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Late Miocene immigrant carnivorans in California, USA highlight a coastal corridor for intercontinental dispersals

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Abstract The Neogene interval witnessed three major waves of intercontinental dispersals by carnivoran mammals, mainly migrating from Eurasia to North America but with rare occurrences going in the opposite direction (e.g., *Sthenictis*, *Leptarctus*). The timing and composition of dispersers are thought to be controlled by filter-bridge mechanisms, but it is unclear what types of regional conditions promoted occasional dispersals outside of the three major waves. We study and report on new occurrences of small-bodied carnivorans from late Clarendonian-aged Black Hawk Ranch and Cuyama Valley fossil mammal assemblages in California. The relatively late occurrences of the mustelids *Sthenictis* and *Hoplictis* and the ailurid *Alopecocyon* in coastal regions of western North America suggest that nearshore dispersal corridors both facilitate and preserve faunal elements later than they might otherwise occur further inland. The availability of both marine- and terrestrially-derived food resources may be an important factor in allowing coastally dispersing taxa to be accommodated in those ecological communities compared to less heterogenous environments further inland.

Key words Cenozoic, paleobiogeography, mammals, Carnivora

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1 Introduction

The Holarctic region is marked by present-day biogeographic distinctions between Nearctic and Palearctic mammal communities (Rodríguez et al., 2006). The deep-time establishment of these modern geographic differences was modified by repeated Eurasian and North American mammal dispersals across the Bering Strait over much of the Neogene (~23 to 2.58 Ma) during shifting environmental conditions (Jiangzuo and Wang, 2023). In particular, Qiu (2003) recognized three major dispersal waves from Eurasia to North America

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by carnivoran mammals across the Beringian land bridge during the Neogene, providing a framework to understand the establishment of present-day carnivoran guilds in the northern continents. In celebration of his long and distinguished career in describing and interpreting the mammalian fossil record, here we report on new occurrences of immigrant carnivorans that inform our understanding of the role that coastal regions such as what is today California played in facilitating and recording carnivoran dispersal events across the northern continents (Fig. 1).

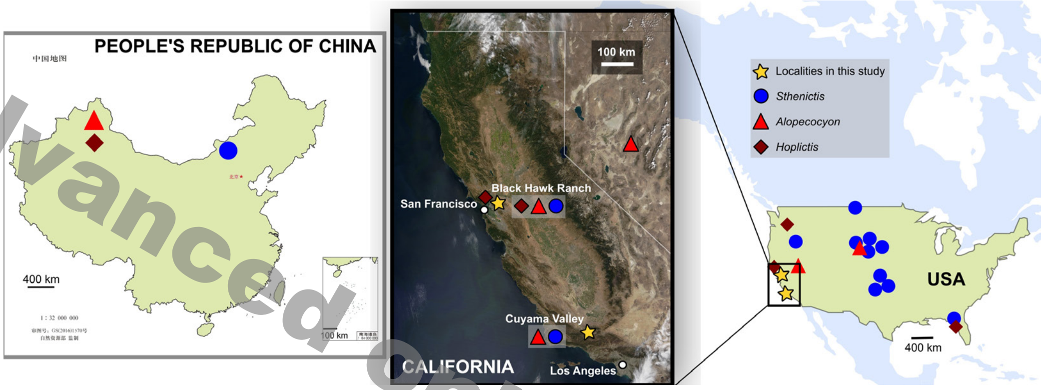

Fig. 1 Fossil localities of carnivorans as discussed in this study

Localities from which new occurrences are reported are indicated by star symbols. Chinese and North American *Sthenictis* localities are in circles, *Alopecocyon* localities in triangles, and *Hoplictis* localities in diamonds. Localities are based on the Paleobiology Database (accessed 27 March 2025)

Map approved number: GS(2016)1570

We studied the Black Hawk Ranch and Cuyama Valley Badlands fossil collections housed in the University of California Museum of Paleontology and the Natural History Museum of Los Angeles County. The Black Hawk Ranch Quarry is a Clarendonian-aged deposit near the paleo-coastline of the San Francisco Bay Area (Prothero and Tedford, 2000) (Fig. 1). Poorly sorted sediments representing a range of clays, sands, and conglomerates preserve both plant and animal fossils. The fossil mammal materials represent a time-averaged series of depositional events controlled by fluvial transport, with evidence of reworked elements being incorporated alongside primary sources of skeletal material. The site was initially excavated by University of California (UC) paleontologists in the 1930s, and collecting continued well into the 1980s through the use of the quarry as a classroom for various paleontology courses taught at UC Berkeley. Collecting activities slowed to a trickle in the 1990s shortly after the Department of Paleontology was terminated by UC Berkeley and when the Museum of Paleontology faculty became affiliated with then newly established Department of Integrative Biology. The UCMP currently houses over 3000 catalogued specimens from the quarry, recording more than 30 genera of fossil mammals (Richey, 1938, 1948; Macdonald, 1948; Savage, 1955; Tseng et al., 2010).

