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A transitional skunk, *Buisnictis metabatos* sp. nov. (Mephitidae, Carnivora), from Baja California Sur and the role of southern refugia in skunk evolution

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Fossil records for basal New World skunks (subfamily Mephitinae) have been slowly but steadily increasing in recent years. Fossils for both living and extinct genera are now dense enough that actual evolutionary steps leading to living clades are beginning to be resolvable. We document a new species of the extinct, transitional genera *Buisnictis*, *B. metabatos* sp. nov., from Early Pliocene San José del Cabo Basin, Baja California Sur, México. *B. metabatos* possesses a combination of primitive and derived features, including a broadened P4 protocone shelf, a notch anterior to the m1 entoconid, and relatively unexpanded M1 lingual cingulum. It thus fills in yet another morphological gap and it is at a basal position within or just outside of the living skunk clade. Although current records are still far too scattered to resolve detailed zoogeographical patterns, we are in a position to speculate that since the Early Pliocene, southern North America and Central America have acted as a refugium for skunks. As a basal skunk, *Buisnictis metabatos* probably gave rise to the modern crown clade. There is evidence to suggest that both spotted skunks (*Spilogale*) and hog-nosed skunks (*Conepatus*) had their centres of diversification in Mexico or Central America. The only exception may be the striped and hooded skunks (*Mephitis*), which have a more northerly distribution.

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Keywords: Mephitidae; *Buisnictis*; Mexico; Pliocene; zoogeography; refugium; Zoobank registration

Introduction

Skunks, family Mephitidae, originated in Eurasia, possibly by as early as the Early Oligocene, some 28.9–34.7 million years ago, based on molecular estimates (Sato *et al.* 2009), and migrated to North America by the Late Miocene about 9–10 million years ago (Wang *et al.* 2005). Although fossil records for Eurasian skunks are all from mid-latitude regions, living Asian skunks have only survived in the islands of Indonesia and Philippines in the form of two species of stink badger, *Mydaus* (Radinsky 1973; Hwang & Larivière 2003, 2004). In the New World, even though the first skunks must have passed through Beringia and have been at least tolerant to cold climates in the Arctic Circle during the Late Miocene, by the Early Pliocene southern North America, especially Mexico, played an important role in the evolution of skunks.

We first recognized that central Mexico in the Early Pliocene held important clues to the evolution of the hog-nosed skunks, *Conepatus* (Wang & Carranza-Castañeda 2008). We now document an even more basal skunk from

the southern tip of Baja California Sur. By its very basal phylogenetic position, just outside the clade for living New World mephitines, it seems reasonable to postulate that southern North America and Central America probably acted as refugia for skunks and at least two of the three living genera of skunks originated there.

Institutional abbreviations

KUVP: vertebrate paleontology collection of University of Kansas, Lawrence, Kansas, USA; **F:AM,** Frick Collections, American Museum of Natural History, New York, New York, USA; **LACM,** Natural History Museum of Los Angeles County, Los Angeles, California, USA; **CGJVP,** Centro de Geociencias Juriquilla Vertebrate Paleontology collection, Juriquilla, Querretaro, México; **MSU,** Midwestern State University collection, now in Texas Natural Science Center (Texas Memorial Museum), Austin, Texas, USA; **UMMP,** University of Michigan Museum of Paleontology, Ann Arbor, Michigan, USA.

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Systematic palaeontology

Order **Carnivora** Bowdich, 1821
 Infraorder **Arctoidea** Flower, 1869
 Parvorder **Mustelida** Tedford, 1976
 Family **Mephitidae** Bonaparte, 1845
 Subfamily **Mephitinae** Bonaparte, 1845
 Genus ***Buisnictis*** Hibbard, 1950

Type species. *Buisnictis meadensis* Hibbard, 1950 (= *Brachyprotoma breviramus* Hibbard, 1941b).

Included species. *Buisnictis meadensis* Hibbard, 1950 (= *B. schoffi* Hibbard, 1954b); *B. burrowsi* Skinner *et al.*, 1972; *Buisnictis metabatos* sp. nov.

Emended diagnosis. *Buisnictis* is intermediate in morphology between the more primitive *Martinogale* and the more derived *Spilogale*, *Mephitis*, *Conepatus*, and other genera within the crown clade of extant mephitids. Derived characters that differ from *Martinogale* include a notch between m1 metaconid and entoconid crest. Primitive characters compared to living clades include narrow forehead (postorbital constriction) region, conical-shaped P4 protocone (except in *B. metabatos* sp. nov.), M1 not broadened anteroposteriorly, M1 internal cingulum (hypocone) not expanded posteriorly, narrow p4, and shallow jaws. An autapomorphy for some species of *Buisnictis* (*B. meadensis* and *B. burrowsi*) is their reduction of m1 metaconid and slight tendency toward hypercarnivory, such as a more slender M1.

Distribution. Early Blancan of Baja California Sur, Mexico (Fig. 1); middle Blancan through Irvingtonian of Nebraska, Kansas and Oklahoma.

