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# Saber-Toothed Cats from the Plio-Pleistocene of Nebraska

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## SABER-TOOTHED CATS FROM THE PLIO-PLEISTOCENE OF NEBRASKA

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*Dinobastis* is reported from the late Pleistocene of Nebraska, and *Smilodon* from the middle through the late Pleistocene. *Ischyrosmilus* is a synonym of *Homotherium*, but *Dinobastis* is not. *Ischyrosmilus* should not be confused with “*Smilodon*” *gracilis*, which is considered an advanced species of *Megantereon*.

† † †

### INTRODUCTION

Blancan through Pleistocene saber-toothed cats are not common in Nebraska. Matthew (1918) made a brief reference to *Smilodon* from the Sheridan Beds near Hay Springs, Nebraska, which he referred to a new species, *S. nebrascensis*. However, he did not figure or describe his new species and it remains a *nomen nudum*. Schultz (1934) only mentioned this record of *Smilodon*, but that genus has been included in a number of subsequent faunal lists (see for instance Schultz and Tanner, 1957). The first paper to include any substantial description and figures of Nebraska sabercats within this age range was by Schultz and Martin (1970). This paper described a new species of scimitar-toothed cat, *Ischyrosmilus crusafonti*, and for the first time recognized that the Blancan sabercat, “*Machairodus*” *hesperus*, was a member of the Eurasian dirk-toothed cat genus *Megantereon*. This assignment was based in part on the recognition of new material of *M. hesperus* in the Broadwater Local Fauna. The present paper is a continuation of our general review of the fossil feloids of Nebraska, and it gives our viewpoints concerning the later saber-toothed cats in North America.

In this paper we intend to evaluate *Ischyrosmilus* in terms of *Homotherium* and *Smilodon gracilis*. We also report on *Smilodon fatalis* from Nebraska and the first record of *Dinobastis serus*.

### “ISCHYROSMILUS”

Schultz and Martin (1970) assigned material from the Blancan Broadwater and Lisco local faunas to the homotherine genus *Ischyrosmilus*. The Broadwater specimens were small and were

made the type of a new species, *I. crusafonti*. There are three other described species in the genus: *I. ischyryus* (probably early Blancan), *I. johnstoni* (possibly late Blancan), and *I. idahoensis* (late Blancan). These taxa seem to cover a time span of about 2.5 million years, and some taxonomic differentiation is possible. Kurtén and Anderson (1980) only recognized the type species, *I. ischyryus*. *Ischyrosmilus crusafonti* compares favorably in size with the skull from Delmont, South Dakota, that was referred to *Ischyrosmilus* by Martin and Harksen (1974). The Delmont skull (Fig. 1) is very small when compared to other material that has been assigned to *Ischyrosmilus*, but is of the right size to occlude with the holotype of *Ischyrosmilus crusafonti*. The presence of *Procastoroides* cf. *sweeti* (ancestral giant beaver) in the Delmont Local Fauna (Martin and Harksen, 1974) suggests that this local fauna is roughly equivalent in age to the Broadwater Local Fauna that produced the holotype of *P. sweeti*, and the absence of the more advanced species *P. idahoensis* would indicate that the Delmont Local Fauna is not as late as the Senecan (Martin and Schultz, 1985).

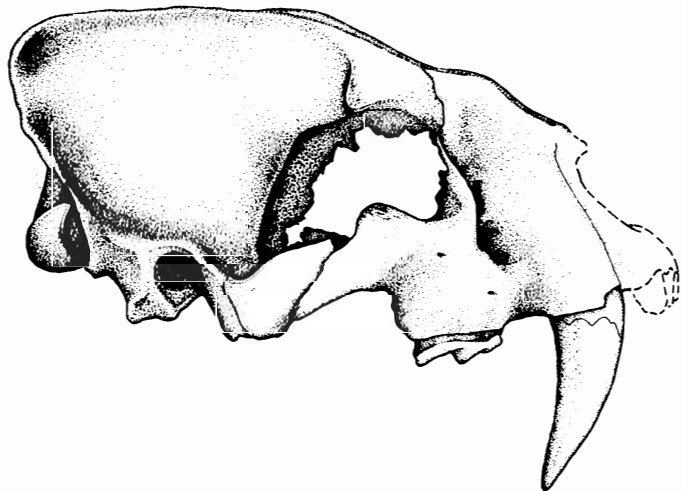


FIGURE 1. Delmont, South Dakota, skull of *Homotherium* based on Martin and Harksen (1974, fig. 5).

The Delmont cranium does not seem to differ in any substantial way from the material of *Homotherium crenatidens* reported by Ballesio (1963), and has in fact been assigned to that species (see Kurtén and Anderson, 1980). The canine is somewhat more slender than in the European specimens, and it resembles more closely the American material of "*Ischyrosmilus*" in this respect. The shape of the canine is much more variable in *Smilodon* than it is among all the canines that have been referred to *Homotherium* and *Ischyrosmilus*. For instance, there is more difference between the two sabers illustrated by Churcher (1984, fig. 9) as *Smilodon neogaeus* than there is between any of the canines that have been referred to *Ischyrosmilus* and those belonging to *Homotherium*. So few complete canines are known from either *Homotherium* or *Ischyrosmilus* that it is probably presumptuous to infer that their variation is distinctive at the specific level, especially since one scimitar-toothed cat (*Nimravides*) seems to have enormous sexual dimorphism (Kitts, 1958; Martin and Schultz, 1975).

The assignment of *Ischyrosmilus* to *Homotherium* has had a varied history. Mawby (1965) maintained the distinction between the two although he indicated that they were probably congeneric. Kurtén and Anderson (1980) listed the Delmont cranium, referred to *Ischyrosmilus* by Martin and Harksen (1974), as *Homotherium*, and it was mapped as such in Rawn-Schatzinger and Collins (1981).

Schultz, Schultz and Martin (1970) accepted Churcher's (1966) assignment of *Dinobastis* to *Homotherium*, but maintained separate origins for *Ischyrosmilus* and *Homotherium* (from different species of *Machairodus*). Schultz and Martin (1970) reaffirmed this same interpretation, citing differences in the development of the flange between the two genera. Martin and Schultz (1975) once again maintained that *Ischyrosmilus* was a separate genus independently derived from *Machairodus*.

In 1979, Martin was able to make direct comparisons with the *Homotherium crenatidens* material reported by Ballesio (1963) from the Villafranchian of Europe. These comparisons convinced him that the separation of the North American *Ischyrosmilus* from *Homotherium* could no longer be maintained (Martin, 1980). Churcher (1984) took exception to this arrangement and stated (Churcher, 1984: 40) the following;

"*Homotherium* is not a possible congener of *Ischyrosmilus*. Last, to my knowledge, the scimitar cats (genus *Homotherium*) have never been intentionally placed in *Ischyrosmilus*, except by Martin (1980), probably because their dental and basicranial characters are essentially dissimilar."

However, Churcher missed a number of references, including Savage and Russell (1983) and de Beaumont (1978), which refer *Ischyrosmilus* to *Homotherium*. Berta and Galiano (1983) referred *Ischyrosmilus johnstoni*, *I. idahoensis* and *I. crusafonti* to *Homotherium*, but synonymized the genotypic species *I. ischyryus* Merriam, 1905, with *Dinobastis* Cope, 1893.

