tail is also used as a muffler to insulate

paws and head from the cold at high altitude when resting (Rieger, 1984).

Laryngeal Anatomy

The genus *Panthera*, including the snow leopard, is characterized by the epihyal bone of the hyoid complex being replaced by an elastic ligament that allows the larynx to move away from the pharynx and, hence, permits roaring and other loud vocalizations. This anatomical feature is usually cited as being of taxonomic significance (Pocock, 1916a) and explains why *Panthera* cats roar and other cats cannot. Peters and Hast (1994) showed that most *Panthera* cats have large vocal folds with large fibroelastic pads, which, they hypothesized, vibrate to produce low-frequency sounds that are amplified by the long larynx, and bell-shaped pharynx and mouth, resulting in loud low-frequency vocalizations, including roars. The elastic epihyal allows the larynx to lower the formant frequencies of vocalizations and does not affect a cat's ability to purr, as thought previously (Weissengruber et al., 2002). However, snow leopards have the small pointed vocal folds of smaller cats and are unable to roar, although they produce long moaning calls to partners, grunts and moans, and they can apparently purr when inhaling and exhaling like smaller cats (Hemmer, 1972).

Physiological Adaptations

Living at high elevations, it would be expected that snow leopards should show physiological adaptations for breathing air with low levels of oxygen. However, surprisingly little information is available. Marma and Yunchis (1968) found that like other montane mammals, they have small red blood cells (RBCs) (mean 5.5 μm diameter, range 4.73–6.15 μm; cf. tiger 7.3 ± 0.45 μm; Shrivastav and Singh, 2012), a high concentration of hemoglobin (16.4 g%), high hematocrit value (47%; relative volume of RBCs), and a large number of RBCs (14.1–16.8 million/mm^3).

A high concentration of small RBCs with a high surface-area-to-volume ratio probably helps the snow leopard to extract sufficient oxygen while breathing at high elevations. Recently it has been shown in studies of the human genome that two loci, EGLN1 (Egl nine homolog 1) and EPAS1 (endothelial PAS domain-containing protein 1) are involved in mediating physiological adaptation to high altitude (Cho et al., 2013). A recent comparison of whole genomes between members of the *Panthera* showed that the snow leopard has a specific genetic determinant in EGLN1 (Met39 (nonpolar)→Lys39; positively charged), which is probably also associated with physiological adaptation to high altitude (Cho et al., 2013). EGLN1 is typically highly conserved in mammals, so this change in the snow leopard genome may alter protein function. Also, two changes specific to snow leopards have been recorded in EPAS1 (Ile663 and Arg794); the latter was predicted to bring about a functional change of this protein (Cho et al., 2013). Further studies are required to determine how these changes to the snow leopard's genome provide adaptation to high altitude. However, recently Janecka et al. (2015) have investigated the ability of snow leopard hemoglobin to bind oxygen. Typically cats have hemoglobin with a low oxygen-binding affinity and reduced sensitivity to the allosteric cofactor 2,3–diphosphoglycerate (DPG), and the snow leopard is surprisingly no exception. Further studies are required to determine compensatory mechanisms in the oxygen transport pathway that allow snow leopards to show extreme hypoxia intolerance at altitudes of up to 6,000 meters or more.

CONCLUSIONS

Owing to its rarity in the wild and in museum collections, the snow leopard's anatomy and physiology have not been well studied in comparison with those of most other *Panthera* cats. The current large captive population offers

good opportunities for studying these aspects from studies of living and dead animals. However, from what we do know, the snow leopard is adapted for leaping and turning to capture ungulate prey on steep mountain slopes, it is well insulated and camouflaged to survive in this cold environment and it has anatomical and physiological adaptations that allow it to maximize oxygen extraction from the low levels at high elevations while conserving heat energy. We recognize the potential for further areas of fruitful research, including relative lung volume in relation to low oxygen levels, eye anatomy in relation to the snow leopard's diurnal behavior, and whether there is any significant geographical variation in morphology and genetics, which could affect the snow leopard's conservation.

References

Allen, W.L., Cuthill, I.C., Scott-Samuel, N.E., Baddeley, R., 2011. Why the leopard got its spots: relating pattern development to ecology in felids. Proc. Royal Soc. B 278, 1373–1380.

Brandt, F., 1871. Neue Untersuchungen über die in den altaischen Höhlen aufgefundenen Säugethierreste, ein Betrag zue quaternären Fauna des Russischen Reiches. Bull. Acad. Imp. Sci. St. Pétersb. 15, 147–205.