Remarks. Hibbard's (1950) original description of this genus, based on a single upper P4 (UMMP 25769) from the Rexroad Formation, Fox Canyon, XI Ranch, Meade County, Kansas, was largely a comparison with the weasels (genus *Mustela*), even though he was aware of similar-sized skunks within his fossil assemblage. Two years later, additional upper dental materials were described (Hibbard 1952), and this time, Hibbard began to compare the genus with the spotted skunks (*Spilogale*). Finally by 1954, enough associated upper and lower dental materials were accumulated that led to the recognition that the upper teeth of his *Buisnictis meadensis* actually belonged to the same species as *Brachyprotoma breviramus* (Hibbard 1941b). However, Hibbard's (1954b) proposed new combination, *Buisnictis breviramus*, effectively redesignating *breviramus* as the type species, is invalid because *meadensis* was earlier fixed as the type species of *Buisnictis* (International Commission on Zoological Nomenclature 1999, Article 67.4), as also pointed out by Stevens & Stevens (2003).

Since Hibbard's initial recognition of *Buisnictis meadensis*, three additional species have been named under the

genus: *B. schoffi* Hibbard, 1954a from the Rexroad Formation, Buis Ranch, Beaver County, Oklahoma (Hibbard 1954a), *B. burrowsi* Skinner *et al.*, 1972 from Sand Draw Quarry, Keim Formation, Brown County, Nebraska (Skinner *et al.* 1972), and *B. chisoensis* Stevens & Stevens, 2003 from Screw Bean Local Fauna in the Bench member, Banta Shut-in Formation, Brewster County, Texas (Stevens & Stevens 2003). Of these, Stevens & Stevens (2003, p.199) pointed out that the Buis Ranch *B. schoffi* is probably the same as the similarly aged and sized *B. meadensis* from the XI Ranch in neighbouring Meade County, an assessment with which we agree. As for *B. chisoensis*, Wang *et al.* (2005) and Wang & Carranza-Castañeda (2008) placed it in a paraphyletic *Martinogale*. The somewhat later (~2–3 Ma, Blancan IV) *B. burrowsi*, on the other hand, is largely established on its much reduced m1 metaconid, a character that appears to be first initiated in *B. meadensis*. This seems to suggest that a slight tendency toward hypercarnivory can be identified in the *B. meadensis*–*B. burrowsi* lineage.

By strict cladistic criteria, our new species of *Buisnictis* from Baja California Sur may warrant a genus of its own because of its transitional position (see Phylogeny below). However, we refrain from naming a new genus, preferring its present paraphyletic status, because of the subtlety of its derived characters (a broad P4 protocone crest and an inflated mastoid sinus) and the uncertainty that the Mexican species may be related to spotted skunks.

***Buisnictis metabatos* sp. nov.**
(Figs 2–6)

2010 *Buisnictis* sp., Carranza-Castañeda *et al.*:79.

Holotype. CGJVP 2140, partial skull with left M1 (broken), right P4–M1, left horizontal ramal fragment with m1–m2 (broken) and right ramal fragment with p4–m2.

Diagnosis. Differs from known species of *Buisnictis* in that the P4 protocone is broadened into a wide shelf and the m1 metaconid not reduced. Characters that are primitive relative to living mephitine clades include: narrow forehead, M1 anteroposteriorly narrow and internal cingulum (hypocone) not expanded posteriorly, relatively narrow p4, and shallow jaw.

Etymology. From *meta*, Greek, transition; *vato*, Greek, step; Latinized as *metabatos* to mean 'transitional, the next step'.

Type locality and associated fauna. CGJVP 2140 was collected in locality BCSM 41, El Zorrillo, about 4 km east of Miraflores, San José del Cabo Basin, Baja California Sur, México (Fig. 1). Associated fauna includes *Equus simplicidens*, *Rhynchotherium falconeri*, *Hemiauchenia* sp., *Borophagus diversidens*, *Felis* cf. *F. studeri*, *Felis lacustris*, *Hypolagus vetus*, and cf. *Ammospermophilus* (Carranza-Castañeda & Miller 1999; Miller & Carranza-Castañeda

