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The cheetah lineage is a group of large, slender, and long-limbed cats with a distinctive skull and dental morphology, of which only the extant cheetah (*Acinonyx jubatus*) is present today. The lineage is characterized by having abbreviated, tall, and domed crania, and a trenchant dentition with a much reduced, posteriorly placed protocone on the upper carnassial. In this article, we report on a new discovery of a Late Pliocene specimen from China with an estimated age of 2.2-2.5 million years, making it one of the oldest specimens known to date. A cladistic analysis confirmed that it is the most primitive cheetah known, and it shares a number of unambiguous derived cranial traits with the Acinonyx lineage, but has more primitive dentition than previously known cheetahs, demonstrating that the many unusual skull and dental characters hitherto considered characteristic of cheetahs evolved in a gradual fashion. Isolated teeth of primitive cheetahs may not be recognizable as such, but can be confused with, for instance, those of leopards or other similar-sized pantherine cats or pumas. The age and morphology of the new specimen supports an Old World origin of the cheetah lineage, not a New World one, as has been suggested. We name the new species Acinonyx kurteni in honor of the late Bjo¨ rn Kurte´n.

A primitive Late Pliocene cheetah, and evolution of the cheetah lineage

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Acinonyx | *Miracinonyx* | Felidae | morphology | systematics

The cheetah lineage (*Acinonyx* sp.) is a group of large, long-limbed felids with small, domed skulls, which lived in open habitats across much of Eurasia in the Late Pliocene-Pleistocene, of which only the species *Acinonyx jubatus* is present today (1–3). *Acinonyx jubatus* is an unusual type of felid with a distinct craniodental and skeletal morphology, and, uniquely among felids, it is anatomically adapted for high-speed pursuit in open landscapes (3–7). Cheetahs are now found almost exclusively on the African grasslands and semideserts (3, 7, 8), but they used to be present in open-forest type habitats in Asia before being exterminated by humans (3, 6, 9). Cheetahs are usually rare in fossil assemblages and are most often found as isolated fragmentary specimens (2, 10–12). In the Plio-Pleistocene of North America, another lineage of cheetah-like cats (*Miracinonyx* sp.) was present, which also had long limbs and small, tall and abbreviated skull shapes (2, 13).

Remains of cheetahs and cheetah-like cats are known from the Late Pliocene (early Villafranchian) to the Late Pleistocene of Africa and Eurasia (*Acinonyx* sp.), and North America (*Miracinonyx* sp.), but complete skulls are very rare and are only known for derived species such as the Late Pleistocene *Miracinonyx trumani* (13), and the giant Eurasian cheetah *Acinonyx pardinensis* from the middle-late Villafranchian (1, 14). Although larger, the latter is morphologically very similar to the extant cheetah, and both species are derived members of the cheetah lineage, whereas more primitive members of this lineage are very poorly known, making hypotheses on the evolution of the many unusual characters in the skull, mandible and dentition tentative. In this article, we present a new discovery from the Late Pliocene of China of a new species of primitive cheetah, whose skull shows a unique combination of primitive and derived characters, and demonstrates gradual evolution of the many derived craniodental traits considered characteristic of cheetah lineage, thus shedding new light on the early evolution of the cheetah lineage. The dentition is far more primitive than in all other cheetah-like cats, raising doubts on the identification of isolated dental finds of large cats from the Pliocene-Pleistocene of Eurasia and Africa, which are often attributed to leopards.

Results

The new specimen of a primitive cheetah consists of an almost complete skull (Fig. 1) from the Late Pliocene, fossiliferous-rich "Hezheng" locality, Linxia basin, South-eastern part of Gansu Province, China (15), with an estimated age of 2.55–2.16 MYA, as indicated by paleomagnetic analysis (16). Thus, it is among the oldest known cheetahs, rivalling other finds, such as European *Acinonyx pardinensis* from the Late Pliocene (middle-late Villafranchian), with an estimated age of ≈2.2 MYA (1, 12, 14), and North African *A. aicha*, with an estimated age of ≈2.5 MYA (17); furthermore, it is from China, not Europe or Africa, as are other very early finds (1, 2, 10, 18). The skull is almost complete except for the occipital condyles, basioccipital region and upper canines. It has undergone very little postmortem distortion, other than the middle and anterior parts of the nasals having been crushed slightly into the nasal cavity, and the dorsal part of the skull having been distorted very slightly to the right hand side. Unlike *A. pardinensis*, the new specimen is no larger than crania of extant cheetahs (Table 1).

