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Journal

PaleoBios, 29(1)

ISSN

0031-0298

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Publication Date

2009-06-22

DOI

10.5070/P9291021804

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A new immigrant mustelid (Carnivora, Mammalia) from the middle Miocene Temblor Formation of central California

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A new mustelid genus from the Barstovian (middle Miocene) marine Temblor Formation in California is described. The material of *Legionarictis fortidens* includes an incomplete cranium with partial upper dentition. The straight lingual border and slightly expanded posterointernal cingulum of M1 are plesiomorphic traits, as in the European *Dehmictis*. However, the M1 is not as posteriorly expanded, and the P4 does not have a lingual hypoconal crest, differentiating *L. fortidens* from younger North American forms. Furthermore, the P4 protocone is posteriorly placed from the paracone, as in the extant South American *Eira*. An autapomorphic feature of *L. fortidens* is its highly hypertrophied P4 paracone with a bulbous crown. The robust upper carnassial, very strong development of the sagittal crest, and derived enamel microstructure all suggest a hard food component in its diet. The coastal depositional environment indicated by the presence of marine taxa in the Temblor Formation suggests that hard shelled invertebrates might have been a food source of *L. fortidens*. A combination of plesiomorphic and derived dental characteristics puts the new form at an evolutionary stage basal to otters and closer to the living *Eira*. Cladistic analysis of craniodental characters suggests that *L. fortidens* is more derived than generalized basal mustelines of the Old World, and may have diverged from the lutrine lineage in a separate immigration event to the New World.

INTRODUCTION

Paleontological exploration in 1913 by the University of California Museum of Paleontology to the western edge of the San Joaquin Valley in central California uncovered fossiliferous marine sandstone deposits of middle Miocene age (Merriam 1914) (Fig. 1). The local fauna, subsequently named the “*Merychippus* zone”, contains both terrestrial and marine taxa (Merriam 1915). Collections by other institutions since then have produced additional large and small mammals (Bode 1935). In 2004, one of us (JDS) oversaw a paleontological mitigation project for the construction of a power transmission line near Monocline Ridge north of Coalinga, and uncovered a new bone bed in the Temblor Formation (Kelly and Stewart *in press*) (Table 1). Among the more than 1,200 vertebrate fossils collected from the new bone bed is a partial cranium of a new, unusual form: a large mustelid with very robust carnassial morphology and enamel microstructural modification towards durophagy. Considering the proximity of the *Merychippus* zone fauna to the coast during the middle Miocene, this new mustelid might have consumed shelled invertebrates using its robust carnassials. The distinctive features of the new form warranted the naming of a new genus and species. Its phylogenetic affinity lies in the middle Miocene diversification of basal mustelines. Furthermore, its basal position to the otters suggests that this new form probably split off from the lutrine lineage sometime in the early to middle Miocene, representing a distinct immigrant lineage from the Old World.

MATERIALS AND METHODS

The new material studied is housed in the University of

California Museum of Paleontology in Berkeley, California. Comparative materials are housed at the Natural History Museum of Los Angeles County, California and the American Museum of Natural History, New York. Cladistic analysis was conducted using PAUP* (Swofford 1993) with the heuristic search algorithm. All measurements were taken with a Mitutoyo

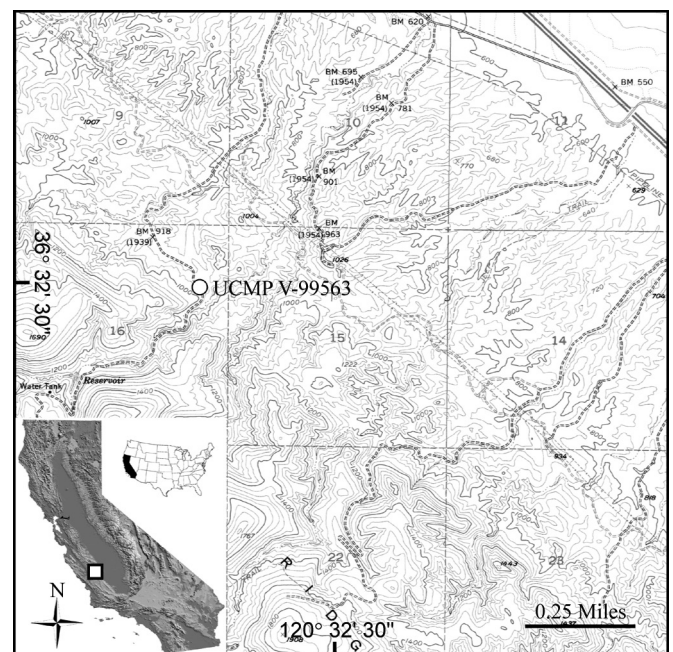


Figure 1. Map showing location of the Monocline Ridge assemblage locality (UCMP V99563). Topographic map modified from 1:24000 scale U.S. Geological Survey map.

vernier caliper to the nearest 0.1 mm. Reconstructed illustration of the cranium was done using a traced outline of a photograph of the specimen. Examination of enamel microstructure was done using a dissection light microscope.

INSTITUTIONAL ABBREVIATIONS

F:AM: Frick collection, American Museum of Natural History, New York, NY, USA

BM: British Museum, London, UK

KUVP: University of Kansas Museum of Natural History, Lawrence, KS, USA

LACM: Natural History Museum of Los Angeles County, Los Angeles, CA, USA

LACM[M]: Mammalogy Collection, LACM

NMNH: National Museum of Natural History, Washington, DC, USA

UCMP: University of California Museum of Paleontology, Berkeley, CA, USA

UMMP: University of Michigan Museum of Paleontology, Ann Arbor, MI, USA

SYSTEMATIC PALEONTOLOGY

CLASS: MAMMALIA Linnaeus 1758

ORDER: CARNIVORA Bowdich 1821

FAMILY: MUSTELIDAE Fischer de Waldheim 1817

SUBFAMILY: MUSTELINAE Fischer de Waldheim 1817

Legionarictis fortidens

(Table 2, Figures 2–10)

Holotype—UCMP 166190, partial cranium with left I1-2, P2-4, right P2, and fragmentary left and right M1s.

Type locality—UCMP V99563 “Monocline Ridge assemblage,” 30 km north of the North Coalinga quarry near Coalinga, California. The locality is on a small hill of the Monocline Ridge between Panoche Creek and Arroyo Cierro (Kelly and Stewart *in press*). See Table 1 for a preliminary faunal list of the locality.

Age and stratigraphy—UCMP V99563 is near the top of the marine sandstone/pebble conglomerate Temblor Formation, which is overlain by the non-marine cross-bedded calcareous sandstone, mudstone, claystone, and pebble conglomeratic Oro-Loma Formation (Bartow 1996). Based on a study of perissodactyl and artiodactyl biochronology (Kelly and Stewart *in press*), the locality is of early to early late Barstovian North American Land Mammal Age (middle Miocene) in age.

