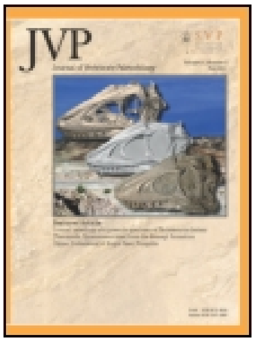

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A NEW BASAL SKUNK *MARTINOGALE* (CARNIVORA, MEPHITINAE) FROM LATE MIOCENE DOVE SPRING FORMATION, CALIFORNIA, AND ORIGIN OF NEW WORLD MEPHITINES

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ABSTRACT—We describe an associated skull and lower jaws of a new species of primitive skunk, *Martinogale* (subfamily Mephitinae), from the late Miocene Dove Spring Formation (late Clarendonian), Kern County, California. It is also the first occurrence of this genus in the Tertiary of the West Coast of North America. The new species is among the best-preserved primitive fossil skunks and represents one of the earliest members of the New World mephitines. As the smallest skunk so far known, the new *Martinogale* features some of the most primitive cranial and dental morphologies in mephitines. The new information permits a phylogenetic analysis of basal taxa from North America, which suggests a New World clade for all known fossil and living taxa from North and South America. We place this New World clade in a tribe (Mephitini) of its own. New World mephitines share the following derived characters: presence of a P4 parastyle, m1 hypoconid dominant in talonid, and presence of a lingual cingulum on lower canines. We further postulate that New World skunks are the result of a single immigration event, and the new California skunk is close to the origin of the New World skunks.

INTRODUCTION

In 1930, E. Raymond Hall named a new genus and species of weasel-sized mustelid, *Martinogale alveodens*, based on a jaw fragment with p4–m1 from the late Hemphillian Edson Quarry of Kansas. He compared it with living *Mustela* (weasels), but wished he had a skull to settle its relationships. Hall (1930:147) wrote: "knowledge of the tympanic bullae and other structures of the basicranial region would go far toward answering the question [of its relationships]. . ." A few years later, Dunkle (1938:183) described a second, slightly better-preserved jaw of *M. alveodens* from the same quarry and recognized its close similarity to that of the extant spotted skunk *Spilogale*. Dunkle, too, lamented the lack of a skull to work out its relationships: ". . . the discovery of the skull shall indicate its true phylogenetic position." Hall and Dunkle's wishes finally come true more than half a century later in the form of a nearly complete skull and associated lower jaws. The new skull bears out Dunkle's insight that *Martinogale* is indeed a skunk.

The new skull and lower jaws were recovered from the Dove Spring Formation, Kern County, California, by a Natural History Museum of Los Angeles County field party under the supervision of one of us (DPW). The new specimen was collected in the upper section of the Dove Spring Formation that is paleomagnetically dated between 9.2–9.3 Ma in the late Miocene (late Clarendonian). Representing both a new species and the earliest and most primitive *Martinogale* (and possibly North American mephitines), the California material supplies much that is unknown about the primitive conditions of New World skunks, and presents an important opportunity to evaluate the early evolution of this group of carnivorans.

The phylogenetic position of the mephitines has become highly controversial in recent years, with the traditional view of a subfamily Mephitinae within the family Mustelidae (Muizon, 1982; Bryant et al., 1993; Wyss and Flynn, 1993; Baskin, 1998) clashing with new molecular evidence that places the skunks in a distinct family of their own outside a clade of Procyonidae-Mustelidae (Wayne et al., 1989; Vrana et al., 1994; Ledje and Arnason, 1996a, b; Dragoo and Honeycutt, 1997; Flynn et al., 2000; Sato et al., 2004). Fossil evidence has been introduced into this debate (Wolsan, 1999), but lack of a systematic synthesis of the early mephitines renders the fragmentary historical record difficult to evaluate and the plesiomorphic condition for mephitines remains speculative. Our new information on a basal New World mephitine helps to bridge the morphological gaps of early musteloids, and when properly integrated into a broader analysis of relevant basal musteloids, could bring a fresh paleontologic perspective to bear on the controversy.

Institutional Abbreviations—FMNH, Division of Mammals, Field Museum of Natural History, Chicago, Illinois; **KUVP**, Department of Vertebrate Paleontology, Natural History Museum of the University of Kansas, Lawrence, Kansas; **LACM**, Department of Vertebrate Paleontology, Natural History Museum of Los Angeles, Los Angeles, California; **LACM(M)**, Department of Mammalogy, Natural History Museum of Los Angeles, Los Angeles, California; **TMM**, Texas Memorial Museum, University of Texas, Austin, Texas; and **USNM**, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

MATERIALS AND METHODS

A large sample of late Miocene *Promephitis* from China (see Wang and Qiu, 2004 for lists of specimens) offers a good example of a Eurasian lineage of mephitines. The rich Chinese materials afford a rare opportunity to describe the basicranial anatomy, an important area for musteloid systematics. While descriptions of the basicranium will be published in a separate study, character coding in our cladistic analysis will make use of those data.

For character polarity determinations, we chose outgroups that are closest to the initial divergence of ursoids and musteloids, instead of basal mustelids as has been assumed to be the case, because of the contention that mephitines are far more basal than had been realized. We use *Amphicynodon* to represent a basal ursoid and *Mustelavus* a basal musteloid (Wang et al., in press).

Comparative materials for living mephitines include the following: spotted skunk *Spilogale putorius* (LACM(M) 8337, 8338, 9954, 29313, 34928, 34930, 34931, 34933); striped skunk *Mephitis*

mephitis (LACM(M) 8047, 31230, 31639, 49585, 52244, 52248); hooded skunk *M. macroura* (LACM(M) 34934, 34935, 34939, 35463); hog-nosed skunk *Conepatus mesoleucus* (LACM(M) 53556, 59421, 59423, 59424, 59627, 78074); striped hog-nosed skunk *C. semistriatus* (LACM(M) 26686); Palawan stink badger *Mydaus marchei* (FMNH 62877); and Javan stink badger *Mydaus javanensis* (FMNH 68731).

SYSTEMATIC PALEONTOLOGY

Order CARNIVORA Bowdich, 1821
Infraorder ARCTOIDEA Flower, 1869
Superfamily MUSTELOIDEA Fischer de Waldheim, 1817
Subfamily MEPHITINAE Bonaparte, 1845

Remarks—All mephitines share an expansion of the epitympanic recess into the mastoid and squamosal areas to form an elaborate mastoid sinus (Schmidt-Kittler, 1981; 1984; Bryant et al., 1993; Wolsan, 1999), a derived character that is unique among skunks. Such an accessory middle ear space can easily be detected as an inflated bulge on the lateral wall of the braincase dorsal to the mastoid process. Mephitines feature a primitively uninflated bulla (type A bulla of Hunt, 1974). This lack of entotympanic inflation is presumably compensated by the mastoid sinus as an auxiliary air space of the middle ear cavity. Mephitines also lack postsylvian and sylvian sulci on the external brain morphology, a primitive condition for Carnivora (Radinsky, 1973). Dentally, skunks are also unique in their possession of extra roots on the labial and lingual sides of m1 between the main anterior and posterior roots. The M1s of all mephitines have primitively subequal paracone and metacone and a postprotocrista, in contrast to many mustelids that have an extremely reduced or absent metacone and a lack of a postprotocrista.

Mephitines have traditionally been included in the family Mustelidae, often allied to the lutrines (otters) or melines (badgers) (Muizon, 1982; Bryant et al., 1993; Wyss and Flynn, 1993; Baskin, 1998). Skunks fit well in the traditional concept of Mustelidae by their possession of such well known morphological characters as loss of M2 and m3, lack of a carnassial notch, absence of alisphenoid canal, and presence of an enlarged anal gland. Exceptions in external brain morphology were noted (Radinsky, 1973), but a mustelid relationship for the skunks remained the conventional wisdom. Recently several molecular studies suggest that mephitines occupy a more basal position in the arctoids, i.e., mephitines are not mustelids and belong to a family of their own (Vrana et al., 1994; Ledje and Arnason, 1996a, b; Dragoo and Honeycutt, 1997; Flynn et al., 2000; Sato et al., 2004). Wolsan (1999) countered with a study of a purported basal mephitine from the middle Miocene of Germany, *Palaeomephitis steinheimensis*, which has a mustelid suprameatal fossa. It is difficult to reconcile these two lines of evidence, and morphologically mephitines are everything a mustelid should be. If the molecular studies are correct, a large number of homoplasies must have occurred in the skunks, a situation that conventional parsimony analysis cannot easily overturn without adequate understanding of the primitive conditions of the mephitines.

Tribe MEPHITINI Bonaparte, 1845

Type genus—*Mephitis* Geoffroy Saint-Hilaire and Cuvier, 1795.

Included Genera—*Martinogale* Hall, 1930, *Pliogale* Hall, 1930, *Buisnictis* Hibbard, 1950, *Brachyopsigale* Hibbard, 1954, *Brachyprotoma* Brown, 1908, *Osmotherium* Cope, 1896, *Spilogale* Gray, 1865, *Mephitis* Geoffroy Saint-Hilaire and Cuvier, 1795, and *Conepatus* Gray, 1837.

