PALEONTOLOGY

Insights on the evolution and adaptation toward high-altitude and cold environments in the snow leopard lineage

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How snow leopard gradually adapted to the extreme environments in Tibet remains unexplored due to the scanty fossil record in Tibet. Here, we recognize five valid outside-Tibet records of the snow leopard lineage. Our results suggest that the snow leopard dispersed out of the Tibetan Plateau multiple times during the Quaternary. The osteological anatomy of the modern snow leopard shows adaptation to the steep slope and, to a lesser extent, cold/high-altitude environment. Fossils and phylogeny suggest that the snow leopard experienced a gradual strengthening of such adaptation, especially since the Middle Pleistocene (~0.8 million years). Species distribution modeling suggests that the locations of the fossil sites are not within most suitable area, and we argue that local landscape features are more influential factors than temperature and altitude alone. Our study underscores the importance of integrating morphology, fossil records, and species distribution modeling, to comprehensively understand the evolution, ecology, and inform conservation strategies for endangered species.

INTRODUCTION

The snow leopard (*Panthera uncia*) is one of the iconic animals of the Tibetan Plateau and distributes also in the ranged mountainous regions of central Asia as the Mongolian Plateau (*1–6*). It has distinctive morphological features, e.g., long and dense pelage, long tail, short face, steep and wide forehead, enlarged anterior chamber (ectotympanic) of the auditory bulla, high and steep mandibular symphysis, and relatively large cheek teeth (*1, 7–10*), that clearly distinguish it from the other members of genus *Panthera*. Although historically classified in its own genus, *Uncia* (*1, 11, 12*), modern phylogenetic analyses based on genetic and genomic data have conclusively placed it within the *Panthera* genus, particularly as the sister species of the tiger (*Panthera tigris*) (*13–16*).

The snow leopard typically inhabits within high alpine regions, above 3000 m, or above the tree line (*17*) but may also occur at much lower elevations below 1000 m in some areas of Russia (*18*). The status of the snow leopard in the International Union for Conservation of Nature Red List is vulnerable, with ~4000 individuals (*17*). However, under global warming, its distribution is expected to be substantially affected, as moving northward (*19*) or upward to a higher altitude (*20*) based on species distribution modeling (SDM) methods on current known distribution.

While the distinctive characteristics of the snow leopard have long been acknowledged, the correlation between these traits and its adaptation to the Tibetan Plateau environment, as well as their evolutionary history, remains largely unexplored. This gap in understanding is primarily due to the scarcity of snow leopard fossils in the Tibetan Plateau and its surrounding regions. Nevertheless, several potential records from northern China and Europe (*8, 21–23*) provided insight into the evolution and adaptation of this species. However, these records have yet to be rigorously tested using phylogenetic or statistical approaches, leaving their validation and phylogenetic positions uncertain.

In this study, we provide in-depth analyses of potential snow leopard records (Fig. 1, A to D; see a review in the Supplementary Materials), especially the best-preserved skull from Manga Larga (Portugal) and a mandible from Longdan (China) with the implementation of phylogenetic and geometric morphometric analyses. We explored the ecological adaptation of the modern and fossil snow leopards, focusing on the function of their unique traits using anatomical study, finite element analysis, and morphometric approaches, and investigated how these traits evolved through the Quaternary. Then, we used species distribution models to predict the past distribution under the last glacial maximum (LGM) condition, which represents the potential largest distribution of the snow leopard, and this predicted distribution was compared with the fossil records to see whether the past adaptation of the snow leopard lineage is equivalent to that of the modern one. These analyses were then combined to infer the evolution and ecological adaptation/requirements of the snow leopard.

RESULTS AND DISCUSSION

Systematics

Order Carnivora Bowdich, 1821
    Family Felidae Batsch, 1788

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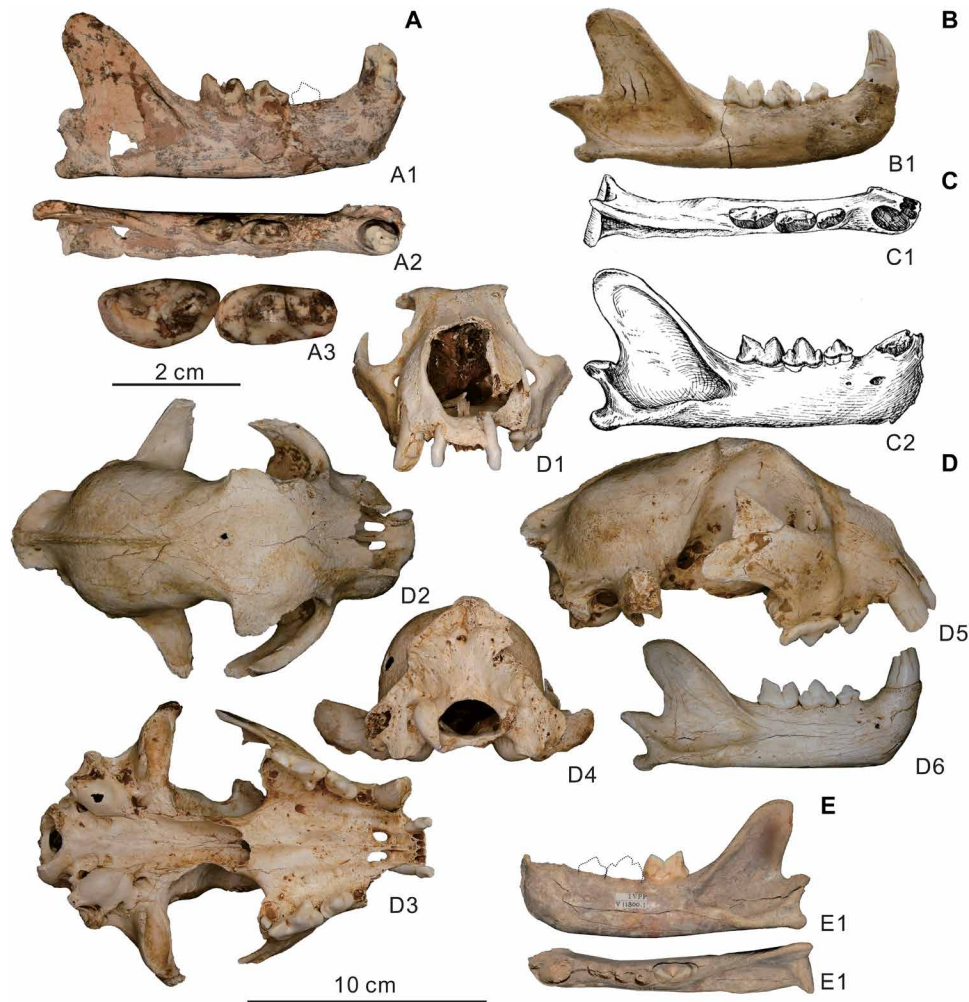
Fig. 1. Fossil snow leopards from Eurasia. (**A**) *Panthera* aff. *pyrenaica*, IVPP V31895, Longdan, Linxia Basin, northeastern Tibet, China. (**B**) *Panthera pyrenaica*, E14-EFNI-1001, Arago Cave, Southeastern France. (**C**) *Panthera* aff. *uncia*, Zhoukoudian Loc. 3, Beijing, China. (**D**) *Panthera uncia lusitana* subsp. nov., MG1355.0001-0002, Manga Larga, Portugal. (**E**) *Panthera uncia*, IVPP V11800.1, Niuyan Cave, Beijing, China.

Subfamily Felinae Batsch, 1788
Genus *Panthera* Oken, 1816
Panthera uncia (Schreber, 1775)
Panthera uncia lusitana subsp. nov.

Diagnosis—small-sized pantherine cat (extant snow leopard-sized). Cranium broad and high, with short rostrum. Forehead slightly concave (in lateral view) and wide; orbit large; bony choana not widened; bulla relatively flat, with enlarged ectotympanic. Deep corpus, with vertical symphysis and low coronoid process; ventral margin of masseteric fossa not laterally expanded. P4 with straight buccal border; m1 slender with antero-buccal corner. Cheek teeth enlarged relative to skull overall size (large ratio of m1 length/mandible length).

Differential diagnosis—differs from modern *P. uncia* by having slightly narrower frontal and less inflated auditory bulla, P4 with straight buccal border; differs from *P. pyrenaica* by having slightly smaller size, shorter c-p3 diastema, larger cheek teeth, lower coronoid process; differs from all other *Panthera* species by having smaller size, wider frontal, concave forehead in lateral view, more inflated auditory bulla, more enlarged ectotympanic chamber, shorter rostrum, lower coronoid process.

Etymology—referred to Lusitania, the ancient region of the western Iberian Peninsula which became a Roman province and corresponds to most of the present-day Portugal and Spanish provinces of Salamanca and Cáceres.

Holotype—MG1355.0001-9, mostly complete skull with broken zygomatic arches and missing both upper second premolars and a few associated postcranial bones.

Type locality and age—Manga Larga (39.51972°N, 8.83114°W), Porto de Mós Municipality, central Portugal, Late Pleistocene.

Description and comparisons—See the Supplementary Materials.
Panthera aff. *pyrenaica*

Diagnosis—small-sized pantherine cat (extant leopard-sized). Symphysis relatively vertical (relative to horizontal plane) in orientation; ventral margin of masseteric fossa not laterally expanded. m1 buccolingually robust.

Differential diagnosis—differs from *P. pyrenaica* by having less elevated symphysis, buccolingually wider m1; differs from modern *P. uncia* and *P. u. lusitana* by having less elevated symphysis, longer c-p3 diastema, higher coronoid process, smaller cheek teeth; differs from *P. palaeosinensis* by having smaller size, lower symphysis, less

ventrally extended angular process and non-expanded ventral border of the masseteric fossa; differs from all other *Panthera* species by having smaller size, non-expanded ventral border of the masseteric fossa.

Material—Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences, Beijing, China, V31895.

Locality and age—Longdan, Linxia Basin, China, Early Pleistocene, 2.5 to 2.2 Ma.

Description and comparison—See the Supplementary Materials.

Ecomorphological adaptation of fossil snow leopard

The peculiar cranial morphology of the modern snow leopard has been noticed by many previous works (*8*, *11*, *12*, *24*, *25*). In the present study, we mainly compared its cranial anatomy with other pantherine cats, especially the similar-sized leopard *Panthera pardus* to elucidate the function of these traits.

The overall cranium morphology of the snow leopard is characterized by the wide and high skull, with an expanded and domed forehead and frontal sinus (*24*). An enlarged frontal sinus (often posteriorly extended) is quite common in Carnivora, especially *Ailuropoda* and bone-cracking hyaenids, as well as other fossil groups (*26*–*31*) and is suggested to be related to resisting high stresses during biting on hard substances (*32*). This is unlikely to be the case for the snow leopard, whose frontal sinuses are not posteriorly expanded and the cheek teeth are not robust. The overall cranial morphology of the snow leopard is very similar to that of cheetah *Acinonyx jubatus*. A greatly laterally expanded frontal sinus was observed in both *P. uncia* and *A. jubatus* (*24*). Anatomical studies suggest that the frontal sinus is connected with nasal passages through small ostia and is normally in continual communication with the nasal air (*33*). An expanded frontal sinus in *P. uncia* and *A. jubatus* can serve as warming the cold air, or heat dissipation during running, and help in promoting the respiratory efficiency of the animals (*31*, *34*– *36*). *P. uncia* lives at high altitudes with low-oxygen concentration, and *A. jubatus* has a chasing hunting behavior with vigorous locomotion (*1*, *10*, *37*, *38*). Therefore, although the adaptations of *P. uncia* and *A. jubatus* are different, the enlarged frontal sinus can help in both cases in respiratory efficiency during hunting. We interpret this anatomical feature in the snow leopard, as an adaptation to high-altitude and cold environments. The enlarged cheek teeth are often correlated with slicing meat, and resisting forces of tendons and skin often seen in sabertoothed cats (*39*, *40*). In the Tibetan Plateau, food sources and competitors are relatively rare, and snow leopards stay near its kills for longer periods than do other large cats to consume its prey (*41*–*43*). In high-altitude and cold environments, the kills will soon freeze, and the large cheek teeth of the snow leopard are also helpful in chewing hard frozen meat.