Significantly, an unusual combination of characters, hitherto unknown in cheetah-like cats, indicates a basal position for this specimen within the Eurasian-African cheetah lineage. Numerous unambiguous synapomorphies identify this skull as a cheetah-like cat (Fig. 2), and at least three unambiguous synapomorphies identify the current specimen as belonging to the lineage of the true cheetahs (*Acinonyx* sp.): a very wide braincase relative to skull length; enlarged frontal sinuses; and a large P^3 parastyle. It also has a well developed P^4 ectoparastyle, as in other *Acinonyx* sp., in particular *A. jubatus*, but this is a slightly more variable character. As in other *Acinonyx* sp., the enlarged P^4 is situated such that its aboral edge is markedly anterior to the aboral rim of the orbital aperture, which may or may not have evolved convergently in *M. trumani*, because of its absence in *M. inexpectatus*. Although the canines are not preserved, the alveoli and root size indicates a small upper canine, similar to those of other *Acinonyx* sp. and *M. trumani*. The postcanine dentition is surprisingly primitive for a cheetah.

Upper premolar teeth of cheetahs are instantly recognizable from those of all other Eurasian-African felines from the Pliocene-Pleistocene, owing to several unique apomorphies

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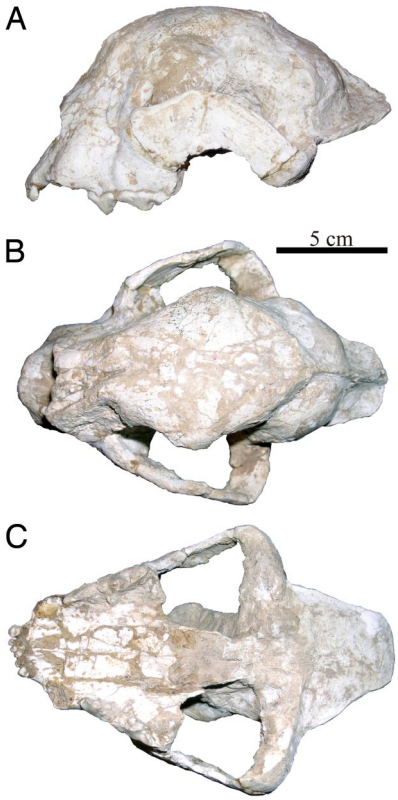

Fig. 1. Holotype of *A. kurteni*, n. sp. SHNM8.1.07 (Shanghai Science and Technology Museum; People's Republic of China) in lateral (*A*); dorsal (*B*); and ventral (*C*) views.

(Figs. 2 and 3). A highly diagnostic feature of all cheetah-like cats is the reduction of the P^4 protocone and frequent absence of a protocone cusp, culminating in the extant cheetah, where it is often little more than a lingual bulge. Protocone position distinguishes *Miracinonyx* sp. from most *Acinonyx* sp., because in *Miracinonyx* sp. it is situated at the normal position for felids, medial to the parastyle or parastyle/paracone junction, whereas in *Acinonyx* sp. it is situated posteriorly to the parastyle/paracone junction (Fig. 3 *D* and *E*). Upper premolars in cheetahs are also more slender and blade-like than in other large felids. This unique and easily identifiable P^4 character combination is ubiquitously used to identify isolated carnassials as belonging to

Table 1. Some numerical values (in millimeters) of the skull of *Acinonyx kurteni*, n. sp. SHNM8.1.07

Characteristic	Measurement
Greatest skull length	184.6
Condylobasal length	166est
Rostrum width	52.0
Infraorbital width	55.2
Interorbital width	47.6
Postorbital constriction	54.4
Zygomatic width	129.4
Greatest nasal length	55.9
Width of braincase	67.4
Palatal length	71.2
Palatal width across P^4	81.7
Pterygoid fossa width	24.4

Condylobasal skull length was estimated based on comparisons with extant *A. jubatus*.