Geologic and Geographic Distribution—Late Miocene through Recent of North America and late Pliocene through Recent of South America.

Diagnosis—New World skunks share derived characters that are absent in Old World skunks: a posterior ridge on the m1 protoconid and associated crest-like M1 paracone-metacone, a small P4 parastyle, and a well-developed lingual and posterior cingulum on lower canines (except in *Mephitis*). On the other hand, Mephitini lack such derived characters for Eurasian skunks as anterior extension of P4 protocone crest to form a prominent anterolingual corner of the P4 and cuspules in front of m1 entoconid to make a fully basined talonid.

Remarks—We use the tribal designation Mephitini for all New World skunks similar to the contents in Baskin (1998). Our phylogenetic analysis (below) demonstrates that Mephitini belong to a clade of their own. The beginning of this clade can be traced to the new species of *Martinogale* described in this paper.

MARTINOGALE Hall, 1930

Type Species—*Martinogale alveodens* Hall, 1930.

Included Species—*Martinogale alveodens* Hall, 1930; *M. chisoensis* (Stevens and Stevens, 2003); and *M. faulli* new species.

Geologic and Geographic Distribution—Late Clarendonian (early late Miocene) of California, early Hemphillian of Texas, and late Hemphillian (late late Miocene) of Kansas and Nebraska (Baskin, 1998).

Emended Diagnosis—As the most basal New World mephitine, *Martinogale* is distinguished from *Buisnictis* in its small size, its lack of a conical m1 entoconid and lack of a notch between the entoconid and metaconid, its relatively narrow p4, and its low M1 internal cingulum. *Martinogale* differs from the crown clade of New World mephitines (*Spilogale*, *Mephitis*, *Conepatus*, *Brachyprotoma*, *Osmotherium*) in its primitively small P4 protocone that is not broadened into a crest, its narrow postorbital constriction, its relatively unexpanded mastoid sinus, and its small paroccipital process that is not detached from the bulla.

Remarks—When Hall (1930) named *Martinogale*, he also referred another species to the new genus: *Martes nambianus* Cope, 1874, from the 'Santa Fe Marls,' New Mexico (Cope, 1874, 1877), which are now considered early Clarendonian in age (Baskin, 1998). The New Mexico species is based on a rather fragmentary ramus with p3–4 and a broken m1 with paraconid only, and Hall (1930:149) admitted that, based on such a poor knowledge of the species, "it probably will be impossible to make a definite generic allocation." In fact, Hall did not realize that *Martinogale* was a skunk (he compared it with *Mustela*). A connection to the skunks was later made by Dunkle (1938) and further confirmed by Harrison (1978; 1983). It is unlikely that a close relationship between *M. alveodens* and *Martes nambianus* can be recognized based on the p3–4 and m1 paraconid only, which are not very diagnostic at this stage of skunk evolution. We did not examine the type specimen of *Martes nambianus*, but believe it is unlikely to be related to *Martinogale*.

If our exclusion of Cope's *Martes nambianus* from the mephitines is correct, then *Martinogale faulli* sp. nov. becomes the earliest and most primitive New World skunk. The California species thus represents the first skunk immigrant, presumably from Asia, to arrive at the west coast of North America in the late Clarendonian, to give rise to a transitional form in western Texas in early Hemphillian, and to spread to the Great Plains in the late Hemphillian. Furthermore, if our phylogenetic analysis is correct (see below), there is only one immigrant event for the New World skunks, i.e., the rest of the New World mephitines were all derived locally, as opposed to assumptions of multiple immigration events (Baskin, 1998:fig. 9.7).

MARTINOGALE FAULLI, sp. nov.

Martinogale alveodens Hall, 1930: Baskin, 1998:159; Stevens and Stevens, 2003:200.

Holotype—LACM 56230, nearly complete skull and both jaws with right C–P3 alveoli and P4–M1, left P3–4 alveoli and M1, left and right p2–m1 and alveoli for i1–c and m3s. Collected by J. MacConnell and family in November 1974.

Type Locality and Age—Powerline Road Tom Quarry, locality LACM 3776, USGS Cross Mountain Quadrangles, Sect. 21, T. 29 S., R. 37 E., Red Rock Canyon, Kern County, California. The type was collected from a light tan siliceous sandy mudstone in the upper part of the Dove Spring Formation. Fossils from this locality are concentrated in small pockets along the bedding plane. Stratigraphically, locality LACM 3776 is bracketed by two volcanic ashes, Ash 15 (fission-track dated 8.4 ± 1.4 Ma) and Ash 16 (K/Ar dated at 8.50 ± 0.13 Ma) (Whistler, 1969; Burbank and Whistler, 1987; Whistler, 1991; Whistler and Burbank, 1992). Ashes 15 and 16 are separated by 258 m of strata in the vicinity of locality LACM 3776, and the locality is 123 m below Ash 16. Locality LACM 3776 falls within a paleomagnetically reversed zone that can be correlated to the paleomagnetic Chron C4Ar.1n, which has a revised age range of 9.230–9.308 Ma (Cande and Kent, 1995). Ash 16 falls within a normal magnetic interval that can be correlated to paleomagnetic Chron C4An with a revised age range of 8.699–9.025 Ma (Cande and Kent, 1995), consistent with the K/Ar date presented by Whistler and Burbank (1992). These magnetic correlations suggest that the fission-track date of 8.4 ± 1.8 Ma for Ash 15 presented by Whistler and Burbank (1992) is anomalously young. Thus, the best estimate of age for locality LACM 3776 is between 9.2 and 9.3 Ma (early late Miocene).

Whistler and Burbank (1992:fig. 4) listed the local range of *Martinogale* as occurring in a short span in the Dove Spring Formation. The type specimen of *M. faulli* is apparently on top of this range, whereas a second specimen, LACM 147445, was responsible for the downward range extension. Our re-examination of this second specimen has ruled out it pertaining to *Martinogale*, and therefore the local occurrence of *Martinogale* is confined to the single type locality of *M. faulli*.

Etymology—In honor of Mr. Mark Faull, former ranger of Red Rock Canyon State Park and avid naturalist, whose guidance and encouragement has been instrumental in the success of fieldwork that help to secure the present specimen.

Diagnosis—*Martinogale faulli* differs from *M. alveodens* in its smaller size, lower p4 crown, narrower premolars, less well-developed anterior and posterior cingular cusps on p4, less well-developed ridge on posterior face of m1 protoconid, and absence of a shallow notch between entoconid and metaconid of m1.

Description—LACM 56230 is crushed laterally, especially on the right side. The entire right half of the skull is thus broken into many pieces and heavily distorted. The left half of the skull, on the other hand, is almost perfectly preserved. The associated left and right lower jaws are also well preserved. LACM 56230 was mentioned by Baskin (1998:161) who used it to briefly characterize the upper dentition of *Martinogale*, but provided no detailed description.

Skull—With a maximum basal length (from anterior edge of C alveolus to posterior margin of occipital condyle) of 40.1 mm, the skull (Fig. 1) of *Martinogale faulli* is the smallest skunk so far known. The cranial bones are smooth and lightly constructed because of its small size. Sutures between bones are mostly fused beyond recognition, even though the lack of dental wear indicates a relatively young individual.

The overall proportions of the skull are similar to those of *Spilogale*. The rostrum is short relative to the temporal region of the skull. Bone sutures are completely fused and the relationships of premaxillary, maxillary, and nasal are not clear. As in living mephitines, the infraorbital canal is small in diameter, short, and oval in cross section. The antorbital rim is not sharply defined, as is also the case in living New World mephitines. The forehead is flat in contrast to a more domed (inflated) condition in *Mephitis* and *Conepatus*, as well as advanced species of *Promephitis*. The postorbital process of the frontal is also poorly developed, and is no more than a minor protrusion along the antorbital rim. The postorbital constriction is narrower than that of living taxa and about the same as that in *Promephitis*. The temporal crest is extremely vague and there is no sagittal crest. The nuchal crest is also indistinct. Both left and right zygomatic arches are broken off at the bases. Bones in the orbital mosaic are also too fused to show their relationships. A vertical slit dorsal to the posterior opening of the infraorbital canal is the site for the lacrimal foramen.

Although the palate is heavily crushed, the posterior border of the palatine seems slightly behind the posterior border of the M1. A vertical septum seems to be in place near the posterior opening of the internal naris (damage to this area prevents a definitive observation), a feature noted by Baskin (1998) to be present in North American mephitines but probably having a wider distribution including both New and Old World skunks.

Basicranium—The right bullar region has caved in toward the left ear region and too many broken pieces of bones are out of original alignment to permit a sense of original morphology. The left auditory region, however, is almost perfectly preserved (Figs. 2, 3).

The bulla is flask-shaped and modestly inflated for a small individual. The degree of inflation is within the range for living skunks, and can be categorized as a type A bulla as defined by Hunt (1974), although the exact bullar composition is not known because of the fusion of individual elements. Baskin (1998:159) mentioned a "moderately inflated entotympanic" of this specimen, but we were unable to delineate the boundary of the entotympanic and cannot verify this statement. The main axis of the bulla forms a small angle with the parasagittal direction, as is the case in most arctoids. A very short bony external auditory meatus, no more than 1 mm long, is present, and this meatus is the shortest among all known mephitines. The bony meatal tube appears to wrap around behind the glenoid process, and forms a complete tube, instead of relying on the squamosal shelf to form the dorsal wall of the meatus. Limited preparation of the meatal tube reveals a rather uniform inner wall of the meatus and shows no sign of a suprameatal fossa, other than a very gentle concavity on the dorsal wall.

