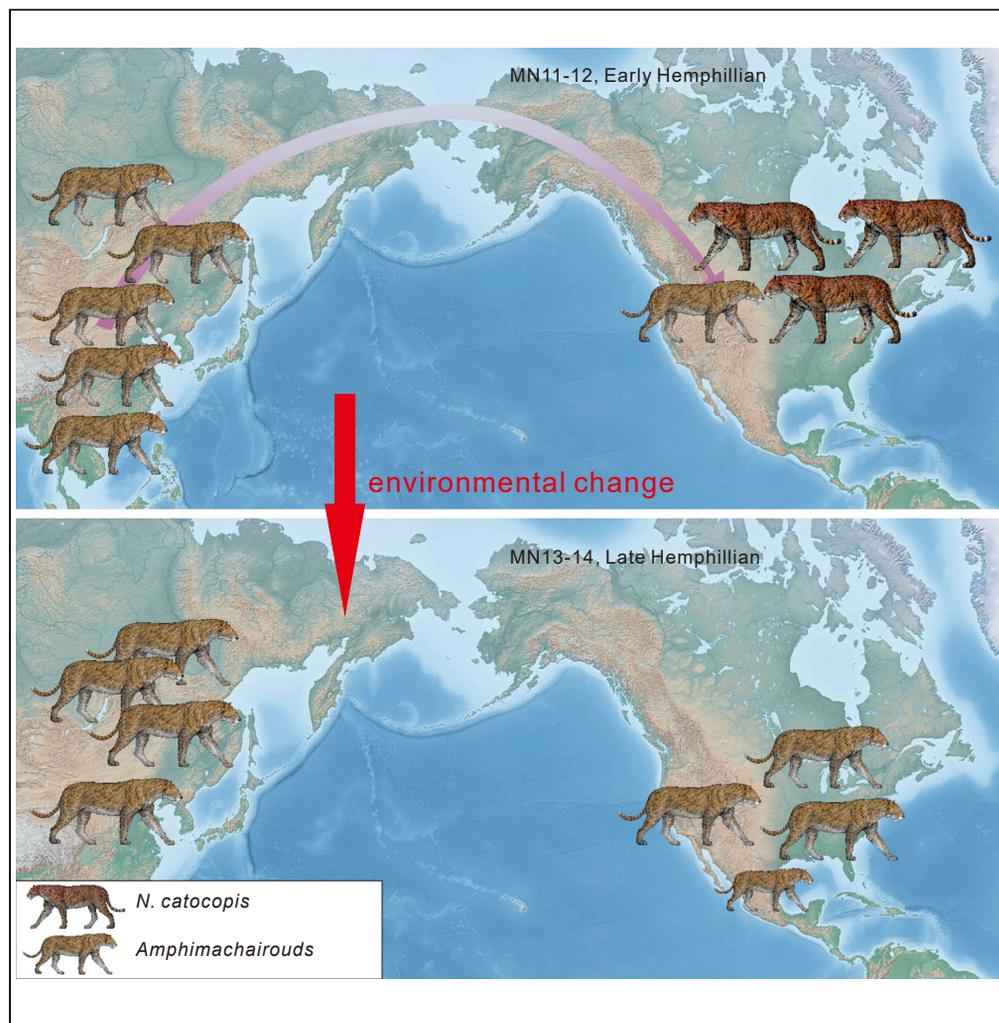


Article

Parallelism and lineage replacement of the late Miocene scimitar-toothed cats from the old and New World



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Highlights

North American
sabertoothed cat
Nimravides are described

Nimravides parallels the
Old-World scimitar-
toothed cats

Lineage replacement by
different survival rate
during the environmental
change

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Article

Parallelism and lineage replacement of the late Miocene scimitar-toothed cats from the old and New World

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SUMMARY

In contrast to large-scale convergence/parallelism, the small-scale convergence/parallelism of sabertooth adaptation within closely related genera and species has been seldom investigated. Here, we describe and analyze the rich material of *Nimravides catocopis*, and provide evidence using a new phylogenetic analysis that *Nimravides* was endemic to North America. The late Miocene (10.5–6.5 Ma) *Nimravides* represents a lineage that shows clearly parallelism with the contemporary Old World lineage of *Machairodus–Amphimachairodus*. The Old World lineage experienced a higher evolutionary rate of cranial trait than the New World one did. The low density of *Amphimachairodus* at its first appearance in North America suggests that the derived traits did not provide a direct competitive advantage over *Nimravides*, but allowed *Amphimachairodus* to survive the significant faunal change in the early–late Hemphillian (~6.5 Ma) in North America, a process that probably can be applied to most replacement of closely related lineages.

INTRODUCTION

Sabertooth is one of the most common adaptations among synsapsids, with at least six independent occurrences within the group in the past 250 Ma, including gorgonopsians (therapsids), thylacosmilid sabertooths (marsupials), machaeroidine sabertooths (Creodonta), hoplophonine and barbourfelid sabertooths (Nimravidae), and felid sabertooths (Felidae).^{1–4} The remarkable convergence has attracted the interest of many researchers, on the mechanism of this convergence and the pattern of the correlated functional adaptation.^{3,5–10} Compared with abundant research on the large-scale convergence/parallelism of different families of sabertooths, the investigation on evolutionary convergence/parallelism within a clade is rare and such convergence is difficult to detect. Among the known members of sabertoothed cats, the North American *Nimravides* has been interpreted as such a case that paralleled with the Old World *Machairodus*.^{11,12} However, there is still debate on whether *Nimravides* is really a nature group, and the taxonomical position of the younger species of the genus, *Nimravides catocopis* is still controversial.¹³ Even though this species has been known since the 19th century,¹⁴ very few published materials and data are known for this species. So far, the best published material is a skull from Sebastian Place, Kansas,¹³ whereas most other records were fragmented. In this circumstance, the intraspecific variation is virtually unknown, which hampers a deep study of its true affinity.

In this study, we describe the best-preserved material of *N. catocopis* (detail in Table 1, and measurements in Tables 2 and 3 in the way shown in Figure 1) and provide evidence that Martin and Schultz¹² are most probably right that North American Late Miocene sabertoothed cat *Nimravides* forms an independent lineage from the Old World *Machairodus*. The parallelism and lineage replacement of the Old and New World lineages of scimitar-toothed cat is discussed based on within lineage morphological evolution and between lineage comparison, and chronological framework.

RESULTS

Order Carnivora Bowdich, 1821.

Family Felidae Fischer, 1817.

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Table 1. The fossil localities with *N. catocopsis* remain analyzed in this study, and their age and corresponding references

Locality	Land mammal age	Source
Jack Swayze Quarry, Clark County, Kansas	Hh1	Janis et al. ¹⁶
Port of Entry Pit (Arnett Locality), 5 mi east of Higgins, Texas, in Ellis County, Oklahoma	Hh1	Janis et al. ¹⁶
Rhino Quarry, Young Brothers Ranch, Vicinity of Ashland, Clark County, Kansas,	Hh1	Janis et al. ¹⁷
Sebastian Place, 1 mi southwest of Oberlin, Decatur County, Kansas	Hh1	Janis et al. ¹⁶
John Dakin Quarry, Clark County, Kansas	Hh2	Janis et al. ¹⁶
Beecher Island, Wray area, Yuma County, Colorado	Hh2	Janis et al. ¹⁷
Box T Quarry, Lipscomb County, Texas	Hh2	Janis et al. ¹⁶
Higgins Local Fauna (=Sebits Ranch), V. V. Parker Place, Lipscomb County, Texas	Hh2	Janis et al. ¹⁶

Subfamily **Machairodontinae** Gill, 1872.

Nimravides Kitts (1958).

Type species

Nimravides thinobates.

Emended diagnosis

Rostrum expanded at canine with marked postcanine constriction, facial and neurocranial part of the cranium folded with distinct angle, glenoid fossa not ventrally projected, mastoid slightly enlarged, and paroccipital process not reduced. Mandibular flange absent. Upper incisors small and not procumbent, canine mostly with bifurcated anterior ridge, with serrated edge, P3 with distinct postero-lingual convexity, P4 with preparastyle and large protocone, m1 mostly with metaconid-talonid.

Included species

*N. catocopsis*¹⁴ and *Nimravides galiani*.

Occurrence

Late Clarendonian to Early Hemphillian (11-6.5 Ma), North America.

Remark

The Late Barstovian to Clarendonian species *Nimravides pedionomus* is too primitive to be included in the genus and will be the topic of another research.

N. catocopsis (Cope, 1887).

(Figures 2, 3, 4, and 5).

Emended diagnosis

Large-sized sabertoothed cat. Occipital plane moderately to strongly posteriorly inclined. Mandibular with distinct antero-ventral angle. Upper canine with serrated edge, P2 absent, P4 with distinct preparastyle, p2 generally absent, m1 with progressively reduced metaconid-talonid.

Differential diagnosis

Differs from *Machairodus* in having expanded rostrum with distinctly more marked postcanine constriction, mostly presence of bifurcated anterior ridge of the canine; differs from *Amphimachairodus* in having less

Table 2. Mean values of craniodental measurements and ratios of *Nimravides* and *Amphimachairodus*

elements	<i>Nimravides galiani</i>	<i>N. thinobates</i>	<i>N. catocopis</i> Hh1	<i>N. catocopis</i> Hh2	<i>Amphimachairodus coloradensis</i>	<i>A. horribilis</i>
CL	25.65		32.16	34.74	31.91	37.57
CW	13.31		14.17	18.67	12.53	15.02
CH	51.18		72.73		90.67	91.92
CW/L	0.52		0.44	0.54	0.40	0.40
CH/L	2.21		2.23		2.46	2.42
P3L	20.22	19.67	22.79	23.73	26.33	23.27
P3W	10.21	9.45	12.22		10.69	10.15
P3H						12.34
P3W/L	0.53	0.48	0.48		0.41	0.43
P3H/L						0.55
P4L	35.86	33.36	40.01	42.77	42.39	41.68
P4W	16.71	16.10	17.36		16.61	16.74
P4BW	11.94	11.81	12.98	14.10	12.87	13.40
P4PaL	9.47	8.15	10.56	10.76	11.24	11.09
P4MeL	13.48	12.55	15.26	17.27	17.52	16.87
P4H	16.26				23.25	20.50
P4W/L	0.47	0.48	0.44		0.39	0.40
P4BW/L	0.33	0.35	0.32	0.33	0.30	0.32
P4paL/L	0.26	0.24	0.26	0.25	0.26	0.27
P4meL/L	0.38	0.38	0.38	0.40	0.41	0.41
M1L	7.74		8.94	7.44		7.36
M1W	13.17		13.91	13.02		11.58
M1W/L	1.71		1.56	1.75		1.58
CL/P4L	0.61		0.84		0.69	0.86
P3L/P4L	0.55	0.59			0.59	0.56
M1W/P4L	0.34					0.27
L1			313.80	356.92		361.26
L2			285.22	300.52		314.51
L3		~236	268.24	282.02		318.00
LT		93.25	108.33	108.65		122.36
W1			170.22 (crushed)	231.66		228.80
W2		91.97		122.56		122.18
W3		67.82		89.88		82.04
LDP		13.87	14.06	10.39		17.93
LDP/TL		0.15	0.13	0.10		0.15
W3/W2		0.74		0.73		0.67

Part I, cranium, and upper dentition. For more detailed information, including sample size, range, and standard deviation, see appendix.

evolved traits in addition to the differences above, including the more folded cranium (angled facial and neurocranial parts), wider cranium, glenoid fossa not projected, mandibular flange absent, coronoid process larger, smaller and less procumbent incisors, larger P3 postero-lingual convexity, larger P4 protocone, and smaller P4 preparastyle. Differs from *Nimravides thinobates* in having a slightly larger size, larger P4 preparastyle, more posteriorly located P4 protocone, more distinct angle in the antero-ventral corner of the mandible; differs from *N. galiani* in having a distinctly larger size, narrower upper canine, the general absence of the P2 and p2.