Berta and Galiano (1983) put the type species of *Ischyrosmilus*, *I. ischyryus*, into *Dinobastis*. Berta (1987: 44) gave five characters to unite these taxa: 1) strongly rectangular symphyseal margin; 2) angular process long and bulbous; 3) deeply excavated masseteric fossa; 4) single mental foramen on the flange; and 5) shorter, dagger-like teeth. However, characters 2 and 5 are not known for *Ischyrosmilus ischyryus*. The difference in the form of the flange was noted by Martin and Schultz (1975), but later observations showed that it is encompassed by European *Homotherium* material (Martin, 1980). In many respects, *Homotherium crusafonti* is more like *Dinobastis* (see Fig. 10) than is "*Ischyrosmilus*" *ischyryus*. The character of the masseteric fossa and the mental foramen are probably diagnostic for *Dinobastis* but *I. ischyryus* is not greatly different (in these features) from the species of "*Ischyrosmilus*" — *I. idahoensis*, *I. johnstoni* and *I. crusafonti* — referred to *Homotherium* by Berta and Galiano (1983).

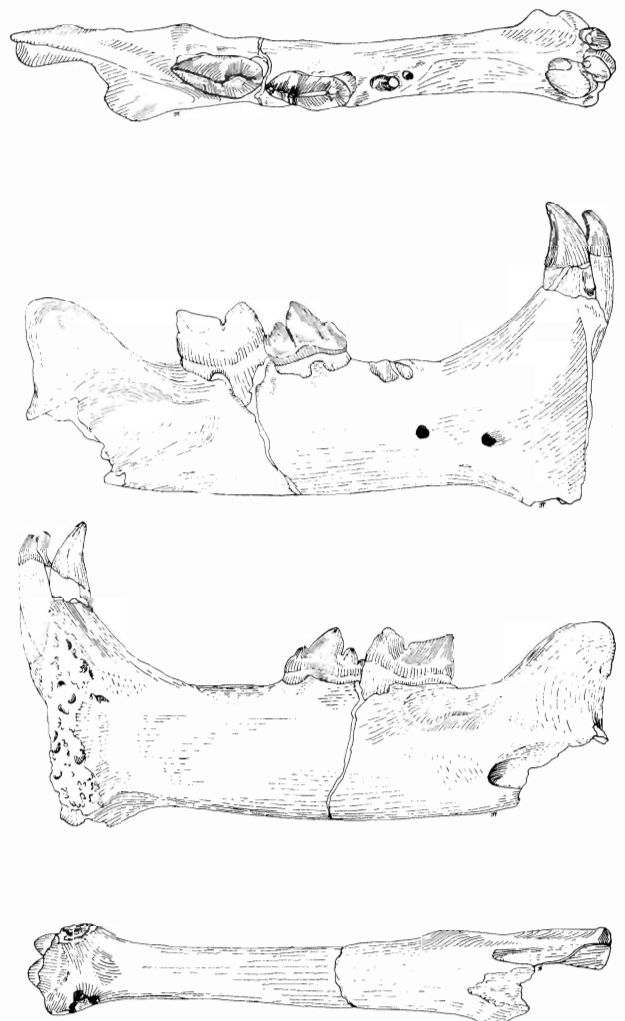


FIGURE 2. *Megantereon gracilis* (*Uncia mercerii* Cope, 1895) right ramus, dorsal, lateral, medial and ventral views. Line = 5 cm.

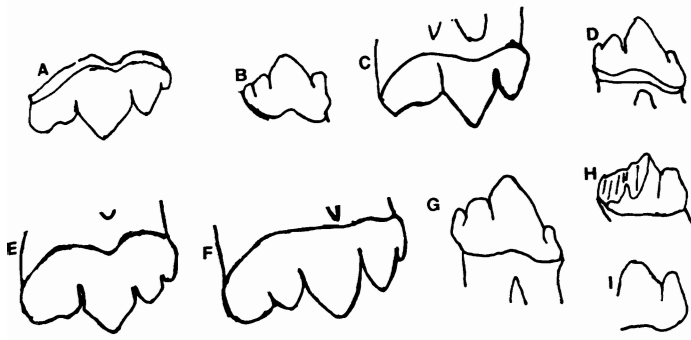


FIGURE 3. Upper carnassials,  $P_4$  and lower last premolars,  $P_3$ : *Megantereon cultridens*, A-B; *M. gracilis*, C-D; *Smilodon fatalis* (holotype), E; *S. floridanus*, F-G; *Homotherium* right  $P_3$ ; *H. crusafonti* (holotype), H; *H. crenatidens*, I. All  $\times 1$ . A-B based on Viret, 1954, Pl. 13; C based on Churcher (1984, fig. 11); F-G based on Merriam and Stock (1932, Pl. 13); I based on Ballesio (1963, fig. 13).

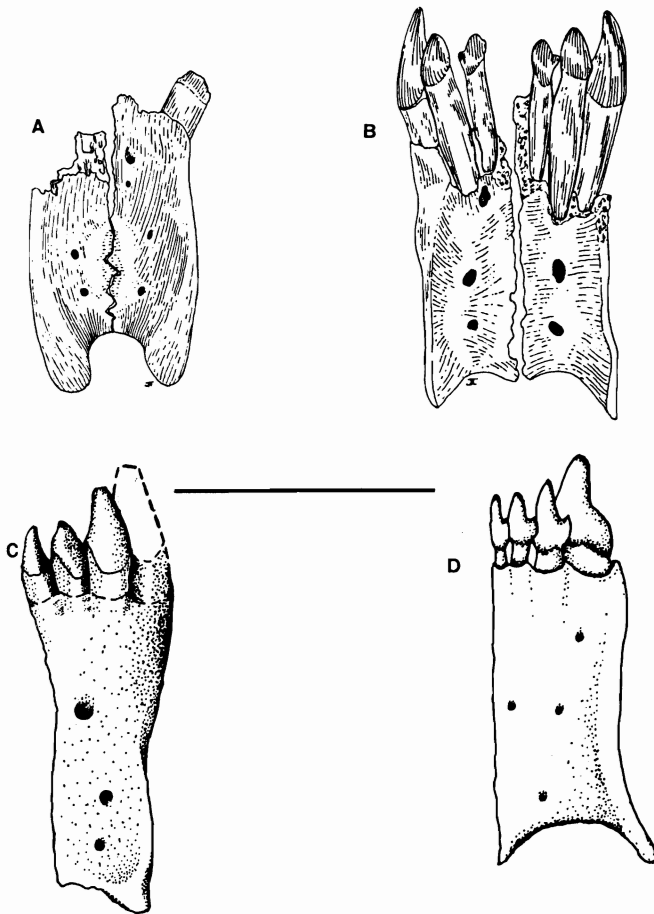


FIGURE 4. Anterior views of mandibles: A. *Megantereon hesperus*, UNSM 25494; B. *M. gracilis*; C. *Homotherium (Ischyrosmilus) crusafonti* (holotype) UNSM 25493 composite of both sides; D. *Megantereon gracilis* [after Churcher, 1984, fig. 1, e].