The entire mastoid region is inflated to the point that the mastoid process is no longer easily discernable, except by a slight swelling on the ventral end of the lambdoidal crest. This mastoid inflation, characteristic of all living and fossil mephitines, is easily recognized externally by a distinct furrow on the lateral side of the braincase (triangle marks on Fig. 3), which precisely correspond to the extent of mastoid inflation. Using this furrow as a guide, the volume of the mastoid sinus is estimated to be greater than the bullar volume itself, if one take into consideration the middle ear space taken up by the petrosal. Since the posterior wall of the external auditory meatus is complete, the air connection between the hypotympanic space and the mastoid sinus is probably via a passage way just behind the epitympanic recess. This is not actually observed because this part of the anatomy was not dissected for fear of damage to the delicate bones.

The paroccipital process is very small, consisting of a tiny, nearly vertically oriented bony plate no more than 1.5 mm long and deep. The base of the process still touches the posterior face of the bulla, in contrast to a more posteriorly detached condition in living skunks due to a further posterior expansion of the mastoid sinus.

The posterior carotid foramen opens along the medial wall of the bulla and is situated in the middle aspect of the bulla, as

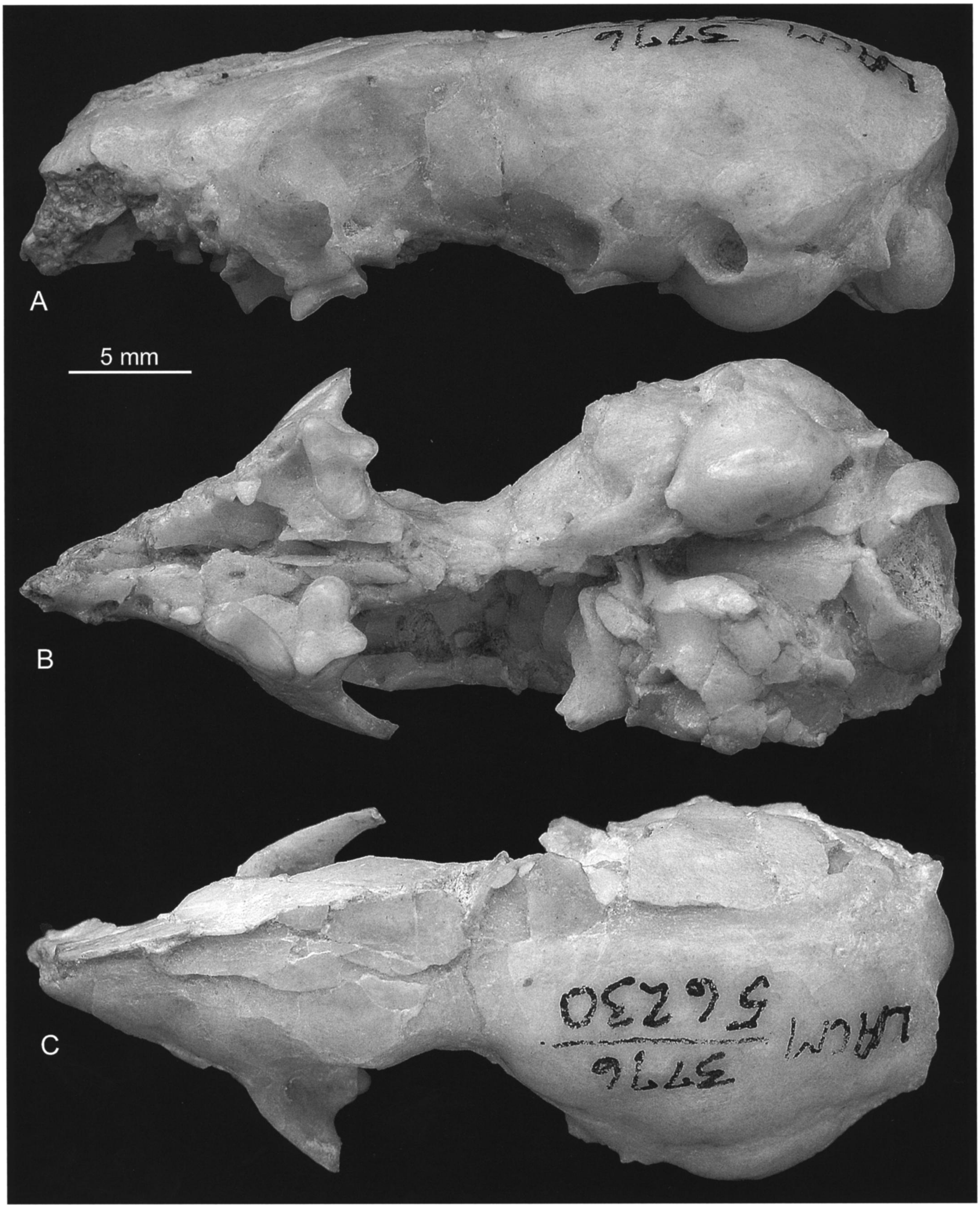

FIGURE 1. Skull of *Martinogale faulli* (LACM 56230, holotype). **A**, lateral, **B**, ventral, and **C**, dorsal views.

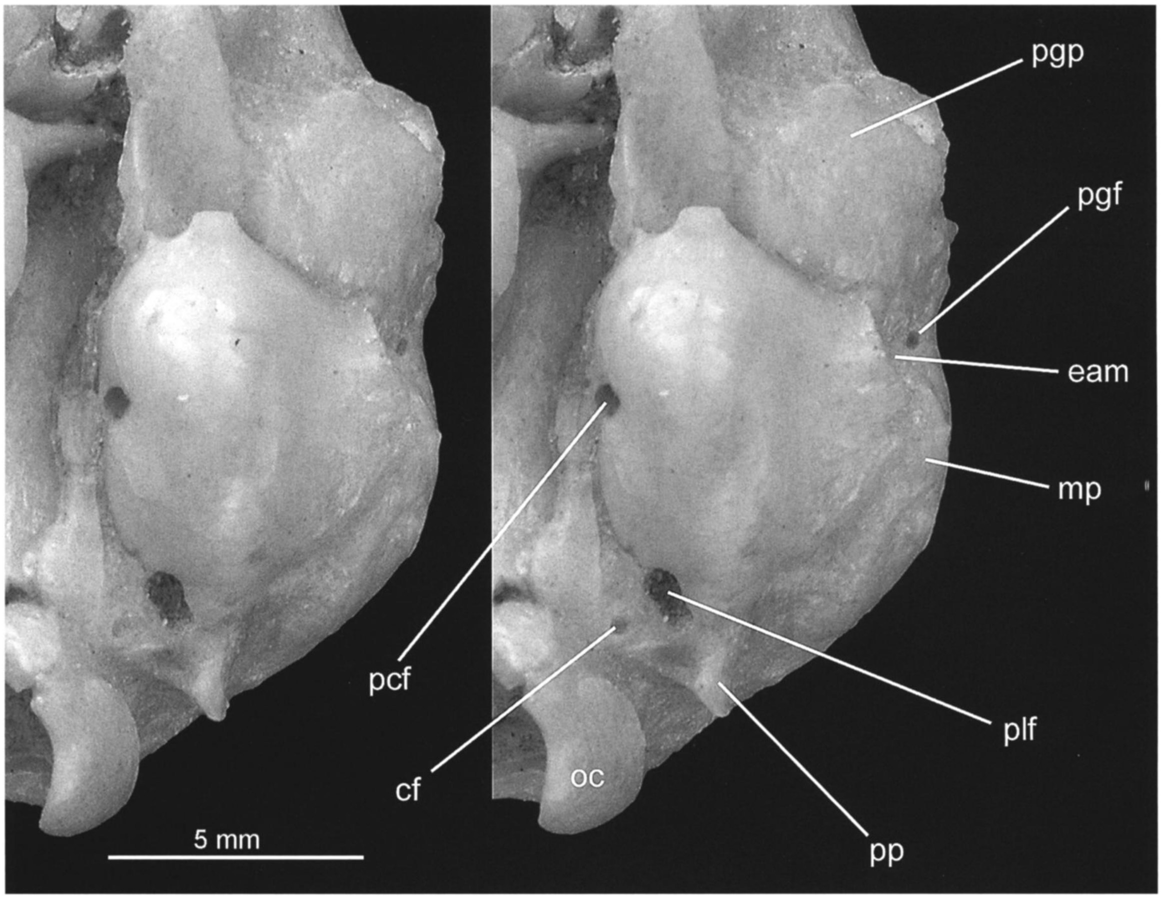

FIGURE 2. Ventral view (in stereo) of the auditory region of *Martinogale faulli* (LACM 56230, holotype). **Abbreviations**: **cf**, condyloid foramen; **eam**, external auditory meatus; **mp**, mastoid process; **oc**, occipital condyle; **pcf**, posterior carotid foramen; **pgf**, postglenoid foramen; **pgp**, postglenoid process; **pp**, paroccipital process. Top is anterior.

compared to a more anteriorly positioned foramen in living skunks. The course of the internal carotid artery can be traced along the nearly transparent wall of the carotid canal (matrix filling along the canal is visible from the external surface of the bulla), presumably enclosed dorsally by the rostral entotympanic and ventrally by the medial edge of the ectotympanic. The canal forms a short arch and appears to open anterodorsally into the brain cavity.

