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Abstract: The cheetah *Acinonyx pardinensis* apparently inhabiting most open habitats of the Old World in the whole Villafranchian up to the lower Middle Pleistocene. Remains of this species have been found at several sites in Europe, northern China and India. Fossils cheetahs also exist in some African faunas of Lower Pleistocene or lower Middle Pleistocene age but are still concealed under other generic and specific names. The distributional history and the origin of the modern cheetah are completely unknown at present.

Le guépard *Acinonyx pardinensis* occupe apparemment la plupart des habitats ouverts de l'Ancien Monde pendant tout le Villafranchien jusqu'au Pléistocène Moyen Inférieur. Les restes de cette espèce ont été trouvés dans plusieurs sites d'Europe, au nord de la Chine et en Inde. Les fossiles de guépards existent également dans des faunes africaines de l'âge du Pléistocène Inférieur ou au Pléistocène Moyen Inférieur mais sont encore cachés sous d'autres genres et noms d'espèce. La distribution historique et l'origine du guépard actuel sont totalement inconnues.

# Fossil History of Living Felidae

Helmut Hemmer

To understand the population decline observable in many cat species today, it is not only necessary to know the effects of direct influences by man but also the ecological adaptations reached in the course of the evolution of these forms. The present distribution of any one species cannot be seen as more than one moment of biogeographical situation, one which has perhaps changed many times in the past. We may be sure that not all restrictions of cats, known for the span of man's history, are due to the activities of this higher primate species alone. Changes in ecosystems by climatic fluctuations determined real reductions and so led to relic populations or gave some species the opportunity to enlarge their distributional ranges considerably. The knowledge of a species' history may also help us to interpret better its present situation for conservational purposes. So it seems to be of some interest, not only for paleontologists, to present here a short account of cat distribution in the Pleistocene and the facts known at present on the evolution of the living cat species.

The greatest difference between maximal and recent distribution in all cats may be found in the lion. Today restricted to parts of Africa and a small population in India, and known from historical times in most of the African and southwestern Asiatic regions, lions once lived in the Upper Pleistocene in the open landscapes of Europe, southern Asia including Ceylon, Siberia and North and Middle America down to the northwest of South America. The known history of this species begins in the lower Middle Pleistocene with fossil remains from Europe, northern Asia and Africa. The oldest documents of the lion in Europe date from the late Cromerian or the onset of the Mindel/Elster glacial. They include two nearly complete skulls from deposits at Mauer in Germany and at Petralona in Greece, numerous mandible and skull fragments from the Mosbach gravels in Germany and some mandible fragments and teeth, as well as postcranial skeleton bones, from a few other sites (Hemmer and Schutt, 1970; Hemmer, 1974). These very large lions of the European lower Middle Pleistocene are characterized by a skull which still resembles, in its frontal proportions, more that of the other species of the subgenus *Panthera* than that of Upper Pleistocene European lions or of modern lions. In the shape of their mandibular bone early European lions of the Mosbach gravels are strictly comparable to the somewhat smaller and presumably oldest lion's fossil presently known, that found in the upper Bed II of Olduvai Gorge in eastern Africa. This lower jaw was originally thought to be possibly related to the tiger (Ewer, 1965) but later was shown to belong to a lion (Hemmer, 1976b; Petter, 1973). Beds II and III of this site are older than the boundary between the Matuyama Reversed and Brunhes Normal epochs on the evidence of geomagnetic polarity measurements (Leakey, 1971). This boundary is dated at about 700,000 years, whereas potassium/argon-dating gave a figure of about 500,000 years for the upper Bed II (Oakley, 1968). Independently of this obvious discrepancy in absolute dating by different methods, the Olduvai mandible must be considerably older than the European lion remains, as the Mauer deposit and the main fauna of the Mosbach gravels, according to corresponding paleomagnetic dates, are younger than the boundary in question (Koci, Shirmer and Brunnacker, 1973). Deposits

yielding lion fossils in the Kolyma region in northeastern Siberia possibly correspond by relative chronology to the Tiraspol faunal complex of the late lower Middle Pleistocene age (Vangenheim and Sher, 1970; Vereshchagin, 1971); therefore, they are younger than the first European lions. This species cannot have originated in Europe where the jaguarlike *Panthera gombaszoegensis* lived from upper Villafranchian time to the lower Middle Pleistocene (Hemmer, 1971d) but was a newcomer in the Cromerian interglacial. These datings suggest the evolution center of the species *Panthera leo* is to be found in the later Lower Pleistocene or early lower Middle Pleistocene of Africa. Other African lion remains of a possibly comparable age are known from Swartkrans and Kromdraai in the south of the continent (for the problem of dating these deposits see: Oakley, 1968; Wright and Skaryd, 1972; Hemmer, 1973; Maier, 1973; Howells, 1973).