The relationships of *Ischyrosmilus* have recently been further complicated by the assignment of all the putative species of that genus to "*Ischyrosmilus*" *gracilis* by Churcher (1984). This taxon is based on "*Smilodon*" *gracilis* from the Port Kennedy

Cave Local Fauna. Martin (1980) accepted Kurtén's (1963) claim that the upper canines of "*Smilodon*" *gracilis* are unserrated. This along with the double-rooted  $P_3$  in at least some individuals (Fig. 2), the lack of a well-developed preparastyle (ectostyle) (Fig. 3), and greater development of the flange than in *Smilodon*, led Martin (1980) to assign the Port Kennedy species to *Megantereon*. Churcher (1984: 2) agreed that the Port Kennedy sabercat is closely related to *Smilodon*, but he argued that it is not congeneric with that genus. His referral of it to *Ischyrosmilus* led him to state that part of the Port Kennedy fauna may be Blancan in age (Churcher, 1984: 36). We think that this is unlikely because of the advanced nature of most of the fauna (*Ondatra*, *Neofiber* and *Microtus*), and suggest that it must be near to the age of the Cudahy faunas in Kansas (around 600,000 BP). A similar age is likely for the Conard Fissure fauna in Arkansas. Churcher (1984) assigned the sabercat from the Conard Fissure Local Fauna to *Smilodon fatalis*, as do Kurtén and Anderson (1980), but the age of the Conrad fissure indicates a need for a more careful comparison with *Smilodon gracilis*.

Churcher's assignment of the Blancan *Ischyrosmilus ischyryrus*, *I. johnstoni*, *I. idahoensis*, and *I. crusafonti*, to *Smilodon gracilis* must have been based on lower jaw characters as Churcher disassociated all of the cranial material previously referred to the Blancan *Ischyrosmilus* and refers it to *Homotherium*. He then relied on the few cranial fragments that are associated with "*Smilodon*" *gracilis* for the cranial features of *Ischyrosmilus*. All modern workers (Kurtén, 1963; Kurtén and Anderson, 1980; Martin, 1980; Berta and Galiano, 1983; Berta, 1987) have accepted a close and usually congeneric relationship between "*Smilodon*" *gracilis* and the later species of *Smilodon*, so it is no surprise that Churcher (1984) finds that the small amount of cranial material of his "*Ischyrosmilus*" *gracilis* supports such a relationship. Unfortunately, the cranial evidence cannot resolve the question of whether Churcher was right in assigning "*Smilodon*" *gracilis* to *Ischyrosmilus*. That must be addressed solely on the basis of the lower jaws that compose the holotypes of the various species.

The following features of the lower jaw are present in one or all of the Blancan material assigned to *Ischyrosmilus* and can be compared to that of "*Smilodon*" *gracilis*. The canines and incisors are relatively much larger in the Blancan *Ischyrosmilus* species than they are in "*Smilodon*" *gracilis* where the canine is only about the size of the  $I_1$  in *Ischyrosmilus crusafonti* (Fig. 4). The shapes of the incisors are also different, with "*Smilodon*" *gracilis* having small, blunt crowns with distinct lateral cusps almost exactly as in later *Smilodon* (Fig. 4), while the crowns of the incisors of *Ischyrosmilus* are more conical and recurved posteriorly as in *Homotherium*. The dorsal margin of the diastema between the canine and  $P_3$  is thin and sharp in "*Smilodon*" *gracilis*, as it is in *Megantereon hesperus* and in *Smilodon*, and different from the condition in the Blancan *Ischyrosmilus* specimens, all of which have the more rounded dorsal margins found in *Homotherium*. The diastema is shorter in

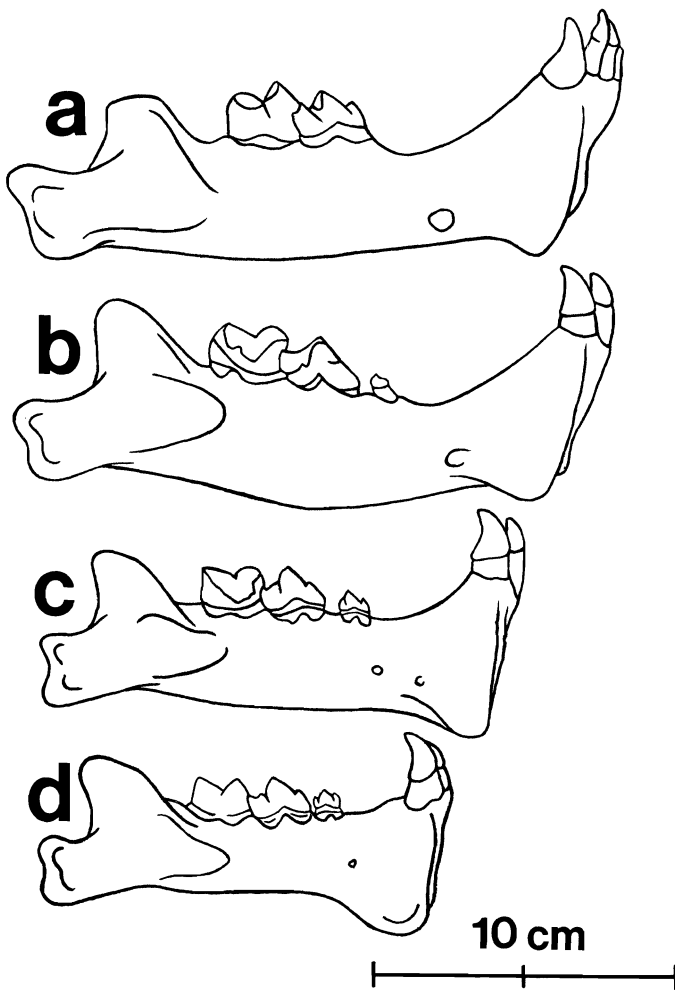


FIGURE 5. Right rami of Smilodontine cats: a. *S. floridanus*; b. *S. cf. fatalis* (composite of UNSM 25500 and 25499); c. *Megantereon gracilis*; d. *M. hesperus* UNSM 25494. Restoration of  $P_4$  and posterior ramus on *Megantereon* based on *M. cultridens* and the type of *M. gracilis*.