Etymology—*Legionarius*, a legionary soldier of the Roman Republic Period; *ictis*, weasel—generic name refers to the prominent sagittal crest of the holotype, reminiscent of the longitudinal helmet ornamentation of Roman legionaries and centurion officers. *Fortis*, strong; *dens*, tooth—specific name refers to the robust carnassial of the holotype specimen.

Diagnosis—large mustelid, with very prominent sagittal crest similar to older individuals of the Eurasian badger (*Meles Boddaert 1785*); infraorbital foramina small, immediately

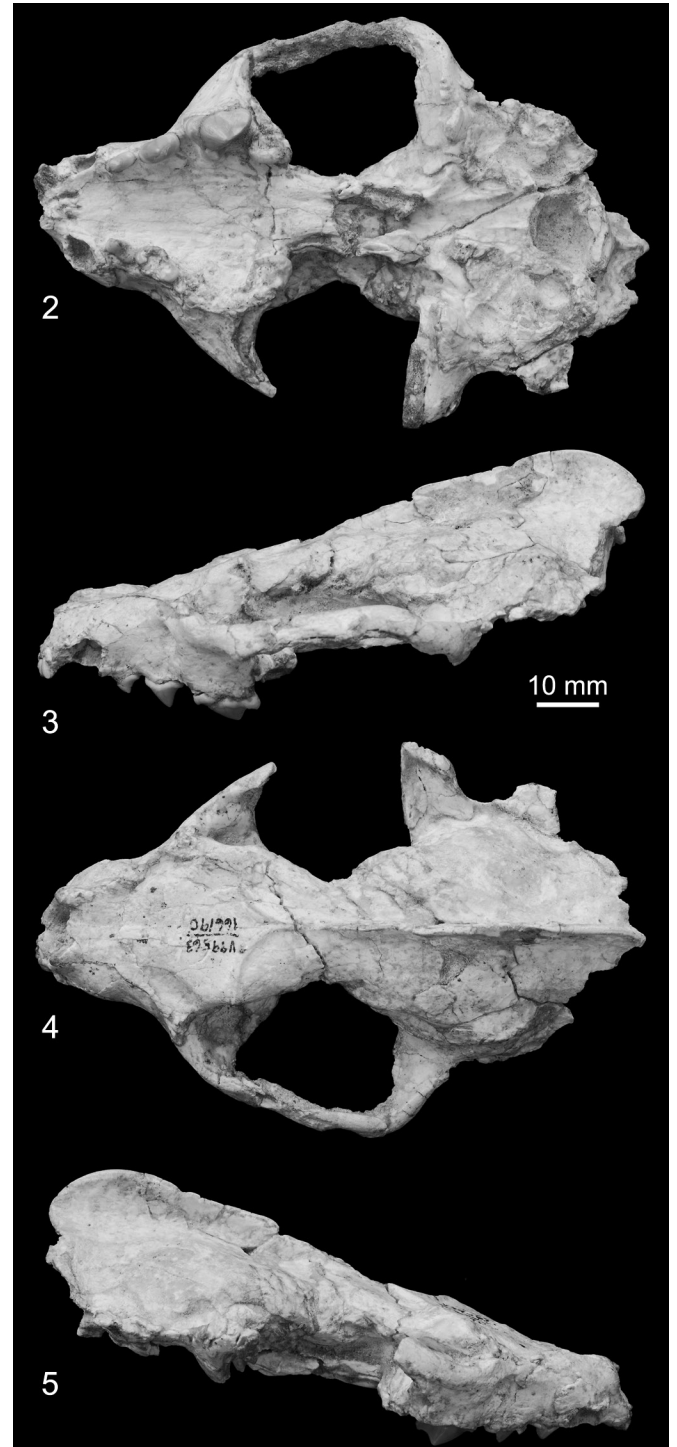
Table 1. A preliminary faunal list of the Monocline Ridge assemblage (UCMP V99563). Modified from Kelly and Stewart (*in press*).

Amphibia	<i>Anura</i> , sp. undetermined
Eureptilia	
Ophidia	Colubridae
	<i>Masticophis</i> or <i>Coluber</i> sp.
Testudines	Testudinidae
	<i>Hesperotestudo</i> sp. of the <i>H. osborniana-orthopyga</i> lineage
Aves	
Anseriformes	Anatidae
	<i>Branta</i> cf. <i>B. woolfendeni</i>
	anatid, sp. undetermined
	Podicipidae
	Passeriformes, sp. undetermined
Mammalia	
Artiodactyla	Antilocapridae
	Cosorycinae, gen. and sp. indeterminate
	Camelidae
	<i>Miolabis</i> sp.
	camelid, sp. undetermined
Carnivora	Felidae
	<i>Pseudaelurus marshi</i>
	Mustelidae
	<i>Legionarictis fortidens</i> sp. et. gen. nov.
	<i>Martes</i> cf. <i>M. glarea</i>
	Amphicyonidae
	<i>Amphicyon ingens</i>
	Canidae
	<i>Microtomarctus conferta</i>
	Borophaginae, sp. undetermined
Lagomorpha	Leporidae, sp. undetermined
Perissodactyla	Equidae
	<i>Archaeohippus mourningi</i>
	<i>Desmatippus avus</i>
	“ <i>Merychippus</i> ” <i>californicus</i>
	“ <i>Merychippus</i> ” <i>brevidentus</i>
	“ <i>Merychippus</i> ” cf. “ <i>M.</i> ” <i>relictus</i>
	Rhinocerotidae
	cf. <i>Peraceras</i> sp.
	Proboscidea, sp. undetermined
	Rodentia, two undetermined. spp.

above posterior root of P3 as in most basal mustelines; upper tooth formula 3/1/3/1/; I3 unenlarged, as in basal mustelines; P2-3 slender and simple, without accessory cusps; P4 protocone posteriorly offset from parastyle crest, slightly anterior in position to paracone, similar to *Martes* Frisch 1775; carnassial notch absent as in all neomustelids, P4 paracone very robust, labially and lingually inflated, invading the protocone space; P4 hypoconal crest absent as in basal mustelines; M1 triangular in occlusal view, with well-formed, straight lingual cingulum; posterior cingulum slightly expanded, M1 labial roots close together or fused, intermediate between the morphology observed in basal mustelines and lutrines.