Even these early lions show differences between the hitherto known forms of Africa, Europe and northern Asia in absolute size and in some proportions of the teeth. These possibly took place as a result of genetic drift in the spreading of the species over the continents (Hemmer, 1974). At present we have very few lion remains dating from the upper Middle Pleistocene but numerous ones from the Upper Pleistocene. This fossil material indicates that there was local evolution in the different parts of the whole distributional area, which was influenced and piloted to a considerable extent by the changing climatic events of the Pleistocene. This led to the different subspecies of lions, such as the famous European cave lion, *Panthera leo spelaea*, and the American lion, *Panthera leo atrox*, at the end of this epoch (Hemmer, 1974). It is supposed that a main factor determining this evolution was the ecological effect of the Riss or Illinoian glacial at the end of the Middle Pleistocene. In Europe and northern Asia the lion's distributional area was apparently partially split up into some refugial centers by ice covering wide regions in the north of central and eastern Europe, by the Caspian transgression enlarging the Caspian Sea far to the north and perhaps also by the damming up of a gigantic ice lake in the western Siberian lowlands with possible connection to Lake Aral. At the same time the marine regression resulted in a broad land connection in the region of the Beringian Sea between northern Asia and Alaska. So the eastern Siberian population of the lion got the chance to spread over the partially ice-free Alaskan region of the North American continent (Hemmer, 1974). Thus began the history of the American lion. This very large form was first described as a separate species, *Panthera atrox*, and later was thought to be related to the jaguar (Simpson, 1941); however recently different authors have simultaneously shown (Vereshchagin, 1971; Hemmer 1971d, e, and 1974) that in fact it is a true lion of the *spelaea*-group distributed in the Upper Pleistocene over the whole northern holarctic region. Whereas only an uncertain find from a supposed Illinoian deposit in Alaska, a specimen from a presumably Illinoian fauna in Idaho and a lion's fossil from the Sangamon interglacial age in Kansas record the species' existence before the ultimate glacial in North America (Harrington, 1969; Kurten, 1973b), a rich documentation exists from the last period of the Upper Pleistocene. *Panthera leo atrox* obviously reached Middle

America at this time as well and spread down to Peru in the northwest of the South American continent (see distributional map given by Harington, 1969). Then the distributional decline of the lion took place rapidly in the northern holarctic at the end of the Upper Pleistocene and at the beginning of the Holocene when, with rising temperatures, the open landscapes of the lion's favored habitat disappeared more and more.

The lion's history is a model for mainly local evolution guided by the ecological events of the Pleistocene and leading, after the initial spreading over the distributional area, to the ultimate diversity of subspecies found in the Upper Pleistocene and in the Holocene. A comparable pattern of evolution holds good for other cat species. The oldest fossil documents of the leopard (*Panthera pardus*) seem to be an upper carnassial from Jharakki (determined as *Sivafelis potens* by Pilgrim, 1932, a species, the holotype of which belongs to *Acinonyx pardinensis* as shown by Schutt, 1970) and a mandibular fragment (B.M. 16537 a; *Felis* non det. allied to *F. pardus* Lydekker, 1884; *Felis* aff. *pardus* Matthew, 1929; *Sivafelis potens* Pilgrim, 1932; *Panthera csomai* Kretzoi, 1929). Both originate in the Pinjor zone of the Indian Siwaliks paralleling in age the upper Villafranchien Djetis complex of Java (von Koenigswald, 1968). The relatively long P3 of this mandible reveals the situation in *Panthera gombaszoegensis* and *Panthera onca* and therefore suggests a very primitive form of the leopard. The upper carnassial resembles in size and proportions a tooth from the lower Middle Pleistocene Trinil complex of Djeruk in Java. In Africa the first leopards are also found in the lower Pleistocene or lower Middle Pleistocene according to the moot dating of the South African deposits in question (Ewer, 1956; Sterkfontein, Swartkrans; see e.g., Oakley, 1968; Wright and Skaryd, 1972; Hemmer, 1973; Maier, 1973; Howells, 1973).