The area between the glenoid process and external auditory meatus is highly inflated and gives the appearance that the glenoid process is being shifted forward to make room for an inflated cavity dorsally. A tiny postglenoid foramen is located just dorsal and lateral to the meatal tube. There is no alisphenoid canal.

A condyloid canal is present toward the dorsal part of the occipital condyle on the inner wall of the foramen magnum. The canal is near the juncture of the dorsal limit of the condyle with the posterior wall of the supraoccipital. This canal is lost in most living New World skunks (Bryant et al., 1993).

Lower Jaw—Nearly the entire horizontal portions of both left (Fig. 4) and right rami of the lower jaw are intact. Only a small anterior segment of the left ascending ramus is preserved. The symphysis is short, stopping just posterior to the p2. A very modest chin is visible in lateral view, as also seen in living skunks and *Promephitis*. Two mental foramina are present on the right ramus, whereas three are present on the left side. The anterior one on the right is between p2–3; the anterior two on the left are in similar position, and are closely spaced together. The posterior mental foramen is between the roots of the p4. The anterior border of the ascending ramus is erect.

Teeth—In the upper dentition (Figs. 1, 5), the right premaxillary preserves the alveoli of the upper incisors. The size of the I3 alveolus seems to be similar to that of the I2. The right C alveolus is crushed and seems to be no more than 1.5 mm in anteroposterior diameter, suggesting a very small upper canine. Almost immediately behind the canine is a tiny alveolus for the P2. Thus the P1 is absent. The P2 is single rooted. The right P3 is represented by two roots and a broken posterior talon. A vague indication of a posterior cingular cusp is present on the posterior talon, and the posterior cingulum is poorly developed. The right P4 is almost perfectly preserved except that the posterior-most tip of the metastylar blade. The P4 has a very slender, elongated appearance not only because of its long shearing blade but also because of its extremely reduced protocone. The protocone is located behind the anterior edge (cingulum) of the paracone and it is formed by a slight elevation of the anterolingual cingulum. The apex of the protocone is so low that it barely rises above the cingulum. There is no trace of a lingual or labial cingulum on the shearing blade. A slight swelling at the anterolingual corner of the tooth, seen in *Promephitis*, is absent in *Martinogale*. An anterior cingulum in front of the paracone is developed into a moderate parastyle. A carnassial notch is absent.

Both left and right M1s are perfectly preserved. The M1 is transversely elongated. A prominent parastyle is developed as part of the expansion of the labial cingulum that achieved the same size and crown height as the paracone. A notch separates the parastyle from the paracone. The labial cingulum narrows posteriorly and wraps around to be continuous with a posterior

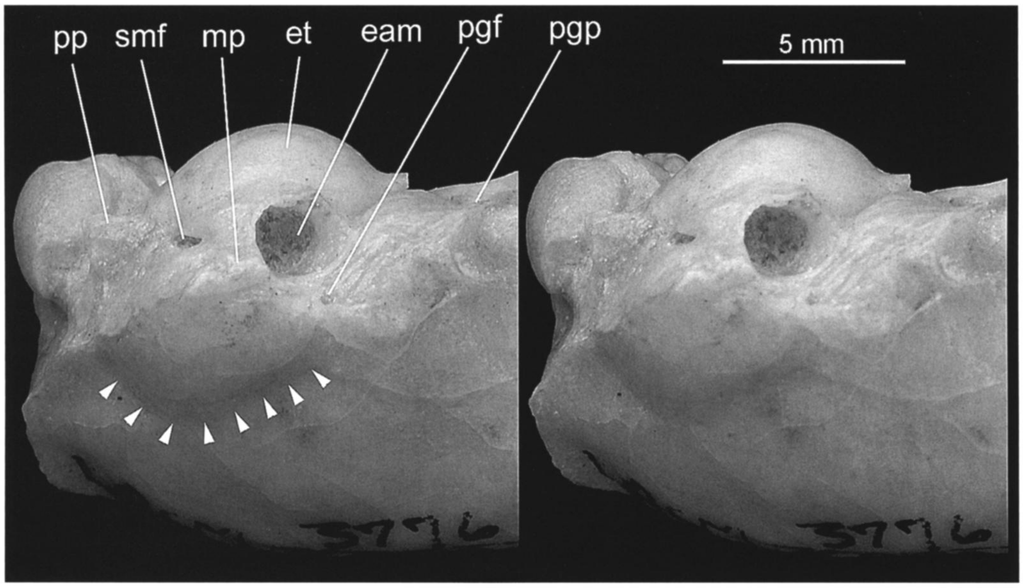

FIGURE 3. Lateral view (in stereo) of the auditory region of *Martinogale faulli* (LACM 56230, holotype). **Abbreviations**: **eam**, external auditory meatus; **et**, ectotympanic; **mp**, mastoid process; **pgf**, postglenoid foramen; **pgp**, postglenoid process; **pp**, paroccipital process; **smf**, stylomastoid foramen. Arrowheads indicate dorsal edge of mastoid sinus. Top is ventral.

ridge of the metacone. The paracone and metacone are nearly the same size and height and are connected by a continuous anteroposterior ridge in between, a feature seen in mephitines and lutrines. The crest-like protocone has a distinct pre- and postprotocrista, but a paraconule and metaconule are not present. The postprotocrista does not reach to the base of the metacone, leaving a posteriorly open basin for the talon. The internal (lingual) cingulum is widest at the posterolingual corner and it ends anteriorly on the lingual side of the protocone apex, i.e., there is no anterior extension of the internal cingulum to wrap around the protocone. The M2 is lost.

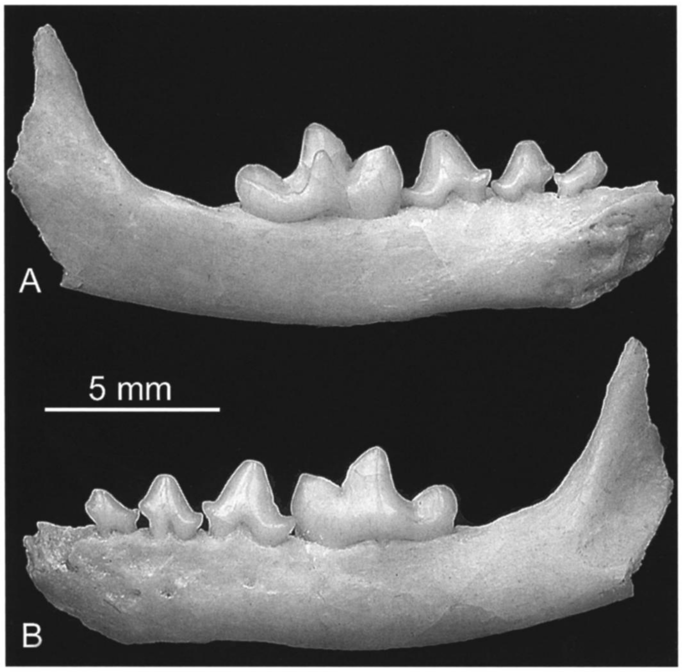

FIGURE 4. Mandible of *Martinogale faulli* (LACM 56230, holotype). **A**, lingual, and **B**, labial views of left ramus.

In the lower dentition (Figs. 4, 5), only the alveoli for i1 through c are preserved. The lower incisors are crowded and imbricated, with the i2 behind the i1 and i3. The lower canines are small in diameter, measuring 1.6 × 1.0 mm in alveolar dimensions. The p1 is lost. The p2 follows immediately behind the canine. The left p2 is double-rooted, whereas the roots on the right p2 are nearly squeezed together into one. A single procumbent main cusp is followed by a tiny posterior cingular cusp on the p2. The p3 has an incipient anterior cingular cusp, but has no lingual or labial cingulum. A distinct ridge runs along the lingual surface of the main cusp, and at the base of this ridge is a small swelling that helps to broaden the tooth in occlusal view. This swelling is even better developed on the p4. The p4 also has better developed anterior and posterior cingular cusps, but has no lingual or labial cingulum. The crown height of lower premolars is generally low compared to those of living skunks.

The m1 is elongated, and its trigonid shearing blade is oriented rather parasagittally with an anteriorly pointed paraconid. The trigonid is relatively low, with the paraconid below the tip of the p4 main cusp. The paraconid shearing blade is longer than that of the protoconid. The metaconid is nearly equal in height to the paraconid. A faint ridge is present on the posterior face of the protoconid. The talonid is narrower than the trigonid, and it is also quite short compared to living skunks. The talonid is basined, although the entoconid crest is very low and barely encloses the basin. The crest-like hypoconid is the dominant cusp on the talonid, and it ends anteriorly at the base of the protoconid, separated from it by a tiny notch. The hypoconid crest is located toward the labial side in occlusal view, and loops around posteriorly to be continuous with the entoconid crest. The entoconid crest is very smooth, and with the exception of a faint indication of a cuspule at its anterior end, the entire entoconid is not divided by cuspules. The m2 is indicated by a single-rooted alveolus.