Description—Cranium. The entire cranium is dorsoventrally deformed; the compression is more severe on the right half in the ventrolateral direction (Figs. 2–5). Associated with this asymmetrical deformation, much of the right upper dentition and zygomatic arch are destroyed. The nasal opening is dorsoventrally compressed to a width of 9.1 mm and a height of 4.0 mm; the nasal bones have been pressed into the nasal cavity, displacing the premaxilla and maxilla laterally. The entire rostrum is 30 mm long between the anterior tip of the premaxilla and the anterior edge of the orbit. The antorbital fossa extends 11.5 mm anterior of the orbit. The infraorbital foramina are 2.4 mm wide and 3.34 mm high; they are situated ~11 mm dorsal of the posterior base of P3. Postorbital processes are not particularly prominent; two prominent frontal ridges lead from the postorbital processes and converge to form the sagittal crest ~8.4 mm posterior of the orbit. The sagittal crest rises gradually over the posterior cranium, reaching a maximum height of 14.0 mm; the crest measures 61.9 mm from the convergence of the frontal ridges to the posterior end, which terminates into a notch that overhangs the occiput. The narrowest region of the cranium is a gradual constriction 13.3 mm posterior to the postorbital processes. The zygomatic arch is slender, measuring 6.5 mm in depth. The lateral sides of the frontal and parietal regions are badly damaged; no foramina are visible. The cranial region does not appear particularly inflated or box-like, even after dorsoventral compression is taken into account. On the dorsolateral surface of the posterior cranial region there are vertical linear rugosities. The lambdoidal crests are destroyed, but at the junction between the lambdoidal and sagittal crests there is a short ridge running ventrally and smoothly merging with a vertical occiput.

There are three incisive foramina immediately behind the incisors on the palate. The paired palatine canals originate at a position adjacent to the P4 protocone, and extend anteriorly as far as the position of P2. The overall shape of the palate is a tapering triangle, with the distance between labial boundaries of M1 approximately equal to that of the toothrow length between C1-M1. The posterior end of the palate extends well beyond the position of M1; the pterygoid bones extend posteriorly to at least the position of the glenoid fossae. The post-glenoid processes are prominent; they are broken at the ventral tips, so it is impossible to discern whether they would



Figures 2–5. Skull of *Legionarictis fortidens* gen. et. Sp. nov., UCMP 166190. 2. Skull in ventral view. 3. Left lateral view. 4. Dorsal view. 5. Right lateral view.

lock the mandibular condyles in articulation. The foramen ovale is immediately medial to the glenoid fossa. The ventral wall of tympanic bulla has been destroyed; the ventral part of the petrosal and the dorsal roof of the tympanic chamber is exposed. The foramen rotundum is missing, the postero-

Table 2. Upper cheek teeth measurements for *Legionarictis fortidens*, compared with the first known upper dentitions of *Dehmictis vorax*, *Mionictis* sp., *Sminthosinis bowleri*, *Trochictis depereti*, and *Trigonictis kansasensis*. L, length; W, width; WaP4, width of anterior P4 at the position of the paracone and protocone; WpP4, width of posterior P4 at the position between the paracone and metastyle. Unless otherwise noted, measurements were taken using vernier calipers to the nearest 0.02 millimeters.

	<i>Dehmictis vorax</i>	<i>Legionarictis fortidens</i>		<i>Mionictis</i> sp.		<i>Sminthosinis bowleri</i>	<i>Trochictis depereti</i>	<i>Trigonictis kansasensis</i>
	Dehm, 1950	UCMP 166190		F:AM 63296		UMMP V52868	BM M5313	KUVP 4604
		left	right	left	right	Holotype ¹	Holotype ²	Holotype ³
LP2		5.22	5.54	6.50	6.16	5.38	5.0	5.5
WP2		2.88	3.26	3.40	3.26	2.15	2.7	3.6
LP3		7.30	7.96	7.52	7.48	8.01	6.0	7.0
WP3		4.10	4.74	4.30	4.26	2.63	3.4	4.4
LP4	9.7	11.50	—	12.34	12.30	4.60	9.5	11.9
WaP4	6.9	8.28	—	—	—	5.35	6.7	7.8
WpP4		5.44	—	5.86	5.88			6.6
LM1	5.8	7.72	7.28	11.96	11.82	4.76	5.5	6.8
WM1	9.8	—	—	12.92	~14.28	7.47		12.1

¹Bjork (1970); ²Pilgrim (1932); ³Hibbard (1941)

ventral part of the basisphenoid is also partially destroyed. No evidence of the mastoid process was present. The right paroccipital process is not enlarged; it is anteroposteriorly compressed, and points posteroventrally.

Dentition: Only left I2-3 are preserved; the I3 is only slightly larger in size than I2, and both are unicuspid. No canine teeth were preserved, but the canine alveoli position indicates the presence of a small diastema between C1 and I3. Post-canine teeth are not crowded; there is a small diastema between each of them. Right P2 and left P2-3 are unicuspid, with only a weak posterior cingulum. The P4 is the most prominent tooth in the dentition; a low parastyle crest is present at the anterior base of the tooth. The paracone is bulbous, occupying more than half the total length of P4. There is no carnassial notch; the posterior face of the paracone runs into a lower, small metastyle. A strong conical protocone is present, posteriorly set from anterior edge of the parastyle crest. There is no hypoconal crest, but there is a weak lingual cingulum running along the lingual base of the tooth crown. On the right M1, only the posterolingual side is preserved; there is a strong posterior cingulum, surrounding a small cusp at the lingual corner of the tooth. Only the lingual cingulum is preserved in left M1; the cingulum runs parallel to the sagittal plane of the cranium, and the anterior border of the tooth appears more or less perpendicular to this cingulum. No postprotocrista could be seen on what remains of the M1. The labial roots of M1 appear to be very close together, and it is possible they might be fused; this gives the M1 a triangular outline in occlusal view. Cheek tooth measurements and comparison to other taxa are shown in Table 2.

Hunter-Schreger enamel microstructural bands (Stefen 2001) are visible on the cheek teeth under a dissecting microscope at 35 times magnification (Table 3). All of the premolars and molars show the basal carnivoran condition of undulating Hunter-Schreger bands, except for the carnassial. In the left P4, the top ~66% of the enamel exhibit acute-undulating bands (Figs. 8–9), which are considered to be more derived than the undulating bands (Stefen 1997).