Other craniodental and postcranial traits are, however, not directly adapted to cold environments themselves. The short rostrum brings (Fig. 1) a high mechanical advantage to the anterior part of the jaw. The high and steep symphysis suggests a strong resistance to stresses induced by the canine bite (*44*). Our finite element analyses on the mandibular profile also show averaged low Von Mises stress (reflected by the stress contour diagram) at the symphysis part in modern *P. uncia* given by the same bite force (Fig. 2). These findings suggest that the anterior portion of the jaw has better mechanical performance, enabling the snow leopard to withstand high bite forces in this region more effectively. The relatively short braincase and absence of a posteriorly extended lambdoidal crest imply that the

temporal muscle has a more vertical component and a small posterior component. Such muscle direction benefits a strong upward force during occlusion and a lower force to track the coronoid backward and resulted in low speed of occlusion. All these traits, as well as the rounded canine cross section (*1*, *45*), support a strong canine bite of the snow leopard compared with *P. pardus* (Fig. 2). The short rostrum and low speed of occlusion lead to a relatively slow bite. This is in accordance with the fact that *P. uncia* predates mainly on Caprini bovids (*3*, *46*–*48*), which have short metapodial bones. The short distal limbs in mammals are correlated with a low speed but higher strength (*49*, *50*). Another important cranial trait of the snow leopard is the large and more anteriorly oriented orbit. The orbit diameter/condylobasal length ratio of *P. uncia* reaches 0.278 (0.264 to 0.296, $n = 13$), much larger than that of other species of *Panthera* (mean 0.226, 0.189 to 0.254, $n = 48$), suggesting a larger eye, and R square of lineal model ($n = 90$) of orbit diameter/condylobasal ratio and condylobasal of *Panthera* is very low at 0.24, suggesting that there is no significant allometry. The angle between the long axis of the orbit and the sagittal plane (in dorsal view) is significantly larger than other species of *Panthera* and *Puma* but comparable to *A. jubatus* (Fig. 3A2). A large angle suggests that the orbit is oriented more anteriorly, therefore with a large overlap of eyesight range of both eyes. This, together with the short rostrum, leads to a better stereo vision of *P. uncia* compared with the other species of *Panthera*, which is needed in prey discovery and focusing on the open mountainous region, as Caprini bovids generally have protective coloration in rock cover. Similar adaptation with a short rostrum and a more anteriorly oriented orbit can be seen in many open environment felid species, e.g., *Otocolobus manul*, *Felis margarita*, or *Felis nigripes* (fig. S12). The enlarged ectotympanic chamber (Fig. 3A3) is also similar to that of *Acinonyx* but unlike that of other *Panthera* being adapted to hearing ability in the open environment (*51*). These cranial traits of the snow leopard are adapted to hunting Caprini bovids in the open mountainous region.

Our analyses of postcranial skeletal proportions suggest that the snow leopard has relatively long distal limbs, a cursorial adaptation in congruence with previous results (*52*). In the principal components analyses (PCAs) of 16 proportions (see the Supplementary Materials for details of these proportions), the morphospace of *P. uncia* is remote from those of other felid species. The PC1 is positively correlated with humerus distal condyle height, femur medial side distal condyle height, scapular length, and pelvis length and negatively correlated with tibia length. The species with positive scores have large girdle bones allowing the powerful muscle attachment with high mechanic advantage. The PC2 is mainly positively correlated with radius length and, to a lesser extent, tibia length, and species having positive scores have cursorial adaptations. The postcranial morphology of *P. uncia* is therefore built for speed not strength. The long distal limb bones, especially the tibia, as well as the long lumbar vertebral column and the long tail (*52*), support a strong jumping ability and are adapted to mountain life on steeped slopes. On the other hand, the distal condyle heights of the humerus and femur (table S3), which directly correlated with a cross-sectional area that sustains the stress of joint, are related to sustaining the force from body mass and locomotion. In this aspect, the relatively low condyle of the snow leopard reflects its relatively small body size within *Panthera*. Alternatively, low condyle height of humerus can be balanced to retain high flexibility of foreleg for hunting.
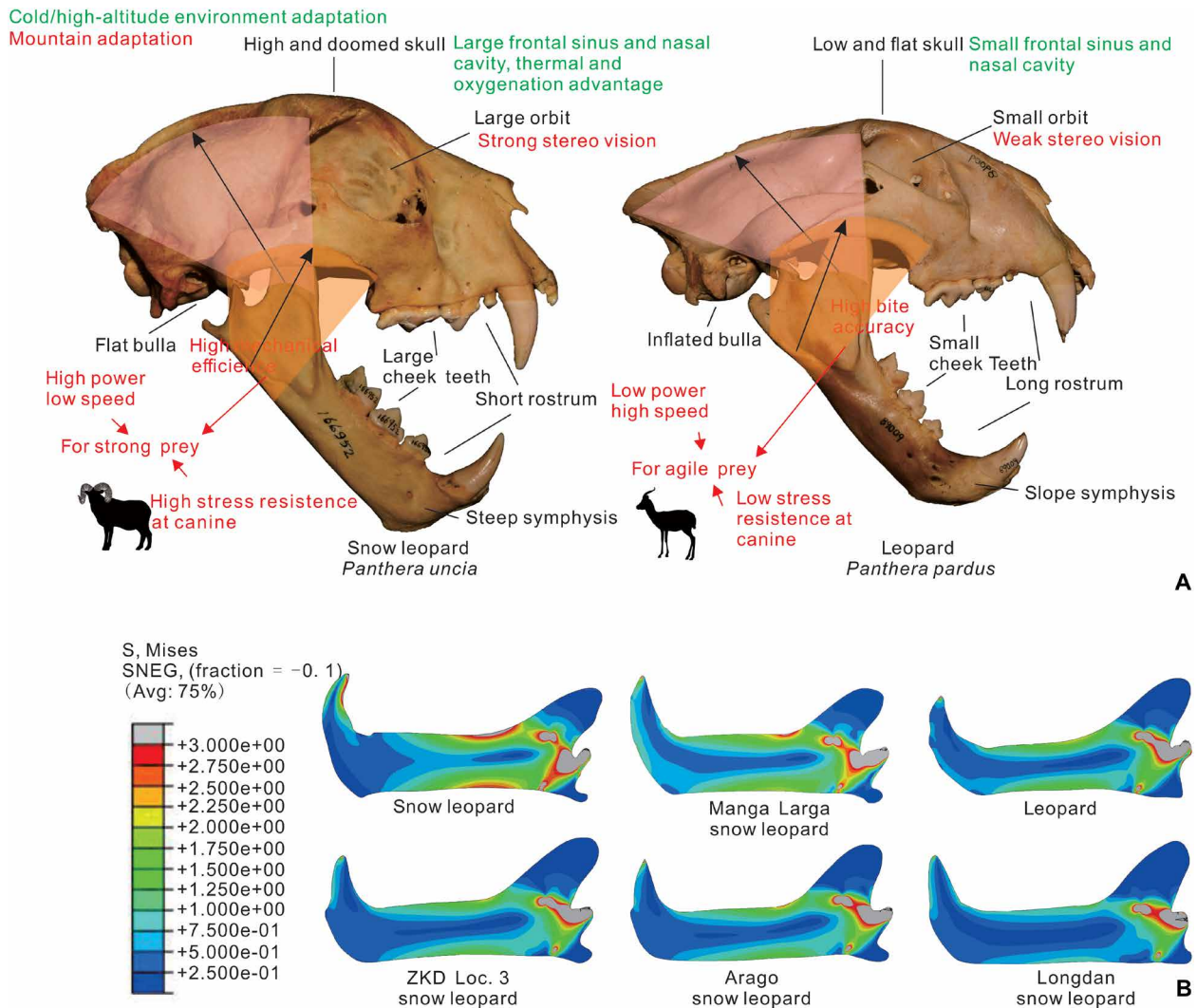
Fig. 2. Craniodental ecomorphology of the snow leopard and related taxa. (**A**) Cranial comparison of *P. uncia* AMNH M166952 and *P. pardus* AMNH M89009, highlighting functional traits related to high/cold adaptation (green) and (prey type related) mountain life (red). (**B**) Finite element analyses of mandibles of modern and fossil *P. uncia*, modern *P. pardus*, and several fossil snow leopards.

In summary, the overall craniodental and postcranial morphology of the modern snow leopard shows the combination of adaptation to hunt in steeped slopes in open mountainous regions and adaptation to high altitude. The adaptations to mountainous regions exhibited in cranial and skeletal morphology (cranium mechanic design, skeleton proportions, and enlarged ectotympanic) seems to be more prominent than those to a high-altitude, cold, and low-oxygen environment (enlarged frontal sinuses and enlarged cheek teeth), suggesting that the local environment is probably more important concerning on the locomotion and hunting behavior than the climate for snow leopards. On the other hand, the white coat, long hair, and some physiological traits in the snow leopard represented adaption to the cold environment (*10*).

Multiple out-of-Tibet dispersal and the rapid evolution of the snow leopard during the Middle and Late Pleistocene

As our results show, the unique craniodental and postcranial traits of the snow leopard are adapted to mountainous regions, prey type,

and climate. The fossil record could help to explore how these traits evolved during the Quaternary.

We identified and analyzed five potential records in Europe and northern China (including the specimen from Longdan, northern China) that putatively belonging to the snow leopard lineage (see the detailed morphological comparison in the Supplementary Materials). Unexpectedly, most of these records are located far away from the Tibetan Plateau. Four of these records are of relatively recent age [i.e., <0.6 million years (Ma)]. To better study their evolutionary position, we perform total evidence phylogenetic analyses of the Pantherini, including both modern and fossil species (the poorly preserved Plio-Pleistocene species are not included).