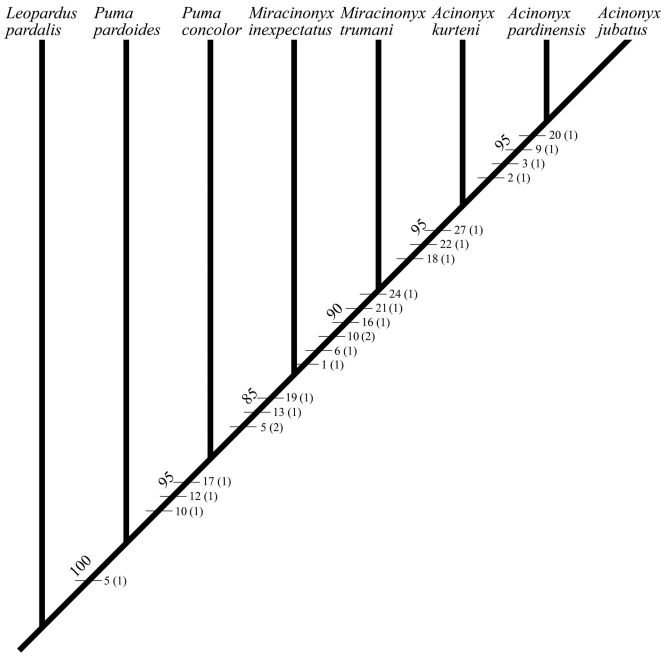

Fig. 2. Phylogenetic relationships of the *Miracinonyx–Acinonyx* lineage; numbers along stems are bootstrap values (1,000 replications), with characters and character states listed along stems to indicate node-based synapomorphies (see *SI Appendix*). Unambiguous synapomorphies of the included groups are: *Puma*+*Miracinonyx*+*Acinonyx*: posterior nasals wide. *P. concolor*+*Miracinonyx*+*Acinonyx*: anterior edge of P^4 at level with anterior edge of orbital aperture; frontals above orbits square or concave; zygomatic arch posterior to postorbital process tall. *Miracinonyx*+*Acinonyx*: posterior nasals very wide, often almost square; premaxilla-maxilla suture relative to gumline not steeply inclined (typically 65–75°); greatly reduced P^4 protocone, often lacking cusp. *M. trumani*+*Acinonyx*: greatly reduced preglenoid process; single mental foramen; anterior edge of P^4 distinctly anterior to orbital aperture; tall, vaulted skull (height at mid-skull typically 45–50% of condylobasal skull length); reduced C_1; large, pointed and trenchant P_3 paraconid. *Acinonyx*: very wide braincase (typically 35–42% of condylobasal skull length); large P^3 parastyle; distinctly inflated frontal sinus. *A. pardinensis*+*A. jubatus*: muzzle in dorsal view distinctly tapering toward premaxilla (triangular profile); frequently double infraorbital foramen; distinctly posteriorly truncated, even V-shaped frontal-maxilla suture; P^4 protocone posterior to the parastyle/paracone junction.

Acinonyx sp. in the Eurasian and African Pliocene-Pleistocene. The new Chinese cheetah demonstrates that the unusual cheetah-like skull morphology precedes the development of the highly sectorial P^4, because it has a prominent, aborally situated and cusped P^4 protocone (Fig. 3*F*), like other felines (Fig. 3 *A–C*), and the shape of P^4 is also typical of that of other felines in being heavy relative to length, rather than slender, as is typical of *Acinonyx* sp. The Late Pliocene *Acinonyx aicha* also has a more primitive, aborally situated P^4 protocone (17), although it is distinctly more reduced than in the Chinese cheetah, indicating that reduction of protocone size and its posterior shift were two separate events in cheetah evolution.