Comparisons—Morphologically, *Martinogale faulli* is closest to a recently described species, "*Buisnictis*" *chisoensis*, from the early Hemphillian Screw Bean Local Fauna of western Texas (Stevens and Stevens, 2003), which falls within *Martinogale* in our phylogenetic analysis below. Dental measurements of *M. chisoensis* are, on average, 39% larger than those of *M. faulli* (Table 1). In addition to the large size difference, Stevens and

FIGURE 5. Occlusal views (in stereo) of upper and lower teeth of *Martinogale faulli* (LACM 56230, holotype). **A**, right upper P3 (broken)–M1. **B**, left lower p2–m1. Scale bar equals 5 mm.

Stevens (2003:200) noted the following differences between LACM 56230 and *M. chisoensis*: a less inflated entotympanic bulla, a less expanded mastoid region, slightly better developed anterior and posterior cingula on lower premolars, a more transversely elongated M1, and a taller m1 metaconid of LACM 56230. See the Phylogeny section below for additional comments on *M. chisoensis*.

In overall dental dimensions (Table 1), *Martinogale faulli* is small in almost all measurements and falls outside the lower limits of the three known specimens of *M. alveodens*, although the absolute magnitude of size difference is rather small. For example, the m1 length of *M. faulli* is only 0.4 mm shorter than the smaller of the two specimens of *M. alveodens*. When larger sample size eventually become available, it is conceivable that dental dimension of the two species may overlap somewhat.

The main distinctions between *Martinogale faulli* and *M. alveodens* lie in several proportional and qualitative differences. First, the main cusp of the p4 in *M. alveodens* is taller than that of *M. faulli*; its apex is considerably above the m1 paraconid, especially in the better-preserved referred specimen KUVP 3833

TABLE 1. Dental measurements of *Martinogale* (in mm). Those for *M. alveodens* are adopted from Hall (1930), Dunkle (1938), and Harrison (1983), and those for *M. chisoensis* from Stevens and Stevens (2003)

	Martinogale alveodens			*Martinogale faulli*	*Martinogale chisoensis*
	KUVP 3473	KUVP 3833	KUVP 3922	LACM 56230	TMM 42247-29
P3 length	—	—	—	2.5*	—
P4 labial length	—	—	—	4.4*	5.6
P4 width (across protocone)	—	—	—	1.8	2.4
M1 labial length	—	—	—	3.3	4.7
M1 width (across labial cingulum)		—	—	3.7	—
M1 maximum transverse width	—	—	—	4.6	6.1
p2 length	—	—	2.0	1.6	2.3
p2 width	—	—	1.0	0.9	1.3
p3 length	2.5	—	2.1	1.7	2.6
p3 width	1.0	—	1.3	1.1	—
p4 length	3.0	2.8	—	2.6	2.9
p4 width	1.5	1.8	—	1.4	—
m1 length	5.8	5.3	—	4.9	6.8
m1 trigonid width at metaconid	2.1	2.5	—	2.3	3.3
m1 talonid width	2.0	2.1	—	1.9	2.9
depth of jaw at ant. border of m1	3.3	3.4	—	3.2	4.6

*Indicates an estimate.

(Dunkle, 1938:pl. XXI). Second, the p4 of *M. alveodens* is wider, particularly in KUVP 3833 (Table 1; Dunkle, 1938:pl. XXI), although the holotype of *M. alveodens* seems to be similar to that of *M. faulli*. Third, the anterior and posterior cingular cusps on p4 are very distinct, as compared to incipient developments of these cusps in *M. faulli*. Fourth, the posterior crest of the m1 protoconid in *M. alveodens* is also more prominent than in *M. faulli*. Finally, a very vague notch is beginning to take shape in front of the m1 entoconid in *M. alveodens*.

The above five features in *M. alveodens* are incipient developments that become much more prominent in later New World skunks. It is possible that *M. alveodens* is a transitional form between *M. chisoensis* and *Buisnictis*, and as such the relationship among species of *Martinogale* is that of an anagenetic progression, a possibility that needs more intermediate materials to test. Given the above size, proportion, and qualitative differences, as well as their more than 2 million year age difference, we feel justified to erect a new species. As shown in the phylogenetic analysis (Fig. 6), our establishment of the new species from California and our placement of '*B.*' *chisoensis* in this genus also render *Martinogale* a paraphyletic stem genus at the base of the New World mephitine clade.

PHYLOGENY OF NEW WORLD MEPHITINES

This study is intended to trace the origin and early evolution of New World mephitines, taking advantage of *Martinogale faulli*, which permits a sense of a basal mephitine. This paper does not intend to deal with the species-level taxonomy of fossil and living skunks, which were recently summarized by Baskin (1998). We limit our scope to a generic level analysis, with the exception of species of *Martinogale*, and we generally only treat fossil taxa that are well known enough cranially and dentally. The following outline lists the taxa we did or did not use in this study.

New World Mephitine Taxa Included in This Study—Living mephitines are represented by three New World genera, *Spilogale* (spotted skunks), *Mephitis* (striped skunks), and *Conepatus* (hog-nosed skunks), and one Asian genus *Mydaus* (stink 'badger'). Modern New World skunks share the following synapomorphies that strongly indicate a monophyletic clade of their own: posterior expansion of mastoid sinus and associated reduction and posterior shifting of the paroccipital process, and enlargement (both anteroposteriorly and lingually) of the P4 protocone crest. Of the three genera of living skunks, *Spilogale* appears to retain the most primitive conditions, based on the character polarity assessment afforded by *Martinogale faulli*. For example, *Spilogale* has a relatively flat forehead, presence of a condyloid canal (in 83% of individuals; n = 29), a transversely elongated M1, and a relatively unreduced P2. This is in contrast to a domed forehead, loss of a condyloid canal [in 84% of *Mephitis* (n = 31) and 54% of *Conepatus* (n = 15)], quadrate or anteroposteriorly elongated M1s, and reduced or lost of P2 in *Mephitis* and *Conepatus*. Early records of living genera of New World skunks can be traced to early to late Blancan Rexroad (Kansas), Mt. Blanco (Texas), and Beck Ranch (Texas) localities for *Spilogale* and early Blancan Broadwater (Nebraska) and Rexroad (Kansas) localities for *Mephitis* (Anderson, 1984; Baskin, 1998). *Conepatus*, on the other hand, first appeared in the fossil record as one of the earliest carnivoran immigrants to South America at approximately 2.4–2.5 Ma (Hunt, 1996), but its North American record started in the Pleistocene of the east coast (Anderson, 1984). For the present study, we use living representatives of these genera (see Materials and Methods) to assess the cranial and dental characters and to evaluate