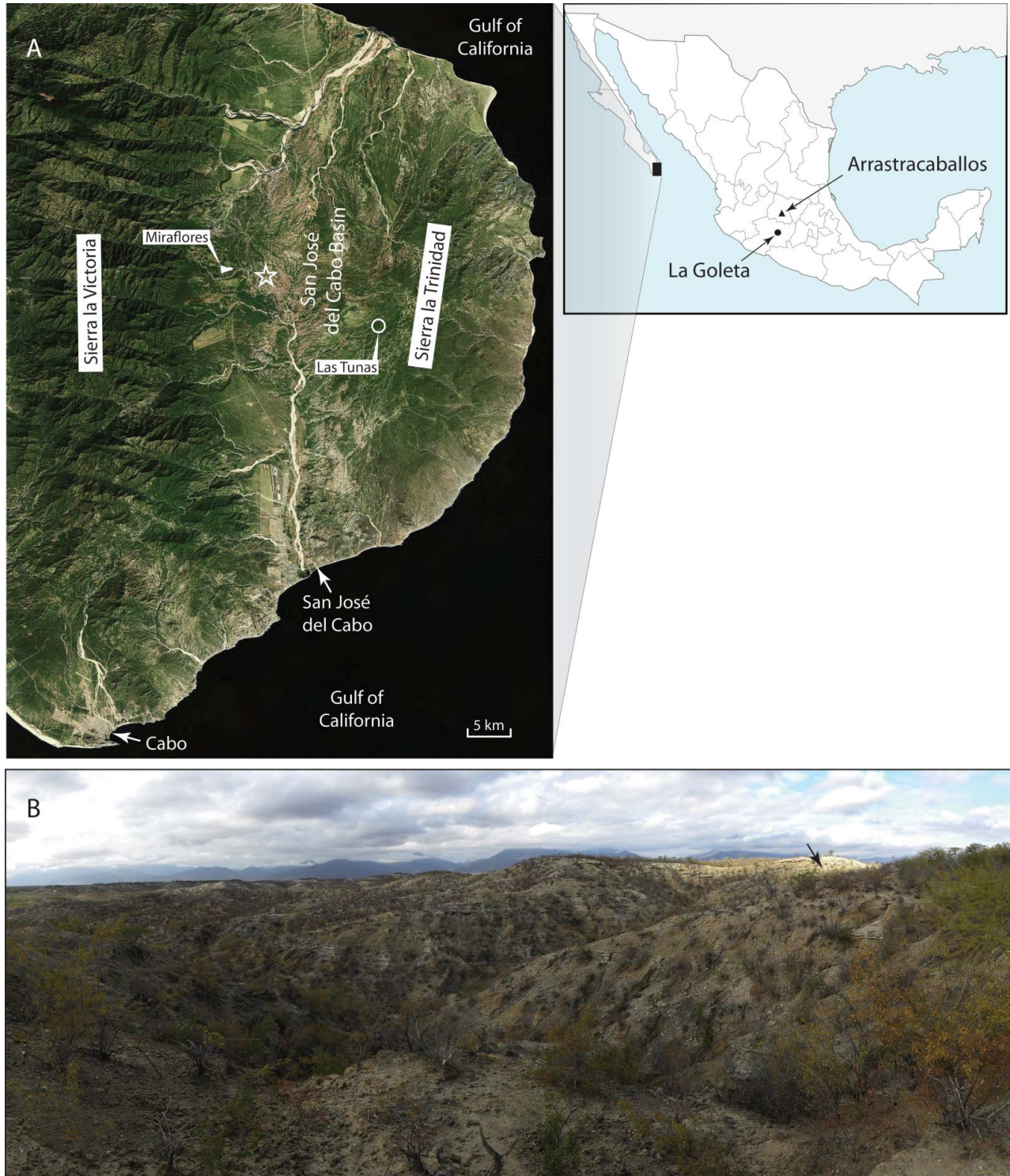


Figure 1. A, Satellite map of the San José del Cabo Basin and Miraflres locality (indicated by white star), which is approximately 3 km east of the village of Miraflres, and the Las Tunas locality (white circle); B, photograph of locality BCSM 41 (El Zorrillo), indicated by a black arrow; the skunk skull was recovered about 5 m from the top of the section in greyish yellow, coarse to medium sandstone layers, which alternate with light grey sandstone and conglomerate.

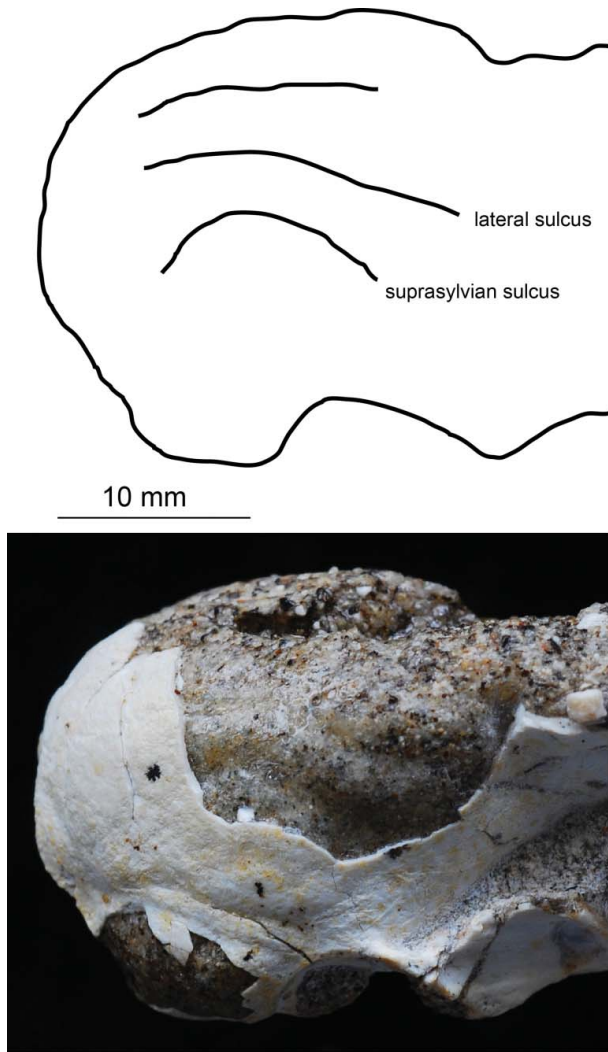


Figure 2. *Buisnictis metabatos* sp. nov., holotype, CGJVP 2140, dorsolateral aspect of skull showing endocast morphology (lower) and interpretation of the sulci (upper) combined from both left and right sides of the endocasts.