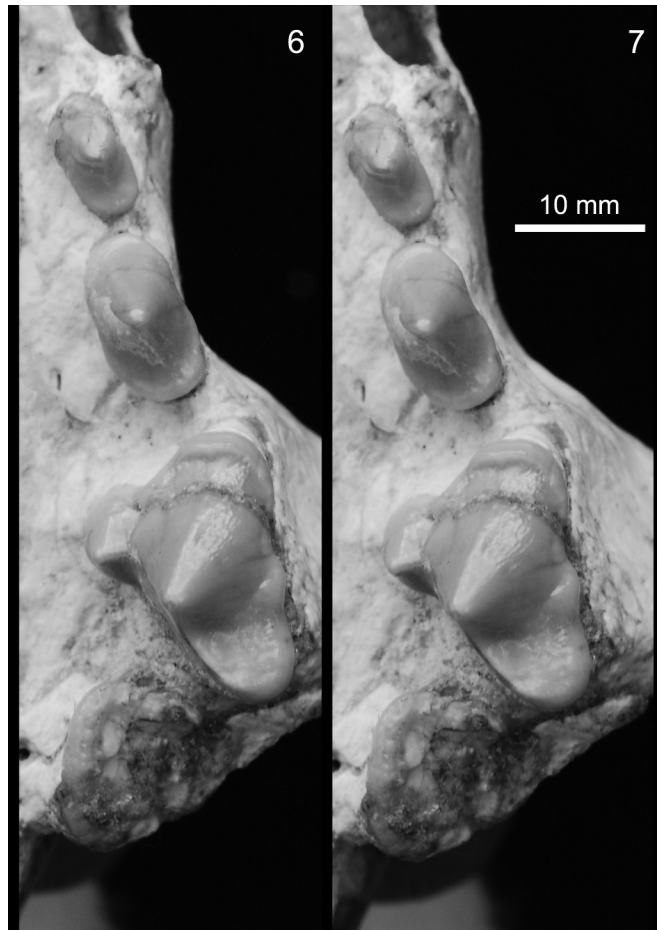
Comparison—The presence of both plesiomorphic and highly autapomorphic characters in *Legionarictis*, along with the paucity of diagnostic synapomorphic characters shared with a particular group of mustelids, made phylogenetic placement of this new form difficult. The suite of plesiomorphic neomustelid characters includes small infraorbital foramina, unenlarged I3 and P4 with simple protocone. A few synapomorphies, namely enlarged P4 protocone, smaller M1 metacone relative to paracone, and strongly ridged M1 lingual cingulum, are shared by *Legionarictis*, early and middle Miocene basal Old World mustelines, the South American *Eira* Jardine 1842, and what has been referred to as Galictini by Baskin (1998). Morphological affinity among basal Old World mustelines *Dehmictis* Ginsburg and Morales 1992, *Eirictis* Qiu et al. 2004, *Iberictis* Ginsburg and Morales 1992, *Trochictis* Meyer 1842, New World forms *Sminthosinis* Bjork 1970, *Trigonictis* Hibbard 1941, and extant South American taxa *Galictis* Bell 1826 and *Eira* have been suggested (Pilgrim 1932, Ray et al. 1981, Ginsburg and Morales 1992, Baskin 1998, Ginsburg 1999). In addition, the otter-like forms *Enhydriactis* Stefani 1891, *Lutravus* Furlong 1932, and *Mionictis* Matthew 1924 have been suggested to take their root in the *Dehmictis* group (Baskin 1998, Ginsburg 1999). In light of

these suggestions, comparisons were made between *Legionarictis* and these taxa.

The basal taxon *Dehmictis vorax* of early Miocene time from Europe was described by Dehm (1950) and designated by Ginsburg and Morales (1992) as a possible ancestral form

Table 3. Hunter-Schreger enamel banding patterns in the cheek teeth of *Legionarictis fortidens*. The microstructure was observed at three regions in each tooth: (1) the top 33% of an unworn tooth or the occlusal surface if worn; (2) the middle 33% of the tooth, and (3) the bottom 33% of the tooth near the base of the tooth crown.

	Occlusal	Mid-section	Crown base
Left P2	undulating	undulating	undulating
Left P3	undulating	undulating	undulating
Left P4	acute	acute	undulating
Left M1	-	undulating	undulating
Right P2	undulating	undulating	undulating
Right P3	-	-	undulating
Right M1	-	undulating	undulating

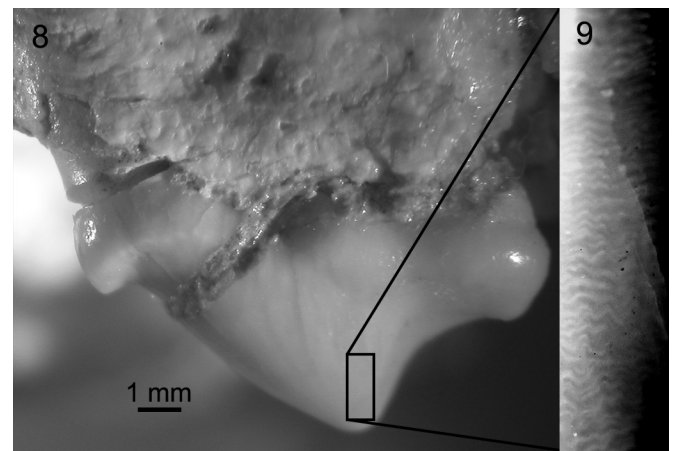


Figures 6–7. Stereopair photos of the left dentition of *Legionarictis fortidens*.

from which more derived mustelines and also lutrines originated. *Dehmictis* is similar to *Legionarictis* in having conical P4 protocone, a very weak P4 lingual cingulum, and a straight M1 lingual cingulum. The position of the P4 protocone is more anteriorly situated in *Dehmictis*; this is a plesiomorphic feature also seen in *Martes*. In addition, the M1 metacone of *Dehmictis* remains more comparable in size to the paracone as in *Martes*, and not reduced as in more derived fossil taxa. Considering these basal features, *Dehmictis vorax* was used as the fossil outgroup while several species of *Martes* were included as an extant outgroup in the cladistic analysis conducted in this study.

An interesting form similar to South American *Eira* was recently described from the late Pliocene (2.58–2.15 Ma) Longdan Fauna of Gansu Province, China (Qiu et al. 2004). The mustelid *Eirictis robusta* has a high rostrum, and nasal bones that are slightly convex at the anterodorsal margin. The maxillary portion of the zygomatic arch is deep above P4, as in *Legionarictis*. Whereas the antorbital arch is located dorsal to the space between the P4 roots in *Eirictis*, it appears to be more anteriorly placed in *Legionarictis*; the arch is situated over the anterior P4 root. *Eirictis* has enlarged I3 which is not observed in *Legionarictis*. As in *Eirictis*, *Legionarictis* shows clear antorbital fossa, delineating the orbit. The distinctiveness of the P4 protocone, having constricted anterior and posterior boundaries, is a symplesiomorphy between *Eirictis* and other mustelines (Qiu et al. 2004). The more conical shape of the P4 protocone, and the complete lack of a posterior cingulum or hypoconal ridge, both being plesiomorphic traits, prompted Qiu et al. (2004) to distinguish *Eirictis* from *Pannonictis* Kormos 1931, *Enhydriactis*, *Trigonictis*, and *Sminthosinis*.