In the Middle Pleistocene several leopard remains are known for eastern and southeastern Asiatic regions. Teeth from southern China are comparable with teeth of the recent subspecies *Panthera pardus sinensis* and have led to the supposition of local evolution from Middle Pleistocene times up to the present in this area (Hemmer and Schutt, 1973). Apparently very large leopards occurred in the Upper Pleistocene Ngandong fauna of Java where very large tigers of Chinese affinities were also found (Hemmer and Schutt, 1973). Several fossil mandibular remains from Japan, Choukoutien in northern China and from Java which were originally thought to come from large leopards in fact belong to small tigers (Hemmer 1967a, 1968a; Hemmer and Schutt, 1973). In Pleistocene faunas of Europe several different forms of leopards may be distinguished. Their spreading over this subcontinent can at present be dated in the lower Middle Pleistocene and obviously occurred somewhat earlier than the invasion of the lion in this country (Hemmer and Schutt, 1970). Mandibular remains of some of these early European leopards show affinities in their shape with Pleistocene North American jaguars. It is to be supposed that another subspecies was existent from the end of the Middle Pleistocene or the beginning of the Upper Pleistocene in south and southeastern European areas. Leopards of this group apparently spread from this center in the Mediterranean region after the Riss glacial over some central European areas (Hemmer, in press). The modern leopard subspecies found in the Caucasus is represented by some remains from a cave fauna at Rubeland, Harz (Germany) which are to be dated not younger than in the Podhradem(Hengelo-) interstadial of the middle Wurm glacial (Schutt, 1968, 1969; Hemmer 1971b). This suggests a distributional connection of leopard populations from central and eastern Europe sometime at the end of the Upper Pleistocene.

The history of the jaguar (*Panthera onca*) in North America dates back to the late Blancan parallel with the late Villafranchian of the European Lower Pleistocene (Kurten, 1937b). From the base of the Blancan deposits in Crosby County, Texas a felid skull was described as *Panthera paleoonca* (Meade, 1945). However it could be shown that this is not a true jaguar or other pantherine cat but belongs to the extinct genus *Dinofelis* which was, ecologically speaking, the forerunner of the genus *Panthera* in the Pliocene and Lower Pleistocene of Africa, Europe, Asia and North America (Hemmer, 1973; Kurten, 1973b). In the course of the Pleistocene a gradual size decrease from earlier to later forms was shown for the North American jaguars. "The earlier form also has relatively longer limbs and less shortened hands and feet" (Kurten, 1973b). Middle Pleistocene remains of South American jaguars were found in the Tarija region in Bolivia (Hoffstetter, 1952). In the Upper Pleistocene the species is well documented in Argentina. Gigantic jaguars lived at this time in the most southern parts of the South American continent (Cabrera, 1934).

On the basis of the dating of the earliest members of the subgenus *Panthera*, it can be supposed that the jaguarlike ancestor of this subgenus spread over Africa, Europe, southern and northern Asia and North America in the middle Lower Pleistocene. Then the differentiation into the living species took place in the second phase of the Lower Pleistocene. At the same time the first members of the monospecific subgenus *Tigris* are known from southeastern Asia. *Panthera tigris* is documented with a mandibular fragment from G. Boetak in the Lower Pleistocene Djetis complex of Java (von Koenigswald, 1934) and with some teeth of the first dentition from the same stratigraphical complex (Kurten, 1962). A complete skull of a very primitive small tiger from a northern Chinese deposit showing some jaguarlike features and originally described as a separate species, *Panthera palaeosinensis* (Zdansky, 1924), probably also dates from the early Pleistocene (Hemmer, 1967a). A relic population of such small tigers comparable in size to the recent Bali population lived in Japan up to the Upper Pleistocene (Hemmer, 1968a). The study of the good documentation of fossil tigers in Java from the lower Middle Pleistocene on led to the supposition that, when this island was connected with the Asiatic continent by glacial marine regressions, genetic exchanges of the Javanese tiger population with populations on the continent occurred, at times interrupting the local evolution of tigers in Java (Hemmer, 1971a). Except for the Pleistocene occurrence of the species in Japan, the presently known fossil remains of the tiger show no other distribution than that known from the Holocene.