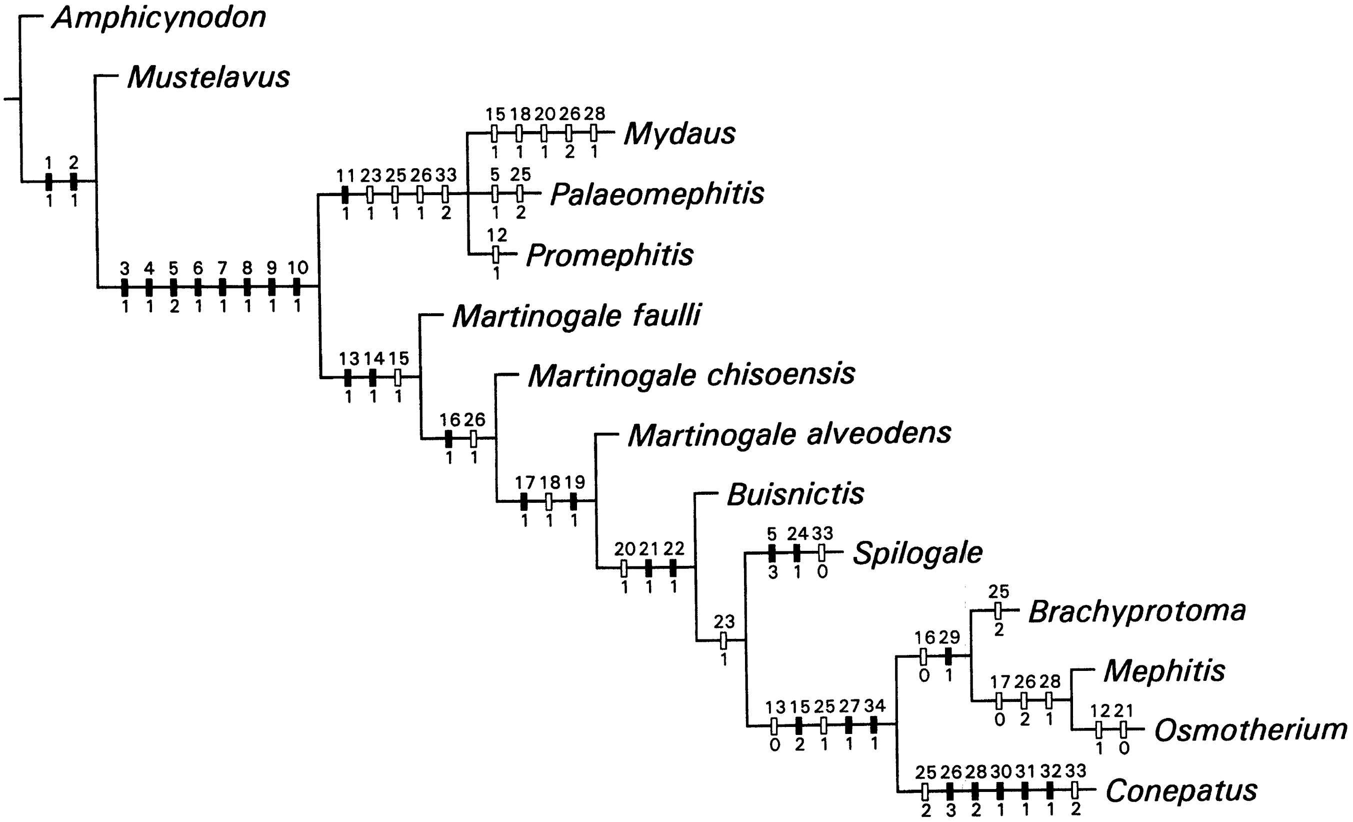

FIGURE 6. One of six shortest trees (length = 56) found by the Branch and Bound option of the PAUP program, showing the most resolved topology among New World mephitines (the Old World clade is collapsed into a trichotomy due to poor resolution). Solid bars indicate synapomorphies and open bars indicate homoplasies and reversals. Numbers above the bars are character numbers that correspond to those in Definitions of Characters in Appendix I and in Table 2, and numbers below the bars are character states.

variations within species of mephitines (e.g., Van Gelder, 1959, 1968).

Martinogale chisoensis (Stevens and Stevens, 2003) from the early Hemphillian Screw Bean Local Fauna, Texas, is only slightly more derived than *M. faulli*. Stevens and Stevens placed the Texas species in *Buisnictis* and further linked it to the living spotted skunk *Spilogale*, mainly due to its well-inflated mastoid region. In our own phylogenetic analysis (below), however, the Screw Bean form is still several steps removed from *Buisnictis* and even more so from *Spilogale*. Significantly, '*B.*' *chisoensis* lacks advanced dental features such as distinct cingular cusps on premolars, a notch anterior to the m1 entoconid, and a very high-crowned p4 to be placed in *Buisnictis*. Cranially, '*B.*' *chisoensis* appears to retain a small paroccipital process that is still attached to the posterior wall of the bulla (Stevens and Stevens, 2003:fig. 9.8), rather than being displaced posteriorly as in *Spilogale*.

Buisnictis Hibbard, 1950 (type species *Brachyprotoma breviramus* Hibbard, 1941), from the early Blancan Hagerman Local Fauna, Idaho (Bjork, 1970) and Fox Canyon (Hibbard, 1950) and Rexroad local faunas of Kansas (Hibbard, 1950, 1954) possesses an intermediate morphology between *Martinogale* and *Spilogale* (well-preserved materials of *B. breviramus* are available from Rexroad local fauna of Kansas). While the P4 protocone of *Buisnictis* remains primitively small and anteriorly located, its elevated m1 entoconid separated by a notch from the metaconid and a high-crowned p4 have reached the stage of development in *Spilogale* (see figures in Hibbard, 1941, 1952; Hibbard, 1954). *Buisnictis* thus represents an important transitional form that bridges the morphologic gap between *Martinogale* and the crown clade of North American skunks.

Brachyprotoma Brown, 1908 [type species *B. obtusata* (Cope, 1899)], from the Pleistocene of the eastern United States (Hall, 1936) and northern Yukon Territory, Canada (Youngman, 1985), is a short-faced genus that has lost the P2 and has a very broad p4. Apart from the autapomorphic short face, *Brachyprotoma* readily falls in the crown clade of New World skunks (*Spilogale-Mephitis-Conepatus*) because of its possession of the following derived characters of the clade: lengthened and posteriorly positioned P4 protocone crest, high m1 entoconid separated from metaconid by a notch, and expanded postorbital constriction. Furthermore, its still transversely elongated M1 and relatively long m1 trigonid suggest that *Brachyprotoma* is somewhat closer to the stage of evolution in *Spilogale*. On the other hand, its P4 protocone crest begins to assume a more conical shape, a character only seen in *Mephitis*.

Osmotherium Cope, 1896 (type species *O. spelaeum* Cope, 1896) is only known from the late Irvingtonian Port Kennedy cave deposits, Pennsylvania (Cope, 1899). In the proportions of the m1 trigonid and talonid length, *Osmotherium* falls in the range of *Mephitis*. On the other hand, the lower carnassial of *Osmotherium* has an entoconid crest that features two or more cuspules, the anterior one of which blocks the lingual notch between metaconid and entoconid seen in the rest of the New World skunks (Hall, 1936). This condition in *Osmotherium* is only seen in the Eurasian *Promephitis* and one species of the hog-nosed skunk (*Conepatus semistriatus*), and presumably represents an independent development in all three taxa. Both Hall (1936) and Anderson (1984) have expressed doubts that *Osmotherium* is generically distinct from *Mephitis*, a problem that cannot be resolved in this study without a detailed evaluation of various species of these two genera.

Other New World Mephitines Not Used in This Study—*Pliogale* Hall, 1930 [type species *P. furlongi* (Merriam, 1911)], from the early Hemphillian Thousand Creek Formation, Nevada, seems to be a mephitine because of its possession of extra roots on the m1 and a posterior ridge on the m1 protoconid (Hall, 1930:pl. 7, figs. c, d). Based on two ramal fragments that only preserve an m1, this genus is too poorly known to be included in this analysis. Judging from published figures (Hall, 1930:pl. 7, figs. a–d, f, g, j, k), the m1 is in a similar stage of evolution as that of *Martinogale*, e.g., lack of a notch in front of the entoconid. A second species, *P. manka*, was named from Wolf Creek, South Dakota (Green, 1956), and it was also based on very fragmentary material (a single right ramus with an m1). Nothing in Green's description indicates any mephitine character for this species. Furthermore, Green remarked about the presence of a p1 root, a condition that most likely rules out a mephitine relationship. It is thus questionable that the Wolf Creek form belongs to *Pliogale*.

Brachyopsigale Hibbard, 1954, is another genus of short-faced skunk from the Rexroad Fauna of Kansas. This precociously derived form (very short rostrum) is still poorly known by a jaw fragment, and is not included in this study.

Old World Mephitine Taxa Included in This Study—Living mephitines are traditionally regarded as endemic to the New World. Recently, however, the Oriental stink 'badger,' *Mydaus*, from some southeast Asian islands is increasingly placed in the mephitines (Schmidt-Kittler, 1981; Schmidt-Kittler, 1984; Bryant et al., 1993), as had also been suggested earlier by Pocock (1921), Pilgrim (1933), and Radinsky (1973). This mephitine relationship is further confirmed by molecular studies (e.g., Dragoo and Honeycutt, 1997). However, *Mydaus* is the only mephitine that has an elongate rostrum, in contrast to shortened muzzles in all other skunks, and its peculiar dental morphology is quite unlike most other skunks (Schmidt-Kittler, 1984:fig. 3a; Hwang and Larivière, 2003). Its large number of autapomorphies indicates a separate evolutionary history while in isolation from the rest of the mephitines.

Beside the peculiarities of the living stink 'badger,' Old World fossil skunks are often represented by forms that feature disparate morphologies (see *Palaeomephitis* below) that lack the kind of continuities seen in the New World mephitines. The best-represented Old World fossil skunk is the genus *Promephitis* Gaudry, 1861, from the late Miocene to Pliocene of northern Eurasia (see Wang and Qiu, 2004 for a recent summary). *Promephitis* has a large shelf-like P4 protocone (except in the most primitive species, *P. pristinidens* Petter, 1963) that is expanded at the anterolingual corner and lacks a deep notch between the m1 entoconid and metaconid, characteristics that are lacking in the New World skunks. *Promephitis* seems to have an independent history from the New World skunks as suggested by Pilgrim (1933).