The total evidence phylogenetic analyses using combined morphological and genetic data were performed to investigate the position of these putative fossil snow leopards. Our phylogenetic tree (Fig. 4) supports the four potential records as a basal snow leopard and supports the oldest record *P.* aff. *pyrenaica* from Longdan as a very basal snow leopard (but with relatively low posterior probability
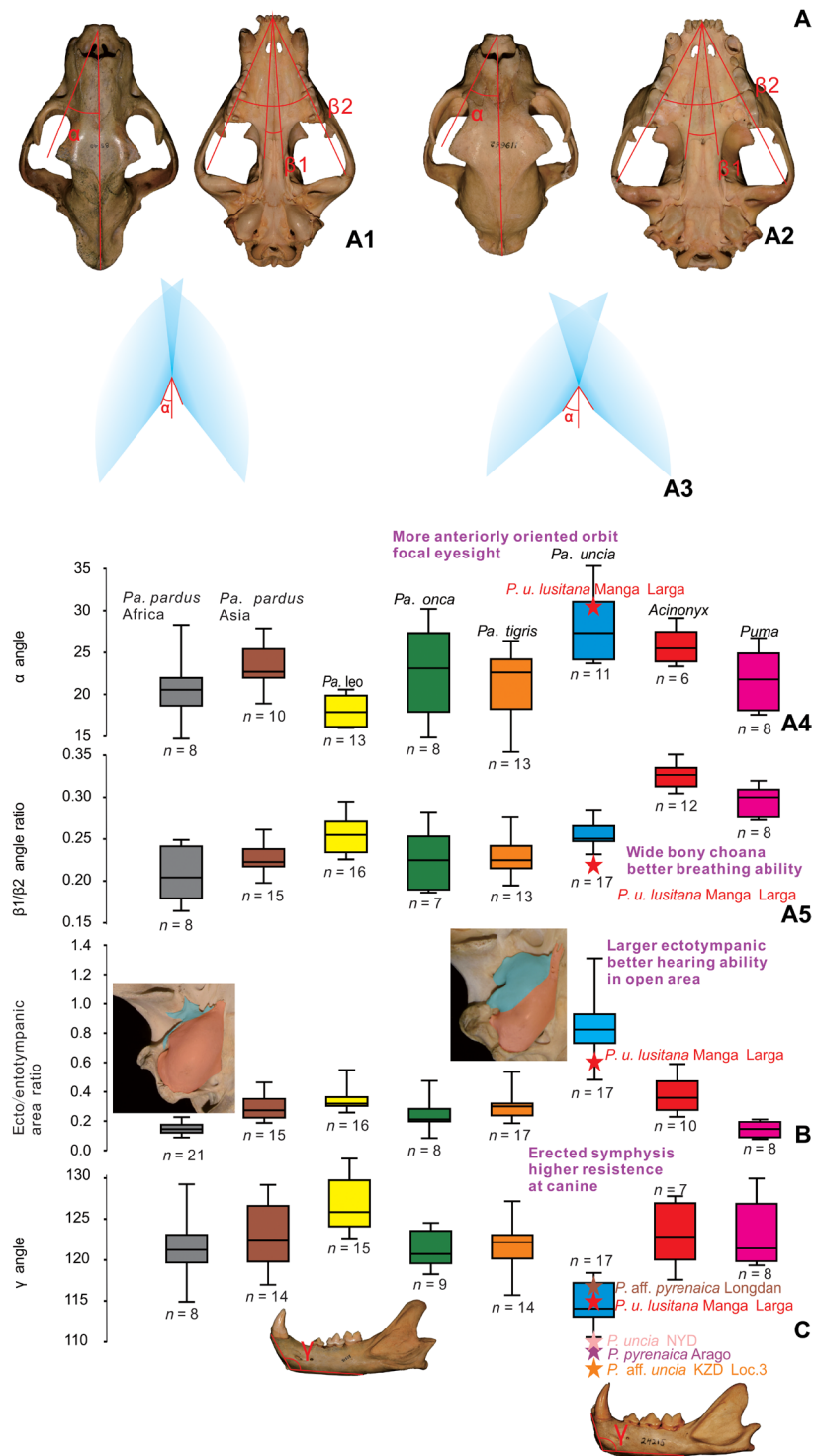
Fig. 3. Functional statistical traits of *Panthera uncia* and its fossil relatives in comparison with other felids. (**A**) Cranial angles of felids; (A1) Angle in the lion *P. leo*; (A2) angle in the snow leopard *P. uncia*; (A3) angle α and its impact on eyesight; (A4) comparison of angle α in modern and fossil felids; (A5) comparison of angle β in modern and fossil felids; (**B**) comparison of the ratio of ectotympanic and entotympanic area in modern and fossil felids; (**C**) comparison of angle γ in modern and fossil felids.

at the latter, suggesting the presence of uncertainty). The phylogenetic tree using pure morphological data gives a similar result (fig. S13), with a different position of *P. uncia* lineage, but the same interspecies relationship within the *P. uncia* lineage. Both analyses support a successive sister group relationship of fossil records and modern species, which are fully consistent with their age (younger species are closer to living species). The topology supports a roughly rapid evolution of the snow leopard lineage since the Early Pleistocene.

Among these five records, only the latest Pleistocene Niuyan Cave one shows nearly the same traits as the modern snow leopard and should be assigned to the modern species *P. uncia*. The Late Pleistocene skull from Manga Larga shows partial discrepancy from the modern *P. uncia*, out of the range of modern species in some measurements, and is regarded as distinct subspecies. All other fossil records show significant differences from the modern species and should be regarded as distinct species. In general, the late Middle

and Late Pleistocene (0.3 to 0.01 Ma) snow leopards already have basic adaptations similar to the modern species (wide forehead, short rostrum, elevated symphysis, enlarged cheek teeth, and enlarged ectotympanic) but still with certain differences. Specifically, *P. u. lusitana* from Manga Larga has a forehead (mainly frontal) with a less concave profile, and its bony choana is relatively narrower, whereas the mandibular corpus is much deeper than in modern *P. uncia*. Therefore, *P. u. lusitana* has less specialization of traits adapted to the cold environment compared with the modern species and also has a somewhat different feeding behavior from that of the modern species (deep mandibular corpus). The early Middle Pleistocene (0.6 to 0.5 Ma) snow leopard *P. pyrenaica*, however, does not have similar traits, as it has small cheek teeth similar to other pantherine cats, and the snout is also relatively longer, and these primitive traits are symplesiomorphic shared with *P. pardus* (*23*). The putative Early Pleistocene snow leopard *P.* aff. *pyrenaica* is basically similar to *P. pyrenaica*, although the symphysis is yet to be so
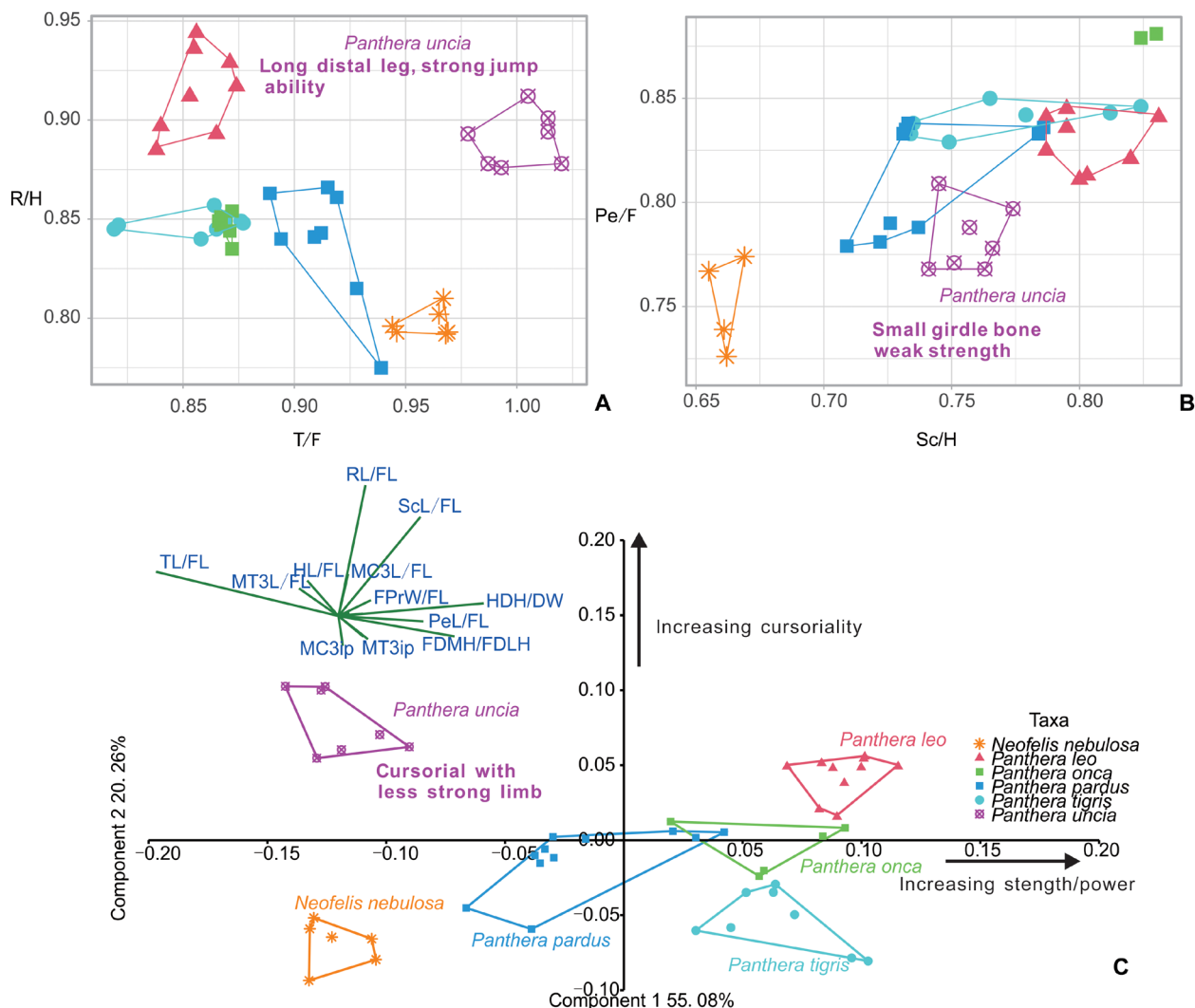

Fig. 4. Functional statistical postcranial traits of *Panthera uncia* in comparison with other felids. (**A**) Plot on tibia/femur length ratio and radius/humerus ratio. (**B**) Plot on pelvis/femur length ratio and scapular/humerus ratio. (**C**) PCA plot of 16 postcranial skeleton ratios; see the explanation in the appendix and raw data in table S3. R, radius; H, humerus; T, tibia; DH, distal antero-posterior height (of long bone); DW, distal medio-lateral width (of long bone); Pe, pelvis; Sc, scapular; F, femur; L, length; MC, metacarpal; MT, metatarsal; P/p, upper/lower premolar.

verticalized, which is primitive in regard to modern *P. uncia*. The lack of large cheek teeth, short snout, and vertical symphysis (for *P.* aff. *pyrenaica*), as analyzed above, suggests less adaption to the cold environment and less reliance on Caprini prey type for *P. pyrenaica* and *P.* aff. *pyrenaica*. In the Longdan fauna, there is no Caprini recorded (*53*).

As a species showing clear adaptation to the environment of the Tibetan Plateau, the majority of its evolutionary history is likely to occur there. The records outside the Tibetan Plateau are rare and incomplete. Longdan in the Linxia basin is located at the northeastern border of Tibet, has a high altitude of ~2000 m (*53*, *54*), and probably represents the general marginal distribution of the snow leopard at that time. The four other records are likely to represent the occasional spread of the snow leopard out of Tibet at (or shortly before) the age of the fossil records. These records can thus be used to trace the rapid specialization of the snow leopard during the Quaternary.

Although the overall shape [inferred from geometric morphometric (GM) analysis in Fig. 4] does not show a clear pattern, in regard to the most functional traits analyzed above and PCA plots (Fig. 5B), two periods can be distinguished. The first period is from the Early Pleistocene and early Middle Pleistocene. The snow leopard in this period gradually developed verticalized symphysis suitable to prey on Caprini, but the rostrum is relatively long, so its adaption is initial. Its cheek teeth are small, implying that its adaptation to the cold environment is less developed than that of the modern snow leopard. The second period is from the late Middle Pleistocene to the present day. The snow leopard in this period already has basically the same functional traits as in modern species, with a short rostrum and enlarged cheek teeth, enlarged frontal sinus, enlarged ectotympanic chamber, large orbit, and better adapted to prey on Caprini-type species and cold environments than the snow leopard from the first period. This is supported by morphological evolutionary rates inferred from Bayesian analyses using the approach of Zhang and Wang (*55*). The lineage leading to the modern *P. uncia* shows the highest morphological evolutionary rates among the branches in the tree (Fig. 4A). This is especially marked in the Middle-Late Pleistocene period. Such rapid evolution during the Early-Middle Pleistocene Transition is likely to be correlated with the onset of glaciation in the Tibetan Plateau in the Middle Pleistocene (*56*, *57*), with the extensive period in marine isotope stages 18 to 16, 12, 6, and 4 to 2 (*58*). The climate and environmental change provided stronger selective pressure on the snow leopard adapted to living and catching unique prey in Tibet. The out-of-Tibet dispersal of the snow leopard is in accordance with its major prey, the Caprini bovids. The early evolution of Caprini is endemic to Tibet (*59*, *60*). Since the Plio-Pleistocene, some species already began to spread out of Tibet (*61*–*63*), but the large wave of such dispersals only occurred since the Middle Pleistocene, with the appearance of *Ovis* and *Hemitragus* in Europe (*64*, *65*) and *Pseudois* in lowland northern China (Beijing) (*66*, *67*). The increased amplitude of glaciation since the Early-Middle Pleistocene Transition brought a long period of the colder environment in Eurasia during several glacial stages (*68*), providing both Caprini bovids and the snow leopard the opportunity to spread from Tibet to other mountainous regions in Eurasia. The functional trait PCA (Fig. 6) also supports a gradually shift of the snow leopard lineage from a leopard-like space to a more specialized space.