2002; Carranza-Castañeda 2006; Carranza-Castañeda *et al.* 2010). A Late Pliocene fauna, the Las Tunas local fauna, found in an area located 18 km SE of the town of Miraflores but also within the San José del Cabo Basin, has been described by Miller (1980). Based on the presence of *Equus simplicidens*, the Miraflores fauna is considered to be early Blancan in age. Furthermore, the Miraflores Fauna is similar to those from Arrastracaballos in the San Miguel de Allende Basin and also to the La Goleta Fauna in the state of Michoacan (Fig. 1). Preliminary dates by both fission track and potassium-argon methods have yielded an age of 3.6 Ma for ash samples near the Arrastracaballos locality and 3.4 Ma for the La Goleta (Carranza-Castañeda 1991; Carranza-Castañeda & Miller 1996).

Geological setting. The San José del Cabo Basin (McCloy 1984) is at the southern tip of the Baja California peninsula, and is bounded by the Sierra La Victoria to the west and the Sierra La Trinidad to the east. It is interpreted as a half-graben controlled by the San José del Cabo normal fault, which is the largest fault in an array of active structures caused by the rifting of Baja California from the mainland (Fletcher *et al.* 2000; Busch *et al.* 2012) and by transform displacements associated with the spreading centres in the Gulf of California. Neogene sediment accumulation in the basin has been affected by the combined effect of local tectonism (syndepositional extension and transform displacements) and global sea-level change. Terrestrial alluvial, transitional and shallow marine sediments are represented by Middle to Upper Miocene La Calera Formation, through Late Miocene Trinidad Formation and Pliocene Refugio and Los Barriles formations, and terminating in Pleistocene El Chorro Formation (Martínez-Gutiérrez & Sethi 1997 and references within). The Miraflores fossil assemblage was recovered in an area where outcrops are dominated by a shallow marine regression unit, the Early Pliocene Refugio Formation (Martínez-Gutiérrez & Sethi 1997), from sediments that we interpret as a fan-delta facies. Vertebrate fossils are preserved in clayey to fine-grained sandy sediments interbedded with coarser grained weakly cemented arkosic sandstones.

Description. CGJVP 2140 is preserved in a sandstone matrix. Maximum anteroposterior preserved length of the skull is 33.2 mm, maximum breadth across the braincase is 18.2 mm, and maximum breadth across the mastoid sinuses is 20.6 mm. Although much of the delicate bones on the left side of the skull are missing, a well-preserved endocast is still intact, permitting observations on the external brain morphology as well as middle ear cavities. The skull bones surrounding the brain are thin-walled and the missing skull bones reveal nearly the entire left endocast and anterior half of the right brain. The left and right endocasts thus combine to make a composite endocast for the hemisphere, although that on the left side is poorly preserved. The overall endocast morphology is very close to those of *Spilogale* illustrated by Radinsky (1973, fig. 3), with the lateral and suprasylvian sulci being the most readily visible (Fig. 2). A sylvian sulcus is not visible, although we cannot rule out poor preservation on the fully exposed left side of the braincase as the cause. Assuming this absence is not due to poor preservation, the lack of this sulcus is consistent with conditions in all mephitines (Radinsky 1973).

The mastoid sinuses are well preserved, a condition typical of all mephitines. The right sinus is filled with sandstone matrix and the left one is represented by a calcite endocast. Both sinuses are inflated well beyond the lateral wall of the braincase, and as is typical of *Spilogale*, also expand posteriorly and medially into the space occupied