Wolsan (1999) identified the holotype of *Palaeomephitis steinheimensis* Jäger, 1839, from the middle Miocene of Steinheim am Albuch, Germany, as the oldest and most primitive mephitine cranium. A partially expanded epitympanic recess in *Palaeomephitis* was considered a transitional stage leading to the fully expanded accessory chamber (mastoid sinus) in all other mephitines. It is also the only mephitine that possesses a mustelid-like suprameatal fossa. Based on a hypothesized transformation series of increasingly blocked suprameatal fossae within mustelids (Schmidt-Kittler, 1981; Wolsan, 1993), the condition in *Palaeomephitis* appears to be that of a primitive mustelid and from this condition, mephitines may have ultimately lost the fossa, an argument that was advanced to support a mustelid relationship of the skunks (Wolsan, 1999). However, the bulla of *Palaeomephitis* seems to have a partially inflated entotympanic, a condition not seen in any other known mephitines. Wolsan (1999) postulated this latter feature to be the primitive condition for skunks and by extension, the lack of the entotympanic inflation (type A bulla of Hunt, 1974) in the rest of the mephitines becomes a secondarily derived condition, a scenario contrary to the general trend of bulla inflation in carnivorans. Wolsan further associated the basicranium of *Palaeomephitis steinheimensis* with the dentition of *Trochotherium cyamoides* (the latter was considered a subjective junior synonym by Wolsan), which is extremely derived with numerous roots on the P4 and m1 and peculiar carnassial morphology of almost a single domed cone without differentiation of other cusps (Fraas, 1870; Wegner, 1913), a pattern that is difficult to compare to any known carnivorans (Baskin, 2003, compared it to the procyonid genus *Potos*). If Wolsan's association is correct, *Palaeomephitis* possesses a peculiar combination of a relatively conservative mastoid sinus, a derived bulla, and highly derived dentitions.

Other Old World Mephitines Not Used in This Study—*Mesomephitis* Petter, 1967 from the Vallesian (early late Miocene) of Spain seems to offer some transitional morphology leading to *Promephitis*. Its lack of a notch between the m1 entoconid and metaconid rules out a relationship with the New World mephitines (Petter, 1967:pl. I, fig. 13, pl. II, figs. 2–3). Poor preservation for this genus prevents us from including it in our analysis.

Additional European genera that have alleged mephitine affinities (Ginsburg, 1999) but were not considered include taxa that are either questionably referred to mephitines or too poorly known to be of much help in our phylogeny. For example, *Trocharion* has been proposed to play a role in the early radiation of the mephitines (Pilgrim, 1933) but has recently been demonstrated to be a leptarctine mustelid (Qiu and Schmidt-Kittler, 1982). Another purported skunk *Nanomephitis* Kretzoi, 1952, from the late Miocene of Hungary, was briefly described but not figured. Unfortunately its holotype was destroyed in Budapest in 1945 (Petter, 1967), and its systematic status remains uncertain. The European middle to late Miocene *Proputorius* is also reported to have an accessory root in m1 (Baskin, 1998), but this genus is mostly known by fragmentary lower jaws (e.g., Ginsburg, 1961).

Descriptions of Characters—Discrete morphological characters are coded to compile a 14 taxa × 34 characters data matrix (Table 2) for parsimony analysis. Most of the characters listed here have been used by previous authors (e.g., Bryant et al., 1993; Baskin, 1998; Wolsan, 1999; Wang and Qiu, 2004). Our own usage of these characters is often in a very different context and they may be coded somewhat differently, e.g., a finer partitioning of some character states. For *Promephitis*, a working hypothesis of a species relationship is available (Wang and Qiu, 2004), and we use a primitive species, *P. parvus*, to code for the genus, in order to avoid homoplasies developed during the long history of the *Promephitis* clade. Similarly, for genera with more than one species, we strive to code the primitive states for the genus concerned.

Character polarities are determined by using *Amphicynodon* and *Mustelavus* as outgroups. *Amphicynodon* is the most basal ursoid from the early Oligocene of Eurasia, and *Mustelavus* is the most basal musteloid from the late Eocene of North America; both are presumably very close to the initial divergence of arctoids (Wang et al., in press). Appendix 1 lists definitions of characters used in our analysis and corresponds to those in the data matrix in Table 2.

Cladistic Analysis—The present phylogenetic analysis focuses on a generic relationship of the basal New World skunks. It is not meant to be an exhaustive analysis of all mephitines—we only selected three Old World genera that are relatively well studied and are represented by good cranial and dental materials. Consequently relationships of Old World mephitines adopted here can only be considered a tentative proposal to be further tested. Nor will this study tackle the more complex problem of the relationships of the mephitines within Arctoidea, although character polarities presented here will have bearing on future discussions of that subject.

Using *Amphicynodon* and *Mustelavus* to root the trees, we performed a parsimony analysis on the 14 taxa × 34 character data matrix using the computer program PAUP (Swofford, 1993). Searches using the 'Branch and Bound' option yielded six shortest trees of 56 steps in length. Relationships among the New World mephitines only vary between a fully resolved topology (Fig. 6) and a trichotomy of *Martinogale faulli*, *M. chisoensis*, and the rest of the advanced clade. Branching patterns among Old World mephitines are less constrained—the reason for an unresolved trichotomy of the Old World skunks in Figure 6. The following is a brief narration of our phylogeny.

We confirm the monophyletic status of the mephitines (including the Asiatic stink 'badger' *Mydaus*), although our present sampling of taxa is not designed to answer that question—a wider selection of basal musteloids will be necessary to fully address that. In the present analysis, the mephitines seem to share the following derived characters: presence of a mastoid sinus, loss of P1/p1, extra roots in m1, a ridge on posterior face of m1 protocone and crest-like cusps in M1, a chin under the mandibular symphysis, and a central septum on the posterior opening of internal naris. Two other derived characters that also support such a relationship in Figure 6, i.e., absence of alisphenoid foramen and loss of carnassial notch, may or may not be synapomorphies for skunks depending on where the Mephitinae are ultimately placed, a larger issue that is not addressed here. If the Mephitinae fall within the Mustelidae, then the above two characters are shared with all other mustelids. On the other hand, if they are outside a mustelid-procyonid clade, as increasingly indicated by molecular evidences (Vrana et al., 1994; Ledje and Arnason, 1996b, a; Dragoo and Honeycutt, 1997; Flynn et al., 2000; Sato et al., 2004), then these characters would be independently derived in the Mephitinae.

The Old World skunks are a monophyletic group supported by four derived characters: presence of an anterior shelf in front of the P4 protocone, broadened P4 protocone crest, reduced or lost P2, and posteriorly located premaxillary-maxillary suture. The first of these appears to be a unique feature of the Old World

TABLE 2. A data matrix of 14 taxa × 34 characters used in the PAUP analysis

Amphicynodon	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0	0 0 ? ?
Mustelavus	1 1 0 0 0	0 0 ? 0 0	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0	0 0 ? ?
Mydaus	1 1 1 1 2	1 1 1 1 1	1 0 0 0 1	0 0 1 0 1	0 0 1 0 1	2 0 1 0 0	0 0 2 0
Palaeomephitis	? ? 1 1 1	1 1 ? ? ?	1 ? 0 ? ?	? ? ? ? 0	? ? 1 0 2	? ? 0 0 ?	? 0 ? ?
Promephitis	1 1 1 1 2	1 1 1 1 1	1 1 0 0 0	0 0 0 0 0	0 0 1 0 1	0 0 0 0 0	0 0 ? 0
Martinogale faulli	1 1 1 1 2	1 1 1 1 1	0 0 1 1 1	? 0 0 0 0	0 0 0 0 0	0 0 0 0 0	0 0 ? 0
Martinogale chisoensis	1 1 1 1 2	1 1 ? 1 1	0 0 1 1 1	1 0 0 ? 0	0 0 0 0 0	1 0 0 0 0	? 0 ? ?
Martinogale alveodens	? 1 ? ? ?	1 1 ? 1 1	? 0 ? 1 ?	1 1 1 1 ?	0 ? ? ? ?	? ? 0 ? ?	? ? ? ?
Buisnictis	1 1 ? 1 ?	1 1 ? 1 1	0 0 1 1 1	1 1 1 1 ?	1 ? 0 0 0	0 0 0 0 0	0 0 ? ?
Brachyprotoma	1 1 1 1 2	1 1 1 1 1	0 0 0 1 ?	0 1 1 1 1	1 ? 1 0 2	0 1 0 1 0	0 0 ? ?
Spilogale	1 1 1 1 3	1 1 1 1 1	0 0 1 1 1	1 1 1 1 1	1 1 1 1 0	0 0 0 0 0	0 0 0 0
Mephitis	1 1 1 1 2	1 1 1 1 1	0 0 0 1 2	0 0 1 1 1	1 1 1 0 1	1 1 1 1 0	1 0 1 1
Osmotherium	? 1 ? 1 2	1 1 ? 1 1	? 1 ? 1 ?	0 0 1 1 1	0 ? ? ? ?	? 1 1 ? ?	? ? ? ?
Conepatus	1 1 1 1 2	1 1 1 1 1	0 0 0 1 2	1 1 1 1 1	1 1 1 0 2	2 1 2 0 1	1 1 2 1

Character numbers correspond to those listed in Appendix 1.

mephitines, whereas the latter three are derived in parallel with some lineages of the New World skunks. These presumed parallel developments of characters, plus the divergent lineages of Eurasian skunks with little morphological cohesion, naturally lead to the suspicion that Old World skunks are not monophyletic. In fact, if mephitines ultimately originated in Eurasia and gave rise to the New World clade, as indicated by current evidence, then it is more likely that the Old World taxa are paraphyletic, forming a series of stem taxa to the monophyletic New World clade. The three selected genera of the Old World skunks are morphologically too disparate to permit a sense of their interrelationships. Indeed all three possible combinations of a three-taxon topology are recovered in the three shortest trees found by PAUP. Further resolution of the Old World mephitines will have to wait for the inclusion of additional taxa to be analyzed.