Table 3. Mean values of craniodental measurements and ratios of *Nimravides* and *Amphimachairodus*

elements	<i>Nimravides galiani</i>	<i>N. thinobates</i>	<i>N. catocopis</i> Hh1	<i>N. catocopis</i> Hh2	<i>Amphimachairodus coloradensis</i>	<i>A. horribilis</i>
cL	16.095		18.859		15.137	17.332
cW	10.323		13.028		10.967	13.033
cH			28.845		27.203	33.400
cW/L	0.643		0.685		0.726	0.756
cH/L			1.596		1.691	
p3L	14.925	18.200	17.911	18.770	19.305	18.866
p3W	7.390	8.240	8.220	7.917	8.443	8.638
p3H	12.015	12.140	12.404	12.970	12.815	12.903
p3W/L	0.496	0.453	0.458	0.424	0.439	0.462
p3H/L	0.806	0.667	0.699	0.645	0.712	0.689
p4L	22.357	24.470	25.220	25.738	27.154	28.613
p4W	9.582	11.260	11.178	11.382	11.288	12.252
p4H	15.059	16.190	16.862	16.790		16.850
p4W/L	0.426	0.460	0.445	0.432	0.427	0.409
p4H/L	0.686	0.662	0.694	0.658		0.633
m1L	26.868	29.735	29.800	31.613	31.177	31.535
m1paL	11.479	12.520	13.545	14.268	14.682	14.493
m1W	11.088	12.595	12.874	14.112	12.643	13.583
m1paL/L	0.429	0.422	0.454	0.453	0.465	0.460
m1W/L	0.413	0.424	0.432	0.447	0.406	0.430
cL/m1L	0.616		0.620		0.463	0.546
p3L/m1L		0.642	0.609	0.573	0.581	0.566
p4L/m1L	0.810	0.825	0.847	0.836	0.881	0.893
L1			222.356		196.300	259.873
LT	99.057		127.721	139.975	122.530	152.080
LDP	19.995		36.863	37.197	31.851	57.836
LM	63.034	71.990	71.773	77.453	76.976	78.408
H1	37.518		53.881	52.750	49.573	63.807
W1	17.544		23.670	23.090	22.113	28.568
H2	32.361	42.580	40.843	40.352	37.100	41.412
W2	14.296	15.625	16.390	19.004	16.356	17.380
H3	35.498	43.615	43.935	43.830	41.703	44.788
W3	16.799	19.135	18.048	18.968	16.756	21.100
LDP/LM			0.513	0.487	0.413	0.680
H1/H3	1.067		1.198	1.224	1.170	1.308
H2/H3	0.938	0.977	0.931	0.887	0.877	0.906
H3/L1			0.196		0.199	0.176
Lm1/H3	0.815	0.683	0.685	0.699	0.774	0.703
Lm1/L1			0.138		0.155	0.125

Part II, mandible, and lower dentition. For more detailed information, including sample size, range, and standard deviation, see appendix.

Description

The cranium from V. V. Parker, AMNH F:AM 146653 (Figure 2B), represents the second cranium of *N. catocopis*. The cranium is complete and not deformed in any significant way. The forehead and braincase are laterally compressed, but the zygomatic seems to be undeformed.

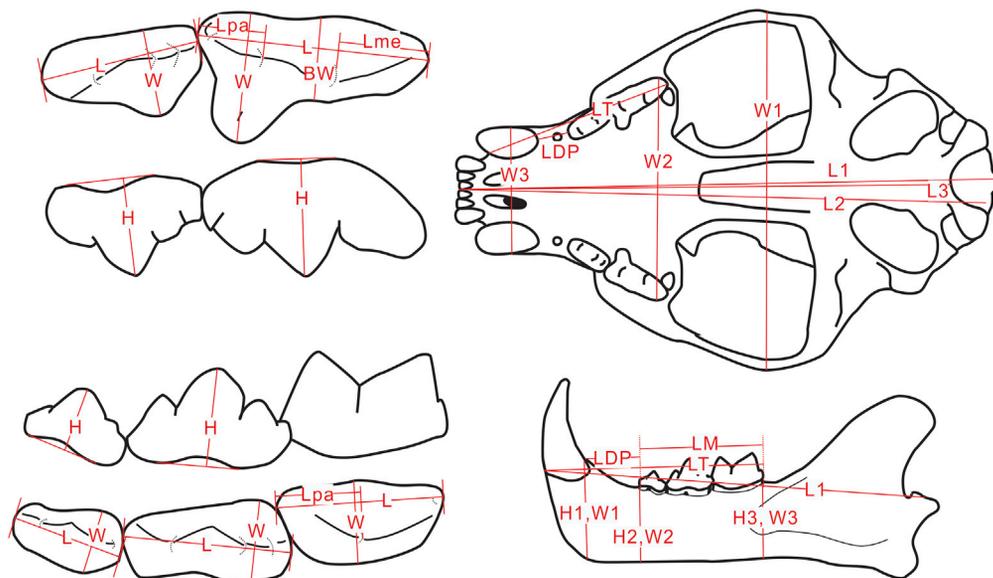


Figure 1. Craniodental measurement for felids

H1-3 and W1-3 in the mandible represent the mandibular height and width behind the canine, before the p3, and behind the m1.

Dorsal view. The cranium is robust. The rostrum is very wide and expanded. There is a distinct postcanine constriction of the rostrum. The nasal has a strongly concave anterior border, with well-developed medial and lateral processes. The nasal tapers backward. The posterior border of the nasal seems to be rounded (but this trait is unclearly seen). The zygomatic arch is very wide. The forehead is somewhat compressed. It seems to be narrow, not wider than the rostrum. The postorbital process of the frontal is weak. The temporal ridge units into the sagittal crest at the anterior part of the rostrum. The mastoid process is slightly laterally expanded and can be seen in the dorsal view.

Lateral view. The skull is domed. The anterior border of the naris opening is slightly concave. The dorsal contour of the skull is symmetric, with the anterior part and posterior part forming a rounded angle slightly posterior to the postorbital process of the frontal. The infraorbital foramen is relatively large, and slightly posteriorly inclined. It is located at the level of the P4 parastyle/paracone boundary. The orbit is moderate in size. Its anterior border lies at the level of the P4 paracone/metacone boundary. The zygomatic is relatively deep and slightly dorsally arched. The anterior border of the jugal is not distinctly anteriorly inclined. The postorbital process of the jugal is weak and blunt. The posterior part of the zygomatic arch becomes shallower. The sagittal crest is well developed, and strongly posteriorly extended. Its posterior border distinctly overhangs the occipital condyle. The mastoid process is ventrally extended, but still does not reach the ventral border of the auditory bulla. Two distinct branches can be seen in the mastoid lateral surface. The anterior branch is directed antero-ventrally, nearly parallel to the postglenoid process, whereas the posterior branch was directed ventrally, nearly perpendicular to the basioccipital plane. The posterior branch extends slightly more ventrally than the anterior branch does. The two branches unit near the base of the mastoid process. The tip of the paroccipital process is broken, but this process does not seem to retreat dorsally. The auditory bulla is moderately domed. Its highest point is located at its anterior part, nearly the anterior border of the mastoid process. The occipital plane is strongly posteriorly inclined.

Ventral view. The incisor row is not anteriorly arched. The rostrum is expanded. The constriction of the rostrum between the canine and P3 is distinct. The rostrum becomes widened from the P3 to M1. The anterior palatine fissure is antero-posteriorly elongated. The ridge from the palatine fissure to the central part of the palate is weakly developed. The embrasure cavity between the P4 and the M1 for the accommodation of the protoconid of m1 is distinct. The bony choana extends slightly posterior to the level of M1. The glenoid fossa is transversely elongated. The postglenoid process is moderately developed, whereas the preglenoid process is rather weak. Medial to the glenoid, a distinct fossa is present, with two foramina in it. The posterior one represents the oval foramen, and the anterior one represents the posterior opening



Figure 2. Crania of *Nimravides catocopsis*, lateral, dorsal, and ventral views

(A) Sebastian Place, 1 mi southwest of Oberlin, Decatur County, Kansas, AMNH F:AM 104044
(B) V. V. Parker Pit, Lipscomb County, Texas, AMNH F:AM 146653.

of the alisphenoid canal. The lateral bony bridge of the canal is short. A small blur is present between the medial border of the postglenoid process and the oval foramen. The auditory region is in good preservation. The bulla is relatively small. At the antero-medial side of the bulla, there is a large opening with a weak central septum, representing the opening of canalis musculotubarius.¹⁵ The tuber-like bony auditory meatus is absent. Between the mastoid process and bulla, there is a valley that contains the stylomastoid foramen and hyoid fossa. The medial border of the bulla turns laterally backward. There is a large fossa that comprises the posterior lacerated foramen and hypoglossal foramen. The bony bridge that separates the two foramina is distinctly lower than the surrounding bone.

Mandibles. Two mandibular fragments were known from V. V. Parker. AMNH F:AM 146654 (Figure 3E) only preserved the anterior part with p3 and p4. The symphysis is high. The mandible flange is weak, without distinct ventral projection. Two mental foramina are present, with the anterior larger one between the c and p3, and the posterior one under the p3. The diastema between the c and p3 is short. AMNH F:AM 146655 (Figure 3F) only preserves the middle and posterior parts. The horizontal ramus is robust, with a distinct convex ventral border. The anterior border of the masseteric fossa reaches the level of the m1 posterior border. The mandible condyle is located slightly lower than the tooth row. The coronoid process is well developed.

Dentition. The I1 and I2 are broken. The I3 is not enlarged and bears no accessory cusp. The canine is large and robust. No serration can be seen in the edges (but this is probably due to wear, as the serration is present in other specimens). The P2 is absent and there is no corresponding alveolus. The P3 has strong postero-lingual inflation. The anterior accessory cusp is large and in line with the main cusp. The posterior accessory cusp and posterior cingulum cusp are well developed. The P4 has a concave buccal border. The parastyle is large. The preparastyle is distinct but small. It is in line with parastyle. The protocone is slightly reduced. It is located at the level between the parastyle/paracone. The M1 has no clear cusp. It is button-like and transversely shortened.