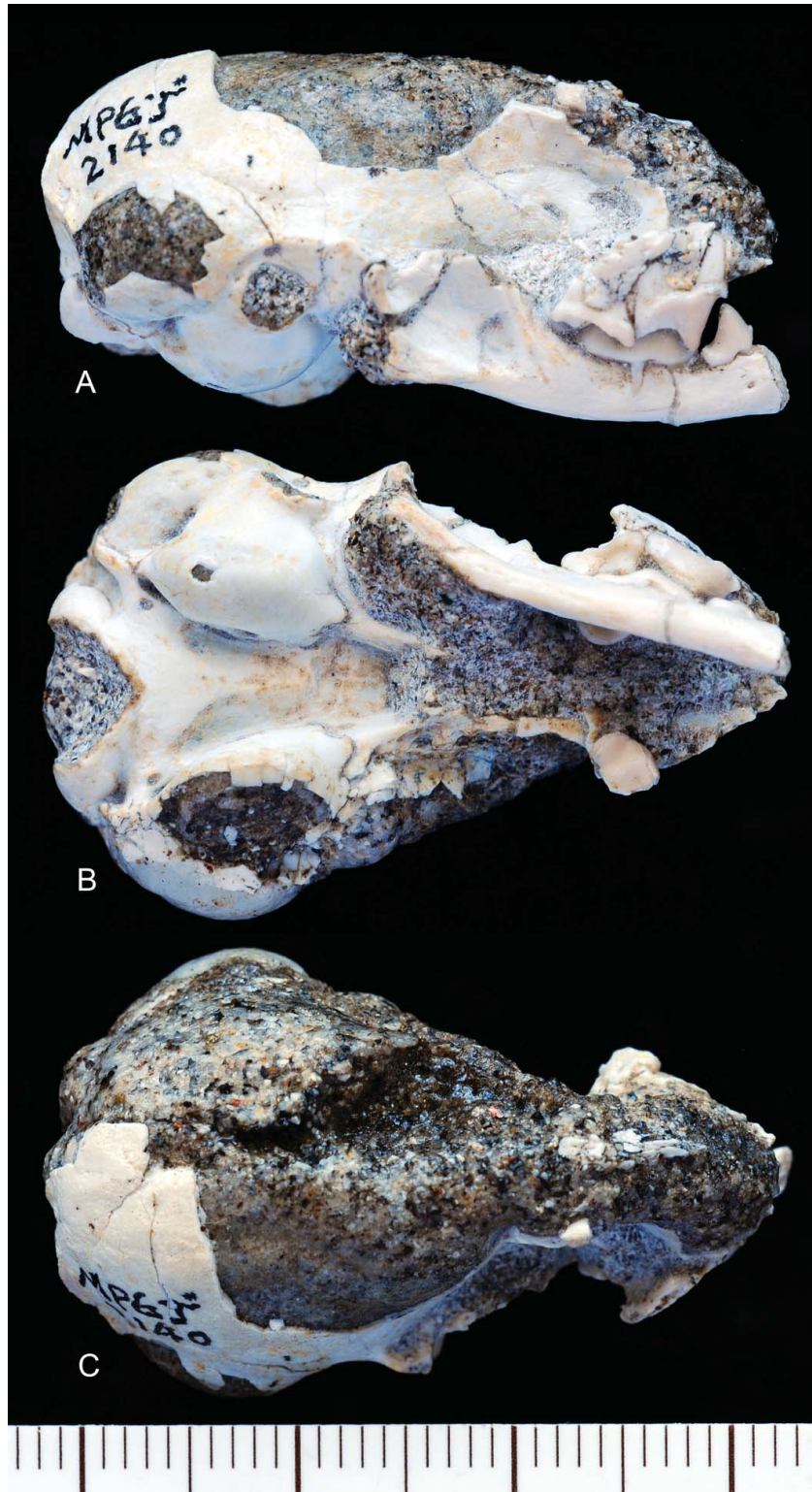


Figure 3. *Buisnictis metabatos* sp. nov., holotype, CGJVP 2140, partial skull. **A**, lateral; **B**, ventral; **C**, dorsal views. Scalebar is in mm.

by the paroccipital process. As a result, the paroccipital process is extremely reduced. The volume of the mastoid sinus is about the same as the tympanic bulla. The tympanic bulla is well inflated, more so than modern North Ameri-

can skunks, and the external auditory meatus is short, as in *Martinogale*. The condyloid foramen is adjacent to, but separate from the posterior lacerate foramen. The foramen for internal carotid artery is located at the medial

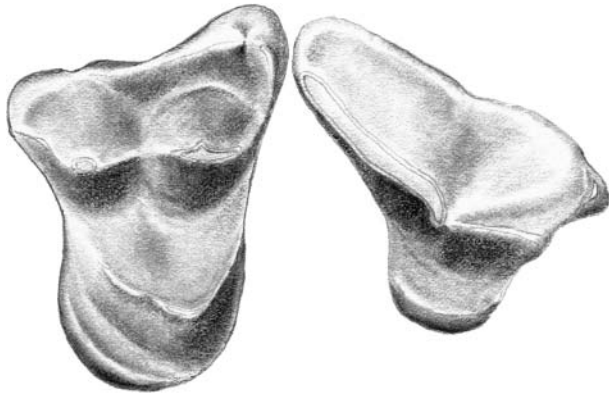


Figure 4. *Buisnictis metabatos* sp. nov., holotype, CGJVP 2140, reconstruction of upper cheek teeth based on the visible outlines in photograph (Fig. 3B) and supplemented by observations on the partial left M1 and revealed cusp morphology (Fig. 3A).

wall of the bullas along the mid-way of the length of the bulla.

Bones on much of the skull top are missing. Based on the matrix endocast, the frontal region appears to be slightly domed. The postorbital constriction also seems to be relatively narrow, although the postorbital process of the frontal is not sufficiently preserved to confidently judge this character. The lower half of the infraorbital canal is preserved, and judging from its calibre, a single infraorbital canal is probably present, as opposed to two foramina in some individuals of *Spilogale*.

Both left and right mandibles are articulated with the skull. The left mandible was successfully separated from the skull, but the right one is too tightly articulated and the risk of damage is too high to attempt separation. Only the lingual half of left M1 remains (Fig. 3B). Combining the partial left M1 with what can be observed on the lingual and labial sides of the right P4–M1, we attempted a reconstruction of the upper cheek teeth (Fig. 4). The cusp morphology in the reconstruction is probably fairly accurate, although the posterior border of M1 is somewhat speculative. We choose to reconstruct the posterior border more like that of *Buisnictis* rather than *Spilogale* because of the overall primitive condition of the dentition.