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The fossil record of the snow leopard (*Uncia uncia*) is limited to some Upper Pleistocene remains from Altai caves (Brandt, 1970; Tscherski, 1892). Mandibular fragments from the Middle Pleistocene of Choukoutien in northern China compared with this species by some authors (Pei, 1934; Kurten, 1960) may belong to true leopards (Hemmer, 1968b, 1971b). Fossil remains of the clouded leopard (*Neofelis nebulosa*) were found with a single lower premolar at Sangiran, Java, presumably in the Lower Pleistocene Djetis complex, and with several teeth in Middle Pleistocene deposits of southern China and of North Vietnam (Hemmer and von Koenigswald, 1964; Kahlke and Nguyen van Nghia, 1965). These teeth differ from recent ones in being somewhat less specialized. Therefore the Middle Pleistocene clouded leopards of southern China were described as a chronological subspecies, *Neofelis nebulosa primigenia*, which can be regarded as the ancestor of the recent subspecies of these regions (Hemmer and von Koenigswald, 1964; Hemmer and Schutt, 1973; Figure 1). From Post-pleistocene, Neolithic cave deposits at Sampung, the former existence of this species in Java, where it is not extant at present, is also documented (Hemmer and von Koenigswald, 1964).

The several species of small cats inhabiting the southeastern Asiatic region are poorly represented in a fossil state. Some mandibles of the leopard cat (*Prionailurus bengalensis*) from the same cave deposits at Sampung in central Java indicate the presence of a very small form of this species (Hemmer, 1971c). The occurrence of this cat in the Sunda Islands dates back at least to the lower Middle Pleistocene with some remains from the Djetis or the Trinil complex of Java (Brongersma, 1935; Hemmer, 1971c). Several remains of cats from Choukoutien and other Chinese localities were assigned to *Prionailurus bengalensis* mainly for geographical convenience (Pei, 1934).

In Sampung, besides the tiger, leopard, clouded leopard and leopard cat, a very small subspecies of the jungle cat (*Felis chaus*) is also recorded with the fragment of a lower jaw (Hemmer, 1971c). The occurrence of this species in the early Holocene of Java, in a region recently not inhabited by jungle cats, is suggestive of the identification of some small cats of the Sunda Islands described under different names as *Felis undata*, *Felis megalotis*, *Felis deliensis* previously regarded as leopard cats, domestic cats or hybrids between domestic cats and jungle cats by different authors (Brongersma, 1935; Hemmer, 1971c). In the western part of the Eurasiatic continent the occurrence of the jungle cat was supposed for the lower Middle Pleistocene cave deposit at Petraion, Greece (Sickenberg, 1971) for travertines from the Upper Pleistocene Eemian interglacial at Unterturkheim, Germany (Helbing, 1934) and for some Upper Pleistocene deposits in France (Koby, 1960). The identifications of these remains, which may belong to *Felis chaus*, seem, however to need confirmation.

The genus *Felis* is represented in the Lower Pleistocene of Europe by *Felis lunensis*, commonly held to be an ancestor of the wild cat, *Felis silvestris*, which occurs in the upper Middle Pleistocene and in the Upper Pleistocene of Europe with very large specimens (Kurten, 1965a, 1968). Possible transitional forms were described from some sites dating from the lower Middle Pleistocene (Kurten, 1968; Sickenberg, 1971). The mean size of *Felis silvestris* in Europe as well as in Palestine declined to a high degree in postglacial times (Kurten, 1968). No fossils seem to be known up to the present from the desert-living species of the genus *Felis*, that is, *Felis margarita*, *Felis bieti* and *Felis nigripes*.

Identification of Pallas' cat, *Otocolobus manul*, in the Wurm glacial in Europe has been seriously doubted (Kurten, 1968). This species however seems to have been clearly identified in the early Middle Pleistocene at Kamyk (Kurten, 1968). The serval (*Leptailurus serval*), presumably related with the *Felis-Lynx*-group is documented with a form somewhat different from the recent ones in the Lower Pleistocene or lower Middle Pleistocene of South Africa (Broom, 1973, 1939). Some later South African remains also are allocated to this species (Ewer and Singer, 1956).