Bivariate and multivariate analyses on 33 linear metric variables corroborate the unusual combination of craniodental traits in the new Chinese cheetah, which shows a clear tendency in cranial morphology to modern African cheetahs (*A. jubatus*), although there are also distinct differences between the two species; the morphology of the P^3 and P^4 in the Chinese cheetah, however, are far more characteristic of pumas or leopards (see *SI Appendix*). The unique combination of primitive and derived traits collectively identify the new Pliocene Chinese find as the most primitive cheetah known to date, and demonstrates gradual evolution of the many derived traits characteristic of later

EVOLUTION

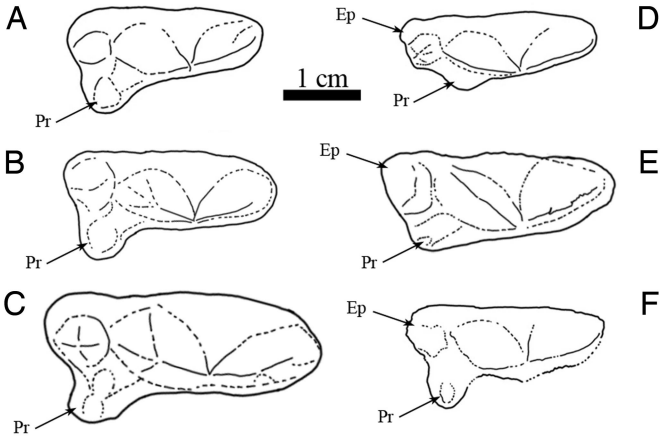

Fig. 3. Comparative morphology of upper carnassials (P^4) in occlusal view. (*A*) Extant puma (*Puma concolor*; NRM595501 ♀). (*B*) Indian leopard (*Panthera pardus fusca*; BM33.2.4.1 ♂). (*C*) Asiatic lion (*Panthera leo persica*; BM31.1.5.1 ♂). (*D*) extant cheetah (*Acinonyx jubatus*; CN3793 ♂). (*E*) Giant Eurasian cheetah (*Acinonyx pardinensis*; MNHN no number). (*F*) Pliocene Chinese cheetah (*A. kurteni* SHNM8.1.07). Ep, ectoparastyle; Pr, protocone.

species. We name it *Acinonyx kurteni* in honor of the world renowned Finnish paleontologist Björn Olof Lennartson Kurtén (1924–1988), in commemoration of his great contribution to carnivore paleontology. Evidently, in the Late Pliocene, several morphological grades of cheetah evolution were present in Eurasia and Africa, because most hitherto-known African and European finds, for instance of *A. pardinensis* and finds attributed to the extant cheetah, appear virtually modern in craniodental morphology, whereas *A. aicha* and in particular *A. kurteni* represent more primitive forms.

A. kurteni may be identified by the following unique combination of characters: Late Pliocene cheetah with a cranium of comparable size to the extant cheetah (*Acinonyx jubatus*); skull shape very tall and abbreviated with domed and lateromedially very wide braincase; frontal sinuses distinctly enlarged and nasal aperture large; occipital crest strongly developed and occipital area distinctly more posteriorly inclined than in other *Acinonyx* sp.; frontal and jugal postorbital processes moderately developed; posterior edge of maxilla broadly rounded; frontals gently concave around middle; posterior temporal bar to occipital crest very short; snout rectangular, not tapering in dorsal or ventral view; zygomatic arch dorsoventrally taller than in *A. jubatus*; moderately developed postglenoid process and weakly developed preglenoid process; nasals posteriorly wide; single infraorbital foramen; incisors small and based on alveolar dimensions, C^1 appears to have been of moderate size with an oval cross-section; entire P^3 anterior to infraorbital foramen; P^3 sectorial with large parastyle; large, wide and nonsectorial P^4 with large, cusped and anteriorly placed protocone; anterior edge of P^4 anterior to infraorbital aperture and far anterior to orbital aperture; P^4 ectoparastyle well developed.

Upper premolar morphology in *A. kurteni* deviates significantly from those of extant cheetahs and bears a much closer resemblance to those of other large cats (Pantherinae and the puma; see *SI Appendix*). Had such carnassials been found isolated, as is the case for most fossil finds, it is doubtful that they would have been recognized as belonging to a cheetah; more likely, they would have been attributed to leopards or other similar-sized pantherine cats. This indicates that at least some of the many fragmentary finds from the Eurasian-African Pliocene-Pleistocene identified as medium-sized pantherine cats, for instance leopards, could belong to primitive cheetahs instead (see also ref. 18 for discussion of possible chimera specimens of cheetahs and leopards), and that primitive cheetahs may not be as rare in faunal assemblages as traditionally believed, although this remains to be verified. It also raises concerns on biogeographical, ecological, and faunistic hypotheses based on fragmentary material, because of the potential for misidentification of early members of phyletic lineages, which have yet to evolve the derived dental characters characteristic of later members of such lineages. Owing to the cheetah lineage being highly adapted for high-speed pursuit in open territory, the presence of cheetahs in Pliocene-Pleistocene deposits has often been used to infer an open-type habitat with shrub and grassland, whereas the presence of leopards is indicative of more wooded habitats (1–3, 6, 19–23). In accordance with the above, it has recently been suggested that some purported discoveries of leopards may instead be of primitive pumas (24), which casts doubts on evolutionary and biogeographical hypotheses of pantherine and puma lineage distribution.