Slightly more derived than *Dehmictis*, the early Miocene *Iberictis* is similar to *Legionarictis* in the conical P4 protocone, straight M1 lingual cingulum, and the overall triangular shape of M1 associated with metacone reduction. *Iberictis* differs in



Figures 8–9. Views of the left P4 of *Legionarictis fortidens* under magnification. 8. Labial view at 6x. 9. Labial view at 25x, note presence of acute-undulating Hunter-Schreger bands.

the presence of a lingual ridge on P4, and anterior P4 protocone position. In addition, the transverse width of M1 in *Iberictis* is longer than the length of P4 (Ginsburg and Morales 1992).

From the early and middle Miocene epochs of Europe, the musteline *Trochictis depereti* (Pilgrim 1932) resembles *Legionarictis* only in its conical P4 protocone. Its P4 has a lingual ridge as well as an anteriorly placed protocone. The M1 is relatively short and not posteriorly expanded. *Trochictis* also retains a P1. Compared to *T. depereti* (BM M5313), the anterior and posterior faces of P2 and P3 appear more asymmetrical in *Legionarictis*. The anterior faces tend to appear convex, whereas the posterior face is concave; this gives an appearance of a posteriorly tilting premolar crown when viewed laterally. Both *Trochictis* and *Legionarictis* have elongate, simple P2, unlike the more oval, nearly circular P2 of *Eirictis*. The P1-3 of *Trochictis* are very similar to that of *Martes*, with its P2-3 being simple, elongate, and P1 small and scoop-like; the loss of P1 in *Legionarictis* notwithstanding, P2-3 in this new form are probably morphologically conservative, and thus represent symplesiomorphies of aforementioned comparative taxa.

Pliocene in age and likely an immigrant from the Old World, *Sminthosinis bowleri* Bjork 1970 from the Hagerman Fauna in Idaho, USA, is similar to *Legionarictis* in its conical P4 protocone (Bjork 1970). The major difference lies in the anteriorly placed protocone position and quadrate M1 with round lingual cingulum of *Sminthosinis*.

Trigonictis kansasensis from the late Pliocene Rexroad Fauna of Kansas shares with *Legionarictis* a conical P4 protocone (Hibbard 1941). It is different from *Legionarictis* in that the P4 protocone is anteriorly placed (not posterior of the parastyle crest), and a P4 lingual ridge is present. The M1 of *Trigonictis* is quadrate, with a rounded lingual cingulum, both different from the triangular M1 with straight lingual cingulum in *Legionarictis*. The P4 of *Trigonictis macrodon* (USNM 23664) is nearly identical in size to that of *Legionarictis*; however, the anterior face of the P4 paracone is straight in lateral view in *Trigonictis*, whereas in *Legionarictis* it is convex. Although both genera lack a carnassial notch, the connection between the paracone and metastyle in *Trigonictis* forms a much deeper arch than in *Legionarictis*, which has only a shallow depression between the two cusps (Figs. 6-7). The lingual ridge in *T. macrodon* is characteristically straight, forming the long edge of the triangular P4 in occlusal view; in *Legionarictis*, the protocone border is well-defined and without a clear lingual ridge or cingulum.

The South American *Eira barbara* is similar to *Legionarictis* in its (1) posteriorly placed, conical P4 protocone, (2) lack of a P4 lingual ridge, (3) slender zygomatic arch, (4) small infraorbital foramina, and (5) small and blunt paroccipital process. One difference is the enlarged I3 in *Eira*, which is not observed in *Legionarictis*.

Also South American in distribution, *Galictis vittata* is similar to *Legionarictis* in the slender zygomatic arch, small infraorbital foramen size, and short paroccipital process. It differs from *Legionarictis* in its enlarged I3, cuplike P4 protocone,

and anteroposteriorly compressed M1 with round lingual edge.

Among the otter-like forms, Pilgrim (1932) placed the genus *Enhydriactis* very close to *Trochictis*. Clear morphological differences are observed between the the *Enhydriactis* and *Legionarictis*. Features like the P4 protocone being anteriorly situated and cuplike, presence of P4 lingual ridge, rounded M1 lingual cingulum and overall quadrate shape of that tooth in *Enhydriactis* all indicate close affinity to the morphology observed in middle Miocene lutrines.

The early Pliocene *Lutravus halli* is similar to *Legionarictis* in the posteriorly placed P4 protocone and straight lingual M1 (Furlong 1932). It differs from *Legionarictis* by its enlarged I3, cuplike P4 protocone, presence of P4 lingual ridge, and unreduced M1 metacone.

Both North American and European specimens have been assigned to the Miocene lutrine *Mionictis*, but the European forms have been renamed *Lartetictis* and *Adroverictis* (Ginsburg and Morales 1996). Ginsburg and Morales (1996) considered these two genera to be melines, convergent with the lutrine *Mionictis*, and both melines and lutrines sharing affinities to *Trochictis*. In addition, Ginsburg and Morales (1992) reassigned *Mionictis artensis* to the genus *Trochictis*, citing the expansion of the M1 talon as a trait shared by *Trochictis*, *Lartetictis*, and *Adroverictis*. The M1 of *Lartetictis dubia* has a prominent posterolingual cingulum, to a more extreme degree than observed in *Legionarictis*; both *Adroverictis ginsburgi* and *A. schmidtkitteri* have anteriorly expanded lingual M1 border, not transversely flat as in *Legionarictis*. Unfortunately, both European genera represent material too fragmentary to be included in the cladistic analysis.

There are no published illustrations or photographs of upper dentition of North American *Mionictis* (Jon Baskin *personal communication*). However, two specimens were brought to our attention: F:AM 63298 and 63296, associated partial lower jaws and partial anterior cranium with full dentition, respectively. The specimens came from the MacAdams quarry of Clarendon Beds of Texas, and are referred to *Mionictis* (Harrison 1981). The lower jaws appear to represent a relatively large species of *Mionictis*. The anterior cranium represents a taxon similar in size. The wide internal M1 cingulum of F:AM 63296 approximately occludes with the m1 talonid and m2 in F:AM 63298, although differential tooth wear indicates they are from two individuals. Comparing *Legionarictis* with F:AM 63296, the former has unenlarged I3; P2-3 are similarly small and simple in both taxa; P4 paracone of F:AM 63296 is not bulbous as in *Legionarictis*; a weak but definite P4 hypoconal crest is present in F:AM 63296; posterior M1 cingulum is more posteriorly extended in F:AM 63296; both exhibit a prominent lingual M1 cingulum that is anteroposteriorly straight; M1 is relatively larger in F:AM 63296.