*Ischyrosmilus* and the homotheres even though the  $P_3$  is more reduced (single rooted) in the oldest Blancan *Ischyrosmilus* (as it is in *Homotherium*), while at least some specimens of the middle Pleistocene "*Smilodon*" *gracilis* still have two roots (Fig. 2). The paraconid on  $P_4$  is comparatively small and low on all of the smilodontine cats (Fig. 3) as compared to that in the Blancan *Ischyrosmilus*, which has a high paraconid as is found in the Homotherini (Fig. 3). The paraconid on  $P_4$  is not as inclined posteriorly in the Blancan *Ischyrosmilus* as it is in the Smilodontini (including "*Smilodon*" *gracilis*) (Fig. 3). In many dirk-toothed cats, including the Smilodontini, there is a progressive trend for the  $P_4$  to overlap the anterior margin of the lower carnassial (Martin, 1980). This may result in some rotation of the carnassial in relation to the premolars (Fig. 5). This is the condition in "*Smilodon*" *gracilis*, while the Blancan *Ischyrosmilus* and European *Homotherium* have the  $P_4$  and lower carnassial in a line and not overlapped. This is the primitive condition, but it is already changed in the Hemphillian *Megantereon*. The lower carnassial is shorter in "*Smilodon*" *gracilis*

than in the Blancan *Ischyrosmilus*. This is quite evident with the holotype of *I. crusafonti*, which has a jaw very nearly the same size as that in "*Smilodon*" *gracilis*. However, the lower carnassial is 3 mm longer. On the other hand, the  $P_4$  is smaller in *I. crusafonti* than in "*Smilodon*" *gracilis* so that the  $P_4$ /carnassial length ratio is 60% in the former and 82% in the latter. This also tends to associate *Ischyrosmilus* with the Homotherini rather than with the Smilodontini. The cheek teeth of the Blancan *Ischyrosmilus* specimens are badly worn, but show traces of serrations as are found on the homotheres but not on the smilodontines. The masseteric fossa in the smilodontines retains the primitive feline condition where it projects a shallow "prefossa" under the  $M_1$ . This is the condition in "*Smilodon*" *gracilis* but not in the Blancan *Ischyrosmilus* which have deep masseteric fossae that are rounded anteriorly as in the Homotherini. The oldest known *Megantereon hesperus* has three mental foramina (Berta and Galiano, 1983), and modern cats usually have two or three. The Broadwater Local fauna *M. hesperus* has one large mental foramen under the anterior root of  $P_3$ , and *Smilodon* usually has one. The "*Smilodon*" *gracilis* jaws have two situated like the anterior two in the Hemphillian *Megantereon hesperus*. The anterior one is small and is clearly the one that is lost in *Smilodon*. The posterior one is larger, roughly circular, and faces laterally. It lies under the anterior root of  $P_3$  (Figs. 2, 5, 6) as it does in species of *Megantereon hesperus*. This foramen seems to maintain its anterior-posterior position in *Smilodon* but becomes progressively more ventral.

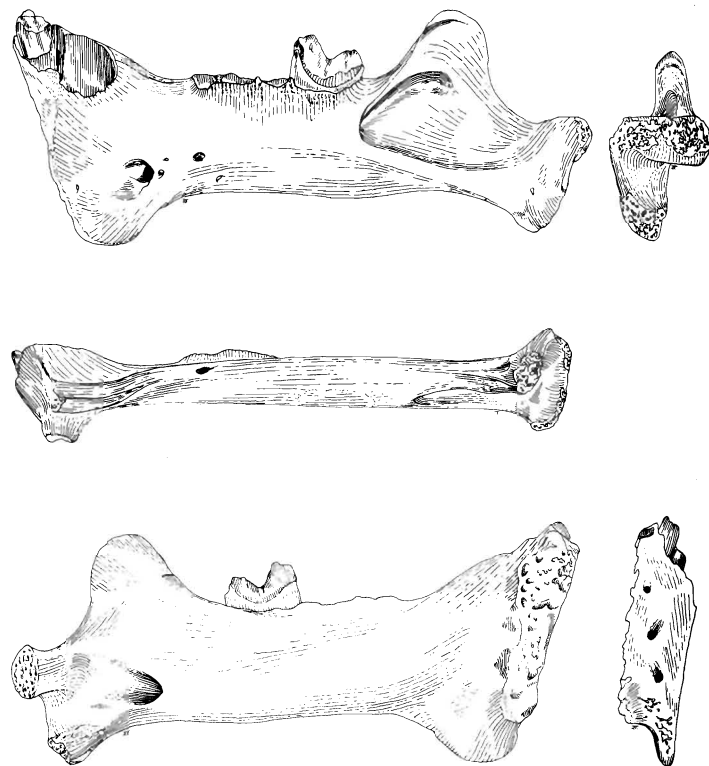


FIGURE 6. *Dinobastis serus*, UNSM 33612, left ramus: lateral, posterior, ventral, medial and anterior views. Line = 5 cm.

Berta and Galiano (1983) emphasized the presence of a distinct medial groove in *Megantereon hesperus*, and a remnant of this groove is retained in "*Smilodon*" *gracilis*. We have not observed such a medial groove in the Blancan material referred to *Ischyrosmilus*.

In the Blancan *Ischyrosmilus*, as in *Homotherium*, the anterior foramen is enlarged, situated ventrally on the flange, and opens anteriorly. The flange itself develops posteriorly from the masseteric line in *Ischyrosmilus* and the Homotherini as opposed to the condition in "*Smilodon*" *gracilis* and the rest of the Smilodontini, where the flange drops directly from the anterior portion of the ventral border of the ramus.

We found no characters not shared by *both* the Homotherini and the Smilodontini that would support a relationship of the Blancan *Ischyrosmilus* species with the Smilodontini or would support a special relationship with "*Smilodon*" *gracilis*, which in all features is a typical smilodontine. On the other hand, we found nothing that would serve to separate these taxa from *Homotherium*, and we think that like the cranial material of similar age they are most usefully assigned to *Homotherium*.

### DINOBASTIS

We here record the first definite occurrence of *Dinobastis* in Nebraska.

#### *Dinobastis serus*

*Referred material* — University of Nebraska State Museum (UNSM) 50764, partial left ramus (Fig. 7).

*Locality* — UNSM collecting locality Md-101, Madison County, Nebraska.

*Horizon* — Late Pleistocene.

*Description* — Incisors flattened laterally and graded in size from  $I_{1-3}$ ; canine alveolus flattened; incisors and canines elevated above carnassial;  $I_1$  alveolus about level with top of coronoid process;  $P_3$  small and single rooted; carnassial with shallow notch; coronoid low and rounded; masseteric fossa forming an anterior "pocket"; angular process at about the same level ventrally as flange and turned slightly medially; one very large and several smaller mental foramina; symphysis large and projected medially with the area of the diasteric insertion a prominent pocket on the ventral-medial border; flange extending about one cm. below symphysis; front of symphysis flat and rough with three large foramina.

*Measurements* (in mm) — Total length, 193; depth of ramus posterior to  $M_1$ , 49.6; depth at coronoid, 62.1; depth at condyle, 40.3; depth of anterior end, 80; length from  $P_2$ - $M_1$  (alveolar), 56.5; length  $P_3$  (alveolar), 8.1; length  $P_4$  (alveolar), 20.8; length  $M_1$ , 26; width  $M_1$ , 10.4.