The Cuyama Valley sits due southwest of the San Andreas fault in southern California in the vicinity of Santa Barbara and Ventura Counties. Sediments of the Caliente Formation crop out in the valley and include up to ~900 m of fluvial and lacustrine deposits that span the Hemingfordian, Barstovian, Clarendonian, and Hemphillian North American Land Mammal Ages (James, 1963; Prothero et al., 2008). Paleontological investigations in the area began in the late 1920s, initially by C. Lewis Gazin of the California Institute of Technology (under the guidance of Chester Stock) (Gazin, 1930). Work steadily continued on the Cuyama Valley mammal faunas and peaked again during the 1960s when Gideon James of UCMP systematically sampled the Caliente Formation and described the stratigraphy and small mammals from across four major east-west trending canyons in the area (James, 1963). Descriptive work on the fossil assemblages of the four major valleys of the Cuyama Badlands continues to this day (e.g., Scarpetta and Ledesma, 2023; Tseng, 2025). The UCMP currently houses over 3500 catalogued specimens from the Caliente Formation, with more than 30 genera of fossil mammals (James, 1963; Kelly and Lander, 1992).

2 Materials and methods

All specimens reported on in this study are from the UCMP collections, and were digitized using high resolution microcomputed tomography (GE Phoenix Nanotom M, Functional Anatomy and Vertebrate Evolution Laboratory, UC Berkeley) at a voltage of 100–120 kV, current of 120–150 μA, and using 1000-1500 projection images depending on specimen size. Images were acquired using isotropic voxel sizes of 14–35 μm. Specimen scans were segmented and converted into 3D mesh models using 3D Slicer (www.slicer.org), and arranged for screen capture using Geomagic Wrap 2020 (Artec 3D, Luxembourg). All measurements were taken using Mitutoyo digital calipers to the nearest 0.1 mm; comparative measurements were taken either from the literature or on specimens and casts using digital calipers.

Institutional abbreviations AMNH, American Museum of Natural History Vertebrate Paleontology collections, New York, USA; CIT, California Institute of Technology collections and localities, now part of LACM; F:AM, Frick Collection of the AMNH; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; LACM, Natural History Museum of Los Angeles County, California, USA; OMNH, Oklahoma Museum of Natural History, Norman, Oklahoma, USA; SAN, Sansan collection in the Muséum d'Histoire naturelle de Toulouse, France; UCMP, University of California Museum of Paleontology, Berkeley, California, USA; UF, University of Florida Museum of Natural History, Gainesville, Florida, USA; UOMNH, University of Oregon Museum of Natural and Cultural History, Eugene, Oregon, USA.

3 Results

3.1 Systematic paleontology

Class Mammalia Linnaeus, 1758

Order Carnivora Bowdich, 1821

Family Mustelidae Fischer von Waldheim, 1817

Genus *Sthenictis* Peterson, 1910

***Sthenictis dolichops* Matthew, 1924**

(Figs. 2A, C–D, G–J, L–N, Q–R, T–V, 3; Appendix 1)

Sthenictis bellus Matthew, 1932

Holotype AMNH FM 18264, left dentary with c, p1 alveoli, p2–m1, and m2 alveolus.

Referred material from California Black Hawk Ranch (UCMP locality V3310), Green Valley Formation: UCMP 33708, partial left p4; UCMP 79520, partial right m1; UCMP 44075, dentary fragment with left m1, partial ascending ramus, and mandibular condyle. Quatal Canyon South (UCMP locality V5656), Caliente Formation: UCMP 200104, partial left dentary with broken p4, almost complete m1 missing protoconid. Quatal Canyon South 9 (UCMP locality V5748), Caliente Formation: UCMP 200105, left dentary fragment with broken m1.

Formation and age Green Valley Formation (locality V3310), late Clarendonian North American Land Mammal Age (NALMA) (Prothero and Tedford, 2000); Caliente Formation (localities V5656 and V5748), late Clarendonian NALMA (Prothero et al., 2008).