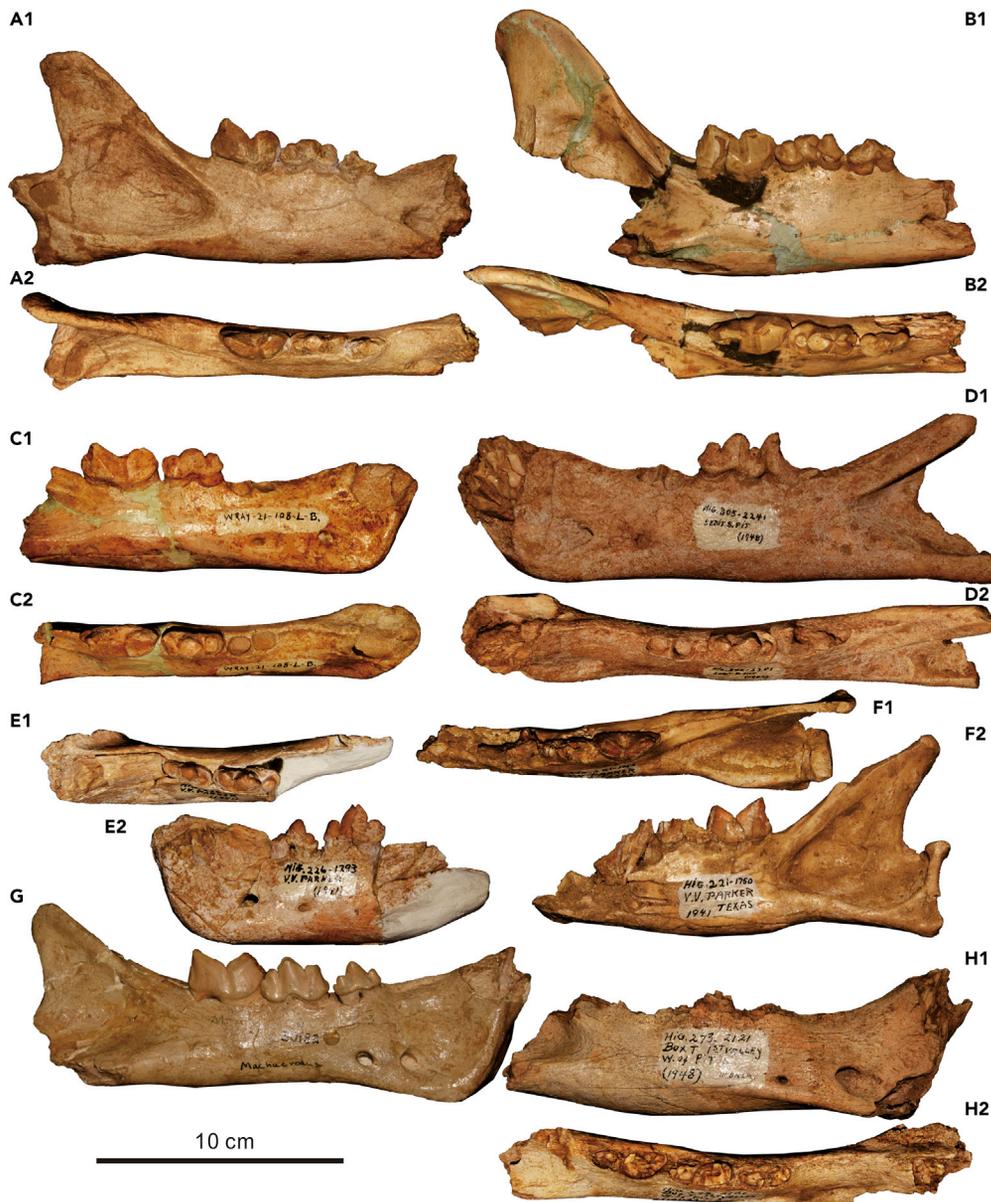


Figure 3. Mandibles of Hh2 population of *Nimravides catocopis* (A–F) and *Amphimachairodus* (G–H), lateral and occlusal views

- (A) Box-T, AMNH F:AM 146667
- (B) Box-T, AMNH F:AM 146668
- (C) Loc. B of Beecher Island, AMNH F:AM 146666
- (D) Higgins Local Fauna (=Sebits Ranch), AMNH F:AM 146670
- (E) V. V. Parker Pit, AMNH F:AM 146654
- (F) V. V. Parker Pit, AMNH F:AM 146655
- (G) Coffee Ranch, UCMP30182
- (H) Box-T, Hig-273-2121.

The p3 and p4 are somewhat posterior inclined. The p3 is distinctly smaller and lower than the p4. Both anterior and posterior accessory cuspids of the p3 are developed. The p4 has similar-sized anterior and posterior accessory cuspids, and the posterior cingulid is weak. The m1 has a protoconid larger and higher than the paraconid. The widest part of the tooth lies slightly anterior to the carnassial notch. The metaco-
nid-talonid complex is virtually absent.

DISCUSSION

Evolution tendency of *N. catocopsis* from the Hh1 to Hh2 population

No previous research has attempted to distinguish the Hh1 and Hh2 populations of *N. catocopsis* due to incomplete knowledge of the material and no comprehensive revision of fossil localities. We were able to distinguish the Hh1 (Figure 5) and Hh2 (Figure 3) populations on this project thanks to the great biostratigraphic work published recently by.^{16–19} The evolution within *N. catocopsis* is especially important, as it has no branch event during this process, and their differences represent the general evolutionary tendency rather than evolution under different selective pressure.

The cranium from V. V. Parker is distinctly larger and much more robust than that from Sebastian Place, Kansas described by Antón et al.¹³ But when the basicranial length is concerned, this difference becomes less distinct. This reflects different proportions between the two crania. Even though the Sebastian Place cranium is slightly laterally crushed and its true width should be larger than what we see in the specimen, the V. V. Parker seems to be still more robust. This is especially the case for the rostrum and zygomatic arch. There is distinct rostrum expansion, with marked postcanine constriction behind this region. Such constriction is also clearly seen in the cranium from Sebastian Place. In lateral view, the occipital plane from V. V. Parker is distinctly posteriorly inclined, and the sagittal crest is more distinctly posteriorly extended (therefore results in a distinctly larger cranial total length). In the cranium from Jack Swayze Quarry of Hh1 age AMNH F:AM 128990 (Figure 4A), this trait is nearly the same as that from Sebastian Place, and different from the situation seen in V. V. Parker cranium.

When all materials available for us were put into the analysis, it is clear that even though the Hh2 *N. catocopsis* is larger in average toothrow length (or carnassial length), there is significant overlap, and the tendency of increasing body size is indistinct (insignificant differences of p4 length, m1 length, and p3-m1 length, with p values all larger than 0.1). Therefore, the significant size difference between the crania from V. V. Parker and those from Sebastian Place and Jack Swayze Quarry is more likely to reflect sexual dimorphism, which is observed on other scimitar-toothed cats like *Machairodus aphanistus*²⁰ and *H. latidens*.²¹ This is also true for most dental or skull proportions. In the biplots shown in Figure 6, *N. catocopsis* from Hh1 and Hh2 are generally close to each other. One exception is the upper canine robustness. The canine of the cranium from V. V. Parker is significantly wider than that of the Hh1 population.

Even though not differs significantly in dental measurements, there are some morphological differences. The most distinct trait is the more reduced m1 metaconid-talonid complex. The m1s from V. V. Parker and Box-T have nearly no metaconid-talonid complex. The m1 from Beecher Island has a very weak talonid, and the m1 from Hiqjins (UCMP V2825 locality) has a larger but poorly separated talonid. In contrast, nearly all m1s from Hh1 localities have a large and well-separated talonid. One exception is a partial mandible AMNH F:AM 146663 from Port of Entry Pit, which has a relatively small talonid comparable to that from Beecher Island, but still more distinct than those from V. V. Parker and Box-T. This trait can, therefore, be used as a reference to distinguish Hh1 and Hh2, though not absolutely. Besides, the p4s from Box-T and Higgins could develop stronger buccal or lingual concavity, which is not seen in the Hh1 population, but this trait is also variable within the Hh2 population. The upper cheek tooth materials from both populations are rare and no effective comparison can be made, but note that the two P3s from Jack Swayze Quarry and Sebastian Place both have small cusp anterior to the anterior accessory cusp, which is absent in that of V. V. Parker, but as the variation is unclear, this difference must be treated with carefulness.

As the size is only very slightly different between the Hh1 and Hh2 populations (see below), the larger size and great robustness of the cranium from V. V. Parker could be merely sexual dimorphism. The V. V. Parker cranium also has a more posteriorly inclined occipital plane, which could be a chronology-related trait, though this hypothesis needs further test with new material.

One notable trait is that the alisphenoid canal is well present in the cranium from V. V. Parker (Figure 7). The posterior opening of this canal is present in the same fossa as the foramen ovale. Antón et al.¹³ did not mention this trait in their description of Sebastian Place cranium, but they stated “a common depression for the foramen ovale and the foramen rotundum is present on the basicranium”. We double-checked the Sebastian Place cranium, and confirm the “foramen rotundum” should be the posterior opening of the alisphenoid canal, as the foramen rotundum should open forward (not backward as seen in the depression of Sebastian Place cranium), and it is never present in the same depression as foramen ovale in felid.

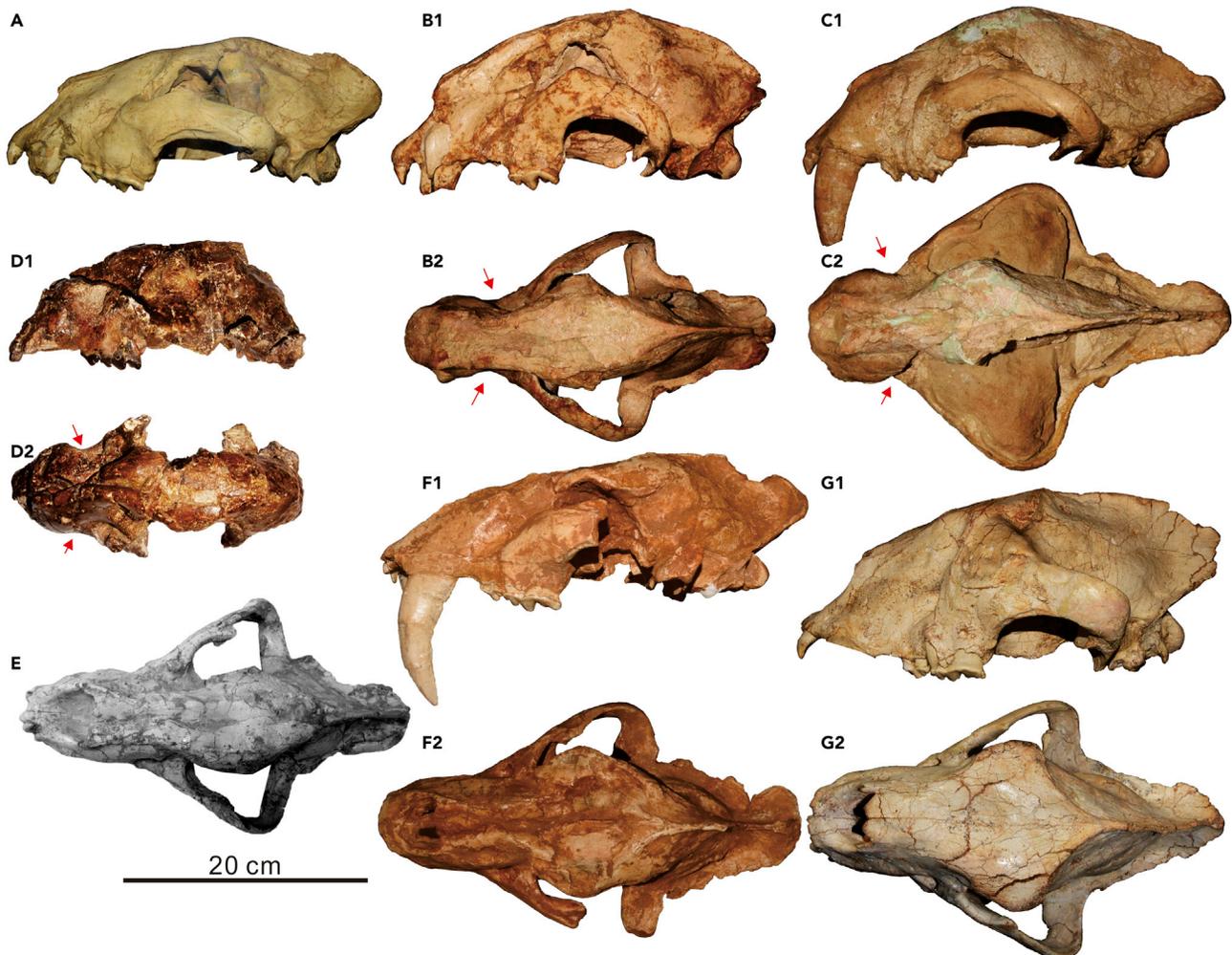


Figure 4. Crania of *Nimravides catocopsis* (A-C), *N. galiani* (D), *Machairodus aphanistus* (E), *Amphimachairodus giganteus* (F), and *A. horribilis* (G), lateral and dorsal views

(A) Jack Swayze Quarry, AMNH F:AM 128990
 (B) Sebastian Place, AMNH F:AM 104044
 (C) V. V. Parker Pit, AMNH F:AM 146653
 (D) Black Hawk Ranch, Green Valley Formation, UCMP V34512
 (E) Batallones-3, BAT-3'09 1622
 (F) Halmypotamos, cast, AMNH FM1-44433
 (G) Baode, IVPP V15642. Red arrows indicate rostrum constriction behind the canine.