Buffon, G.-L., 1761. La panthére, l'once et le léopard. In: Buffon, G.-L., Comte de, L.C., Daubenton, L.J.M. (Eds.), Histoire Naturelle, Générale et Particuliére avec la Description du Cabinet du Roi, vol. 9, De l'Imprimière Royale, Paris, pp. 151–172, pl. 13.

Cho, Y.S., Hu, L., Hou, H., Lee, H., Xu, J., Kwon, S. et al., 2013. The tiger genome and comparative analysis with lion and snow leopard genomes. Nat. Commun. 4 (2433), 1–7.

Christiansen, P., 2007. Canine morphology in the larger Felidae: implications for feeding ecology. Biol. J. Linn. Soc. 91, 573–592.

Christiansen, P., Adolfsen, J.S., 2005. Bite forces, canine strength and skull allometry in carnivores (Mammalia, Carnivora). J. Zool. (London) 266, 133–151.

Davis, B.W., Li, G., Murphy, W.J., 2010. Supermatrix and species tree methods resolve phylogenetic relationships within the big cats, *Panthera* (Carnivora: Felidae). Mol. Phylogenet. Evol. 56 (1), 64–76.

Deng, T., Wang, X., Fortelius, M., Li, Q., Wang, Y., Tseng, Z.J., Takeuchi, G.T., Saylor, J.E., Säilä, L.K., Xie, G., 2011. Out of Tibet: Pliocene woolly rhino suggests high-plateau origin of Ice Age megaherbivores. Science 333 (6047), 1285–1288.

Dennell, R.W., Turner, A., Coard, R., Beech, M., Anwar, M., 2005. Two Upper Siwalik (Pinjor Stage) fossil accumulations from localities 73 and 362 in the Pabbi Hills, Pakistan. J. Palaeontol. Soc. (India) 50, 101–111.

Ehrenberg, M.C.G., 1830. Observations et données nouvelles sur le tigre du nord et la panthère du nord, recueillies dans le voyage de Sibérie fait par M.A. de Humboldt, en l'année 1829. Ann. Sci. Nat. 21, 387–412.

Fox, J.L., 1994. Snow leopard conservation in the wild – a comprehensive perspective on a low density and highly fragmented population. In: Fox, J.L., Jizeng, D. (Eds.), Proceedings of the Seventh International Snow Leopard Symposium. July 25–30, 1992, International Snow Leopard Trust, Seattle, Xining, Qinghai, China, pp. 3–15.

Gonyea, W.J., 1976. Adaptive differences in the body proportions of large felids. Acta Anat. 96, 81–96.

Gray, J.E., 1854. The ounces. Ann. Mag. Nat. Hist. Ser. 2 14, 394.

Haltenorth, T., 1937. Die Verwandtschaftliche Stellung der Großkatzen zueinander VII. Zeitschrift für Säugetierkunde 12, 7–240.

Hemmer, H., 1972. *Uncia uncia*. Mammal. Species 20, 1–5.

Heptner, V.G., Sludskii, A.A., 1992. Mammals of the Soviet Union. Part 2 Carnivora (hyaenas and cats), vol. II, E.J. Brill, Leiden, Netherlands.

Horsfield, T., 1855. Brief notices of several new or little-known species of Mammalia, lately discovered and collected in Nepal, by Brian Houghton Hodgson. Ann. Mag. Nat. Hist. Ser. 2 16, 101–114.

Janecka, J., Nielsen, S.S.E., Andersen, S.D., Hoffmann, F.G., Weber, R.E., Anderson, T., et al., 2015. Genetically based low oxygen affinities of felid hemoglobins: lack of biochemical adaptation to high-altitude hypoxia in the snow leopard. J. Exp. Biol. 218, 2402–2409.

Marma, B.B., Yunchis, V.V., 1968. Observation on the breeding, management and physiology of snow leopards, *Panthera u. uncia*, at Kaunas Zoo from 1962 to 1967. Int. Zoo Yearb. 8, 66–73.

McCarthy, T.M., Chapron, G. (Eds.), 2003. Snow Leopard Survival Strategy. International Snow Leopard Trust and Snow Leopard Network, Seattle.

Medvedev, D.G., 2000. Morfologicheskie otlichiya irbisa iz Yuzhnogo Zabaikalia. Vestnik Irkutskoi Gosudarstvennoi sel'skokhozyaistvennoi akademyi, vypusk 20, 20–30.