CLADISTIC ANALYSIS

A parsimony cladistic analysis was performed using 22 craniodental characters on fifteen mustelid taxa, including

major taxa discussed in the comparison section, with the addition of *Lontra* Gray 1843 as a representative of extant North American lutrine to better evaluate character polarity in the otter-like fossil taxa (Appendices 1–2). Using the heuristic search option, 132 equally parsimonious trees were obtained. The 50% majority-rule consensus tree of those 132 trees is shown in Figure 11. Three species of *Martes* were designated as outgroup taxa. In all 132 most parsimonious trees the taxon *Dehmictis vorax* is basal to all other taxa analyzed except for *Martes*. In 79% of the trees, a clade composed of *Eirictis robusta*, *Sminthosinis bowleri*, *Trigonictis kansanensis*, and *Gulo gulo* appear between *D. vorax* and the sister clade composed of the rest of the taxa, which appears in 97% of the trees. Within this last clade, *Eira barbara* and *Legionarictis fortidens* appear more basal to the well-supported sub-clade which includes the otter-like fossil taxa and *Galictis*. *Lutravus halli* and *Galictis vittata* fall at the base of the highest level clade which includes the extant *Lontra canadensis* and the fossil genera *Mionictis* and *Enhydriactis*.

The cladistic analysis shows that the otter-like clade is well supported (Fig. 11) and is consistent with a recent molecular phylogenetic analysis by Fulton and Strobeck (2006). The clade *Enhydriactis-Mionictis-Lontra* precedes the more basal *Lutravus*. The grison *Galictis* is at the base of the otter clade, and in the case of craniodental morphology this taxon is very close to *Lutravus*. In the same analysis, Fulton and Strobeck (2006) also found a musteline clade more basal to that of the otters and weasel; this clade is composed of *Martes*, *Gulo*, and *Eira*. The morphology cladogram is in overall agreement with the molecular hypothesis; however, the position of *Eira* is closer to that of the otter clade than to the basal musteline clade. In addition, the *Martes-Gulo-Eira* clade is paraphyletic in our morphological analysis. The addition of species of weasels *Mustela* and Eurasian badgers (e.g., *Meles*, *Mellivora*) might provide additional morphological disparity

to resolve the disagreements, but that is beyond the scope of this study. As for the placement of *Legionarictis fortidens* into a position in musteline evolution, the cladistic analysis shows that it is outside of the otter clade, and closest to the living *Eira* in morphology.

Some broad morphological patterns can be observed by comparing the P4-M1 morphology of the taxa across clades (Fig. 11). The paraphyletic group including *Martes* to *Gulo* and the fossil taxa between them are all characterized by relatively more anterior position of the P4 protocone, which is aligned with the P4 parastylar ridge, or at a position between the parastylar ridge and the paracone. In contrast, the clade including otters and the rest of the taxa tends to show a more posterior position of the P4 protocone. There is a minor trend in the aforementioned clade to enlarge the M1 relative to the P4, and develop a postero-lingual cingulum extension which increases the surface area of M1. Among the other taxa, *Gulo gulo* is clearly derived in its reduction of M1 size relative to P4.

As *Legionarictis* is without a closely related taxon in the Miocene fossil record of North America, we suggest that this new form represents an immigrant lineage from the Old World. With its position basal to the clade of Old World and New World lutrines (Fig. 11), *Legionarictis* would have immigrated to North America separately from the invasion of *Mionictis* which occurred during the middle Hemingfordian (Tedford et al. 1987, Tedford et al. 2004). The timing of the *Legionarictis* immigration event would have been sometime after the divergence from basal Old World mustelines during the early to early middle Miocene, before the Barstovian. This scenario would be clarified with discovery of additional related forms in the middle Miocene of North America.

Functional Morphology

The ancestral P4 protocone morphology in mustelines is

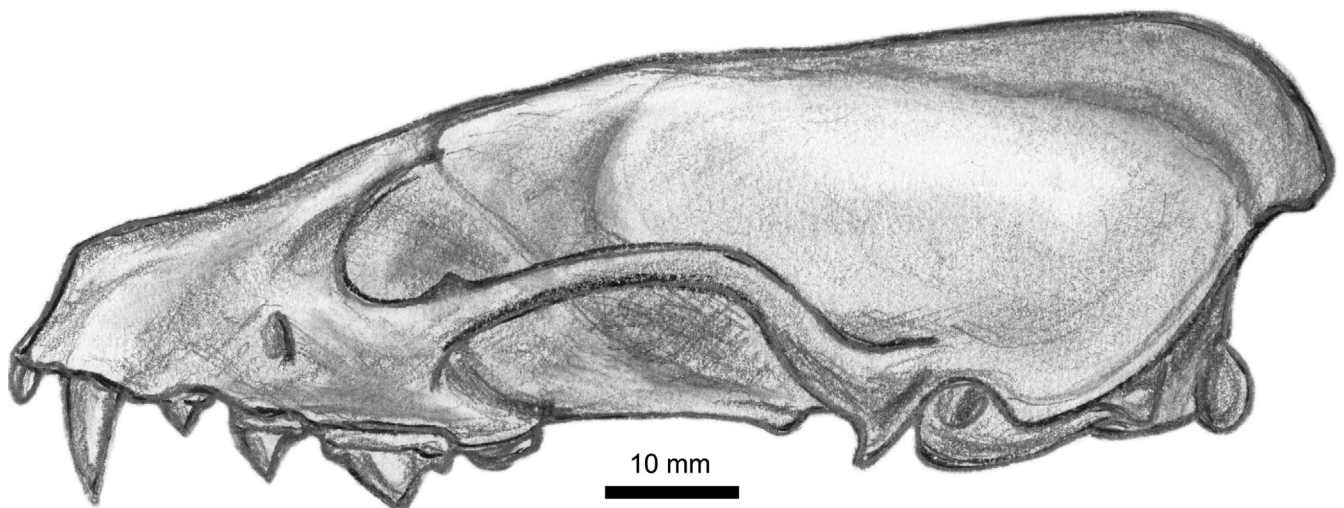


Figure 10. Reconstruction of the cranium of *Legionarictis fortidens*. Left lateral view shown. Illustration by Z.J. Tseng.