Phylogenetic analysis

To test the hypothesis that the large machairodonts from the Old and New World belong to two independent lineages, we performed phylogenetic analysis on machairodonts based on a morphological matrix modified from that of Werdelin and Flink,²² adding our observation. A total of 70 morphological traits and 22 taxa were included in our analyses. We use the tip-dating Bayes Inference method (see detailed settings in *Material and methods*), which has the advantage over other methods^{23–25} and includes the stratigraphic information in analyses.

Our phylogeny (Figure 8) supports that the New World *Nimravides* is a distinct lineage, closely correlated with but independent from the Old World *Machairodus-Amphimachairodus* lineage. The posterior probability supporting the monophyly is relatively high. *M. aphanistus* is grouped with the *Amphimachairodus-Homotherium*, though the posterior probability supporting this node is lower. The New and Old World lineages of large machairodonts form a sister group, in 100%

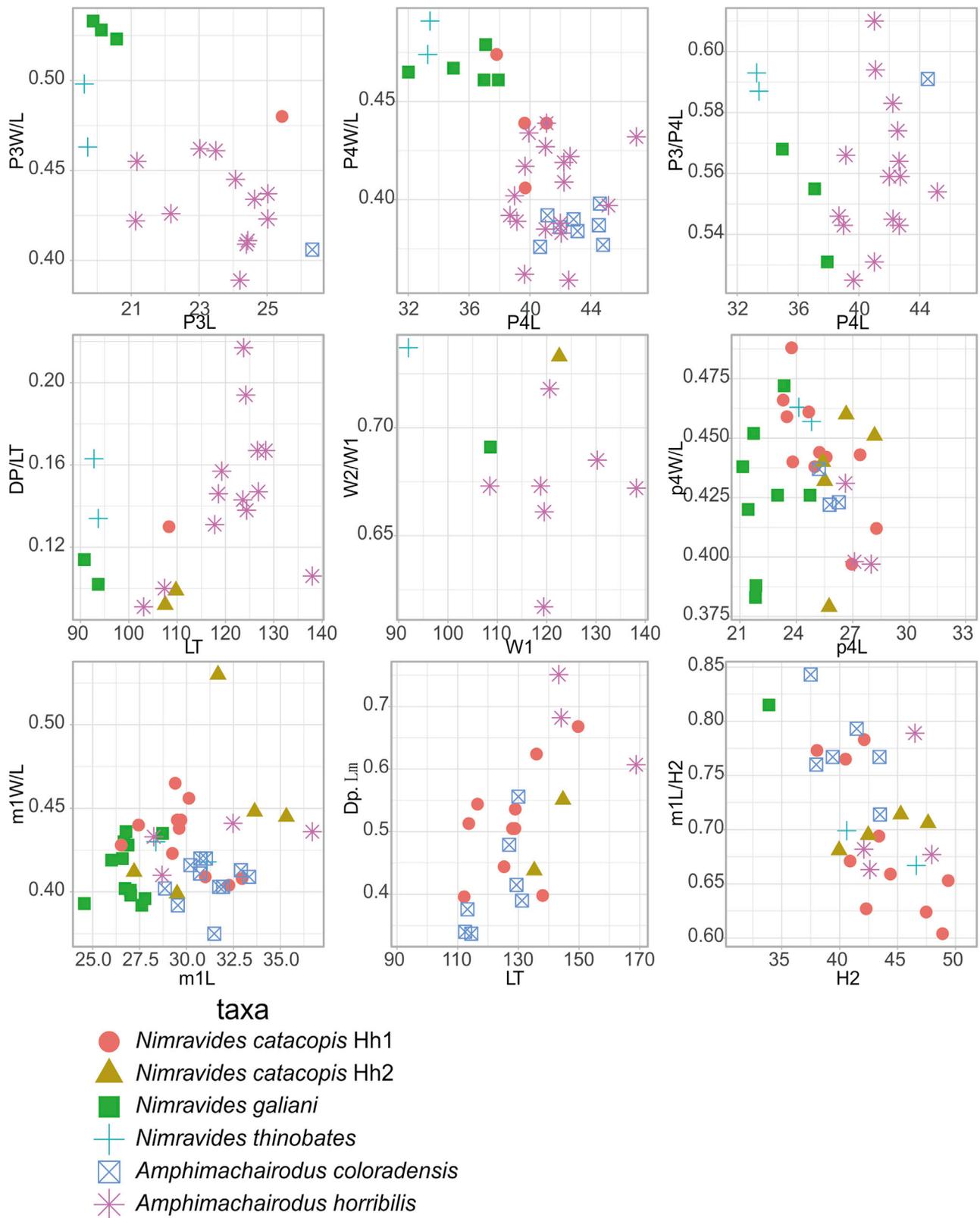


Figure 6. Craniodental measurements and ratios of *Nimravididae* and *Amphimachairodus*

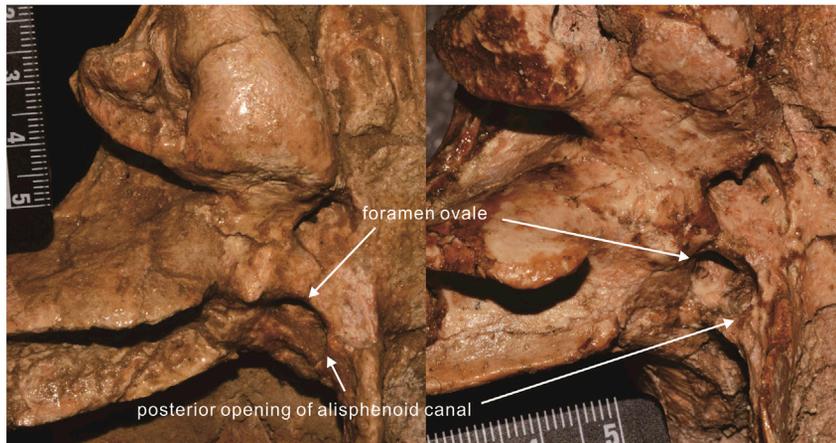


Figure 7. The basicranial area of *Nimravides catocopsis* (left AMNH F:AM 146653 and right AMNH F:AM 104044)
White arrows show the position of depression with the foramen ovale and the posterior opening of the alisphenoid canal.

The Turolian and equivalent aged species of *Machairodus* were either viewed as *Machairodus*^{26–29} or separated into their own genus *Amphimachairodus*.^{10,22} As our phylogeny suggests that these species are closer to *Homotherium* than to *Machairodus*, and there are significant morphological differences (see below), we regard these species as a valid genus *Amphimachairodus*.

Comparison of *N. catocopsis* with *N. thinobates* and *N. galiani*

The taxonomy of *N. catocopsis*, especially its generic assignment, has a long history of debate. The species was established under *Machairodus* by Cope,¹⁴ but at that time *Machairodus* is virtually used to include all sabertoothed cats. Kitts³⁰ established the genus *Nimravides* based on *Pseudaelurus thinobates*, referring to those with initial sabertoothed cat tendency in North America. Martin and Schultz¹² first assign *Machairodus catocopsis* to *Nimravides*, and this view was accepted by later authors.^{11,31} However, as Beaumont³¹ has stressed, the reason that Martin and Schultz¹² assign *M. catocopsis* to *Nimravides* is based on its comparison with the younger species *Amphimachairodus coloradensis*. This is easily understood, as the latter species is clearly more derived, and in fact represents an independent immigrant from Eurasia.^{13,18,32} Beaumont³¹ stated that most characters distinguishing *N. catocopsis* and *A. coloradensis* are invalid to distinguish *N. catocopsis* and the type species of *Machairodus*, i.e., *Machairodus aphanistus*. Meanwhile, Beaumont³¹ also noticed the great similarity of *N. catocopsis* and the Late Clarendonian type species *N. thinobates*, and suggested the possibility that this species could be only a synonym of the type species. Concerning this controversial scenario, he did not give his conclusion regarding this issue.

Antón et al.¹³ described the skull of a complete skeleton of *N. catocopsis* and again they found great similarity of this species to the Old World *M. aphanistus*. After a systematic comparison with the Old World *M. aphanistus* and the younger North American *A. coloradensis*, they concluded that *N. catocopsis* is much closer to *M. aphanistus* in many aspects, and this species, like *A. coloradensis*, is also an immigrant from Eurasia and should be assigned to *Machairodus*. However, they ignored the point already mentioned by Beaumont,³¹ that *N. catocopsis* is also very similar to the North American Late Clarendonian *N. thinobates*, the type species of *Nimravides*, and did not make efficient comparison with the latter species. The similarity between *N. catocopsis* and *M. aphanistus* are more or less sympleomorphic characters compared with *Amphimachairodus*, thus these characters only provide no or weak evidence that these two species should be congeneric. This taxonomic issue is, therefore, still not really pushed forward.