We find that during the late Middle and Late Pleistocene *P. pardus* also show certain adaptation toward Caprini prey (*69*–*71*), probably due to the harsh environment and abundance of Caprini during the different glacial stages (see the Supplementary Materials). Some characters of this leopard show some similarities to *P. uncia* (see details in the Supplementary Materials). However, our geometric morphometric analyses suggest that they are not much different from modern Asian *P. pardus*, and they lack some key traits seen in the snow leopard lineage (especially the auditory bulla). The lesser extent of cold/mountainous adaptations in *P. pardus* is likely due to the brief period during which leopards inhabited this environment and the unstable environmental conditions in Europe during the Middle and Late Pleistocene, which provided inconsistent selection pressures for cold/mountainous adaptations.

SDM analysis of potential LGM distribution and dispersal route of the snow leopard

To test whether the five fossil localities are within the area of suitable climate region of the snow leopard during the Pleistocene, we performed SDM to predict the probability of snow leopard presence under LGM climate conditions. Although none of the records can be precisely dated to LGM, the two Late Pleistocene ones are likely from this age. Nevertheless, during the LGM, the cold environment was predominant than at any other time of the Middle to Late Pleistocene (*72*, *73*), and the snow leopard is likely to spread farthest from Tibet at the LGM. This condition, therefore, represents the largest potential distribution of the snow leopard. Note that the SDM cannot predict the presence or not of glaciation, which definitely present in the Tibetan Plateau during LGM, so the potential range of the snow leopard in the Tibetan Plateau must be much smaller during LGM.

The predicted suitable area (Fig. 6) is much larger than the current condition (see fig. S14 for the prediction under the current conditions for comparison). Except for the Longdan one, none of the other four putative records are located within the highly suitable area predicted by SDM, although they are all closer to the suitable area than they are found today. This makes sense considering the small number of snow leopard records discovered in these regions, and these records probably represent the occasional and marginal distribution of the Pleistocene snow leopard. All four Middle to Late Pleistocene localities are lower than 1000 m in altitude. This is especially true for the Loc. 3 of Zhoukoudian (*74*), which is not in a typical cold environment as in the LGM conditions.

The SDM results suggest that the fossil snow leopards probably have different climate adaptations as the modern snow leopards do. This is in accordance with our morphological analyses that most of these fossil snow leopards have less strong adaptation to cold and high altitudes. On the other hand, the snow leopard from Niuyan Cave, which we identified as modern snow leopard, is also located outside the predicted suitable area under the LGM conditions. Notably, the microenvironments are steeped slopes in mountainous regions in all four cases. We argue that for the snow leopard, climate and altitude only partially influence their distribution, but mountainous steeped slopes are necessary habitat. Most anatomical traits of the snow leopard analyzed above are adapted to preying focusing, catching, and killing in the mountainous region. In lowlands with heavy cover (warm and humid conditions), the advantage of the snow leopard (over the leopard) loses. This explains their rarity or absence in most of the faunae of the lowlands far away from Tibet.
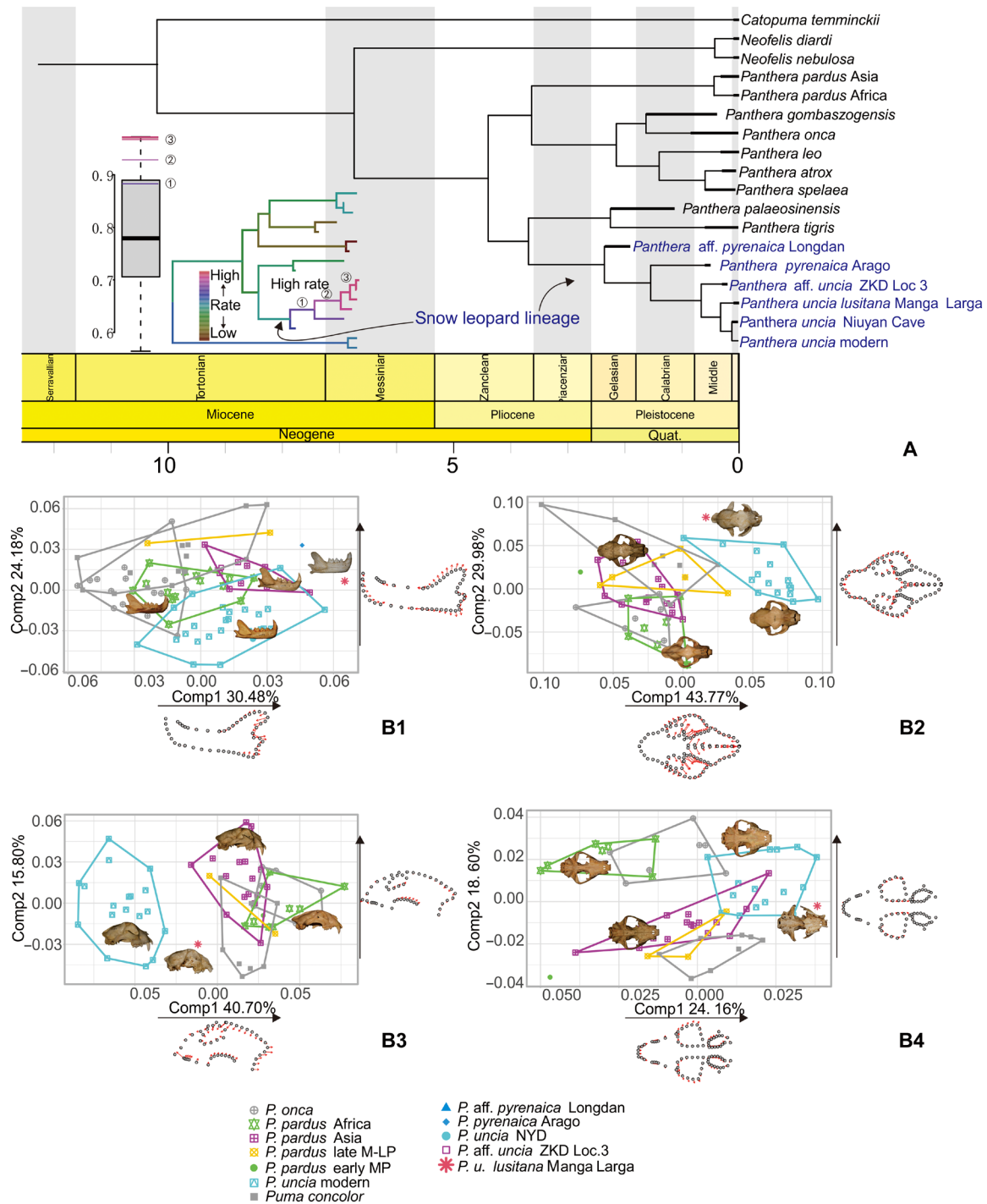
Fig. 5. Phylogenetic position and morphospace of modern and fossil snow leopards. (**A**) Time-calibrated total evidence phylogenetic tree of pantherine cats and the morphological evolutionary rate. (**B**) Geometric morphometric analyses on lateral views of the cranium and mandible of the fossil snow leopard in comparison with modern species. (B1) Mandible lateral profile, (B2) cranial dorsal view, (B3) cranial lateral view, and (B4) cranial ventral view.
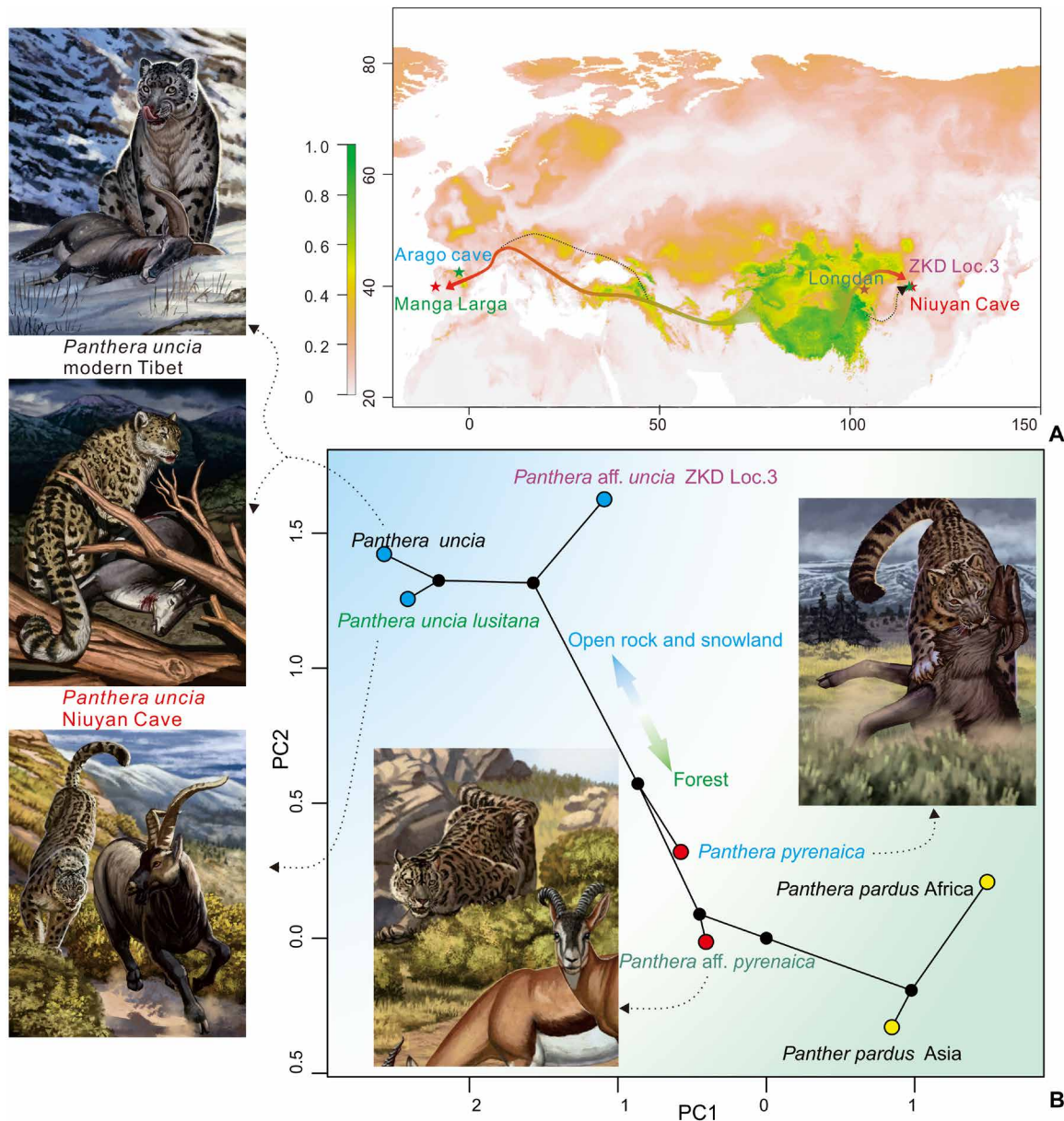
Fig. 6. SDM predicted suitable distribution and morphospace of the modern and fossil snow leopards. (**A**) The predicted probability of snow leopard presence under the LGM climate conditions. (**B**) Functional traits PCA morphospace, with reconstruction of fossil and modern snow leopards. Artwork by Jianhao Ye.