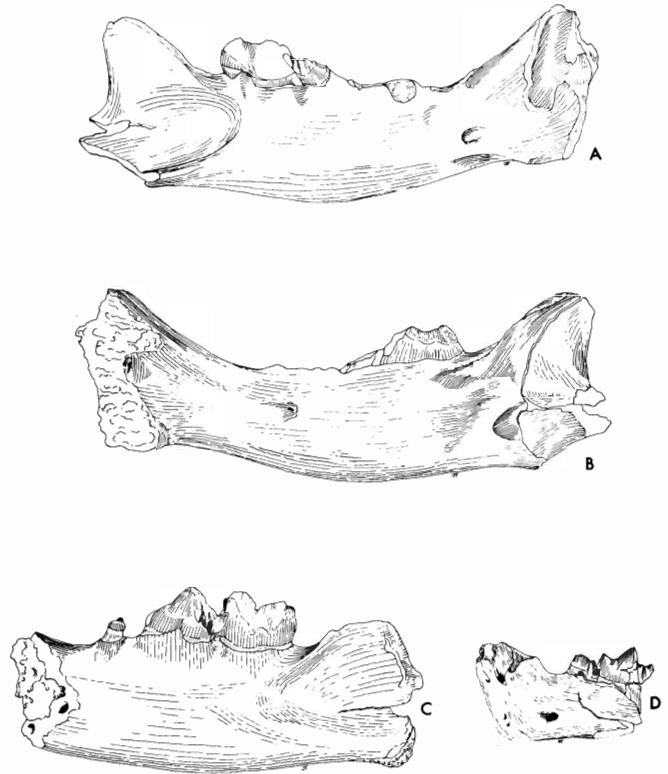


FIGURE 7. Rami of *Smilodon* cf. *fatalis*: A-B, partial right ramus, UNSM 25502, lateral and medial views; C, partial left ramus, UNSM 25500, lateral view; D, anterior part of juvenile, left ramus with  $dp_{3,4}$ , UNSM 83450. Line = 5 cm.

### MEGANTEREON

Schultz and Martin (1970) were the first authors to recognize *Megantereon* in North America, and its North American range was extended back to the late Hemphillian by Berta and Galiano (1983). The latter authors separated *Megantereon* from *Smilodon* on the basis of a smaller postglenoid process, mastoid process, upper canines, and  $P^4$  "ectoparastyle" in *Megantereon*, which also has a larger flange. All these features are primitive in *Megantereon* as opposed to *Smilodon*, and nothing exists to prevent an ancestral-descendent relationship between some species of *Megantereon* and *Smilodon*. In figure 2 of Berta and Galiano, an enlargement of the lower jaw flange is thought to unite all *Megantereon* species. Comparison of the flanges of North American smilodontines arranged stratigraphically (Fig. 5) shows a progressive decrease in flange size, and one form placed by Berta and Galiano (1983) in *Smilodon* (*S. gracilis*) has a perfectly well-developed flange as in *Megantereon*. The prominent groove on the inside of the ramus thought to be characteristic of *Megantereon hesperus* by Berta and Galiano (1983) can

also be found in some specimens of "*Smilodon*" *gracilis* and *Smilodon fatalis*, and the strong dorsoventral ridge of the mandibular flange mentioned by these authors is characteristic of *Smilodon* specimens. Berta and Galiano, (1983, fig. 1, C) seem to figure this ridge for "*Smilodon*" *gracilis* but at the same time deny its presence (Berta and Galiano, 1983: 894). We presently prefer to include "*Smilodon*" *gracilis* as an advanced species of *Megantereon*.

### SMILODON

The genus *Smilodon* was recently reviewed by Berta (1985). In this paper she synonymized all the North American species with the South American species, *S. populator*. We do not believe that her study took into account qualitative differences between South American and North American materials, nor are we convinced that the late Irvingtonian material from North America can be easily included with the Rancho La Brea population. However, we do not at this time wish to do a revision of *Smilodon*, although one is clearly needed. The material from the Irvingtonian of Nebraska is here referred to *Smilodon fatalis*, although the fate of that species must remain doubtful.

#### *Smilodon* cf. *fatalis*

*Referred material.* — UNSM 25500, partial left ramus; UNSM 25499, partial right ramus; UNSM 25502, posterior end of ramus; UNSM 83450, juvenile left ramus, UNSM 20022, posterior portion of cranium (figs. 7-8).

*Localities* — UNSM 25500, 25499 and 25502 all from UNSM Coll. Loc. Sh-5, UNSM 83450 from Coll. Loc. Sh-1, Sheridan County, Nebraska. UNSM 20022 from Cuming County, Nebraska. — *Horizon* — Late Irvingtonian (Sheridanian).

*Description* — Sagittal crest high and slender and brain case little expanded (perhaps even less so than in *S. floridanus*); mastoid process large, facing anteriorly and nearly in contact with the posterior root of the zygomatic arch; glenoid fossa much more ventral than mastoid process; auditory bulla larger than in *S. floridanus*; posterior lacerate and condyloid foramina separate (combined in a single opening in *S. floridanus*); occipital region narrower dorsally than in *S. floridanus*; ramus with single rooted P<sub>3</sub> (usually absent in *S. floridanus*); flange a little better developed than in *S. floridanus*; coronoid process somewhat more pointed and slightly higher than in *S. floridanus* and the masseteric fossa somewhat smaller.

As in other *Smilodon*, the occipital bone extends anteriorly to form the posterior wall of the temporal fossa; the sagittal crests meet to form a single crest above the postglenoid process, and there is a nick point where the two crests join and the single crest is elevated well above the frontals; as in other *Smilodon*, the postero-dorsal corner of the temporal fossa is richly supplied with large foramina; the medial ridge on the occipital surface above the foramen magnum is longer than in *S. floridanus*; the occipital condyles are narrower and the articular surfaces run

further anteriorly in *Smilodon* than in *Felis* or *Panthera* and are even narrower in UNSM 20022 than in *Smilodon floridanus*; the auditory bulla is shorter than in *S. floridanus* so that the anterior margin lies closer to the basioccipital-basisphenoid suture (the bullae are in general more elongated anteriorly and inflated in *S. floridanus*); the foramen ovale seems to be a little more ventrally directed, and the separation between the foramen ovale and the foramen rotundum wider than in *S. floridanus*, which also has the foramen rotundum, orbital fissure and optic foramen in a deeper groove; as in other *Smilodon*, there is a small but distinct carotid foramen enclosed within the entotympanic bulla.

All of the rami from the Sheridan beds of western Nebraska have P<sub>3</sub> as compared to only about six percent of the rami from Rancho La Brea. The rami are small, falling at the very small side of the range of Rancho La Brea material. The masseteric fossa may range a little further anteriorly, and the flange is a little better developed than in the California sample.