To give a better solution to this issue, we perform analyses on the following two points in addition to the phylogeny expressed above:

1. Systematic comparison with both European *M. aphanistus* and other species of North American *Nimravides*, especially the type species *N. thinobates* and another derived species *N. galiani*, with a large sample to exclude the influence of intraspecific variation. If *N. catocopsis* really represents

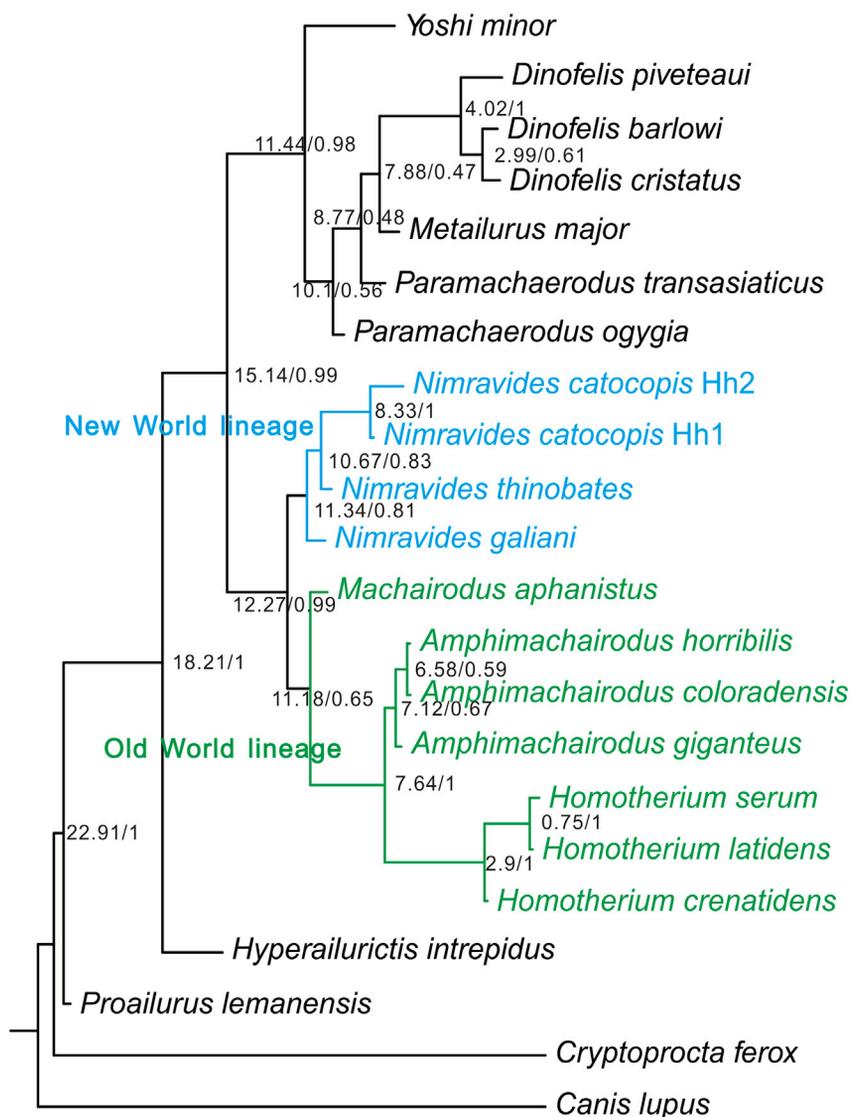


Figure 8. Phylogeny of Machairodonts using Bayes Inference with tip-dating method

The numbers shown in the nodes represent the node age (before “/”, Ma) and posterior probability (after “/”).

a paralleled lineage of the Old World *Machairodus*, then we would expect that should be a synapomorphy of this lineage, that differs from that of *M. aphanistus*.

2. The evolutionary tendency between the Late Clarendonian *Nimravides* and *N. catocopsis* and within *N. catocopsis*. If *Nimravides* really represents a lineage paralleled with the Old World *Machairodus*, then we would see the gradual evolution of related traits without a sudden change in morphology as those between *A. coloradensis* and *N. catocopsis*.

Antón et al.¹³ stressed the great similarity between *N. catocopsis* and *M. aphanistus*. We fully agree with their view, though the same can be applied to *N. catocopsis* and the type species of *Nimravides*, i.e. *N. thinobates*. Antón et al.¹³ suggest that *N. catocopsis* and *M. aphanistus* share similarly developed postorbital processes of the frontal and jugal, the same developmental states of mastoid and paroccipital processes, the tendency of reduction of the P2, P4 with large protocone and presence of preparastyle, no distinct mandibular flange, relatively large coronoid process. If we compare these traits of *N. catocopsis* and *N. thinobates*, except a few that unknown in *N. thinobates* specimens, e.g. the postorbital process of the jugal, mastoid and paroccipital processes, the above-mentioned similarity can be equally applied. This

suggests that a more detailed study should be performed to clarify the affinity of *N. catocopsis* with either *Machairodus* or *Nimravides*. As the material of *N. thinobates* is rare, we also include another contemporary *Nimravides* species, i.e. *N. galiani* in our comparison, which has the largest sample among the Clarendonian species of *Nimravides*. The more derived *Amphimachairodus* and *Homotherium* were also compared, serving as the standard for polarity of character evolution.

The general cranial shape of *N. catocopsis* and *M. aphanistus* is similar. Both species have a relatively narrow forehead, with the width of the postorbital process of the frontal similar or only slightly wider than the rostrum width. The same applied to *N. thinobates*. In both *Amphimachairodus giganteus* and *Amphimachairodus horribilis*, the forehead is much wider than the rostrum. A forehead much wider than the rostrum is inherited in *Homotherium* but shows a reversal pattern in *Xenosmilus*.^{33,34} However, there is one clear difference between *N. catocopsis* and *M. aphanistus*. In both crania of *N. catocopsis*, there is marked post-canine constriction of the rostrum. This constriction is very weak on the two crania figured by Antón et al.²⁰ and Monesillo et al.,³⁵ and also an illustration of Antón et al.²⁰ This constriction is well marked in *N. thinobates*. We checked a large number of published and unpublished skulls of *A. horribilis* from Baode and Linxia Basin and found none of these skulls have distinct postcanine constriction. This constriction is also absent in the crania of *A. giganteus* from Halmypotamus, Greece³⁶ and Hadjidimovo, Bulgaria²⁶ and more derived *Homotherium*. In lateral view, the crania of *N. catocopsis* are clearly folded, which we mean that the facial part and neurocranial part of the cranium forming a large angle. This is clearly seen when the cranium is put horizontally (with the ventral border of maxilla, or base of P4 at the same horizontal plane as the glenoid fossa, as shown in Figure 4), and the occipital condyle is clearly ventrally located, lower than or at the level of the glenoid fossa. This seems to be the case for *M. aphanistus* and *N. thinobates*. In *Amphimachairodus* and *Homotherium*, the cranium is clearly less folded, with the neurocranial part rising compared with facial part, and as a result the occipital condyle is located above the level of the glenoid fossa.

The mandible of *N. catocopsis* shows homogeneous morphology. The mandibular flange is never developed, but there is a distinct angle in the antero-ventral corner of the mandible. Such an angle is developed in *M. aphanistus* and *N. thinobates* and *N. galiani*, but seems to be weaker in these species. In *Amphimachairodus* and more derived *Homotherium*, there is always a developed mandibular flange, either weak or strong, but the flange is very weak in *Lokotunjailurus*.^{37,38} In figured specimens of *M. aphanistus*, the anterior part of the horizontal ramus is somewhat elevated relative to the part with cheek teeth, making the base of the canine alveolus distinctly higher than the alveoli for cheek teeth.^{20,35,39} In most specimens of *N. catocopsis*, such elevation is absent (but see AMNH F:AM 141217). In *N. thinobates*, the anterior part is slightly elevated, whereas this elevation is absent in *N. galiani*. This elevation seems to be absent in *Amphimachairodus*.

The anterior ridge of the upper canine bifurcates at its crown base at a rather high probability in *N. catocopsis*, as has been observed by Beaumont.³¹ The upper canine is not preserved in *N. thinobates*, but *N. galiani* has several upper canines preserved, and most canines also have this bifurcated anterior ridge⁴⁰ (Figure 9). This trait is not mentioned in the description of *M. aphanistus* from Batallones-1 and Batallones-3,^{20,35} but according to personal communication with M. Salesa, it is also present. In all *A. horribilis* specimens we examined, there is no such bifurcated anterior ridge. The upper canine of *N. catocopsis* is similarly wide (concerning the canine width/length ratio) as that of *M. aphanistus*. The situation of *N. thinobates* is unclear, but in *N. galiani* the upper canine is distinctly wider, though having overlaps with *M. catocopsis*. *Amphimachairodus* generally has a narrower upper canine. The P2 is absent in all three specimens of *N. catocopsis* available to us. It is also absent in the only cranium of *N. thinobates*, but present in the cranium of *N. galiani*. The P2 is also absent in most specimens of *M. aphanistus*.^{20,35} It is also absent in the two crania of *A. giganteus*,^{26,36} but present in the majority in *A. horribilis* and *A. coloradensis*.⁴¹ The known P3s of *N. catocopsis* all have prominent postero-lingual convexity. This convexity is variable in *M. aphanistus*, with its presence at a higher frequency in Batallones-1 than that in Batallones-3.^{20,35} The convexity is also present but slightly weaker in *N. thinobates*, though this part is a little broken in the P3 of *N. thinobates*. It is also well developed in most specimens of *N. galiani*, but being weak in one specimen (UF24737). Such strong convexity is absent in *Amphimachairodus*. The P4 of *N. catocopsis* has distinct protocone, located at the level between the parastyle and paracone. The same is true for *M. aphanistus*.^{20,35} In *N. thinobates*, the protocone is similarly large, but located more anteriorly. In *N. galiani*, the protocone is also large, and located variably from *N. thinobates*-like or *N. catocopsis*-like, suggesting the possible variation of this trait in the Late Clarendonian population of

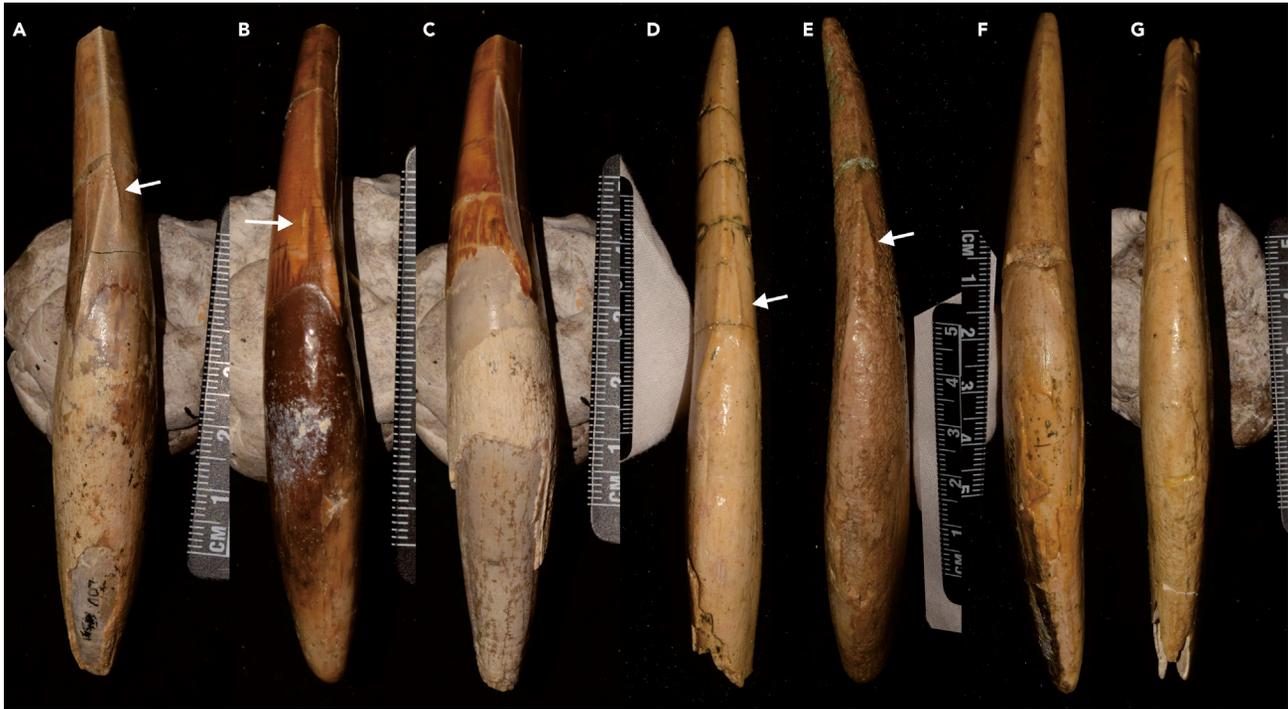


Figure 9. Comparison of anterior view of upper canine of *Nimravides* and *Amphimachairodus*

(A–C) Love Bone Bed *N. galiani*, (A) UF24734, (B) UF25058, (C) UF24465; (D–F) *N. catocopsis*, (D) J. Dakin Quarry, AMNH F: AM146652, (E) Port of Entry Pit, AMNH F: AM146656, (F) Port of Entry Pit, AMNH F: AM102504; (G) Coffee Ranch, *A. coloradensis* AMNH F:AM 30522. Arrows mark the bifurcated anterior ridge.