Overall, our analyses suggest that the mountainous region with steeped slopes and heavy rock cover are probably more important factors that influence the snow leopard distribution during its evolutionary history than the temperature and altitude themselves. This information would benefit further protection.

The predicted suitable area may also infer the dispersal routes of the snow leopard during glacial stages, as this provides potential connectivity. However, topography, prey type, etc., which is not included in the SDM analyses, are also important for real dispersal, so the exact dispersal routes are still waiting for more fossil records.

In summary, our analyses support five fossil records putatively corresponding to the Pleistocene snow leopard lineage. According to the obtained results, the former lineage suffered a rapid evolution during the Quaternary, especially since the Middle Pleistocene. The earliest putative record of the lineage is located at Longdan (Linxia Basin) near the border of Tibet with an estimated chronology of 2.2 to 2.5 Ma. The other four records are far from Tibet and not located in the suitable area predicted by SDM under the LGM conditions. In consequence, snow leopards could disperse out of Tibet to lowland eastern Asia and Europe through different routes. These later four fossil records are still out of the suitable area, representing the marginal distribution at that time. All three aspects (morphology, paleoenvironment of fossil occurrence, and SDM under the LGM conditions) support that the temperature and altitude are less important than the local microscale landscape, and steeped slope and heavy rock are more important factors for snow leopard survival.

Our study suggests climate, prey type, and especially landscape (mountainous region) are important for snow leopard, probably more than altitude itself. This information will be beneficial for the future protection of this iconic animal. We highlight the importance that the combination of morphology, fossil records, and ecological methods (SDM) can have for providing more comprehensive and testable data on the ecology and adaption of modern species and provide information that might be helpful to develop protection strategies for the animal.

MATERIALS AND METHODS

Phylogenetic analyses

To elucidate the evolutionary position of the analyzed specimens, a comprehensive phylogenetic analysis was performed, using a matrix modified from Salles (*24*), Werdelin and Flink (*75*), and Jiangzuo *et al.* (*76*). A total of 160 craniodental and postcranial characters are present in the matrix, which is initially designed for whole members of the family Felidae (including Machairodontinae), so the matrix has some characters not necessarily informative within the species included in this analysis. As we focus on the evolutionary history and trait evolutionary rates of the subfamily Pantherinae, most irrelevant taxa were not added, only leaving *Catopuma temminckii* as the outgroup. Genetic data were adopted from Johnson *et al.* (*14*), and four blocks (autosome DNA, X chromosome DNA, Y chromosome DNA, and Mitochondrial DNA) were set, together with the morphology block.

Bayes inferences with tip-dating under the fossilized birth-death model (*77*, *78*), using the mkv model (*79*) for morphology block, and GTR + gamma for four DNA blocks were performed. MrBayes3.2.7 (*80*, *81*) was used in inference. Two independent runs, each with four chains, were used in analyses. Ten million generations were performed in each run. See the detailed settings in the Supplementary Materials file.

Metric and geometric morphometric analyses

To clarify the morphology and the taxonomical position of the studied specimens, we performed biometric, as well as, geometric morphometric analyses. Only species that has the potential to be misidentified as *P. uncia* was included in metric and geometric morphometric analyses to clarify their differences, i.e., extant *P. uncia*, extant *P. pardus* from Africa and Asia, *Panthera onca*, and *Puma concolor*. Dentognathic specimens from mammalian collection of American Museum of Natural History (AMNH M), New York, USA; Smithsonian National Museum of Natural History (USNM), Washington DC, USA; Museum of Comparative Zoology (MCZ), Boston, USA; Institute of Zoology, Chinese Academy of Sciences, Beijing, China (IOZ); and Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming, China (KIZ), Northwest Institute of Plateau Biology, Chinese Academy of Sciences, Xining (NWIPB) were used in analyses. The landmarks and semilandmarks were obtained using software tpsDig2.32. The measurements of lower dentition and mandible follow the study of Jiangzuo and Liu (*9*). Geometric morphometric analyses were performed using Geomorph 4.0.1 package (*82*) of R 4.0.5 (*83*), and plots were made using the package ggplot2 (*84*). PCA analyses were performed in software past 4.0.3 (*85*).

Anatomical study and fossil records

We reviewed the literature and the available fossil collections in Eurasian Museums and Research Centers to find potential snow leopard fossil records, which are tested and analyzed in this study. The details on the comments on fossil records are provided in the Supplementary Materials. Two of them, Niuyan Cave and Loc. 3 of Zhoukoudian, are both from Fangshan, Beijing, China (*67*, *74*), one from Arago cave, Tautavel, France (*8*, *23*), and one from Manga Larga Cave, Santo António Plateau, Portugal (*21*). None of these four records were identified as the snow leopard when they were first published but as *P. pardus* or *Panthera* sp. (or *Felis* sp.), but the similarity with the snow leopard was mostly recognized. The anatomic, morphometric, and geometric morphometric analyses of the mandible and lower dentition were carried out to study the phylogenetic and taxonomic features of these four records. The faunal composition of the four records was analyzed to infer the paleoenvironment.

Finite element analyses

Finite element analyses were performed in the Abaqus computer-aided engineering (CAE) (v. 6.14) software. For simplicity, two-dimensional (2D) finite element modeling for hemimandibles was used (*86*, *87*). First, photos of the mandibles of *P. uncia* AMNH M166952 and *P. pardus* AMNH M89009 were taken in the right lateral view. The outlines were plotted in the AutoCAD 2018 software, scaled to the same size, and exported .dxf files. The exported outline files were loaded into Abaqus CAE and generated 3D planar shell models with a uniform thickness of 2 mm. The models were assigned the homogeneous material property approximating mammalian cortical bone, with a Young's modulus of 15 GPa and a Poisson's ratio of 0.28, following the study of Drake *et al.* (*88*). As our goal is to compare the mandibular mechanical behavior, we set the same bite force of temporal and masseteric muscles as 3000 and 1000 N, respectively, for all taxa used. The direction of muscle (temporal and masseteric) of the modern species is measured in the case seen in Fig. 1, and the exact angle and bite force are given in table S1. The fossil species related to modern *P. uncia* were set as the same angle. The following boundary conditions were set: 1, one point at the posterior border of the condyle, only allowing vertical movement; 2, one point at the dorsal border of the condyle, only allowing horizontal movement; and 3, the tip point of the canine, all the six movements were constrained.

Species distribution modeling

Data

The snow leopard occurrence data used in this study were from field surveys, literature, and the Global Biodiversity Information Facility database (table S4). Most of the occurrences were derived from camera trap records, and others were from feces or footprints marked during line transect surveys (*20*, *89*, *90*). All occurrences used for SDMs were from recent surveys conducted after 2010, and more than 60% of the records were based on the surveys in the past 5 years. The minimum distance between occurrences is 5 km. All occurrences were recorded using GPS handsets.

We used the 19 bioclimate variables (30 arc sec) from the World-Clim 2.0 dataset (https://worldclim.org/) for current (1960–1990) climate conditions; and we used the WorldClim 1.4 downscaled data for climate conditions at the LGM (about 22,000 years ago) (*91*). For the LGM data, we selected the global climate model CCSM4, because it is a moderate model with temperature and precipitation neither too high nor too low (*92*).

Models

We used environmental variables to explain the presence or absence of the snow leopard using the model $logit(p) = f(x1, x2, \ldots xk)$,

where *p* is the probability of the presence of snow leopard at a location, and *x* are environmental variables.

We applied random forest (*93*) for SDMs. Random forest is a machine learning algorithm and is one of the frequently used SDM approaches (*94–97*). It is especially good for handling high-dimensional data (multiple correlated explanatory variables) and complex relationships such as interaction and high-order effects (*98–100*). We used the R package randomForest (*101*) for the analysis. We set the argument ntree (number of trees) to be 1000 and left others undefined (default settings, including no weights, were used).

For the current distribution of snow leopards, we used the occurrences and evenly distributed $50 \times 50 = 2500$ pseudo absence points as the dependent variables, with the 19 climate variables in the WorldClim dataset as explanatory variables, and build a model to quantify the association between snow leopard occurrences and climate variables. Then, we projected the historical distribution of the snow leopard using the model and the climate data at the LGM. The partial effects of the 12 most important elements and the basic evaluation parameter of the SDM model are provided in the Supplementary Materials.

Supplementary Materials

The PDF file includes:
Figs. S1 to S16
Tables S1 to S7
Legends for data S1 to S3
References

Other Supplementary Material for this manuscript includes the following:
Data S1 to S3