Description and comparison The two dentary fragments from Cuyama Valley (UCMP 200104, 200105) preserve lower carnassial teeth (m1) that are extremely similar to the morphology of AMNH 20501 (the type of the late Hemingfordian *Sthenictis bellus* that was synonymized with *S. dolichops* by Baskin (2020)).

All three specimens show a paraconid that is similar in height and size to the metaconid, a protoconid that is ~50% taller than either cusp, and a shelf-like talonid with a raised hypoconid and a labially sloped occlusal surface (Fig. 2G–H, M–N). The isolated m1 (UCMP 79520) from Black Hawk Ranch also shares all of the above features and thus is referred to *S. dolichops* as well. A second Black Hawk Ranch m1, heavily worn but preserved in situ in a partial hemimandible (UCMP 44075), is approximately 40% longer and wider compared to UCMP 79520 (Fig. 2C–D). Nevertheless, the dimensions of the California *Sthenictis* sample are comparable to those reported from the great plains (Appendix 1), and thus we consider the size differences to represent individual and/or populational variation (Baskin, 2020) (Fig. 3). Finally, a partial p4 (UCMP 33708) from Black Hawk Ranch, consistent in its larger size with UCMP 44075, shows a heavily worn main cusp and posterior wear that indicates the presence of a posterior accessory cusp (Fig. 2A, L). In this regard it is similar to the p4 morphology observed on the Cuyama specimen preserving p4 (UCMP 200104) and also to AMNH 20501.

Although the smaller California specimens are also close in size to *S. junturensis* from the Juntura Basin in Oregon, *S. junturensis* lacks accessory cusps on premolars altogether (Shotwell et al., 1963), whereas the California specimens show evidence of p4 posterior accessory cusps.

Like other *Sthenictis* specimens, the materials from California are larger in size than those of other mustelids such as *Plionictis*, *Dinogale*, and several fossil taxa referred to "*Martes*" (Baskin, 2020). *Sthenictis* also tend to have better developed m1 talonid basin compared to Plionictis and more trenchant talonid with prominent hypoconid relative to *Dinogale* and "*Martes*" which exhibit more basined talonids (Baskin, 1998, 2020).

Fig. 2 Mustelid and ailurid specimens described in this study
A, L, T. *Sthenictis dolichops*, UCMP 33708, Lp4, in medial (A), lateral (L) and occlusal (T) views;
B, K, S. *Alopecocyon* cf. *A. parverratis*, UCMP 33829, Rm1, in medial (B), lateral (K) and occlusal (S) views;
C, J, R. *S. dolichops* UCMP 79520, Rm1, in medial (C), lateral (R) and occlusal (S) views;
D, I, Q. *S. dolichops*, UCMP 44075, left dentary with m1, in medial (D) lateral (I) and occlusal (Q) views;
E, P, X. *Hoplictis* cf. *H. grangerensis*, UCMP 61401, Rp2, in medial (E), lateral (P) and occlusal (X) views;
F, O, W. *Hoplictis* cf. *H. grangerensis*, UCMP 34615, Lp3, in medial (F), lateral (O) and occlusal (W) views;
G, N, V. *S. dolichops*, UCMP 200104, left dentary with broken p4, m1, in medial (G), lateral (N) and occlusal (V) views; H, M, U. *S. dolichops*, UCMP 200105, left dentary with broken m1, in medial (H), lateral (M) and occlusal (U) views

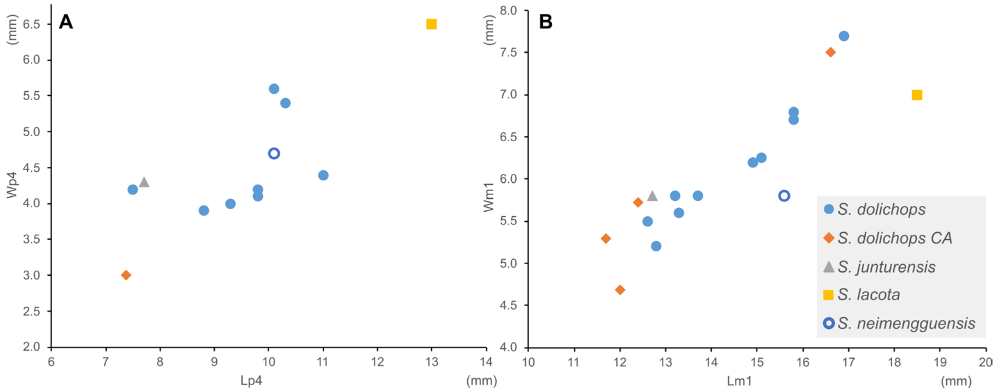

Fig. 3 Comparisons of p4 and m1 dimensions in *Sthenictis* samples
A. length versus width of p4 (in mm); B. length versus width of m1 (in mm).
California specimens of *S. dolichops* are indicated as “*S. dolichops* CA”

Genus *Hoplictis* Ginsburg, 1961

Hoplictis cf. *H. grangerensis*

(Fig. 2E–F, O–P, W–X; Appendix 1)

Beckia grangerensis Bryant, 1968

Referred material from California Black Hawk Ranch (UCMP locality V3310), Green Valley Formation: UCMP 34615, left p3; UCMP 61401, right p2.