Members of the genus *Lynx* are richly documented throughout the Pleistocene in Europe, Asia and North America. The history of this genus may have begun in the late Pliocene of North America with very primitive lynxlike cats (*Lynx rexroadensis* and some of the material assigned to "*Felis*" *lacustris*; Savage, 1960; Kurten, 1968). At the end of the Pliocene and in the Lower Pleistocene, Europe and northern Asia were also inhabited by lynxes (*Lynx issiodorensis*) with the body proportions of normal cats but apparently already with a short tail (e.g., Kurten, 1968). From such basal forms the separation of some speciation centers in the Middle Pleistocene by the glacial ecological events apparently led to the recent species *Lynx lynx*, *Lynx pardina*, *Lynx canadensis* and *Lynx rufus*. The pardeii lynx seems to be the original western European form that found refuge with diminishing body size in the Iberian peninsula after the last glacial (Kurten, 1968; see also discussion in Bonifay, 1971). On the other hand the base of the northern lynx in Europe seems to have been in the southeast and in the east of this subcontinent (Kurten, 1968) where the transition to the Asiatic lynxes of the same species occurs. In the late Middle Pleistocene of Florida lived now extinct subspecies of bobcat (*Lynx rufus koakudsi*) which equaled the Canadian lynx in size (Kurten, 1965b).

In the south of the North American continent, besides the bobcat, remains from other small cat species were also found in Pleistocene deposits. Jaguarundi-like fossils were described from three localities in Florida and from one site in Georgia (Ray, 1967), while the Florida sites probably all date from the Wisconsin (Kurten, 1965b). A fragmentary mandibular ramus from Ladds, Georgia indicates a skull size comparable to that of recent bobcats but larger than in recent jaguarundis (Ray, 1967). In a new paper (1976) states that "Late Quaternary fossils from southeastern United States previously assigned to *Felis yagouaroundi* and new records of small felines from three additional localities represent an extinct new species," called *Felis amnicola*. This form shows characters of the margay and the oncilla as well as the jaguarundi. Its relationship with these modern species is not yet clear. Fossil material from the Cita Canyon quarries, Texas, of Blancan age has been described as belonging to an aberrant species, *Puma studeri*, perhaps ancestral to modern pumas, but with some cheetahlike features (Savage, 1960). At two sites in Florida the ocelot (*Leopardus pardalis*) is also recorded in fossil state (Kurten, 1965b).

Pumas were widely distributed in the Pleistocene of both North and South America (e.g., Simpson, 1941; Hoffstetter, 1952; Savage, 1960). It is suggested that this species is derived autochthonously in North America from some earlier cats assigned to the genus *Pseudailurus* (Savage, 1960). Cheetahs themselves are known with a gigantic species apparently inhabiting most open habitats of the Old World in the whole Villafranchian up to the lower Middle Pleistocene. Remains of this species, *Acinonyx pardinensis*, have been found at several sites in Europe,

northern China and India (Schutt, 1970). Fossil cheetahs of hitherto unknown relationship to the recent species *Acinonyx jubatus* also exist in some African faunas of Lower Pleistocene or lower Middle Pleistocene age but are still concealed under other generic and specific names (Brown, 1937; Petter, 1973). The distributional history and the origin of the modern cheetah is completely unknown at present.

In a new publication Kurten (1976) also argues for an ancestral position of this early pumalike cat to modern pumas but points out an adaptation to a more cursorial mode of predation. Then in 1977 Martin, Gilbert and Adams show that there lived a cheetahlike cat besides the true puma in the late Pleistocene of North America, perhaps derived from Blancan forms related to *studerii*. It will be a task of the future to clarify the evolutionary position of this species.

All other species of modern cats not mentioned here are not yet satisfactorily described from Pleistocene deposits. Otherwise some fossil material, especially from eastern Asiatic sites unidentified at the specific level or described as belonging to separate Pleistocene small cat species, really may belong to some living felids. At present the body of knowledge on the particular species and the number of papers written on their phylogeny seem to be correlated with the body size of the species in question, that is, the larger the species the more papers there are. So a good deal of further work will be necessary to reach a better understanding of the evolutionary and distributional history of all recent cat species.

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