The P4 shearing blade lacks a carnassial notch, as is typical of mephitines. A tiny but distinct parastyle is present at the anterolabial corner. The protocone is crest-shaped, located behind the anterior border of the paracone, and is formed by a large shelf extending nearly half the length of the tooth. The crest is low crowned and runs along the lingual border. A faint ridge is located along the anterior face of the paracone.

The M1 is transversely wider than its anteroposterior length. A prominent parastyle and labial cingulum surrounds the paracone. The metacone is about the same height and size as the paracone. A metastyle is far less

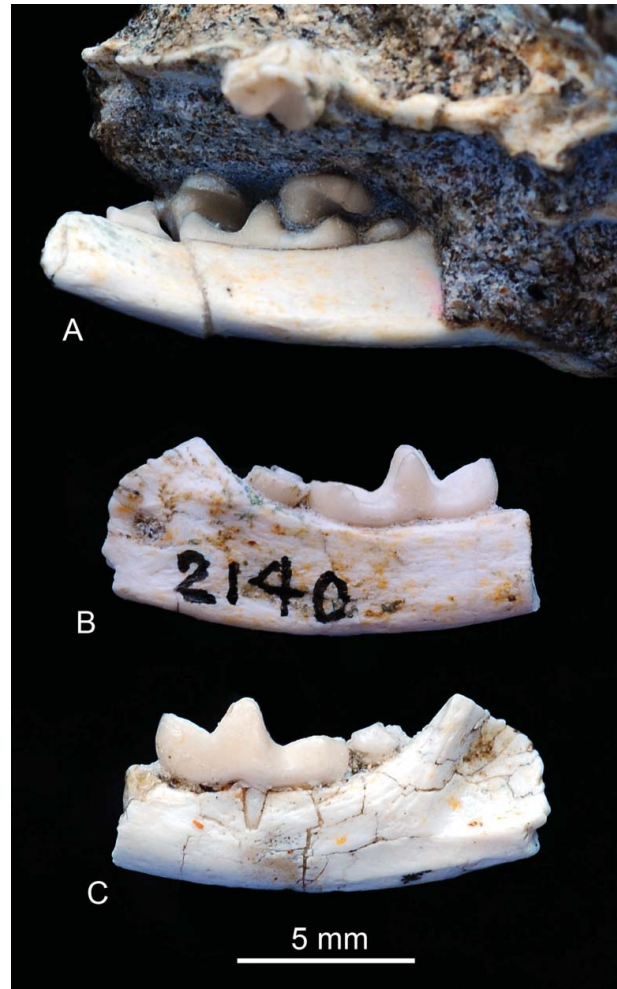


Figure 5. *Buisnictis metabatos* sp. nov., holotype, CGJVP 2140, jaws and lower teeth. **A**, medial view of right mandible in articulation with the upper teeth; **B**, medial view of left mandible; **C**, lateral view of left mandible.

developed than the parastyle. The protocone crest has a well-developed postprotocrista, as is typical for mephitines. Surrounding the postprotocrista is a well-developed internal (lingual) cingulum, or hypocone. The internal cingulum is at the posterolingual corner of the tooth and is lower-crowned than the protocone. The cingulum does not extend forward and wrap around the protocone.

The right mandible is better preserved than the left one. There is a slight indication of a ‘chin’ at the level of the p3, as is common in most modern skunks. The horizontal ramus is shallow and weak. The ascending ramus is partially preserved but its dorsal process is broken. The angular process is blunt and shallow, indicating a poorly developed inferior ramus for medial pterygoid muscle.

The p4 is about the same height as the m1 paracone. It is relatively slender without the conspicuous widening seen in living skunks. The anterior and posterior cingular cusps are modestly developed. There is no accessory cusp.

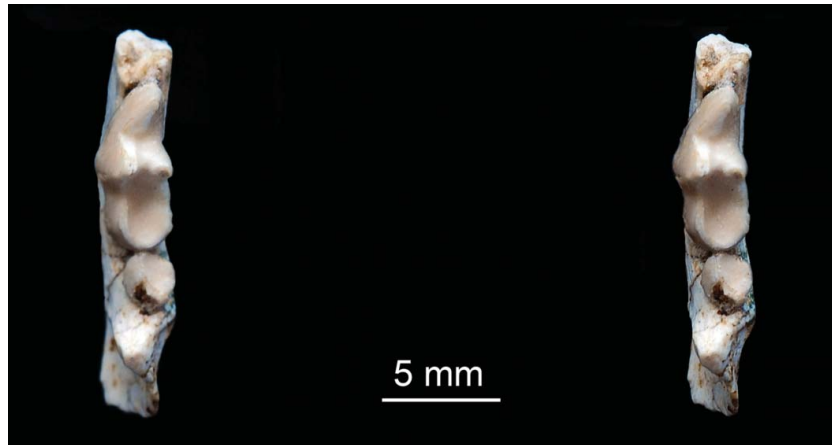


Figure 6. *Buisnictis metabatos* sp. nov., holotype, CGJVP 2140, stereophotos of left lower teeth.