The New World skunks, tribe Mephitini (*Martinogale* and above), share three synapomorphies that are absent from the Old World skunks: a parastyle on P4, a dominant hypoconid on m1, and posteriorly shifted lingual cingulum of M1. These characters, particularly the initial stages of them shown in *Martinogale*, may not be very prominent morphologically; they are nonetheless consistent among all New World skunks, with only occasional exceptions.

Martinogale is probably closest to what a primitive mephitine would look like. With the exception of a fully expanded mastoid sinus and lack of a suprameatal fossa, characters that are somewhat more derived than those in *Palaeomephitis* (which has a partially expanded mastoid sinus and presence of a suprameatal fossa), *Martinogale* retains a primitively small, anteriorly located P4 protocone crest and a lingually closed talonid basin. Of the three species of *Martinogale*, *M. chisoensis* is slightly more derived than *M. faulli* in its possession of a small lingual cingulum on the lower canines (the status of this character in *M. faulli* is unknown) and a slightly less transversely elongated M1. *M. alveodens* is the most derived in its widened premolars with more distinct cingular cusps and tall-crowned p4. *Martinogale* is shown in our cladogram as a paraphyletic genus at the species level, and the three species presently recognized may be an anagenetic progression. This latter scenario cannot be demonstrated with the meager data at hand, but remains a distinct possibility.

Buisnictis plays a critical role as an intermediate form between the basal *Martinogale* and the crown clade of New World mephitines. While still preserving the primitive condition of an isolated P4 protocone on the anterolingual corner of the tooth, it is the first genus that has reached the beginning stage of an m1 entoconid crest that is separated from the base of the metaconid by a wide notch. The talonid basin is thus open lingually. Such a steep notch is often associated with an elevated M1 protocone that fits into this notch. Such a combination of primitive and derived features in *Buisnictis* permits a sense of actual steps in the evolution of the New World skunks—the entoconid notch was first developed in *Buisnictis*, followed by a lengthened and posteriorly located P4 protocone crest in later taxa.

The crown clade of North American skunks (*Mephitis*, *Spilogale*, *Conepatus*, plus two fossil genera *Brachyprotoma* and *Osmotherium* included in this analysis) share a derived character of an anteroposteriorly lengthened P4 protocone crest that is shifted behind the anterior margin of the paracone.

Of the living skunks, *Spilogale-Mephitis-Conepatus* appear to form a morphocline. Morphological trends include progressively more domed forehead, reduction of anterior premolars, broadening and increasing crown height of premolars, increasing height of M1 protocone, broadening of M1 lingual cingulum, lengthening of m1 talonid at the expense of the trigonid, deepening of the m1 entoconid notch and talonid basin, and more crest-like cusps on M1 paracone-metacone complex and the corresponding m1 hypoconid, etc. Our phylogenetic analysis indicates a (*Spilogale* (*Mephitis*, *Conepatus*)) relationship for living North American genera, with the two fossil genera, *Brachyprotoma* and *Osmotherium*, closely related to *Mephitis*. This topology is different from two recent trees based on molecular evidences: (*Conepatus* (*Spilogale*, *Mephitis*)) in two separate studies of skunks and mustelid-like carnivorans (Dragoo et al., 1993; Dragoo and Honeycutt, 1997) and (*Mephitis* (*Conepatus*, *Spilogale*)) in a more restricted analysis of New World skunks only with fewer base pairs (Dragoo et al., 2003). Whereas the first topology (*Conepatus* (*Spilogale*, *Mephitis*)) tends to be supported when more mitochondrial and nuclear genes are used (Dragoo, pers. comm. 2004), a sister relationship for *Mephitis-Conepatus* in our morphological tree (when fossil taxa are subtracted from the tree), on the other hand, is supported by multiple synapomorphies and is consistent with a separate morphologic study (Holmes, 1988).

BIOGEOGRAPHIC REMARKS

Past remarks on the origins of skunks were often highly speculative. Hall (1936:fig. 4) proposed separate origins for living genera of skunks. He postulated a close relationship of *Mephitis* and *Spilogale* that in turn were derived from *Promephitis*, whereas *Conepatus* came from an unknown origin before *Promephitis*. Kurtén and Anderson (1980:161), on the other hand, believed that the ancestry of living (North American) skunks should be sought in the Old World Miocene *Miomephitis*.

More recently, Baskin (1998:170) postulated two independent invasions for North American skunks (he appears to recognize three such invasions in his figure 9.7). The first invasion is by *Pliogale*/*Martinogale*, which was presumed to be derived from an ancestor similar to the European *Mesomephitis*. This first lineage of skunks became extinct in North America after *Buisnictis*. Baskin's second immigration event includes all living genera of North American skunks plus their close relatives (*Spilogale*, *Mephitis*, *Conepatus*, *Osmotherium*, *Brachyprotoma*) and their ancestry is traced back to an ancestor similar to the Eurasian *Promephitis*, although Baskin commented that *Promephitis* is too specialized to be ancestral to the living New World skunks. Stevens and Stevens (2003) accepted Baskin's diphyletic origin of New World skunks, but placed *Spilogale* in a clade that includes *Martinogale* and *Buisnictis* (within Baskin's first invasion), thus rejecting the monophyly of living North American mephitines.

While we are in agreement with Baskin's first immigration event, his second immigration event is not supported by our analysis. We conclude that all fossil and living New World mephitines share several derived characters and form a clade of their own. Furthermore, instead of an unbridgeable gap, we see morphological continuity between *Buisnictis* and the living skunks clade (*Spilogale* and above in our phylogeny, Fig. 6), separated by a single derived character of a broadened P4 protocone crest (character 23). In fact, *Buisnictis* is an ideal intermediate form that bridges the morphological gap between *Martinogale* and *Spilogale*. Therefore, postulation of a second, independent immigration is not necessary, and as allowed by Baskin (1998:170), such an immigration would lack a viable ancestral form in the Old World.

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APPENDIX 1

Definitions of characters and their states used in compiling the data matrix for phylogenetic analysis. Character numbers correspond to those in Table 2.

(1) M2: present (0); absent (1).
(2) m3: present (0); absent (1).
(3) Alisphenoid foramen: present (0); absent (1).
(4) Upper carnassial (P4) notch: present (0); absent (1).
(5) Mastoid sinus (expansion of epitympanic recess into mastoid): absent (0); small and not fully reaching to lateral wall of mastoid process (1); large and fully filling mastoid process (2); further expansion posteriorly to separate paroccipital process from bulla (3).
(6) m1 roots: no extra roots (anterior and posterior main roots only) (0); extra roots on both lingual and labial sides (1).
(7) P1 and p1: present (0); absent (1).
(8) Central septum in internal naris: absent (0); present (1).
(9) Ridge on posterior face of m1 protoconid (presumably associate with crest-like M1 paracone and metacone): absent (0); present (1).
(10) Chin on mandibular symphysis: absent (0); present (1).
(11) Anterior shelf of P4 protocone to expand anterolingual corner: absent (0); present (1).
(12) Cuspules on anterior segment of m1 entoconid crest: absent (0); present (1).
(13) P4 parastyle: absent (0); present (1).
(14) m1 talonid cusps: hypoconid approximately equal in height to entoconid (0); hypoconid dominant over entoconid (1).
(15) M1 lingual cingulum: surrounding protocone lingually (0); posteri-

orly shifted and not surrounding protocone lingually (1); a widened shelf on posterolingual corner (2).

(16) Lower canine lingual cingulum: absent or poorly developed (0); well developed (1).

(17) Premolar anterior and posterior cingular cusps: absent or weakly developed (0); distinctly developed (1).

(18) p4 crown height: relatively low and not much exceeding m1 paraconid (0); relatively high and equal or exceeding m1 protoconid (1).

(19) Premolar width: narrow (0); broadened (1).

(20) Postorbital constriction: narrow (0); widened (1).

(21) m1 entoconid crest: fully enclosed on lingual side (0); notch on anterior end of entoconid crest (1).

(22) M1 protocone height: low (0); high (1).

(23) P4 protocone crest: narrowly constricted and anteriorly located (0); broadened and posteriorly shifted (1).

(24) Paroccipital process: not reduced (0); reduced (1).

(25) P2: normal size (0); much reduced relative P3 (1); lost (2).

(26) outline of M1: 0, transverse width nearly twice anteroposterior length; 1, transverse width less than twice anteroposterior length; 2, approximately equal length and width; 3, anteroposteriorly elongated.

(27) Profile of forehead: flat (0); domed (1).

(28) Relative length of m1 trigonid and talonid: trigonid much longer than talonid (0); trigonid roughly equal to talonid (1); talonid longer than talonid (2).

(29) P4 protocone crest: thin and crest-like (0); swollen and conical (1).

(30) Crista behind M1 postprotocrista: absent (0); present (1).

(31) Nasal and premaxillary: normally proportioned (0); nasal retracted and premaxillary protruded (associated with hog-nose) (1).

(32) P4 paracone crown height: relatively low (0); very high (1).

(33) Premaxillary-maxillary suture in palatal view: across incisive foramen (0); at level of posterior edges of incisive foramen (1); behind posterior edge of incisive foramen (2).

(34) Condyloid canal: present (0); extremely reduce or absent (1).