*Discussion:* UNSM 20022 corresponds closely to Slaughter's (1963) description of the skull of *Smilodon fatalis* (Fig. 8) in that the occiput is narrower and more triangular than in *S. floridanus*; there are deep pockets on either side of the occipital ridge, and there is no distinct basioccipital ridge of the type found in *S. floridanus*. These and the other features listed above that differ from those in *S. floridanus* generally are more *Megantereon*-like and may all be reasonably considered to be primitive in comparison to *S. floridanus*. It seems useful to recognize material having these features as a separate taxon from *S. floridanus*, and this taxon seems to have a stratigraphic range running from the Illinoian (Sheridanian) into the Sangamon, or roughly that of the extinct muskrat *Ondatra nebracensis*. The type of *Smilodon fatalis* is a P<sup>4</sup> (Fig. 3). We suspect that most attempts to synonymize this species with *S. floridanus* have been based on comparisons with other material than the holotype whose exact age is unknown. It is actually too small to occlude with any of the lower jaw material that we have referred to that species in Nebraska and is probably too small for any of the material referred to it by Slaughter (1963). In terms of size it is closer to *Smilodon gracilis*, but it is more advanced than that species in having a distinct preparastyle (etoparastyle). This cusp is not as well-developed as in *S. floridanus*, the tooth is not so high-crowned, and the metacone blade is not so elongated nor is it separated into two parts by a secondary carnassial notch as in *S. floridanus*. In general it seems a little smaller and more primitive than most of the material presently referred to *S. fatalis*, although it may be close to the material synonymized with it from the Conrad Fissure in Arkansas (*Smilodontopsis troglodytes* and *S. conardi*, see Kurtén and Anderson, 1980; Churcher, 1984). For the present time we propose to continue the use of *Smilodon fatalis* for the middle Pleistocene smilodontine sabercats.

*Measurements* (in mm) — UNSM 25500: depth of ramus anterior to M<sub>1</sub>, 44; posterior to M<sub>1</sub>, 39.5; length P<sub>3</sub>, 5.7; P<sub>4</sub>, 26.4; M<sub>1</sub>, 27.2; width P<sub>3</sub>, 6.1; P<sub>4</sub>, 10.6; M<sub>1</sub>, 12.4.

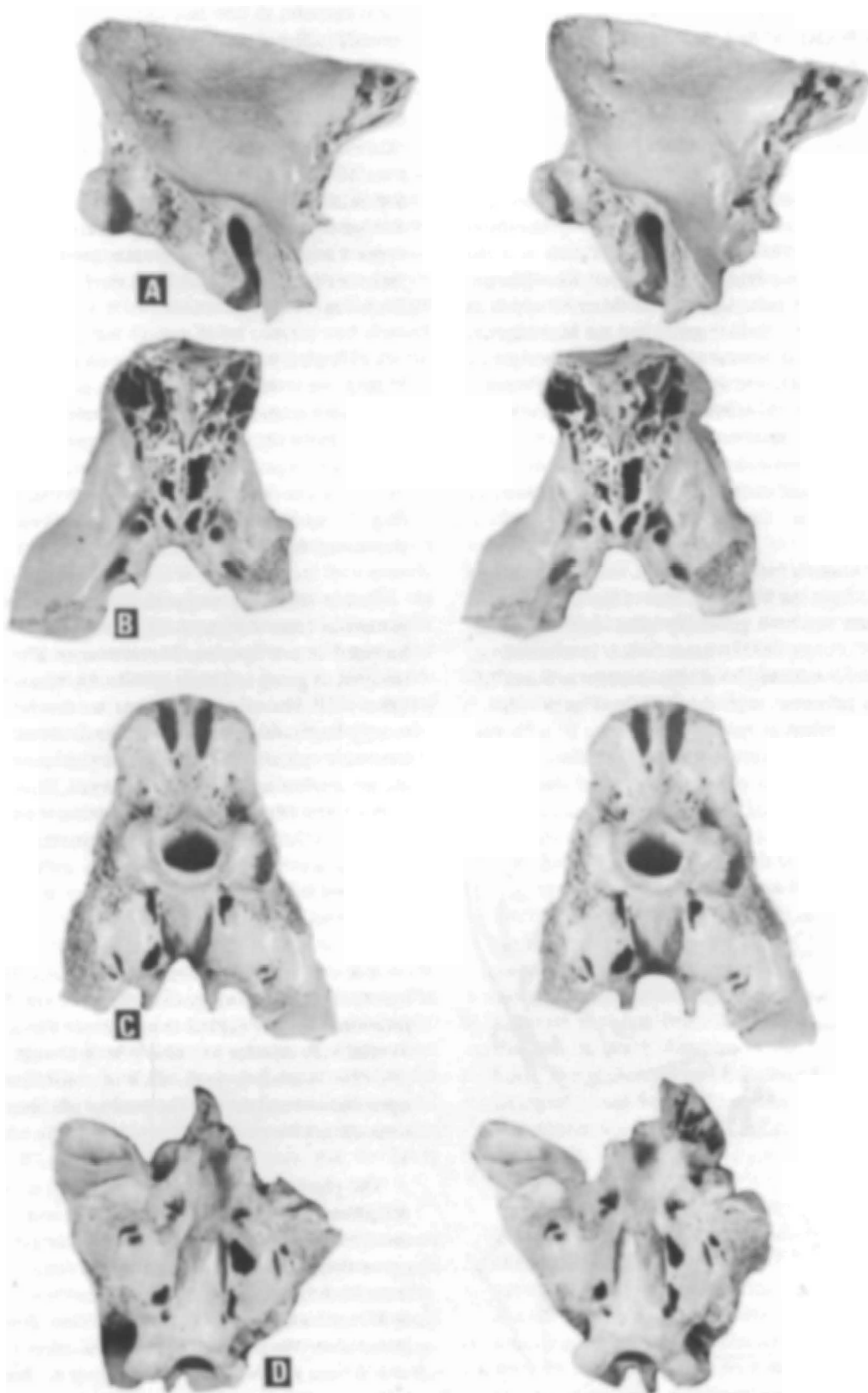


FIGURE 8. *Smilodon cf. fatalis* cranium, UNSM 20022: lateral, anterior, posterior and ventral views.



TEXT—(Continued from page 158)

### SUMMARY AND CONCLUSIONS

It is readily apparent that the bulk of the recent literature on smilodontine and homotherine cats in North America gives conflicting information, and that much of it must certainly be wrong. Both groups require extensive revision. As in the Miocene and Oligocene faunas, we normally get both dirk-toothed and scimitar-toothed predators in the same region. The dirk-toothed feloids are short-limbed ambush predators and the scimitar-toothed feloids long-limbed pursuit predators (Martin, 1980). Kurtén (1968) recognised these two adaptive types as belonging to two tribes, the Smilodontini and the Homotherini respectively. In North America the Homotherini is thought by many workers to be represented by "*Ischyrosmilus*" (Mawby, 1965; Martin and Harksen, 1974; Martin, 1980). A second genus of scimitar-toothed cat has also been recognized in North America by Kurtén (1972). This genus, *Dinofelis* (= *Theralurus*) seems to share a very similar distribution with *Homotherium* and *Megantereon*.

*Megantereon*, *Dinofelis* (= *Therailurus*), and *Homotherium* have been reported from the Villafranchian of Eurasia, while in Africa only the first two have generally been reported (Ewer, 1955). However, Collings (1972) described a machairodont, "*Megantereon*" *problematicus*, from Makapansgat in South Africa which seems referable to *Homotherium* (Fig. 9). "*M.*" *problematicus* is described as having an elongate P<sup>4</sup> with vestigial protocone and well-developed parastyle, serrated upper canines, a very low coronoid process on ramus, and single-

rooted P<sub>4</sub>. The elongate and highly shearing upper carnassials as well as the other characters of its anatomy resemble most closely those of *Homotherium*. In contrast, species of *Megantereon* have unserrated upper canines, and most have double-rooted P<sub>4</sub>'s (Kurtén, 1963). Besides *Megantereon*, *Homotherium problematicus* (Collings) requires comparison with *Dinofelis* and *Smilodon*. *Dinofelis* lacks serrations on its upper canines, while *Smilodon* has less sectorial upper carnassial and more elongate upper canine than *Homotherium problematicus*. Two mental foramina on the ramus of *Homotherium* also distinguish it from *Smilodon*.