N. galiani (Figure 10). There is also a distinct preparastyle in most specimens of *N. catocopsis*, more developed than that of *M. aphanistus*.¹³ The preparastyle is very weak in *N. thinobates*, but quite distinct in *N. galiani*. In *Amphimachairodus*, the preparastyle is definitely larger, and oriented in the same line as the parastyle, not turning buccally as in *Nimravides* and *Machairodus*. The preparastyle tends to reduce in *Homotherium*²¹ and is absent in *Xenosmilus*.^{33,34}

The lower dentition of machairodonts is more conservative. The lower canine is large in all species of *Nimravides* and also in *M. aphanistus*, but smaller in *Amphimachairodus*.¹⁰ The p2 is mostly absent in *N. catocopsis* (3 in 12 specimens of Hh1 population and absent in 4 specimens Hh2 population). The p2 is not mentioned to be present in the *M. aphanistus* in Antón et al.,²⁰ but Monesillo et al.³⁵ suggested that this tooth could be present in Batallones-1 but always absent in Batallones-3. The tooth is present in one specimen of *N. thinobates* but absent in another. It is present in half of the specimens (9 in 18 specimens) of *N. galiani*. *Amphimachairodus* and more derived *Homotherium* lack this tooth. The p3 and p4 do not show any clear differences. Antón et al.¹³ suggested that there is an anterior swollen in the anterior side of the p4 in *N. catocopsis*, but this trait is rather variable in this species, and never be more distinct than the case in Sebastian mandible. *M. aphanistus* and other *Nimravides* species do not have this swollen, but it can be even better developed in younger *Amphimachairodus*, e.g. *A. horribilis*.²⁹ The m1 of Hh1 *N. catocopsis* always has a distinct metaconid-talonid complex, but tends to reduce this structure in the Hh2 population. This structure is always present in *M. aphanistus* in both localities of Batallones-1 and Batallones-3,^{20,35} but can be totally reduced in Can Llobateres 1 population.³⁹ This structure is absent in known specimens of *A. giganteus*, but variable in both *A. horribilis* and *A. coloradensis* (absent in the majority but can be quite large too in both species). The m1 of *N. catocopsis* is more robust than that of *M. aphanistus* from Batallones. The two older species *N. thinobates* and *N. galiani* also have slenderer m1, probably correlated with their longer talonid. *Amphimachairodus* has more sectoral m1, which is also slender.

Regarding the body size (here use dental and mandibular sizes as the criterion), *N. catocopsis* is slightly larger than *M. aphanistus* on average (and also in maximum and minimum), but there is considerable

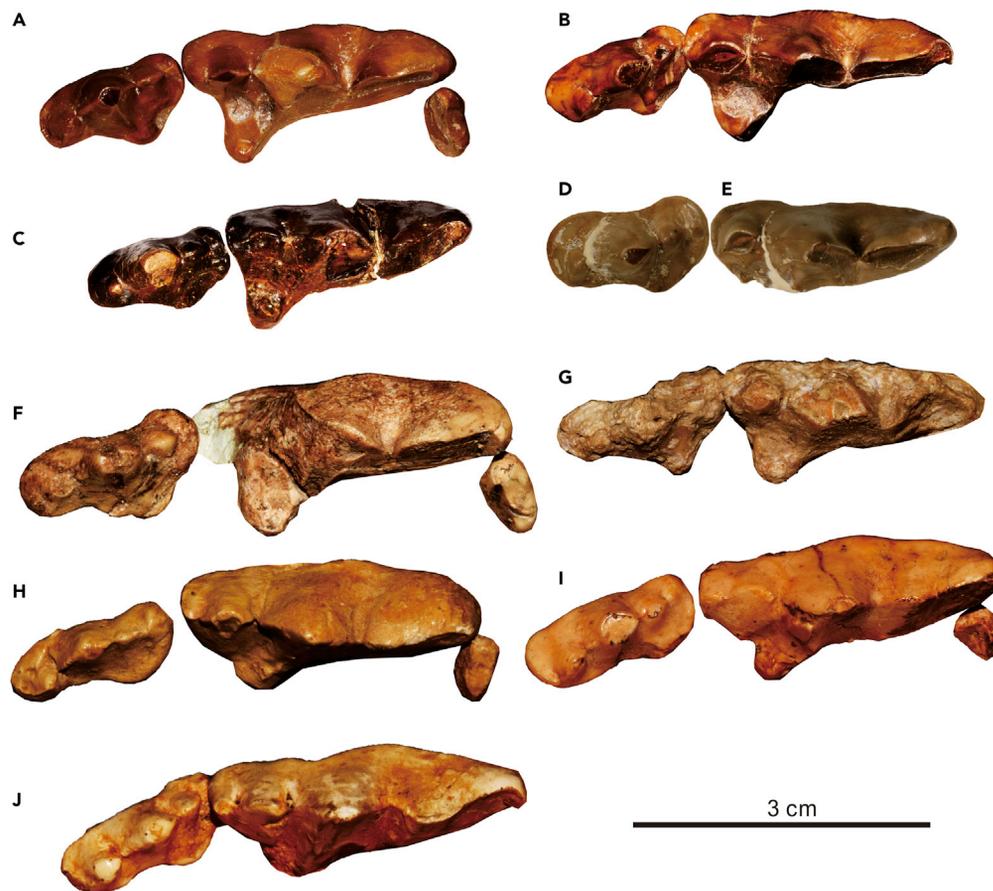


Figure 10. Comparison of upper cheek teeth of *Nimravides* and related taxa

(A and B) *Nimravides galiani* from Love Bone Bed, (A) UF27989, (B) UF24482
 (C) *N. thinobates* from Black Hawk Ranch, Green Valley Formation, UCMP V34512
 (D and E) *Machairodus aphanistus* from Can Llobateres 1, (D) IPS13166, (E) IPS13170, courtesy of J. Madurell-Malapeira
 (F and G) *N. catocopsis* from (F) Jack Swayze quarry, Kansas, AMNH F:AM 146649, and (G) V. V. Parker, AMNH F:AM 146653
 (H) *Amphimachairodus palanderi* Baode, UCMP cast
 (I) *A. horribilis*, Baode, AMNH F:AM 50474
 (J) *A. giganteus*, Halmyropotamos, cast, AMNH FM1-44433.

overlap.^{20,35,39,42} The cranium of *N. thinobates* is clearly smaller than that of *M. catocopsis*, but this specimen is probably female, as the larger mandible of *N. thinobates* from type locality is well comparable to *N. catocopsis* in size. In summary, *N. thinobates* is probably only slightly smaller than *N. catocopsis*, comparable to *M. aphanistus*. *N. galiani* is clearly smaller than *N. catocopsis* without overlap. This species also has a much smaller infraspecific variation in size, suggesting a much smaller sexual dimorphism, unlike that of *N. catocopsis* and *M. aphanistus*. *Amphimachairodus* has a very large variation in body size but is generally similar to or slightly larger than *N. catocopsis* and *M. aphanistus*.

Based on the detailed comparison of craniodental traits, we can clearly see that the majority of similarity between *N. catocopsis* and *M. aphanistus* is sympleisomorphic traits as compared to *Amphimachairodus* and cannot distinguish them from *N. thinobates* and to a less extent *N. galiani*. That is to say, the similarity between *N. catocopsis* and *M. aphanistus* more reflects the evolutionary level. On the contrary, *N. catocopsis* shares important traits with the Late Clarendonian species *N. thinobates* and *N. galiani*, e.g. the marked postcanine constriction on the rostrum. This trait is absent in both *M. aphanistus* and *Amphimachairodus*, and should be regarded as a synapomorphy of *Nimravides*. Even though it cannot exclude that these traits are sympleisomorphic traits of *Nimravides* as compared with the more derived *Machairodus*-*Amphimachairodus* lineage, the age of Late Clarendonian-early Hemphillian *Nimravides* is contemporary to the former lineage and cannot be the ancestor of the former, so it is unlikely that this trait is only sympleisomorphic traits

of *Nimravides*. We, therefore, propose that *N. catocopsis* can be assigned to *Nimravides*, rather than to *Machairodus*, and it is not an immigrant from Eurasia at the beginning of Hemphillian, but a descendant from Late Clarendonian *Nimravides*, mostly probably *N. thinobates*. This is also supported by the stepwise evolution from Late Clarendonian to Hemphillian. See the summary of differences in Table 4.

In summary, as the analysis above, the New World species form a continuously changed line of evolution. As the phylogeny shows, when incorporating stratigraphic information, the monophyly of the New World species is supported, suggesting that *N. catocopsis* is derived from *N. thinobates*, not closely related to *M. aphanistus*. Another reason that *N. catocopsis* is not likely a sister group with *M. aphanistus*, is that the dispersal of Carnivora between Eurasia and North America shows a clear wave-like pattern,^{43,44} and there is small-scale immigration (*Barbourofelis* and *Hoplictis*) within Clarendonian and large-scale immigration between Hh1 and Hh2 (*Amphimachairodus*, *Indarctos*, *Plionarctos*, *Simocyon*, and *Enhydriotherium*), and to a less extent in Hh3 and H4, as has been recently discussed by Jiangzuo and Wang.⁴⁵ It is notable that no Carnivora appeared in North America at the Hh1,¹⁸ and *N. catocopsis* does not seem to be an exception. The ancestor of *M. aphanistus* is not explored here, and a deeper study of the earlier form, i.e., "pseudaelurine" will be needed to survey the ancestor of these large sabertoothed cats.

Parallel evolution of *Machairodus*-*Amphimachairodus* lineage and *Nimravides*

After clarifying the generic affinity of *N. catocopsis* through a systematic morphological comparison and a phylogeny, it will be interesting to revisit the convergent evolution between the New World *Nimravides* lineage and the Old World *Machairodus*-*Amphimachairodus* lineage. Here, we compare the evolution of both lineages from the late Miocene, including two late Clarendonian species of *Nimravides*, and Hh1, Hh2 populations of *N. catocopsis* for the New World lineage, and two populations of *M. aphanistus* from Batallones-1 and Batallones-3, and *A. horribilis* from Baode for the Old World lineage, spanning the age largely contemporary with the New World one.

The Old world lineage experiences a slow evolution between MN9 and MN10, and a quick morphological change in MN11²⁸, resulting in a very different form, *Amphimachairodus*, in MN12. Monesillo et al.³⁵ studied in detail the morphological evolution of *M. aphanistus* from Batallones-1 and Batallones-3. Except a slightly smaller size, the Batallones-3 population shows a slightly more advanced morphotype, e.g. absence of the P2, and presence of P3 with weak postero-lingual convexity, both are derived traits as they are closer to those of *Amphimachairodus*. Nevertheless, the overall morphology did not change in any significant way and does not seem to be different from those from the MN9 population of *M. aphanistus*.³⁹ The lineage experience rapid evolution in MN11 and early MN12, showing a mosaic evolution in some aspects,²⁸ though no good material is known from this age. During MN12, typical *Amphimachairodus*, much more derived than *M. aphanistus* appeared. As mentioned above and being studied by many previous authors,^{10,13,20,31,46} this genus is clearly more derived than *M. aphanistus* in a significant number of traits. These differences make it easily distinguished from the older *M. aphanistus*.