Formation and age Green Valley Formation (locality V3310), late Clarendonian NALMA (Prothero and Tedford, 2000).

Description and comparison The two isolated premolars both exhibit strong basal cingulum that wraps around the entire base of the crown. A single, robust cusp sits near the middle of the tooth, and the p3 also displays a posterior ridge that trends towards the labial edge as it leads down the tip of the tooth. All of these characteristics are consistent with LACM 10642, the holotype of *H. grangerensis* (Bryant, 1968), UCMP 112158, the referred specimen from the Kendall-Mallory quarry a few miles from the Black Hawk Ranch (Edwards, 1976), and UF 25965, a specimen from the Love Bone Bed of Florida referred to *H.* sp., (Baskin, 2005). Given the paucity of additional characters, we tentatively conclude these specimens as being close to *H. grangerensis* and await additional material prior to confirming its species designation. Valenciano (2019) reported on the first occurrences of *Hoplictis* in East Asia, including a late Tunggurian (MN7/8, 12–11 Ma) occurrence of *Hoplictis* cf. *H. helbingi* from the Duolebulejin Formation in the Ulungur River area of Xinjiang Autonomous Region, China (Fig. 1). This updated Eurasian distribution of the genus added a geographic and temporal datum consistent with the subsequent arrival of the genus in North America during middle to late Clarendonian (10–9 Ma).

Family Ailuridae Gray, 1843

Subfamily Simocyoninae Dawkins, 1868

Genus *Alopecocyon* Camp and Vanderhoof, 1940

Type species *A. goeriachensis* (Toula, 1884)

Alopecocyon leardi Stock, 1947

Actiocyon leardi Stock, 1947

Type specimen LACM (CIT) 2747, partial palate with right P1 to M1, left P4–M1.

Formation and age Caliente Formation (UCMP locality V5663 [= CIT 64]), late Clarendonian NALMA, Nettle Springs Local Fauna in the Apache Canyon (James, 1963).

Remarks Webb (1969) synonymized *Actiocyon* with *Alopecocyon*, crediting D.E. Savage for the observation that both genera are characterized by “short, nearly quadrangular upper carnassial and the low connate cusps of the upper molars.” Subsequently several researchers cited similarity between the two genera but either did not offer additional justification to support or refute Webb’s assessment (Baskin, 1998; Salesa et al., 2022), or only generally suggested the similarity in dental morphology between the two genera (Smith et al., 2014). We concur with all of these authors in the numerous morphological similarities between *Actiocyon* and *Alopecocyon*, and follow Webb (1969) in treating *Actiocyon leardi* as belonging to *Alopecocyon*. Additionally, we deem the minor morphological differences between *A. leardi* and *A. parverratis* discussed by Smith et al. (2014) as constituting interspecific variation that do not amount to genus-level differences. Therefore, we hereby treat *Actiocyon parverratis* as belonging to *Alopecocyon* as well. As such, both North American species formerly assigned to *Actiocyon* should belong to *Alopecocyon*.

Alopecocyon cf. *A. parverratis*

(Fig. 2B, K, S; Appendix 1)

Actiocyon parverratis Smith et al., 2014

Referred material from California Black Hawk Ranch (UCMP locality V3310), Green Valley Formation: UCMP 33829, partial right m1 with protoconid, metaconid, and talonid preserved.

Formation and age Green Valley Formation (locality V3310), late Clarendonian NALMA (Prothero and Tedford, 2000).