The m1 is slender. The paraconid blade is long and forwardly extended. The protoconid is bulging to the labial side, and has a low but distinct ridge on its posterior face that is continuous with the anterior extension of the hypoconid ridge. The metaconid is lower than the protoconid but taller than the paraconid. The metaconid also has a ridge along its posterior face but this ridge does not continue to the entoconid ridge. The talonid is dominated by a high hypoconid ridge, which occupies approximately half of the talonid. The hypoconid ridge extends posteriorly and wraps around to be continuous with the entoconid ridge. The entoconid ridge is disrupted anteriorly by a deep notch, which separates the entoconid from the metaconid, resulting in a talonid basin that is open toward the lingual side. In medial view, this notch is broadly U-shaped, which pushes the entoconid backward to occupy less than one-half the length of the talonid.

The left m2 is broken at the posterior end and the right m2 cannot be observed due to tight articulation with upper teeth. The m2 is a simple, rounded peg with distinct protoconid ridge oriented anteroposteriorly along the labial margin. A lingual (metaconid) ridge rims along the inner margin.

Comparison. Presence of an inflated mastoid sinus (Bryant *et al.* 1993), extra roots on lingual and labial sides of m1 (Dunkle 1938; Bjork 1973), and overall dental morphologies leave little doubt that the Miraflores specimen is a mephitine. Within New World skunks, CGJVP 2140 possesses derived dental characters, such as a broad P4 protocone shelf and a distinct notch in front of m1 entoconid ridge, that place it near the crown clade including all living mephitines plus the extinct *Brachyprotoma* and *Osmotherium* (Wang *et al.* 2005; Wang & Carranza-Castañeda 2008). Yet its transversely widened M1 is still in the same grade as *Martinogale* and *Buisnictis*, in marked contrast

to more quadrate or even anteroposteriorly elongated M1s in modern skunks of the Americas. This is mainly due to its lack of a posterior expansion of the hypocone crest (internal cingulum) typical of advanced skunks, as well as corresponding elongation of the labial margin of the tooth. Therefore, the Baja California fossil skunk may provide key insights into the transition from archaic skunks (*Martinogale* and *Buisnictis*) to their living descendants. The following comparisons are mainly between species of *Buisnictis* and *Spilogale*, where the Miraflores specimen seems to lie.

Hibbard (1954a) commented on the overall similarity of *Buisnictis* and *Martinogale* due to what he called a “musteline P4” (small, conical P4 protocones as in *Mustela*) and speculated that *Martinogale* may be ancestral to *Buisnictis*. Although not specifically addressing the systematics of *Buisnictis*, we have previously postulated a transitional position for *Buisnictis* between the stem *Martinogale* spp. and a crown clade that includes all living New World skunks (Wang *et al.* 2005; Wang & Carranza-Castañeda 2008). In our cladogram (Wang & Carranza-Castañeda 2008, fig. 12), we defined *Buisnictis* as having derived characters of an m1 with a notch between the entoconid and metaconid but retaining the primitive condition of a P4 protocone that is not broadened posteriorly. Such a characterization, based primarily on published figures of *Buisnictis meadensis* (Hibbard 1952, 1954b), was still valid when we had the opportunity to examine some original materials of *B. meadensis* during the present study.

Based on the above characterization of *Buisnictis*, the Miraflores specimen is conspicuous in its possession of an advanced P4 with a crested protocone and an inflated mastoid sinus. Such a combination of characters places the Miraflores species one step beyond previously known species of *Buisnictis* (*sensu* Wang *et al.* 2005; Wang & Carranza-Castañeda 2008), but falling short of the crown clade mephitine (see Phylogeny). Morphologically, the