Colling's (1972) determination of a lower Pleistocene age for Makapansgat was based on features of *Homotherium problematicus* that would be highly derived were it a species of *Megantereon*. However, except for the larger size of its carnassials, *Homotherium problematicus* is at a similar evolutionary state to *Homotherium crenatidens* from the Villafranchian of Europe (Fig. 9) and the Blancan species of *Homotherium* (= *Ischyrosmilus*) from North America.

Turner (1987) has suggested that all known material of *Megantereon* from Africa, Asia, Europe, and North America be included in one species, *M. cultridens*. The age range of this material as given in Turner (1987) may be as much as from 3.7–1.5 my BP. The material from Africa that he figures consists of mostly fragmentary lower jaws. We doubt the validity of such an extensive synonymy, but it may be that most of this material is too incomplete for specific assignment. This was the opinion of Schultz and Martin (1970: 37) who stated that "*Megantereon hesperus* (Gazin) is doubtfully separate from *Megantereon megantereon* (Croizet and Jobert), although they probably should not be synonymized until better material of *M. hesperus* can be compared."

A few characters that may be diagnostic of the North American *Metantereon* lineage include: 1) the small size of the mental foramina; 2) less ventral expansion of the anterior ramus; and 3) relatively smaller M<sub>1</sub>. One potential source of error in Turner's (1987) analysis is the lack of consideration given to stratigraphic control so that the pattern of variation over geologic time cannot be evaluated.

The place of origin of *Megantereon* is uncertain. The oldest specimen may be from Florida (Berta and Galiano, 1983), although Turner (1987) questioned that assignment. We tend to agree that *Megantereon* is related to cats like *Adelphaleurus* from the Edson Quarry in Kansas (Harrison, 1983) and possibly to *Metailurus*. Berta and Galiano affiliate *Pontosmilus* with this group also. We do not think that the ancestor of *Megantereon* would have had highly serrated upper canines, although a few incipient serrations may have been present and are widely distributed among individual fields of various taxa.

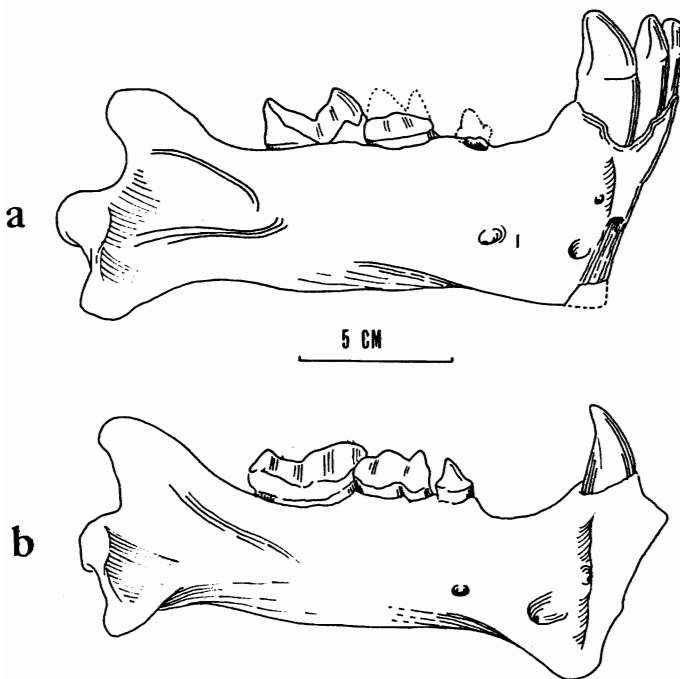


FIGURE 9. *Homotherium*, right rami: A. *H. crenatidens* (from Ballesio, 1963, fig. 13); B. *H. problematicus* (from Collings, 1972, fig. 1).

*Smilodon* probably entered South America in the Irvingtonian. The genus did not get into Asia, and its relatives became extinct in Eurasia and Africa during the middle Pleistocene.

Scimitar-toothed cats are in general less specialized than are dirk-toothed cats. It is thus interesting that the Villfranchian scimitar-toothed cat *Homotherium* is more specialized in many respects (serrated canines, more reduced protocone on P<sup>4</sup>, single rooted P<sub>3</sub>) than is the contemporary *Megantereon*. It would appear that *Homotherium* must have already had a long evolutionary history as a sabercat while *Megantereon* had a substantially shorter one. Many workers have tried to derive *Homotherium* from the Miocene scimitar-toothed cats put in the genus *Machairodus*. It seems that faunas often contain two distinct forms which are commonly included in that genus. In North America there is a lion-like form with canines serrated both front and back, *Machairodus (Heterofelis)*, and a longer legged form with the canine serration best developed posteriorly. The latter form was made the type of *Machairodus catocopsis* by Cope (1887). Another specimen of this cat was assigned to a new genus (*Nimravides*) by Kitts (1958). Martin and Schultz (1975) considered the type species of *Nimravides* conspecific with *Machairodus catocopsis*. Baskin (1981) agreed with their generic assignment, but argued that *Machairodus catocopsis* did not overlap morphologically with the type material of *Nimravides thinobates* and hence was a *nomen vanum*. We would agree that the symphyseal region of a ramus does not make an ideal holotype, but the specimen is virtually identical with the material reported from Smith County, Kansas, by Martin and Schultz (1975), which is not far removed either geographically or in age from the holotype of *Nimravides catocopsis*. Baskin's own diagnosis of *Nimravides galiani* relies to a large extent on size, and with the unusual amount of sexual dimorphism that seems to be present in this species, it seems difficult to reject Cope's name. *Nimravides* has a septum bulla, and we regard it as a felid cat derived from a North American *Pseudaelurus* (Baskin, 1981). Accepting this premise, it is difficult to understand Baskin's (1981) assignment of *Nimravides* to the Machairodontinae unless he also intends to include *Pseudaelurus pedionomus* (the form he takes to be the probable ancestor) in that subfamily. Baskin (1981) reports that the upper canines of *Nimravides galiani* are serrated on both the front and back. *Nimravides* differs from most other sabercats in having considerable occlusion between the upper and lower canines, causing wear so that the presence or absence of serrations may not be easily ascertained.