Owing to its unusual morphology, inferences of relationships of the extant cheetah have been murky, and traditionally, it has been assigned to its own subfamily, the Acinonychinae (25). Modern analyses have all favored a close relationship with the puma within a larger group of small felid species (26–28). The relationship of the Eurasian-African *Acinonyx* lineage and the American *Miracinonyx* lineage has been a subject of debate, with morphological data favoring a relationship of the two, albeit not necessarily a close one, with the early puma, *Puma pardoides* (also known as *Panthera schaubi*) (24, 29) as a possible common ancestor; and molecular data favoring two separate lineages (27), implying great convergence of many craniodental and postcranial traits. The results of the current study indicate a close relationship of the two lineages and that *P. pardoides* may be a possible ancestor of both but also demonstrate that the late Rancholabrean (Wisconsian) *M. trumani* was much more craniodentally derived and cheetah-like and shares a large number of craniodental synapomorphies with *Acinonyx* sp., which are not present in *M. inexpectatus*. The fossil record of the extant puma (*Puma concolor*) in the USA is only ≈400 KYA (21, 30, 31), and thus, the inference that *Miracinonyx* sp. and the puma shared a last common ancestor in the Americas in the mid-late Pliocene (27, 28) is not supported by paleontological evidence. The presence of primitive pumas, such as *P. pardoides*, in the Eurasian Late Pliocene favors a Eurasian-African origin of the *Puma–Miracinony–Acinonyx* group (24), with separate dispersals of the former two into the Americas, perhaps twice in *Miracinonyx*, as discussed by ref. 31. The above is supported by the unusual combination of primitive and derived characters in *A. kurteni*, and, accordingly, a New World origin of cheetahs (as suggested in refs. 28 and 32) appears unlikely. Although our analysis of craniodental characters favors one evolutionary lineage of cheetah-like cats, and indicates a close relationship of *Miracinonyx*, at least *M. trumani*, to *Acinonyx*, *A. kurteni* has a number of primitive traits, notably more primitive dentition, that could indicate two separate lineages, each culminating in craniodentally highly derived predators, and thus, we would not at this time entirely rule out that the highly cheetah-like morphology of *M. trumani* evolved convergently in the Americas, as suggested by ref. 27.

Materials and Methods

Characters of the skull and mandible were scored in two species of extant felids [puma (n = 23) and cheetah (n = 12)] and 4 species of extinct cheetahs and cheetah-like felids, using the extant ocelot (n = 11) as outgroup. All morphometric characters were found by statistical (MANOVA, post hoc Tukey HSD) tests on angular transformed morphometric ratios, to restore normality to the variables (33), and character states were accepted as dissimilar only at $P < 0.001$ and with either no overlap (discrete) or overlap only on extreme

outlier specimens (<5% of sampled population). Phylogenetic analysis (heuristic search) and bootstrap analysis (1,000 replications) were performed in Phylip ver. 3.6 (34, 35). We also conducted a variety of bivariate and multivariate statistical analysis, comparing the proportions of *A. kurteni* to the extant cheetah, puma, and pantherine felids (clouded leopard, jaguar, lion, leopard, tiger, snow leopard) (see *SI Appendix*). Institutional abbreviations used in Fig. 3 are as follows: BM, Natural History Museum, London; CN, Zoological Museum, Copenhagen; NRM, Naturhistoriska riksmuseet, Stockholm; MNHN, Museum National d'Histoire Naturelle, Paris; SHNM, Shanghai Science and Technology Museum.

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