Description and comparison The referred specimen represents an unworn adult tooth fragment, preserving a complete protoconid that is twice the height of a strongly developed metaconid. A low ridge connects the protoconid and metaconid, and a trenchant notch is formed where the two cuspids meet. A similar arrangement is seen between the protoconid and the hypoconid, with a notch forming at the junction between the trigonid and the talonid. There is a hint of a small hypoconulid adjacent to the hypoconid, but the rest of the talonid is enclosed by a continuous ridge that forms a wall around the distal and lingual edges of the talonid basin. This raised ridge connects gradually to the distal face of the metaconid, but no notch is present at their junction. In all of above characteristics, the Black Hawk Ranch specimen is very similar to the conditions observed in the type specimen of *A. parverratis* (UCMP 141928) from the Barstovian Middlegate Local Fauna of Monarch Mill Formation, Nevada (Smith et al., 2014). Furthermore, both the Black Hawk Ranch and Middlegate specimens exhibit similar m1 morphology when compared to a complete dentary of *A. goeriachensis* from Sansan (Salesa et al., 2022). However, given the importance of both P4 and m2 features in distinguishing different species of *Alopecocyon* (Stock, 1947; Smith et al., 2014; Baskin et al., 2020), we refrain from placing the Black Hawk Ranch taxon into a species until additional materials are known. For now, the closest taxon morphologically and spatially to the referred specimen would be *A. parverratis.*

4 Discussion

The Clarendonian age of *Sthenictis dolichops* specimens reported in this study represent the youngest occurrences for the species (Appendix 1). Elsewhere this species is reported from the late Hemingfordian and early Barstovian of Nebraska. *Sthenictis junturensis* and ?*S. lacota* also occur in the late Clarendonian NALMA. All known North American specimens of *Hoplictis* are late Clarendonian or younger in age, and the late Clarendonian occurrence of *Alopecocyon* in Black Hawk Ranch also represents one of the youngest occurrences for the genus in North America, as does an undescribed mandible (F:AM 25212) from the Ash Hollow Formation, Nebraska (Baskin et al., 2020). Taken collectively, these temporally late occurrences of immigrant carnivoran lineages in California indicate the presence of suitable habitats persisting along the paleocoast of western North America from southern California to as far north as potentially Washington state (Fig. 1).

Qiu's (2003) framework for major carnivoran dispersals suggests three major waves at ~20 Ma (near the Arikareean-Hemingfordian NALMA boundary), 8–7 Ma (in the early Hemphillian), and ~4 Ma (in the early Blancan). Based on known temporal ranges, none of the three genera discussed in this study appeared to have participated in those major waves. Rather, *Sthenictis* dispersed from North America to East Asia no later than the late Middle Miocene (Tseng et al., 2009), and *Alopecocyon* dispersed in the opposite direction around the same time (Smith et al., 2014). Even the later-arriving *Hoplictis* likely arrived in North American from East Asia by the end of the Clarendonian (Valenciano et al., 2019). Given the differences in dispersal timing of these coastally-occurring carnivorans compared to those that participated in the major intercontinental dispersal waves, we speculate that a coastal corridor route along western North America may have functioned as a different type of dispersal filter compared to those that accommodated more inland taxa. The availability of both marine- and terrestrially-derived food resources along the coastal ecotone plays a key role in expanding the feeding niches of living mammals in model systems (Luengos Vidal et al., 2021), and may have also played a role in generating favorable dispersal corridors that accommodated higher carnivoran diversity than less heterogenous habitats further inland.

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Supplementary material can be found on the website of Vertebrate PalAsiatica (http://www.vertpala.ac.cn/CN/10.19615/j.cnki.2096-9899.250813).

美国加州晚中新世食肉类扩散类群与其迁移路线及古环境的指示

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摘要：全北界的新近纪脊椎动物化石记录了至少三次大规模的食肉类动物迁移，物种在北美和欧亚大陆之间双向交流。参与这些大规模迁移的类群以及其事件发生的地质年代被认为受白令陆桥过滤性机制主导，但是目前对于在这三波主要的迁移事件之外更罕见的其他物种迁徙现象却缺乏类似的框架来诠释。针对美国加利福尼亚州晚中新世Black Hawk Ranch (黑鹰牧场)和Cuyama Valley (库亚玛谷)动物群里还未报道的小型食肉类化石进行了描述和研究。结果显示鼬科*Sthenictis*, *Hoplictis*两个属和小熊猫科*Alopecocyon*属在北美洲西部的化石记录相对这些属在其它全北界的化石出现时代更晚，这表明北美洲西部沿岸的迁移路线可能代表了比内陆地区更为稳定和有利的生态环境，甚至可能作为残遗种的保护区。居住于现代沿海生态过渡地区的哺乳动物群拥有同时利用海生和陆生资源的地理优势，这一现象指示晚中新世时期，加州、奥勒冈州及华盛顿州一带的生态环境条件可能是促进跨大陆迁移成功的重要因素之一。

关键词：新生代，动物地理，哺乳动物，食肉目

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