REFERENCES AND NOTES

1. H. Hemmer, Uncia uncia. *Mamm. Species*, 1–5 (1972).
2. J. Ma, H. Zou, K. Cheng, The distribution status of Snow Leopard (*Uncia uncia*) in China. *Contributed Papers to the Snow Leopard Survival Strategy Summit*, 209 (2002).
3. W. Shehzad, T. M. McCarthy, F. Pompanon, L. Purevjav, E. Coissac, T. Riaz, P. Taberlet, Prey preference of snow leopard (*Panthera uncia*) in South Gobi, Mongolia. *PLOS ONE* **7**, e32104 (2012).
4. Y. A. Kalashnikova, A. S. Karnaukhov, M. Y. Dubinin, A. D. Poyarkov, V. V. Rozhnov, Potential habitat of snow leopard (*Panthera uncia*, Felinae) in South Siberia and adjacent territories based on the maximum entropy distribution model. *Zool. Zhurnal.* **98**, 332–342 (2019).
5. V. S. Lukarevskiy, M. Dalannast, S. Lukarevskiy, E. Damdin, Factors determining the distribution and status of the snow leopard population (*Panthera uncia*) in Western Mongolia. *Anim. Vet. Sci.* **7**, 127–132 (2019).
6. T. McCarthy, D. Mallon, E. W. Sanderson, P. Zahler, K. Fisher, "Chapter 3 - What is a snow leopard? Biogeography and status overview" in *Snow Leopards*, T. McCarthy, D. Mallon, Eds. (Academic Press, 2016), pp. 23–42.
7. Y. Gao, *Fauna Sinica. Mammalia, Vol. 8: Carnivora*. (Science Press, 1987), vol. 8.
8. H. Hemmer, An intriguing find of an early Middle Pleistocene European snow leopard, *Panthera uncia pyrenaica* ssp. nov. (Mammalia, Carnivora, Felidae), from the Arago cave (Tautavel, Pyrénées-Orientales, France). *Palaeobiodiversity Palaeoenvironments* **103**, 207–220 (2023).
9. Q. Jiangzuo, J. Liu, First record of the Eurasian jaguar in southern Asia and a review of dental differences between pantherine cats. *J. Quat. Sci.* **35**, 817–830 (2020).
10. A. C. Kitchener, C. A. Driscoll, N. Yamaguchi, "Chapter 1 - What is a snow leopard? Taxonomy, morphology, and phylogeny" in *Snow Leopards*, T. McCarthy, D. Mallon, Eds. (Academic Press, 2016), pp. 3–11.
11. T. Haltenorth, Die verwandtschaftliche Stellung der Großkatzen zueinander. I. Beschreibung der Schädelknochen [The relationship between the big cats. I. Description of the skull bones.]. *Z. Säugetierk.* **11**, 32–105 (1936).
12. R. I. Pocock, The classification of existing Felidae. *Ann. Mag. Nat. Hist. Series* **20**, 329–350 (1917).
13. M. Y. Mattern, D. A. McLennan, Phylogeny and speciation of felids. *Cladistics* **16**, 232–253 (2000).
14. W. E. Johnson, E. Eizirik, J. Pecon-Slattery, W. J. Murphy, A. Antunes, E. Teeling, S. J. O'Brien, The late Miocene radiation of modern Felidae: A genetic assessment. *Science* **311**, 73–77 (2006).
15. H. V. Figueiro, G. Li, F. J. Trindade, J. Assis, F. Pais, G. Fernandes, S. H. D. Santos, G. M. Hughes, A. Komissarov, A. Antunes, C. S. Trinca, M. R. Rodrigues, T. Linderoth, K. Bi, L. Silveira, F. C. C. Azevedo, D. Kantek, E. Ramalho, R. A. Brassaloti, P. M. S. Villela, A. L. V. Nunes, R. H. F. Teixeira, R. G. Morato, D. Loska, P. Saragueta, T. Gabaldon, E. C. Teeling, S. J. O'Brien, R. Nielsen, L. L. Coutinho, G. Oliveira, W. J. Murphy, E. Eizirik, Genome-wide signatures of complex introgression and adaptive evolution in the big cats. *Sci. Adv.* **3**, e1700299 (2017).
16. G. Li, B. W. Davis, E. Eizirik, W. J. Murphy, Phylogenomic evidence for ancient hybridization in the genomes of living cats (Felidae). *Genome Res.* **26**, 1–11 (2016).
17. T. McCarthy, D. Mallon, R. Jackson, P. Zahler, K. McCarthy, *Panthera uncia*. The IUCN Red List of Threatened Species; IUCN: Gland, Switzerland, 2017. (2017).
18. T. Mahmood, A. Younas, F. Akrim, S. Andleeb, A. Hamid, M. S. Nadeem, Range contraction of snow leopard (*Panthera uncia*). *PLOS ONE* **14**, e0218460 (2019).
19. J. D. Farrington, J. Li, "Chapter 8 - Climate change impacts on snow leopard range" in *Snow Leopards*, T. McCarthy, D. Mallon, Eds. (Academic Press, 2016), pp. 85–95.
20. X. Li, L. Ma, D. Hu, D. Ma, R. Li, Y. Sun, E. Gao, Potential range shift of snow leopard in future climate change scenarios. *Sustainability* **14**, 1115 (2022).
21. J. L. Cardoso, F. Regala, O. Leopardo, *Panthera pardus* (L., 1758), do Algar da Manga Larga (Planalto de Santo António, Porto de Mós). *Comunicações Geológicas* **93**, 119–144 (2006).
22. B. Kurtén, An attempted parallelization of the Quaternary mammalian faunas of China and Europe. *Societas Scientiarum Fennica Commentationes Biologicae* **23**, 1–12 (1960).
23. A. Testu, A. M. Moigne, H. De Lumley, La panthère *Panthera pardus* des niveaux inférieurs de la Caune de l'Arago à Tautavel (Pyrénées-Orientales, France) dans le contexte des Felidae (Felinae, Pantherinae) de taille moyenne du Pléistocène européen. [The panther Panthera pardus from the lower levels of the Caune de l'Arago at Tautavel (Pyrénées-Orientales, France) in the context of medium-sized Felidae (Felinae, Pantherinae) from the European Pleistocene.]. *Quaternaire H. S.* **4**, 271–281 (2011).
24. L. O. Salles, Felid phylogenetics: Extant taxa and skull morphology (Felidae, Aeluroidea). *Am. Mus. Novit.* **3047**, 1–67 (1992).
25. M. E. Sims, Cranial morphology of five felids: *Acinonyx jubatus*, *Panthera onca*, *Panthera pardus*, *Puma concolor, Uncia uncia*. *Russ. J. Theriol.* **11**, 157–170 (2012).
26. B. Figueirido, Z. J. Tseng, A. Martin-Serra, Skull shape evolution in durophagous carnivorans. *Evolution* **67**, 1975–1993 (2013).
27. B. Figueirido, P. Palmqvist, J. A. Perez-Claros, W. Dong, Cranial shape transformation in the evolution of the giant panda (*Ailuropoda melanoleuca*). *Naturwissenschaften* **98**, 107–116 (2011).
28. W. Dong, Virtual cranial endocast of the oldest giant panda (*Ailuropoda microta*) reveals great similarity to that of its extant relative. *Naturwissenschaften* **95**, 1079–1083 (2008).
29. A. A. Curtis, B. Van Valkenburgh, Beyond the sniffer: Frontal sinuses in Carnivora. *Anat. Rec.* **297**, 2047–2064 (2014).
30. V. Vinuesa, D. A. Iurino, J. Madurell-Malapeira, J. Liu, J. Fortuny, R. Sardella, D. M. Alba, Inferences of social behavior in bone-cracking hyaenids (Carnivora, Hyaenidae) based on digital paleoneurological techniques: Implications for human–carnivoran interactions in the Pleistocene. *Quat. Int.* **413**, 7–14 (2016).
31. V. Vinuesa, J. Madurell-Malapeira, J. Fortuny, D. M. Alba, The endocranial morphology of the Plio-Pleistocene bone-cracking hyena *Pliocrocuta perrieri*: Behavioral implications. *J. Mamm. Evol.* **22**, 421–434 (2015).
32. Z. J. Tseng, Testing adaptive hypotheses of convergence with functional landscapes: A case study of bone-cracking hypercarnivores. *PLOS ONE* **8**, e65305 (2013).
33. G. K. Reznik, Comparative anatomy, physiology, and function of the upper respiratory tract. *Environ. Health Perspect.* **85**, 171–176 (1990).
34. R. M. Joeckel, Unique frontal sinuses in fossil and living Hyaenidae (Mammalia, Carnivora): Description and interpretation. *J. Vertebr. Paleontol.* **18**, 627–639 (1998).
35. J. S. Reidenberg, J. T. Laitman, Sisters of the sinuses: Cetacean air sacs. *Anat. Rec.* **291**, 1389–1396 (2008).
36. V. Negus, The function of the paranasal sinuses. *AMA Arch. Otolaryngol.* **66**, 430–442 (1957).
37. V. Torregrosa, M. Petrucci, J. A. Pérez-Claros, P. Palmqvist, Nasal aperture area and body mass in felids: Ecophysiological implications and paleobiological inferences. *Geobios* **43**, 653–661 (2010).
38. H. J. O'Regan, Defining cheetahs, a multivariate analysis of skull shape in big cat. *Mammal Rev.* **32**, 58–62 (2002).
39. A. Turner, M. Antón, *The Big Cats and Their Fossil Relatives: An Illustrated Guide to Their Evolution and Natural History* (Columbia Univ. Press, 1997).
40. L. Werdelin, N. Yamaguchi, W. E. Johnson, S. J. O'Brien, "Phylogeny and evolution of cats (Felidae)" in *Biology and Conservation of Wild Felids*, D. W. Macdonald, A. J. Loveridge, Eds. (Oxford Univ. Press, 2010), pp. 59–82.
41. G. B. Schaller, *Mountain Monarchs: Wild Sheep and Goats of the Himalaya* (University of Chicago Press, 1977).

42. J. L. Fox, S. P. Sinha, R. S. Chundawat, P. K. Das, A field survey of snow leopard in northwestern India. *Proc. Intl. Symp.* **5**, 99–111 (1988).

43. J. L. Fox, R. S. Chundawat, "Chapter 2 - What is a snow leopard? Behavior and ecology" in *Snow Leopards*, T. McCarthy, D. Mallon, Eds. (Academic Press, 2016), pp. 13–21.

44. F. Therrien, Mandibular force profiles of extant carnivorans and implications for the feeding behaviour of extinct predators. *J. Zool.* **267**, 249–270 (2005).

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

46. S. Lyngdoh, S. Shrotriya, S. P. Goyal, H. Clements, M. W. Hayward, B. Habib, Prey preferences of the snow leopard (*Panthera uncia*): Regional diet specificity holds global significance for conservation. *PLOS ONE* **9**, e88349 (2014).

47. M. K. Oli, I. R. Taylor, D. M. E. Rogers, Diet of the snow leopard (*Panthera uncia*) in the Annapurna Conservation Area, Nepal. *J. Zool.* **231**, 365–370 (1993).

48. D. Mallon, R. B. Harris, P. Wegge, "Chapter 4 - Snow leopard prey and diet" in *Snow Leopards*, T. McCarthy, D. Mallon, Eds. (Academic Press, 2016), pp. 43–55.

49. S. Gutarra, I. A. Rahman, The locomotion of extinct secondarily aquatic tetrapods. *Biol. Rev. Camb. Philos. Soc.* **97**, 67–98 (2022).

50. A. A. Biewener, Biomechanics of mammalian terrestrial locomotion. *Science* **250**, 1097–1103 (1990).

51. G. Huang, J. Rosowski, M. Ravicz, W. Peake, Mammalian ear specializations in arid habitats: Structural and functional evidence from sand cat (*Felis margarita*). *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* **188**, 663–681 (2002).

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

53. Z. X. Qiu, T. Deng, B. Y. Wang, *Early pleistocene mammalian fauna from Longdan, Dongxiang, Gansu, China*. (Palaeontologia Sinica Science Press, 2004), vol. 27, pp. 1–193.

54. T. Deng, Z. X. Qiu, B. Y. Wang, X. M. Wang, S. K. Hou, "Late Cenozoic biostratigraphy of the Linxia Basin, Northwestern China" in *Fossil Mammals of Asia*, X. Wang, L. J. Flynn, M. Fortelius, Eds. (Neogene Biostratigraphy and Chronology, Columbia Univ. Press, 2013), pp. 243–273.

55. C. Zhang, M. Wang, Bayesian tip dating reveals heterogeneous morphological clocks in Mesozoic birds. *R. Soc. Open Sci.* **6**, 182062 (2019).

56. Y. Chen, Y. Li, M. Zhang, Z. Cui, G. Liu, Much late onset of Quaternary glaciations on the Tibetan Plateau: Determining the age of the Shishapangma Glaciation using cosmogenic ^{26}Al and ^{10}Be dating. *Sci. Bull.* **63**, 306–313 (2018).

57. L. A. Owen, J. M. Dortch, Nature and timing of Quaternary glaciation in the Himalayan–Tibetan orogen. *Quat. Sci. Rev.* **88**, 14–54 (2014).

58. J. Ehlers, P. L. Gibbard, P. D. Hughes, "Quaternary glaciations and chronology" in *Past Glacial Environments* (Elsevier, 2018), pp. 77–101.

59. S.-Q. Wang, Q. Yang, Y. Zhao, C.-X. Li, Q.-Q. Shi, L.-Y. Zong, J. Ye, New *Olonbulukia* material and its related assemblage reveal an early radiation of stem Caprini along the north of the Tibetan Plateau. *J. Paleontol.* **93**, 385–397 (2018).

60. X. Wang, Q. Li, G. T. Takeuchi, Out of Tibet: An early sheep from the Pliocene of Tibet, *Protovis himalayensis*, genus and species nov. (Bovidae, Caprini), and origin of Ice Age mountain sheep. *J. Vertebr. Paleontol.* **36**, e1169190 (2016).

61. F. Bibi, E. Vrba, F. Fack, A new African fossil caprin and a combined molecular and morphological Bayesian phylogenetic analysis of Caprini (Mammalia: Bovidae). *J. Evol. Biol.* **25**, 1843–1854 (2012).

62. M. Bukhsianidze, A. Vekua, *Capra dalii* nov. sp.(Caprinae, Bovidae, Mammalia) at the limit of Plio-Pleistocene from Dmanisi (Georgia). *Courier-Forschungsinstitut Senckenberg* **256**, 159 (2006).

63. P. Teilhard de Chardin, J. Piveteau, Les Mammifères fossiles de Nihowan (Chine) [Fossil Mammals from Nihowan (China)]. *Ann. Paleontol.* **19**, 1–154 (1930).