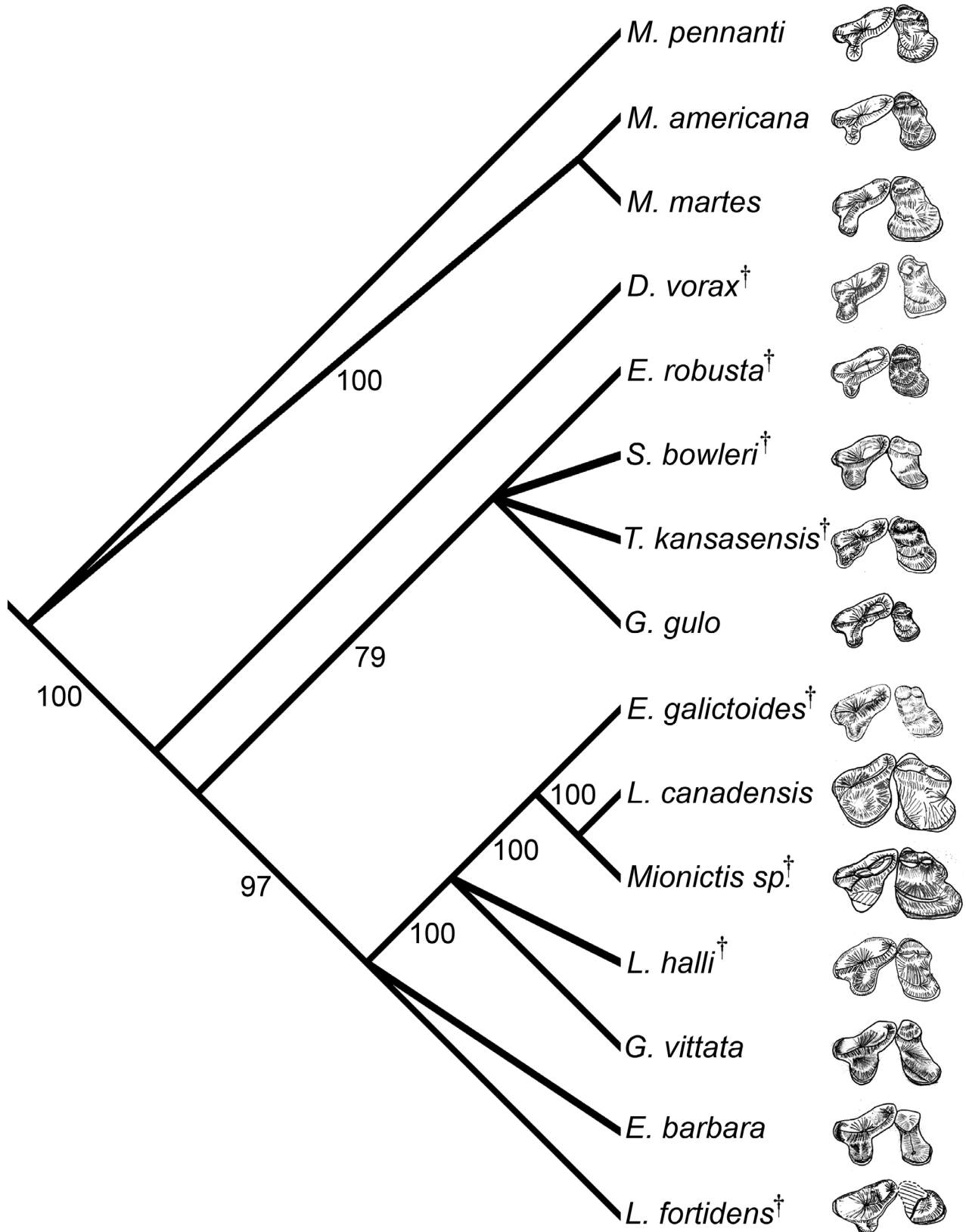


Figure 11. 50% majority-rule consensus tree from 132 most parsimonious trees in a cladistic analysis of basal Old World mustelines and lutrines and their New World relatives. Branch values indicate percentage of all trees with the presence of the clade. Extinct taxa are indicated by a dagger. The P4-M1 dentition of each species is scaled to the same P4 length to show relative differences in dental morphology and size. For character matrix and its description see Table 4 and Appendix.

Table 4. Character matrix used in cladistic analysis. For description of characters and their states see Appendix.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
<i>Dehmictis vorax</i>	?	1	0	0	0	0	0	1	0	0	0	0	?	0	0	0	?	?	?	?	?	?
<i>Eira barbara</i>	1	1	0	0	0	1	2	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0/1
<i>Eirictis robusta</i>	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	?	?	1	?
<i>Enhydriactis galictoides</i>	1	1	1	1	0	1	0	?	0	0	?	0	0	?	1	0	?	?	0	1	?	0
<i>Galictis vittata</i>	1	1	1	1	1	1	2	1	0	1	0	0	0	0	0	0	1	0	0	1	0	0
<i>Gulo gulo</i>	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1
<i>Legionarictis fortidens</i>	1	?	0	0	0	?	0	1	?	1	?	0	0	1	?	1	0	0	0	?	0	1
<i>Lontra canadensis</i>	0	1	2	1	0	1	1	1	1	0/1	0	0	1	0	1	0	1	1	0	1	0	0
<i>Lutravus halli</i>	0	1	1	1	0	1	0	1	0	1	0	0	1	0	0	0	1	?	?	?	?	?
<i>Martes americana</i>	0	0/1	0	0	0	0	0	1	0/1	0	0	0	0	0	0	0	0	0	0	0	0	0/1
<i>Mionictis</i> sp.	1	1	1	1	0	1	0	0	1	0	1	1	1	0	1	0	0	1	?	?	1	?
<i>Martes martes</i>	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
<i>Martes pennanti</i>	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Smintbosinis bowleri</i>	0	1	0	0	0	1	0	?	0	0	?	0	?	0	0	0	?	?	?	?	?	?
<i>Trigonictis kansasensis</i>	?	1	1	0	0	1	0	0	0	0	?	0	?	0	0	0	?	?	?	?	?	?

small, conical, and lingual to the P4 parastyle (Fig. 11). At this position, dental occlusion places the protocone between the main cusp of p4, and the paraconid of m1. Posterior development, either by expanding a P4 hypoconal shelf, or by altering the position of the P4 protocone, would bring it into contact with the m1 paraconid. This suggests that carnassial occlusion in *Legionarictis* would include not only shearing, but also direct overlap of m1 paraconid with lingual P4, as in the crushing occlusion seen in posterior molars. Thus, *Legionarictis* was probably capable of durophagy, the ingestion of tough food, and may have incorporated bone or hard invertebrates as part of its diet. However, the degree of this diet specialization is not as pronounced as in fossil and extant lutrines, which developed morphologies ranging from cup-like P4 protocone (as in *Lutravus*), to more extended P4 hypoconal crest and platform (as in *Mionictis*), to the quadrate P4 seen in many extant lutrines. All of these morphological modifications increased the surface area available for occlusion, and thus probably improved the performance of those teeth as crushing tools.