Compared with the increased evolutionary rate of the Old World lineage, *Nimravides* shows a stepwise evolution throughout its evolutionary history. The late Clarendonian *N. thinobates* is slightly smaller than the Hemphillian *N. catocopsis*, and less derived in smaller P4 preparastyle and more anteriorly located protocone, and p4 never develops anterior swelling. In other aspects, it is virtually not different from *N. catocopsis*. *N. galiani* is more primitive in having a more robust canine, the frequent presence of the P2 and p2, and a distinctly smaller size. *N. galiani* is probably not in the line of evolution toward the Hemphillian species, whereas *N. thinobates* is the most probable ancestor of *N. catocopsis*, as was supported in our phylogeny. The character differences between the Hh1 and Hh2 populations of *N. catocopsis* have been discussed above, and it is just like the differences between the different populations of *M. aphanistus* from Batallones-1 and Batallones-3. The Hh2 population is only slightly more derived than the Hh1 population in the reduction of the metaconid-talonid complex. In conclusion, there is a gradually morphological change from the Late Clarendonian to Hh2, without any abrupt morphological change, therefore refuting the immigration hypothesis.

As is shown above, the evolutionary tendency of both Old and New World lineages of scimitar-toothed cats is mostly the same: the tendency of increasing body size, reduction of anterior premolars (P2/p2), enlargement of P4 preparastyle while reduction of its protocone and m1 metaconid-talonid complex. The latter several characters are correlated with increasing sectorial dentition under the selection of increasing cutting efficiency, very easily convergent traits among all Carnivora. This results in the great similarities

Table 4. Morphological characters of four species/population of *Nimravides*

	<i>Nimravides catocopis</i> Hh1	<i>Nimravides catocopis</i> Hh2	<i>Nimravides galiani</i>	<i>Nimravides thinobates</i>	<i>Machairodus aphanistus</i>	<i>Amphimachairodus</i> spp.
Cranium	cranium folded, with an angled middle point, rostrum expanded, with distinct postcanine constriction, mastoid process moderately enlarged	cranium folded, with an angled middle point, rostrum expanded, with distinct postcanine constriction, mastoid process moderately enlarged	cranium folded, with an angled middle point, rostrum expanded, with distinct postcanine constriction, mastoid process slightly enlarged	cranium folded, with a moderately angled middle point, rostrum expanded, with distinct postcanine constriction, mastoid process unknown	cranium folded, with a moderately angled middle point, rostrum not expanded, without distinct postcanine constriction, mastoid process moderately enlarged	cranium not folded, with a flat middle point, rostrum not expanded, without distinct postcanine constriction, mastoid process enlarged
Mandible	no mental flange, coronoid process large	no mental flange, coronoid process large	no mental flange, coronoid process large	no mental flange, coronoid process large	no mental flange, coronoid process large	weak to moderate mental flange, coronoid process small
upper dentition	canine with bifurcated anterior ridge, P2 absence, P4 with strong preparastyle not in line with parastyle, protocone moderate	canine with bifurcated anterior ridge, P2 absence, P4 with strong preparastyle not in line with parastyle, protocone moderate	canine with bifurcated anterior ridge, P2 presence, P4 with weak preparastyle not in line with parastyle, protocone large	canine unknown, P2 absence, P4 with strong preparastyle not in line with parastyle, protocone moderate	canine with? bifurcated anterior ridge, P2 mostly absence, P4 with moderate preparastyle not in line with parastyle, protocone moderate	canine without bifurcated anterior ridge, P2 presence in most species, P4 with strong preparastyle in line with parastyle, protocone small
lower dentition	p2 absence, m1 with distinct talonid	p2 absence, m1 with very weak or no talonid	p2 absence in half specimens, m1 with distinct talonid	p2 absence (variability unknown), m1 with distinct talonid	p2 mostly absence, m1 with distinct talonid	p2 absence, m1 with no talonid in most cases

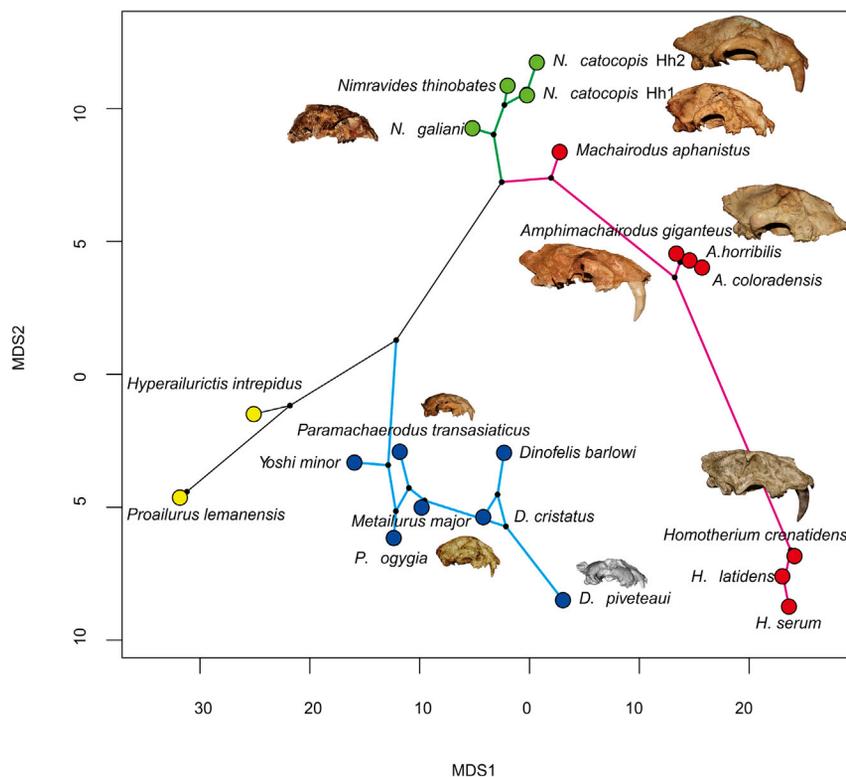


Figure 11. NMDS of 56 morphological traits of felids

The phylogenetic tree is mapped to the plots using *phylomorphospace* function of R package *phytools*.⁴⁷

between *N. catocopis* and *M. aphanistus*, which have a similar evolutionary level. The expanded rostrum of *Nimravides*, with distinct postcanine constriction, is unique to the New World lineage and suggests a possible different hunting behavior between the two lineages. Contrary to the rapid evolution of the Old World lineage, the evolution of *Nimravides* remains slow throughout its evolutionary history.

To more quantitatively show such a parallelism process, a non-metric multidimensional scaling (NMDS) analysis was carried out based on a total of 56 craniodental traits from the phylogenetic matrix (see appendix, traits with incomplete data are discarded as empty data are not allowed in the analysis) were selected for machairodont representatives of both Old and New Old lineages, as well as several metailurine cats and outgroup *Proailurus* and *Hyperailurictis*.

In the plot of NMDS analysis (Figure 11), the Old and New World lineages initially evolved toward different directions, with the primitive species *N. galiani* is located far from *M. aphanistus*. The more derived *N. thinobates* and *N. catocopis* are rather, in the same evolutionary direction as that of *M. aphanistus*, showing the tendency of parallelism. The late Late Miocene to Plio-Pleistocene members of the Old World lineage evolved toward another morphospace, suggesting the exploration of a new morphospace in the Old World lineage. The distance between *M. aphanistus* and *Amphimachairodus* spp. in the morphospace is distinctly larger than that between Hh2 *N. catocopis* and *N. galiani*, suggesting a much faster evolutionary rate in the Old World lineage. Interestingly, our outgroup Metailurini also shows parallelism with the Old World lineage, but discussion on this issue is out of the scope of this study. The generic assignment of the middle and late Turolian species of the Old World lineage is also disputed. Morlo and Semenov²⁸ suggested a gradual evolution of lineage and thought that there is no need to separate the younger form as *Amphimachairodus*. Similarly, Geraads and Spassov²⁶ suggest that there is no branch event from *M. aphanistus* to *Amphimachairodus* and the former species has no apomorphy, and separation of *Amphimachairodus* is not necessary. On the contrary, the phylogenetic analysis of Christiansen⁴⁶ does not support a close relationship between *M. aphanistus* to *Amphimachairodus*. We agree with Geraads and Spassov²⁶ that the result of Christiansen⁴⁶ is probably problematic with the question of taxa sampling,

but as we have shown above, *Amphimachairodus* is more derived than *M. aphanistus*, much more so than that between *Nimravides* and *Machairodus*, so we follow Werdelin et al.⁴⁸ that the younger members of the lineage should be separated as *Amphimachairodus* for convenience, just like the separation of *Homothe-rium* and *Amphimachairodus*.

Lineage replacement of the New World scimitar-toothed cat by the Old World one

The replacement of *Nimravides* by *Amphimachairodus* at the Hh2/Hh3 boundary has been well established; however, it is unclear whether *Amphimachairodus* directly competitively replaced *Nimravides* or rather, *Amphimachairodus* only flourished after the extinction of *Nimravides*. Such a question is always difficult to answer as the process often happened in a short period, and it is often unclear of the causal relationship.

Even though *Amphimachairodus* is clearly more derived than *Nimravides* in craniodental morphology, it does not mean that the Old World genus could competitively replace the New World genus. Among the living Carnivora, the intraguild competition is often not directly correlated anyway with hunting efficiency, but correlated strongly with body size.⁴⁹ For example, rich research suggests that the tiger has a strong influence with smaller-sized competitors wolf and leopard, through direct interference competition that aggressively reduces the abundance of the latter species.^{50–52} The abundance of wolves and leopards is often directly negatively correlated with tiger abundance.^{50,53} These facts provide the basis for discussion of the process of replacement of *Nimravides* by *Amphimachairodus*.

Jiangzuo and Hulbert⁴¹ presented that *Amphimachairodus* has entered North America at Hh2 in Florida, but this locality lacks *Nimravides*. Jiangzuo and Hulbert⁴¹ mentioned that most material from Box-T (Texas, Hh2), said to be *Amphimachairodus* by Martin,¹¹ should represent *N. catocopsis*. We further examined all the material from this locality and found that one edentulous mandible (Figure 3H) clearly has a mandibular flange, and the anterior border of the mandible is concave, and should indeed represent *Amphimachairodus*. This locality, thus, represents the first known locality to have both Old and New World scimitar-toothed cats coexisted. Also, its diverse fauna is composed by several Eurasian immigrant carnivorans (*Indarctos* and *Moralesictis*), as well as Neotropical immigrants (e.g., sloth *Thinobadistes*)^{18,54,55}, which emphasizes the importance of this area for the faunal interchange during the late Miocene.