64. A.-M. Moigne, M. R. Palombo, V. Belda, D. Heriech-Briki, S. Kacimi, F. Lacombat, M.-A. de Lumley, J. Moutoussamy, F. Rivals, J. Quilčs, A. Testu, Les faunes de grands mammifčres de la Caune de l'Arago (Tautavel) dans le cadre biochronologique des faunes du Pléistocčne moyen italien [The faunas of large mammals of the Caune de l'Arago (Tautavel) in the biochronological framework of the faunas of the Italian Middle Pleistocene.]. *Anthropologie* **110**, 788–831 (2006).

65. P. Fosse, J. B. Fourvel, S. Madeleine, Quaternary cliff-dwelling bovids (*Capra, Rubicapra, Hemitragus, Ovis*): Site's typology and taphonomic remarks. *SAGVNTVM Extra* **21**, 137–163 (2020).

66. H. W. Tong, S. Q. Zhang, Q. Li, Z. J. Xu, Late Pleistocene mammalian fossils from Xitaiping Cave, Shidu, Beijing. *Vert. PalAs.* **46**, 51–70 (2008).

67. D. Tao, H. Wanbo, W. Hongjie, The late Pleistocene mammalian fossils from Niuyan Cave in Mentougou, Beijing, China. *Vert. PalAs.* **37**, 156–164 (1999).

68. M. J. Head, P. L. Gibbard, Early–Middle Pleistocene transitions: Linking terrestrial and marine realms. *Quat. Int.* **389**, 7–46 (2015).

69. E. Ghezzo, L. Rook, The remarkable *Panthera pardus* (Felidae, Mammalia) record from Equi (Massa, Italy): Taphonomy, morphology, and paleoecology. *Quat. Sci. Rev.* **110**, 131–151 (2015).

70. D. Nagel, *Panthera pardus vraonensis* n. ssp., a new leopard from the Pleistocene of Vraona/Greece. *Neues Jahrbuch für Geologie und Palaeontologie Monatshefte* **1999**, 129–150 (1999).

71. N. Spassov, T. Raychev, Late Würm *Panthera pardus* remains from Bulgaria: The European fossil leopards and the question of the probable species survival until Holocene in the Balkans. *Historica Naturalis Bulgarica* **7**, 71–96 (1997).

72. P. D. Hughes, "Chapter 46 - Concept and global context of the glacial landforms from the Last Glacial Maximum" in *European Glacial Landscapes*, D. Palacios, P. D. Hughes, J. M. García-Ruiz, N. Andrés, Eds. (Elsevier, 2022), pp. 355–358.

73. N. Shackleton, Oxygen isotope analyses and Pleistocene temperatures re-assessed. *Nature* **215**, 15–17 (1967).

74. W. Pei, *On the mammalian remains from Locality 3 at Choukoutien* (Palaeontologia Sinica, Ser. C, 1936), vol. 7(5).

75. L. Werdelin, T. Flink, "The phylogenetic context of Smilodon" in *Smilodon: The Iconic Sabertooth*, L. Werdelin, H. G. Mcdonald, C. A. Shaw, Eds. (Johns Hopkins Univ. Press, 2018), pp. 14–29.

76. Q. Jiangzuo, L. Werdelin, Y. Sun, A dwarf sabertooth cat (Felidae: Machairodontinae) from Shanxi, China, and the phylogeny of the sabertooth tribe Machairodontini. *Quat. Sci. Rev.* **284**, 107517 (2022).

77. F. Ronquist, S. Klopfstein, L. Vilhelmsen, S. Schulmeister, D. L. Murray, A. P. Rasnitsyn, A total-evidence approach to dating with fossils, applied to the early radiation of the hymenoptera. *Syst. Biol.* **61**, 973–999 (2012).

78. C. Zhang, T. Stadler, S. Klopfstein, T. A. Heath, F. Ronquist, Total-evidence dating under the fossilized birth-death process. *Syst. Biol.* **65**, 228–249 (2016).

79. P. O. Lewis, A likelihood approach to estimating phylogeny from discrete morphological character data. *Syst. Biol.* **50**, 913–925 (2001).

80. J. P. Huelsenbeck, F. Ronquist, MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* **17**, 754–755 (2001).

81. F. Ronquist, M. Teslenko, P. van der Mark, D. L. Ayres, A. Darling, S. Hohna, B. Larget, L. Liu, M. A. Suchard, J. P. Huelsenbeck, MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Syst. Biol.* **61**, 539–542 (2012).

82. D. C. Adams, E. Otárola-Castillo, geomorph: An R package for the collection and analysis of geometric morphometric shape data. *Methods Ecol. Evol.* **4**, 393–399 (2013).

83. R Development Core Team, R: A Language and Environment for Statistical Computing (R Foundation for Statistical Computing, 2016).

84. H. Wickham, *ggplot2: Elegant Graphics for Data Analysis* (Springer, 2016).

85. Ø. Hammer, D. Harper, P. Ryan, PAST: Paleontological statistics software package for education and data analysis. *Palaeontol. Electron.* **4**, 1–9 (2001).

86. T. Fletcher, C. Janis, E. Rayfield, Finite element analysis of ungulate jaws: Can mode of digestive physiology be determined? *Palaeontol. Electron.* **13**, 1–15 (2010).

87. P. Piras, L. Maiorino, L. Teresi, C. Meloro, F. Lucci, T. Kotsakis, P. Raia, Bite of the cats: Relationships between functional integration and mechanical performance as revealed by mandible geometry. *Syst. Biol.* **62**, 878–900 (2013).

88. A. Drake, T. L. Haut Donahue, M. Stansloski, K. Fox, B. B. Wheatley, S. W. Donahue, Horn and horn core trabecular bone of bighorn sheep rams absorbs impact energy and reduces brain cavity accelerations during high impact ramming of the skull. *Acta Biomater.* **44**, 41–50 (2016).

89. L. Xiao, C. Cheng, H. Wan, D. Zhang, Y. Wang, Tsedan, P. Hou, J. Li, X. Yang, Z. Lü, Y. Liu, Defining conservation priority areas of snow leopard habitat in the Sanjiangyuan Region. *Biodiv. Sci.* **27**, 943–950 (2019).

90. Y. Liu, X. Li, X. Liang, Y. Liu, C. Cheng, J. Li, P. Tang, H. Qi, X. Bian, B. He, R. Xing, S. Li, X. Shi, C. Yang, Y. Xue, X. Lian, Awangjiumei, Xierannima, D. Song, L. Xiao, Z. Lü, *Where and How many?* The status of snow leopard (*Panthera uncia*) density surveys and knowledge gaps in China. *Biodiv. Sci.* **27**, 919–931 (2019).

91. S. E. Fick, R. J. Hijmans, WorldClim 2: New 1km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* **37**, 4302–4315 (2017).

92. G. Flato, J. Marotzke, B. Abiodun, P. Braconnot, S. C. Chou, W. Collins, P. Cox, F. Driouech, S. Emori, V. Eyring, C. Forest, P. Gleckler, E. Guilyardi, C. Jakob, V. Kattsov, C. Reason, M. Rummukainen, "Evaluation of climate models" in *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, P. M. Midgley, Eds. (Cambridge Univ. Press, 2013).

93. L. Breiman, Random forests. *Mach. Learn.* **45**, 5–32 (2001).

94. C. Kampichler, R. Wieland, S. Calmé, H. Weissenberger, S. Arriaga-Weiss, Classification in conservation biology: A comparison of five machine-learning methods. *Ecol. Inform.* **5**, 441–450 (2010).

95. T. A. Rather, S. Kumar, J. A. Khan, Multi-scale habitat modelling and predicting change in the distribution of tiger and leopard using random forest algorithm. *Sci. Rep.* **10**, 11473 (2020).

96. L. R. Iverson, A. M. Prasad, S. N. Matthews, M. Peters, Estimating potential habitat for 134 eastern US tree species under six climate scenarios. *For. Ecol. Manag.* **254**, 390–406 (2008).

97. R. Valavi, J. Elith, J. J. Lahoz-Monfort, G. Guillera-Arroita, Modelling species presence-only data with random forests. *Ecography* **44**, 1731–1742 (2021).

98. S. Winham, X. Wang, M. de Andrade, R. Freimuth, C. Colby, M. Huebner, J. Biernacka, Interaction detection with random forests in high-dimensional data. *Genet. Epidemiol.* **36**, 142–142 (2012).

99. Y. Kim, R. Wojciechowski, H. Sung, R. A. Mathias, L. Wang, A. P. Klein, R. K. Lenroot, J. Malley, J. E. Bailey-Wilson, Evaluation of random forests performance for genome-wide association studies in the presence of interaction effects. *BMC Proc.* **3**, S64–S64 (2009).

100. X. H. Li, Y. Wang, Applying various algorithms for species distribution modeling. *Integr. Zool.* **8**, 124–135 (2013).

101. Fortran original by Leo Breiman and Adele Cutler; R port by Andy Liaw and Matthew Wiener, "Breiman and Cutler's Random Forests for Classification and Regression" (2018; https://stat.berkeley.edu/~breiman/RandomForests/).

102. J. N. Woldřich, *Reste diluvialer Faunen und des Menschen aus dem Waldviertel Niederösterreichs in den Sammlungen des K. K. Naturhistorischen Hofmuseums in Wien* [Remains of diluvial fauna and humans from the Waldviertel region of Lower Austria in the collections of the Imperial and Royal Natural History Court Museum in Vienna] (K.K. Hof-und Staatsdruckerei, 1893).

103. E. Thenius, "Die Feliden (Carnivora) aus dem Pleistozän von Stránská Skálá" [Felidae (Carnivora) from the Pleistocene of Stránská Skálá.] in *Stránská Skálá I, 1910-1945*, R. Musil, Ed. (Moravske Museum, 1971), pp. 121-135.

104. H. Hemmer, Zur Kenntnis pleistozäner mitteleuropäischer Leoparden (*Panthera pardus*) [On Pleistocene Central European Leopards (Panthera pardus).]. *Neues Jahrb. Geol. Paläontologie Abh.* **138**, 15–36 (1971).

105. E. Thenius, Über das Vorkommen fossiler Schneeleoparden (Subgenus *Uncia*, Carnivora, Mammalia) [On the occurrence of fossil snow leopards (Subgenus Uncia, Carnivora, Mammalia)]. *Säugetierk. Mitt.* **17**, 234–242 (1969).

106. A. Testu, "Etude paléontologique et biostratigraphique des Felidae et Hyaenidae pléistocènes de l'Europe méditerranéenne," [Paleontological and biostratigraphic study of Pleistocene Felidae and Hyaenidae from Mediterranean Europe]. thesis, Université Perpignan (2006).

107. F. Olive, Évolution des grands Carnivores au Plio Pléistocène en Afrique et en Europe occidentale [Evolution of large carnivores in the Plio-Pleistocene in Africa and Western Europe]. *Anthropologie* **110**, 850–869 (2006).

108. V. Sauqué, G. Cuenca-Bescós, The Iberian Peninsula, the last european refugium of *Panthera pardus* Linnaeus 1758 during the Upper Pleistocene. *Quaternaire* **24**, 13–24 (2013).

109. J. M. Malapeira, D. M. Alba, S. M. Solà, J. A. Garrido, The Eurasian puma-like cat *Puma pardoides* (Owen 1846) (Carnivora, Felidae): Taxonomy, Biogeography and dispersal events. *Cidaris* **30**, 169–172 (2010).

110. P.-E. Moullé, A. Echassoux, F. Lacombat, Taxonomie du grand canidé de la grotte du Vallonnet (Roquebrune-Cap-Martin, Alpes-Maritimes, France) [Taxonomy of the large canid of the Vallonnet cave (Roquebrune-Cap-Martin, Alpes-Maritimes, France)]. *Anthropologie* **110**, 832–836 (2006).

111. J. Madurell-Malapeira, S. R. Montoya, M. P. E. Ortiz, D. M. Alba, J. A. Garrido, Villafranchian large mammals from the Iberian Peninsula: Paleobiogeography, pleoecology and dispersal events. *J. Iber. Geol.* **40**, 167–178 (2014).