Studies of enamel microstructure across Carnivora have shown adaptive trend towards more crack-resistant structure in taxa that incorporate hard food in their diet (Stefen 1994). Examination of Hunter-Schreger enamel banding in mustelid teeth have shown that *Aelurocyon* Peterson 1906, *Brachypsalis* Cope 1890, *Eomellivora* Zdansky 1924, *Gulo* Pallas 1780, *Mionictis*, and *Plesiogulo* Zdansky 1924 all show some degree of specialization (Stefen 2001). Consistent with their robust cranial morphology, the specialized Hunter-Schreger bands probably imply a hard food component in the diet of those taxa. In *Legionarictis*, most of the cheek teeth exhibit the unspecialized undulating enamel banding pattern, but the carnassial has a more derived acute-undulating pattern

(Figs. 8–9, Table 3). Thus there is additional indication that *Legionarictis* might have consumed hard food such as shell or bone. Furthermore, the coastal depositional environment indicated by the presence of both terrestrial and marine taxa in the *Merychippus* zone fauna (Merriam 1915) suggests the proximity of the terrestrial mammals of the Temblor Formation to marine waters. Thus, it is possible that *Legionarictis* might have incorporated marine and/or freshwater shelled invertebrates in its diet. Recent discoveries of a diverse guild of lutrines from the Toros-Menalla sites in Chad (Peigné et al. 2008) suggest that even within the lutrine clade there were terrestrial ecomorphologies near aquatic environments but without extensive adaptations for an aquatic lifestyle. *Legionarictis* could have played a similar ecological role as other Miocene mustelids of near-water environments.

The prominent sagittal crest is additional evidence for strong bites and hard diet in *Legionarictis*. The deep sagittal crest provides a relatively large area for the attachment of the temporalis muscles, which along with the masseter are the primary jaw-closing muscles (Fig. 10). However, it is also possible that the deep sagittal crest observed in *Legionarictis* is a sexually dimorphic trait. The depth of the sagittal crest is sexually dimorphic in Eurasian badgers, but this slight differentiation is obliterated when crest depth is compared across a wider sample of mustelid taxa (Lee and Mill 2004). The great development of the sagittal crest observed in *Legionarictis* could thus be a combination of biomechanical function and sexual selection. Interestingly, when the ratios of sagittal crest height to condylobasal length and width of postorbital constriction to basioccipital width are compared among *Legionarictis*, *Meles* (n=44), and *Lutra* Brunnich 1772 (n=9) using the data from Lee and Mill (2004), *Legionarictis* is more similar to *Meles* in its relatively taller sagittal crest, but

closer to *Lutra* in its relatively narrower postorbital constriction. The intermediate morphology of *Legionarictis* might thus indicate an intermediate diet, as those two morphological indicators have been linked to different predatory strategies between the terrestrial badgers and aquatic otters (Lee and Mill 2004). Judging from the unworn premolars, the *Legionarictis* specimen is probably a young adult individual, even though no bone sutures could be observed on the cranial bones. Given its young age, the prominent sagittal crest is even more impressive as the crest may continue to develop through adult life similar to the patterns seen in some extant mustelids (Marshall 1951, Long 1974, Hancox 1988).

CONCLUSION

A new genus of mustelid carnivoran is described from a newly discovered bone bed of the middle Miocene Temblor Formation near Coalinga, California. *Legionarictis fortidens* exhibits several highly autapomorphic characters, including a prominent sagittal crest, and hypertrophied P4. Our cladistic analysis places this new taxon among mustelines but basal to lutrines, indicating *L. fortidens* had only begun to evolve away from musteline ancestral morphology. Its basal position relative to lutrines indicates that it might have been an immigrant from the Old World during a separate immigration event from the first occurrence of New World lutrines. Its robust upper carnassial morphology, derived enamel microstructure, and cranial shape all suggest a durophagous component in its diet. With a suite of morphological characters intermediate between badgers and otters, *Legionarictis* might have hunted both terrestrial vertebrates and aquatic invertebrate prey.

ACKNOWLEDGMENTS

We thank Pat Holroyd for providing access to the UCMP holotype specimen for study; Bob Purdy and Dave Bohaska for their hospitality and assistance with the collection of the NMNH; Jon Baskin for help on North American *Mionictis* specimens and improving the manuscript; Clara Stefen for constructive comments on the manuscript and illustrations; Ken Finger and Mark Goodwin for editorial assistance; Ted Connors (LACM) for his partial preparation of the specimen. This research was funded by a National Science Foundation Graduate Research Fellowship (to ZJT).

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APPENDIX 1

List of morphological characters and their states used in the cladistic analysis.

- Character 1*: P1 (0) present (1) absent.
- Character 2*: p1 (0) present (1) absent.
- Character 3*: P4 medial shelf (0) absent or restricted to area between paracone and protocone (1) expands anteriorly and posteriorly (2) shelf runs entire lingual side.
- Character 4*: P4 protocone (0) conical cusp (1) shelf only.
- Character 5*: P4 hypocone (0) absent (1) present.
- Character 6*: p4 posterior accessory cusp (0) present (1) absent.
- Character 7*: M1 (0) metacone small relative to paracone (1) metacone as large as paracone (2) metacone lost.
- Character 8: Inter-dental gaps between premolars (0) absent (1) present.
- Character 9: P4 protocone (0) aligned with parastyle (1) offset posteriorly from parastyle.
- Character 10: m1 trigonid length (0) longer than or equal to talonid (1) shorter than talonid.
- Character 11: M1 metaconule (0) absent (1) present.
- Character 12: M1 posterior border (0) slightly bulging internally (1) formation of internal “ear”.
- Character 13: Infraorbital foramen (0) small (1) enlarged.
- Character 14: P4 paracone anterior ridge (0) present (1) absent.
- Character 15: m1 metaconid size (0) small relative to protoconid (1) close to equal in size and level as protoconid.
- Character 16: P4 cusp (0) not inflated (1) inflated and bulbous.
- Character 17*: Anterior opening of palatine canals (0) adjacent to P4 (1) adjacent to P3.
- Character 18*: Orientation of infraorbital foramen opening directed (0) anteriorly (1) antero-ventrally.
- Character 19*: Paroccipital process (0) present (1) absent.
- Character 20: Pre-glenoid process (0) smaller than post-glenoid process (1) same size.
- Character 21: Zygomatic arch depth (0) less than or equal two times the zygomatic width (1) more than twice the zygomatic width.
- Character 22: Sagittal crest (0) ends at occipital (1) hangs over the occipital.

*Characters modified from Bryant et al. (1993).

APPENDIX 2

List of extant specimens used in the cladistic analysis:

- Eira barbara* LACM[M]10078, 13751; *Galictis vittata* LACM[M]70236; *Gulo gulo* LACM[M]31569; *Lontra canadensis* ZJT comparative collection J050607T01; *Martes americana* LACM[M]10668, 27377, 33377, 92393; *Martes martes* LACM[M]74508; *Martes pennanti* LACM[M]54254.