If *Amphimachairodus* has distinct adaptation prominence over *N. catocopsis*, we would expect to see that this new immigrant quickly becomes flourished in the New World, being abundant in many fossil localities coexisting with *N. catocopsis*. Rather, this new immigrant seems to be very rare in Hh2, with only low density when it coexisted with *N. catocopsis*. Therefore, even though *Amphimachairodus* is more derived than *N. catocopsis* in many ways, it does not seem to take the position of the latter immediately after it entered North America. This is expected when we consider the scenario of living species competition, that body size makes a great role through interference exclusion of smaller species by dominant species. The body size of the Hh2 population of *N. catocopsis* is quite large. Among the four femurs from the Ogallala group, the two larger male has a total length of 417.7 and 432.2 mm, larger than that of *Smilodon* and comparable to that of *Panthera atrox*.⁵⁶ Some recent found from Idaho, Oregon, and Texas were erected as a new species *Machairodus lahayishupup* of huge size.⁵⁷ The dental differences they listed from those of *N. catocopsis* are only intraspecific variation when taking into account the large collection analyzed here, though the humerus is indeed much larger than the humeri we observed. We propose this form is more likely to be local subspecies of *N. catocopsis lahayishupup*, of very large body size in southwestern America. The tooth row length of *Amphimachairodus* mandible from Box-T is similar to the larger specimen of *N. catocopsis* (presumably a male) from the same locality, but the mandible is slenderer. We can at least say that *Amphimachairodus* is not larger than *N. catocopsis*. Moreover, *Amphimachairodus* seems to be slightly more cursorial than *N. catocopsis*, with antero-posteriorly more elongated distal humerus (distal humerus a-p height vs m-l width ratio is 0.683 in Withlacoochee River 4A specimen) than that of *N. catocopsis* (corresponding value 0.578–0.668), and a cursorial species is often less strong, with weaker muscle power. Therefore, the above-mentioned evidence does not support a direct replacement of *N. catocopsis* by *Amphimachairodus* through competition.

However, the significant environmental change happened close to the boundary between the Hh2 and Hh3, when the C4 grassland expanded throughout the continental, causing a distinct faunal change.^{58–60} Many carnivores went extinct without new ecologically similar species, e.g. *Barbourofelis* (therefore not from competition). The higher efficient cutting apparatus and more specialized hunting behavior (and

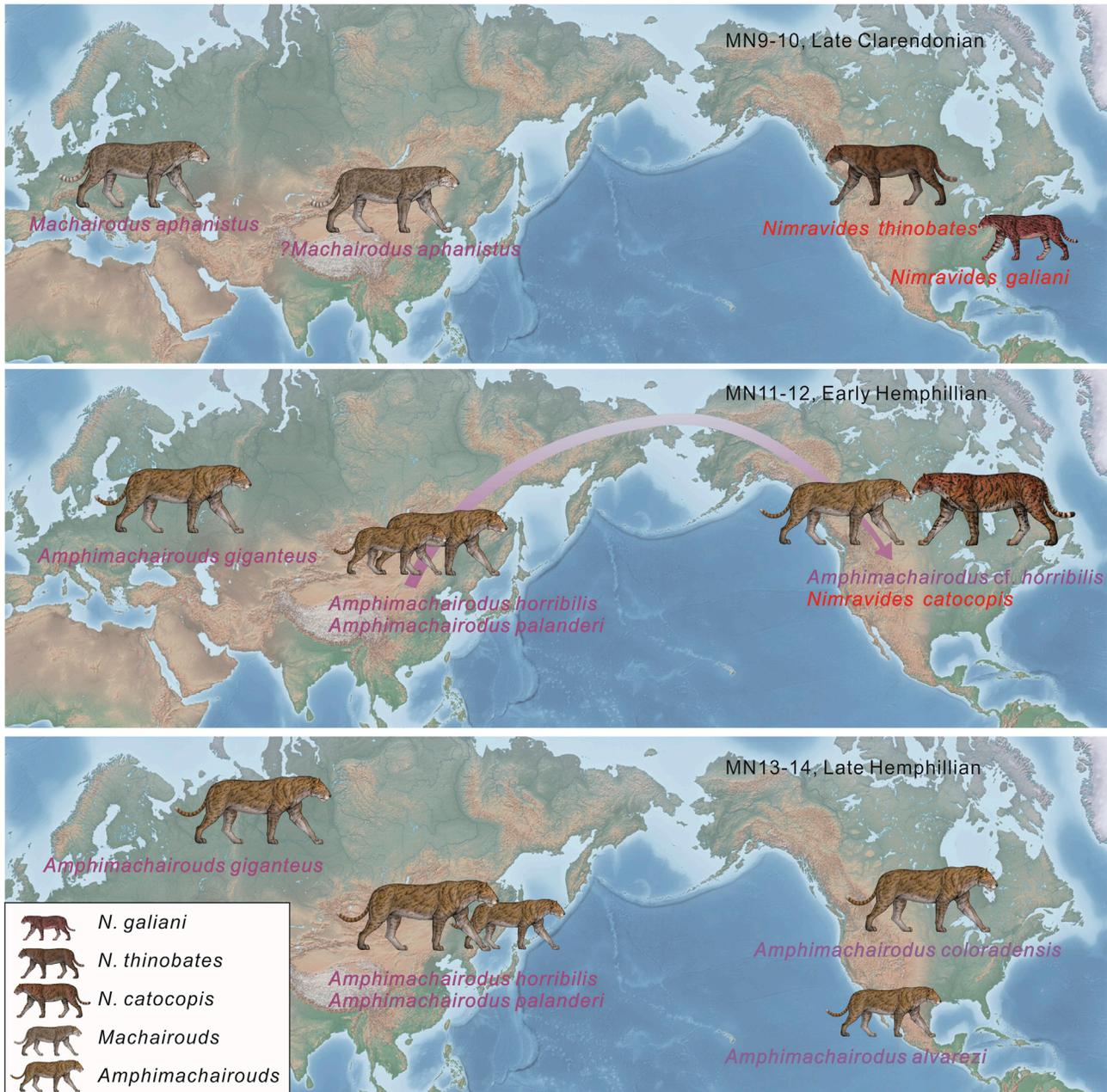


Figure 12. Evolution and dispersal scenario of scimitar-toothed cats from Old and New World
Artwork by Yu Chen.

probably also more efficient) as revealed from craniodental morphology, and slightly more cursorial adaptation of *Amphimachairodus* made it survive, whereas *N. catocopsis* went extinct. A similar process has been found in the Quaternary horses in Eurasia.⁶¹ When caballoid horses appeared in the Old world, it did not directly replace the older stenonid horses, but retained a low density with the later species when coexisted, but when the environment changed to a more arid and unstable one, its higher flexibility made it survive and finally becomes the dominant species.⁶¹

The lineage replacement of scimitar-toothed cats thus provides a good example of how closely related species replace each other (Figure 12). The more derived traits may contribute little in direct competition, but its advantages appeared when the environment changes, and finally contribute to its success. More

evidence from the detailed study of other groups will be welcome to study the mechanism of replacement of creatures in evolutionary history.

Wang et al.⁶² recently proposed an anagenetic evolution of *A. coloradensis-alvarezii* in North America with a tendency of reduction of body size, which is different from the general increasing body size pattern seen in North American *Nimravides* and Eurasian *Amphimachairodus*. The influential factors of body size can be varied from temperature, vegetation coverage, and food source. *Amphimachairodus alvarezii* was found in the southern part of North America, and the warm climate and high vegetation coverage probably contribute to its small size, but more comprehensive studies will be needed to explore this issue.

Conclusions

Through the description of new material and a systematic comparison and phylogenetic analysis, *N. catocopsis* is identified as a North American endemic sabertoothed cat, not an immigrant from Eurasia. The Late Clarendonian and Early Hemphillian *Nimravides* represent a lineage that shows unique morphology, e.g. presence of marked rostral expansion at the canine and strong postcanine constriction.

Both the Old and New World lineages parallel toward larger body size, the tendency of reduction of anterior premolars, and more sectorial dentition. The Old World lineage experiences a higher rate of trait evolution during the MN11, and evolved to a much more derived genus *Amphimachairodus*. This genus immigrated to North America at the Hh2, but did not immediately replace *Nimravides* through direct competition. Rather, it is very rare in Hh2, but when the significant faunal change near the Early/Late Hemphillian in North America, its more derived traits made it survived the environmental change and continue to flourish during the Late Hemphillian in the New World.

Limitations of the study

In this work, we only focus on the Late Clarendonian and Hemphillian member of *Nimravides*, and the earlier form is not included due to time and space limitation. Such the origin of *Nimravides* is insufficiently explored.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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- METHOD DETAILS

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.isci.2022.105637>.

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DECLARATION OF INTERESTS

The authors declare no conflict of interest.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Phylogenetic character matrix	Modified from Jiangzuo et al. ⁶³	NA
Software and algorithms		
	Mrbayes 3.2.7 ^{64,65} ggplot2 3.3.5 ⁶⁶ in R 4.0.5 ⁶⁷ PAST 4.03 ⁶⁸	NA

RESOURCE AVAILABILITY

Lead contact

Further information and requests for related data should be directed to and will be fulfilled by the lead contact, Qigao Jiangzuo (jiangzuo@ivpp.ac.cn).

Materials availability

All *Nimravides* materials are housed in scientific museum, colleges or research institute (see details in text).

Data and code availability

Any details of phylogenetic analysis is provided in [supplemental information](#).

METHOD DETAILS

Abbreviations

AMNH American Museum of Natural History, New York, USA.

AMNH FM Fossil Mammal collection in American Museum of Natural History, New York, USA.

AMNH F:AM Frick collection (Fossil Mammals), Division of Paleontology, AMNH.

IVPP Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Science, Beijing, China.

P/p upper/lower premolar.

M/m upper/lower molar.

Hh1 Hemphillian1, early Early Hemphillian North American Land Mammal 'Age' (NALMA).

Hh2 Hemphillian2, late Early Hemphillian NALMA.

Hh3 Hemphillian3, early Late Hemphillian NALMA.

Hh4 Hemphillian4, Latest Hemphillian NALMA.

MN Neogene land Mammal age of Europe.

UCMP University of California Museum of Paleontology, Berkeley, California, USA.

UF Florida Museum of Natural History at University of Florida, Gainesville, Florida, USA.

In this study, we exam the rich collection of Hemphillian *Nimravides* (all from the Ogallala Group) remains of Frick collection in AMNH, which have not been published before except a skull (AMHN F:AM 104044) described by Antón et al.¹³ Of especially importance is a cranium and two mandibular fragments from V.V. Parker of Higgins Local Fauna, which is described in detail, and data for other materials (largely mandibles or isolated dentition) were used for comparison. A complete cranium of *N. catocopsis* from Jack Swayze Quarry is also figured, but without a detailed description, since it is in the exhibition and unavailable for close study.

For comparison, two derived Late Miocene *Nimravides* were studied. The material includes *N. thinobates* housed in UCMP and *N. galiani* from UF. In addition, *A. horribilis* housed in AMNH, IVPP, *A. giganteus*, and *Homotherium* specimens and cast housed in AMNH, and *A. coloradensis* housed in UCMP and AMNH are checked for comparison. Other sabertoothed cats were compared through literature.

There were eight localities with rich *N. catocopsis*, all from the Early Hemphillian localities within the Ogallala Group (Table S1). Thanks to the great biostratigraphic work published recently by,^{16–19} we were able to distinguish these materials into Hh1 and Hh2 age.

Terminologies for the skull follow, with minor modifications, Qiu et al.⁶⁹ The measurements follow and are shown here in Figure 1. Parts of figure plots were made in the software package ggplot2 3.3.5⁶⁶ in R 4.0.5⁶⁷ and NMDS analysis was performed using PAST 4.03.⁶⁸

The phylogenetic using tip-dating Bayes Inferences was performed using the software Mrbayes 3.2.7.^{64,65} The analysis was set for 4 chains, including three cold chains and one hot chain. Two independent runs were performed, each 10 million generations. The Mkv and fossilized birth-death models^{70,71} were used in the analysis.