Martin and Schultz (1975) pointed out similarities between their new subspecies, *Machairodus coloradensis tanneri*, and *Ischyrosmilus*. Churcher (1984) commented on this paper, stating that: "Martin and Schultz (1975) described and figured *Machairodus* cf. *coloradensis* from the Kimball Formation (Upper Pliocene) of Cheyenne County, Nebraska, and from the upper part of the Ash Hollow Formation (Pliocene, Hemphillian) of Sherman County, Nebraska, the latter as a new sub-

species, *M. coloradensis tanneri*." This is in part a *lapsus* as Churcher has reversed the two specimens (*M. coloradensis tanneri* is from Cheyenne County). However, his discussion and figure 13 seem to correctly refer to the Cheyenne County specimen. The use of "Upper Pliocene" by Schultz and Martin in this paper seems to have confused Churcher, as he placed it in a Blancan age relationship (Churcher, 1984: fig. 13). Martin and Schultz (1975: 59) clearly state that the type is from the Ogallala group, a stratigraphic assignment that would put it in the Late Miocene as shown on Churcher's chart. It cannot be Blancan as the associated fauna includes *Teleoceras*, *Calippus* and *Neohipparion*. Churcher (1984: 40) goes on to discuss the *Machairodus* in Martin and Schultz stating that: "Their two *Machairodus* are typical of the early stages of the genus *sensu lato*, probably at the level of *Homotherium crenatidens* or *H. palanderi*, and show none of the derived characters that typify the *Ischyrosmilus* state in the *Megantereon* to *Smilodon* lineage." In his figure 13 he shows *Homotherium crenatidens* as being derived from the Cheyenne Co. form (*M. coloradensis tanneri*); "Cita Canyon Texas records," and independently in Europe from *Machairodus maximiliani* through "*Machairodus*" *nihowanensis* and *Machairodus nestianus*.

We are uncertain about the origin of *Homotherium*. The species of *Machairodus* that we have compared with it have relatively elongate mandibles (Fig. 10), and this may exclude them from consideration in spite of similarities in details of the mandible including the flange.

Churcher (1984) has taken a somewhat questionable approach to his analysis of *Ischyrosmilus*. He has disassociated the skull placed by Mawby (1965) in *Ischyrosmilus johnstoni* from the lower jaw used by Mawby as the holotype of *Ischyrosmilus johnstoni* (WT 1239), although both are from sabercats of the same size and are from the same locality and horizon (Mawby, 1965). Churcher assigns the skull to *Homotherium*, and retains the lower jaw in *Ischyrosmilus*. Churcher's interpretation requires him to accept the co-existence of two sabercats similar in size and adaptation in the same fauna. The only other cranial material that has been assigned to *Ischyrosmilus* from the Blancan of North America is the premaxilla from the Lisco Local Fauna (Martin and Schultz, 1970) and the skull from the Delmont Local Fauna (Martin and Harksen, 1974). Churcher was apparently unaware of the latter skull (Fig. 1) and did not discuss it.

*Dinobastis* differs from *Homotherium* in details of the mandible and also in the postcranial skeleton. Although both genera are short-tailed and somewhat long-legged, *Dinobastis* does not appear to be as adapted for running as its European relatives. Kurtén has produced a restoration of *Dinobastis* based on the mounted skeleton at the University of Texas. This restoration shows a plantigrade rear foot that seems incongruous with its relatively long legs. For comparison, we include a restoration of the skeleton (Fig. 11) based on Meade (1961) with a normal digitigrade rear foot.

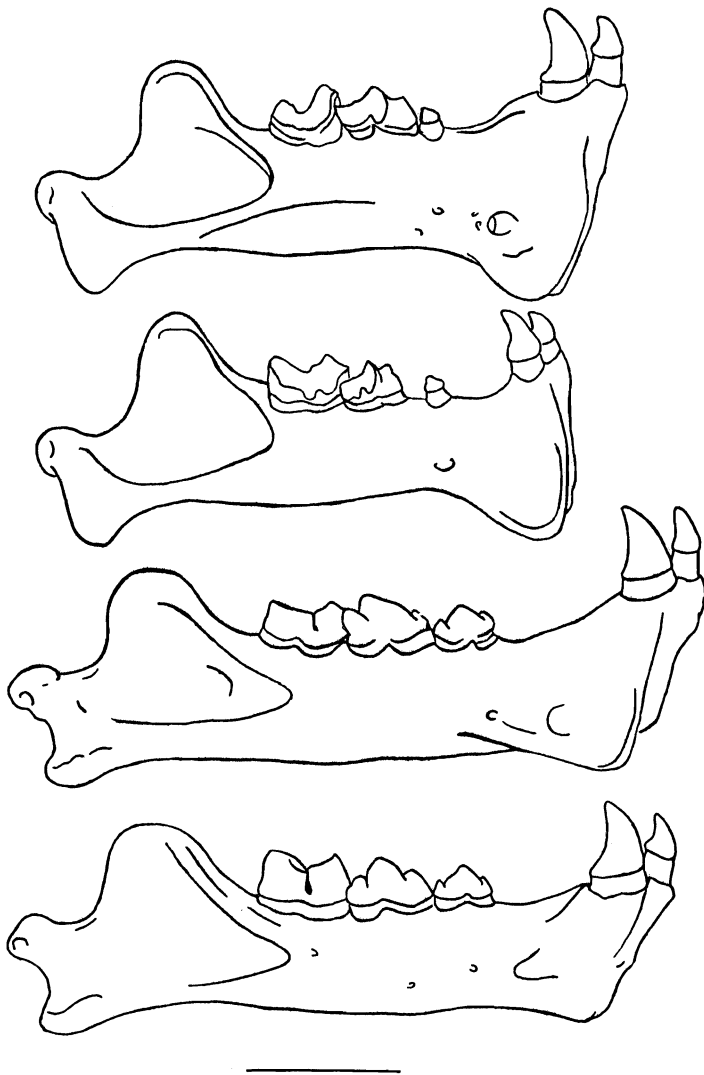


FIGURE 10. Comparison of right rami of scimitar-toothed cats from top to bottom: *Dinobastis serus*; *Homotherium crusafonti*; *Machairodus coloradensis tanneri*; *Machairodus coloradensis*. Line = 5 cm.

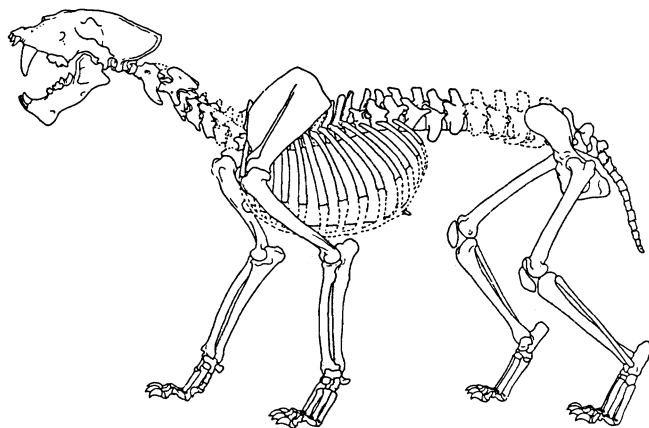


FIGURE 11. Restoration of the skeleton of *Dinobastis serus* based on the figures of the skeleton in Meade (1961).

At the present time we would include the American *Ischyrosmilus* within the Eurasian genus *Homotherium*, but retain *Dinobastis*. "*Smilodon*" *gracilis* is included in *Megantereon*, but we accept its close affinity to *Smilodon*. It should not be included in "*Ischyrosmilus*." We also accept *Smilodon fatalis* as a valid species that does not include *S. floridanus*. Both smilodontin and homotherin cats in North America are in need of extensive additional revision.

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