112. C. G. Diedrich, Late Pleistocene leopards across Europe–northernmost European German population, highest elevated records in the Swiss Alps, complete skeletons in the Bosnia Herzegowina Dinarids and comparison to the Ice Age cave art. *Quat. Sci. Rev.* **76**, 167–193 (2013).

113. T. Kotsakis, M. R. Palombo, Un cranio di *Panthera pardus* (L.) del Pleistocene medio superiore di Monte Sacro (Roma) [A skull of Panthera pardus (L.) from the Upper Middle Pleistocene of Monte Sacro (Rome)]. *Geologica Romana* **18**, 137–155 (1979).

114. B. Kurtén, A. Poulianos, Fossil Carnivora in Petralona Cave: Status of 1980. *Anthropos* **8**, 9–56 (1981).

115. H. Hemmer, "Die Feliden aus dem Epivillafranchium von Untermassfeld" in *Das Pleistozän von Untermassfeld bei Meiningen (Thüringen), Monographien des Römisch-Germanishes Zentralmuseums* ["The Felids from the Epivillafranchium of Untermassfeld" in The Pleistocene of Untermassfeld near Meiningen (Thuringia), Monographs of the Roman-Germanic Central Museum]. R.-D. Kahlke, Ed. Römisch-Germanisches Zentralmuseum, Mainz, (2001), pp. 699–782.

116. I. Cáceres, J. Canyelles, M. Esteban, S. Giralt, F. González, R. Huguet, N. Ibáñez, C. Lorenzo, M. Mata, A. Pinto, Estudi d'un exemplar de *Panthera pardus* i un de *Panthera leo spelaea* localitzats a l'Abric Romaní (Capellades, Anoia) i anàlisi de la problemàtica dels carnívors en aquest jaciment [Study of one specimen of Panthera pardus and one Panthera leo spelaea located in the Abric Romaní (Capellades, Anoia) and analysis of the problem of carnivores in this site]. *Estrat* **6**, 31–41 (1993).

117. W. V. Koenigswald, D. Nagel, F. Menger, Ein jungpleistozaner Leopardenkiefer von Geinsheim (nördliche Oberrheinebene) und die stratigraphische und okologische Verbreitung von *Panthera pardus* [A Late Pleistocene leopard jaw from Geinsheim (northern Upper Rhine Plain) and the stratigraphic and ecological distribution of

118. W. Pei, Carnivora, Proboscidea and Rodentia from Liucheng *Gigantopithecus* Cave and other caves in Guangxi. *Memoirs of Institute of Vertebrate Palaeontology and Palaeoanthropology, Academia Sinica* **18**, 1–119 (1987).

119. C. K. Hu, T. Qi, *Gongwangling Pleistocene Mammalian fauna of Lantian, Shaanxi* (Palaeontologia Sinica, New series C, Science Press, 1978), vol. 21.

120. W. Z. Pei, On the Carnivora from Locality 1 of Choukutien. *Palaeontol. Sin.* **8**, 1–217 (1934).

121. Q. Jiangzuo, Y. Wang, J. Ge, S. Liu, Y. Song, C. Jin, H. Jiang, J. Liu, Discovery of jaguar from northeastern China middle Pleistocene reveals an intercontinental dispersal event. *Historical Biology* **35**, 293–302 (2023).

122. H. W. Tong, B. Zhang, X. Z. Wu, S. M. Qu, Mammalian fauna of Middle Pleistocene Bailongdong site. *Acta Anthropologica Sinica* **38**, 613–640 (2019).

123. B. Zhang, S. L. Zou, X. Chen, K. L. Zhao, J. Wen, L. Deng, H. W. Tong, Mammalian fossils from Yangjiawan Cave 2 of Pingxiang, Jiangxi Province and their age estimation. *Quat. Sci.* **37**, 155–165 (2017).

124. Q. G. Jiangzuo, B. Zhang, L. Deng, X. Chen, J. Wen, H. W. Tong, "Fossil Carnivora (Mammalia) from Yangjiawan Cave 2, Pingxiang, Jiangxi, with remarks about the tooth identification of quaternary carnivores" in *Proceedings of the Sixteenth Annual Meeting of the Chinese Society of Vertebrate Paleontology*, W. Dong, Ed. (China Ocean Press, 2018), pp. 119–146.

125. W. Liu, M. Martinon-Torres, Y. J. Cai, S. Xing, H. W. Tong, S. W. Pei, M. J. Sier, X. H. Wu, R. L. Edwards, H. Cheng, Y. Y. Li, X. X. Yang, J. M. de Castro, X. J. Wu, The earliest unequivocally modern humans in southern China. *Nature* **526**, 696–699 (2015).

126. J. Y. Liu, L. T. Zheng, Q. Q. Xu, C. K. Sun, J. Y. Lv, X. C. Xie, Study on carnivora fossil remains from the Jinpendong Cave, Wuhu, Anhui. *Acta Anthropologica Sinica* **25**, 227–241 (2006).

127. Y. Zhang, C. Jin, Y. Cai, R. Kono, W. Wang, Y. Wang, M. Zhu, Y. Yan, New 400–320 ka *Gigantopithecus* blacki remains from hejiang cave, chongzuo City, guangxi, South China. *Quat. Int.* **354**, 35–45 (2014).

128. Y. Pan, Y. Zhang, L. Yang, M. Takai, T. Harrison, K. Westaway, C. Jin, Preliminary description of a late Middle Pleistocene mammalian fauna prior to the extinction of Gigantopithecus blacki from the Yixiantian Cave, Guangxi ZAR, South China. *Anat. Rec.*, 10.1002/ar.25200 , (2023).

129. T. Shikama, The Kuzuu Ossuaries: Geological and Palaeontological Studies of the Limestone Fissure Deposits, in Kuzuu, Totigi Prefecture. *Geology* **23**, 1–201 (1949).

130. T. Shikama, G. Okafuji, On some Choukuotien mammals from Isa, Yamaguchi Prefecture, Japan. *Sci. Rep.* **9**, 51–58b (1963).

131. H. Hemmer, G. Schütt, Pleistozäne Leoparden (Panthera pardus) aus Java und Südchina [Pleistocene leopards (Panthera pardus) from Java and southern China]. *koninkl. Nederl. Akademie van wetenschappen* **76**, 37–49 (1973).

132. A. Filoux, C. Lespes, A. Wattanapituksakul, C. Thongcharoenchaikit, Note about new Pleistocene faunal remains from Tham Prakai Phet, Chaiyaphum Province, Thailand. *J. Sci. Technol.* **33**, 378 (2013).

133. A.-M. Bacon, F. Demeter, P. Duringer, C. Helm, M. Bano, V. T. Long, N. T. K. Thuy, P.-O. Antoine, B. T. Mai, N. T. M. Huong, Y. Dodo, F. Chabaux, S. Rihs, The Late Pleistocene Duoi U'Oi cave in northern Vietnam: Palaeontology, sedimentology, taphonomy and palaeoenvironments. *Quat. Sci. Rev.* **27**, 1627–1654 (2008).

134. T. Harrison, The palaeoecological context at Niah Cave, Sarawak: Evidence from the primate fauna. *Bull. Indo Pacific Prehistory Assoc.* **14**, 90–100 (1996).

135. Q. Jiangzuo, J. Liu, J. Wagner, W. Dong, J. Chen, Taxonomical revision of fossil *Canis* in Middle Pleistocene sites of Zhoukoudian, Beijing, China and a review of fossil records of *Canis mosbachensis variabilis* in China. *Quat. Int.* **482**, 93–108 (2018).

136. F. T. Regala, J. L. Cardoso, Vestígios paleontológicos do Algar da Manga Larga [Paleontological remains of Algar Manga Larga]. *Trogle* **5**, 4–17 (2007).

137. H. Jayne, *Mammalian Anatomy, Part I. The Skeleton of the Cat* (Lippincott Company, 1898), vol. 116, pp. 210–212.

138. Z. X. Qiu, T. Deng, B. Y. Wang, A Late Miocene *Ursavus* skull from Guanghe, Gansu, China. *Vert. PalAs.* **52**, 265–302 (2014).

139. J. H. Mazak, P. Christiansen, A. C. Kitchener, Oldest known pantherine skull and evolution of the tiger. *PLOS ONE* **6**, e25483 (2011).

140. L. Werdelin, M. E. Lewis, *Koobi Fora Research Project Volume 7 The Carnivora* (California Academy of Sciences, 2013).

141. D. Geraads, Carnivores du Pliocène terminalde Ahl al Oughlam (Casablanca, Maroc) [Carnivores of the terminal Pliocene Ahl al Oughlam (Casablanca, Morocco)]. *Geobios* **30**, 127–164 (1997).

142. J. Viret, Le lœss à bancs durcis de Saint–Vallier (Drôme) et sa faune de mammifères villafranchiens [The hardened loess of Saint-Vallier (Drôme) and its fauna of Villafranchian mammals]. *Nouv. Arch. Mus. Hist. Nat. Lyon* **4**, 3–67 (1954).

143. D. Geraads, S. Peigné, Re-Appraisal of '*Felis' pamiri* Ozansoy, 1959 (Carnivora, Felidae) from the Upper Miocene of Turkey: The Earliest Pantherin Cat? *J. Mamm. Evol.* **24**, 415–425 (2016).

Panthera pardus]. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen* **2006**, 277–297 (2006).

144. N. Chatar, M. Michaud, V. Fischer, Not a jaguar after all? Phylogenetic affinities and morphology of the Pleistocene felid *Panthera gombaszoegensis*. *Pap. Palaeontol.* **8**, e1464 (2022).

145. H. Hemmer, The evolution of the palaeopantherine cats, *Palaeopanthera* gen. nov. *blytheae* (Tseng et al., 2014) and Palaeopanthera pamiri (Ozansoy, 1959) comb. nov. (Mammalia, Carnivora, Felidae). *Palaeobiodiversity Palaeoenvironments* **103**, 827–839 (2023).

146. Q. Jiangzuo, L. Li, J. Madurell-Malapeira, S. Wang, S. Li, J. Fu, S. Chen, The diversification of the lynx lineage during the Plio-Pleistocene—Evidence from a new small *Lynx* from Longdan, Gansu Province, China. *Biol. J. Linn. Soc.* **136**, 536–551 (2022).

147. S. Lovari, M. Ventimiglia, I. Minder, Food habits of two leopard species, competition, climate change and upper treeline: A way to the decrease of an endangered species? *Ethol. Ecol. Evol.* **25**, 305–318 (2013).

148. P. J. Buzzard, X. Li, W. V. Bleisch, The status of snow leopards *Panthera uncia*, and high altitude use by common leopards *P. pardus*, in north-west Yunnan, China. *Oryx* **51**, 587–589 (2017).

149. N. P. Koju, P. Buzzard, A. Shrestha, S. Sharma, K. He, J. Li, R. C. Kyes, C. Chen, W. V. Beisch, Habitat overlap and interspecific competition between snow leopards and leopards in the Central Himalayas of Nepal. *Glob. Ecol. Conserv.* **52**, e02953 (2024).

150. S. Lovari, S. Kachel, L. Xueyang, F. Ferretti, "Snow leopard, common leopard, and wolf: Are they good neighbors?" in *Biodiversity of World: Conservation from Genes to Landscapes, Snow Leopards (Second Edition)*, D. Mallon, T. McCarthy, Eds. (Academic Press, 2024), pp. 137–147.

151. GBIF.org, "GBIF Occurrence Download https://doi.org/10.15468/dl.sn4azx." (2021).

152. Wolong National Nature Reserve, "Ten-year monitoring of snow leopard at Wolong" (2019).

153. S. M. Watts, T. M. McCarthy, T. Namgail, Modelling potential habitat for snow leopards (*Panthera uncia*) in Ladakh, India. *PLOS ONE* **14**, e0211509 (2019).