Ognev, S.I., 1962. Mammals of the USSR and adjacent countries, vol. III Carnivora (Fissipedia and Pinnipedia). Israel Program Scientific Translations, Jerusalem.

Peters, G., Hast, M.H., 1994. Hyoid structure, laryngeal anatomy, and vocalization in felids (Mammalia: Carnivora; Felidae). Zeitschrift für Säugetierkunde 59 (2), 87–104.

Pocock, R.I., 1916a. On the hyoidean apparatus of the lion (*F. leo*) and related species of Felidae. Ann. Mag. Nat. Hist. Ser. 8 18, 222–229.

Pocock, R.I., 1916b. On the tooth-change, cranial characters and classification of the snow-leopard or ounce (*Felis uncia*). Ann. Mag. Nat. Hist. Ser. 8 18, 306–316.

Pocock, R.I., 1930. The panthers and ounces of Asia. Part II. J. Bombay Nat. Hist. Soc. 34, 307–336, pls. VII–XIII.

Rieger, I., 1984. Tail functions in ounces, *Uncia uncia*. Blomqvist, L. (Ed.), International Pedigree Book of Snow Leopards, *Panthera uncia*, 4, Helsinki Zoo, Helsinki, pp. 85–97.

Schauenberg, P., 1969. L'identification du chat forestier d'Europe *Felis s. silvestris* Schreber 1777 par une méthode ostéométrique. Revue Suisse de Zoologie 76, 433–441.

Schauenberg, P., 1971. L'indice crânien des Félidés. Revue Suisse de Zoologie 78, 317–320.

Schreber J.C.D., 1775. Die Säugethiere in Abbildungen nach der Natur mit Beschreibungen, vol. 2(14), Wolfgang Walther, Erlangen.

Shrivastav, A.B., Singh, K.P., 2012. Tigers blood: Haematological and biochemical studies. In: Moschandreou, T.E. (Ed.). Blood Cell – An Overview of Studies in Hematology, pp. 229–242. INTECH Open Access Publisher. http://dx.doi.org/10.5772/50360.

Stroganov S.S.U., 1962. Zveri Sibiri: Khishchnye. Akademiya Nauk SSSR, Moscow, (In Russian).

Sunquist, M., Sunquist, F., 2002. Wild Cats of the World. Chicago University Press, Chicago.

Torregrosa, V., Petrucci, M., Pérez-Claros, J.A., Palmqvist, P., 2010. Nasal aperture area and body mass in felids: ecophysiological implications and paleobiological inferences. Geobios 43 (6), 653–661.

Tscherski, J.D., 1892. Wissenschaftliche Resultate der von der kaiserlichen Akademie der Wissenschaften zur Erforschung des Janalandes unde der Neusibirischen Inslen in den Jahren 1885 und 1886 ausgesandten Expedition. IV.: Beschreibung der Sammlung posttertiärer Säeugetiere. Mém. l'Acad. Imp. Sci. St. Pétersbourg, 7th ser. 40 (1), 1–511.

Tseng, Z.J., Wang, X., Slater, G.J., Takeuchi, G.T., Li, Q., Liu, J., Xie, G., 2014. Himalayan fossils of the oldest known pantherine establish ancient origin of big cats. Proc. Royal Soc. B 281 (1774), , 20132686.

Weissengruber, G.E., Gerhard Forstenpointner, G., Peters, G., Kübber-Heiss, A., Fitch, W.T., 2002. Hyoid apparatus and pharynx in the lion (*Panthera leo*), jaguar (*Panthera onca*), tiger (*Panthera tigris*), cheetah (*Acinonyx jubatus*) and domestic cat (*Felis silvestris* f. *catus*). J. Anat. 201, 195–209.

Werdelin, L., Olsson, L., 1997. How the leopard got its spots: a phylogenetic view of the evolution of felid coat patterns. Biol. J. Linn. Soc. 62, 383–400.

Wozencraft, W.C., 2005. Order Carnivora. In: Wilson, D.E., Reeder, D.M. (Eds.), Mammal Species of the World. A Taxonomic and Geographic Reference, vol. 1, third ed. Johns Hopkins University Press, Baltimore, MD, pp. 532–722.

Zukowsky, L., 1950. Grossäuger, die Hagenbeck entdeckte. Der Zoologischer Garten (N.F.) 17, 211–221.