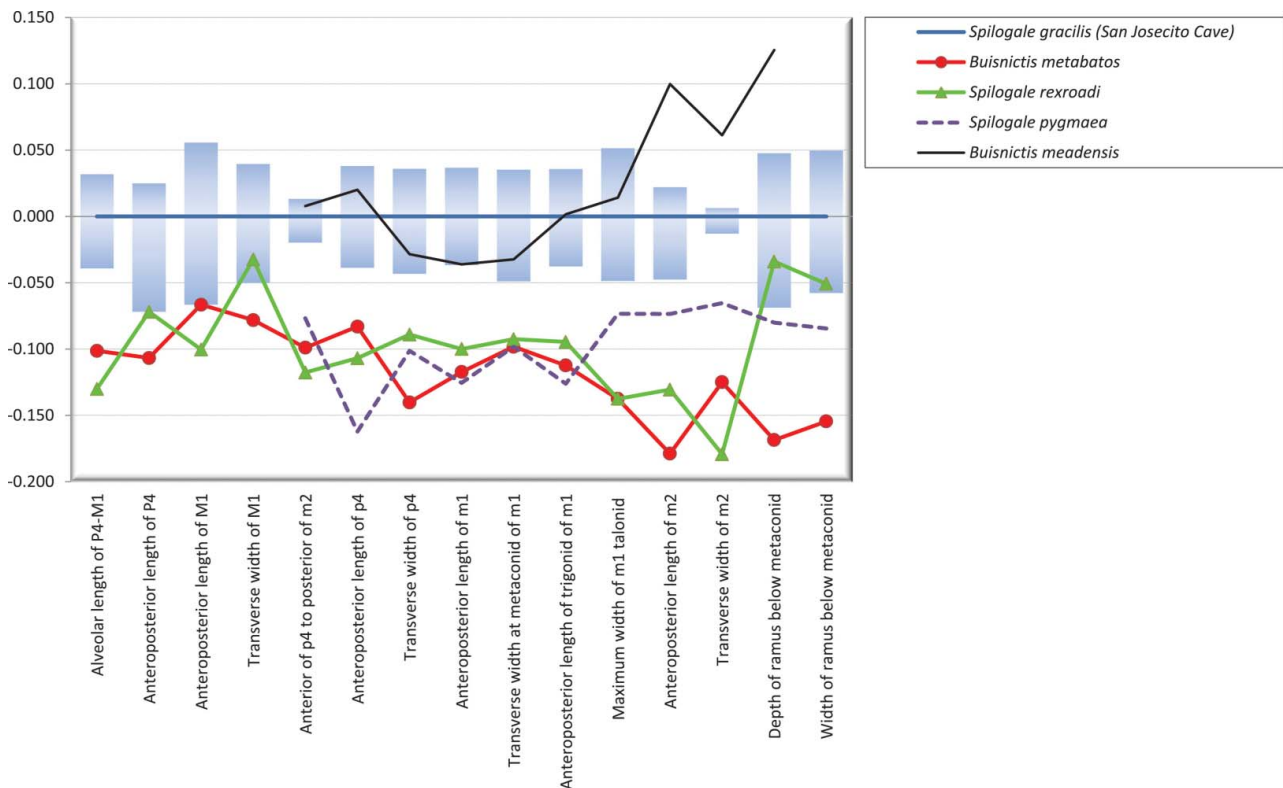


Figure 7. Simpson's (1941) log-ratio diagram of dental measurements for species of *Buisnictis* and selected *Spilogale* using *S. gracilis* from San Josecito Cave as the standard (means) for comparison (straight line at zero). Grey bars extending from the mean of the standard are the observed upper and lower ranges for *S. gracilis*. See text for explanations and Table 1 (Online Supplementary Material) for measurements.

Miraflores form is also very close to some fossil species previously placed in *Spilogale*, and a close comparison is warranted.

The earliest reported fossil spotted skunks are *Spilogale rexroadi* from Rexroad 3 locality, Meade County, Kansas and Beck Ranch, Scurry County, Texas (Hibbard 1941a, b; Dalquest 1972) in the Middle Pliocene (3–3.5 Ma, Blancan III) (Bell *et al.* 2004), and *S. marylandensis* from the Irvingtonian (Early Pleistocene) Cumberland Cave, Maryland (Gidley & Gazin 1933). The latter is close in size and morphology to the eastern spotted skunk, *S. putorius* (Kinlaw 1995), although living eastern and western spotted skunks are distinguished more by their reproductive patterns (Mead 1968a, b) than by morphology (Van Gelder 1959). Baja California is presently occupied by the western spotted skunk *S. gracilis* (Verts *et al.* 2001). *S. pedroensis* from the latest Blancan Curtis Ranch of Arizona is somewhat larger than the Miraflores form. By the latest Rancholabrean, fossil *Spilogale* at Rancho la Brea tar pit of southern California (referred to *S. phenax microrrhina*) (Stock 1929, 1930) and San Josecito Cave of Nuevo León, Mexico (referred to *S. putorius leucoparia*) (Hall 1960) (Online Supplementary Material Table 1) are largely referable to the living western spotted skunks, as are most Pleistocene records (Kurtén & Anderson 1980).

At an m1 length of 5.4 mm, the Miraflores skunk falls in the same size range as *Spilogale rexroadi* (5.2–6.0 mm) and is also near the smallest living skunks, *S. pygmaea* (5.3 mm), from the Pacific coast of mainland Mexico (Medellín *et al.* 1998). A log-ratio diagram of preserved dental dimensions (Fig. 7) shows that the main difference between the Baja skunk and other small species of *Spilogale* is its relatively unwidened p4, a primitive character seen in *Martinogale* and *Buisnictis*.

Phylogeny

We use a modified data matrix from Wang & Carranza-Castañeda (2008, table 2, appendix 1) to assess the phylogenetic position of *Buisnictis metabatos*, plus two previously known species of the genus. Modern species of *Spilogale* are mostly distinguished by coat patterns and colours (Van Gelder 1959; Verts *et al.* 2001) and our character coding is thus at the generic level. The matrix was manipulated in Mesquite (Maddison & Maddison 2011) and parsimony analysis was done in TNT made available with the sponsorship of the Willi Hennig Society (Goloboff *et al.* 2008). A character matrix of 21 taxa by 39 characters was searched by the 'implicit enumeration' algorithm, an exact search

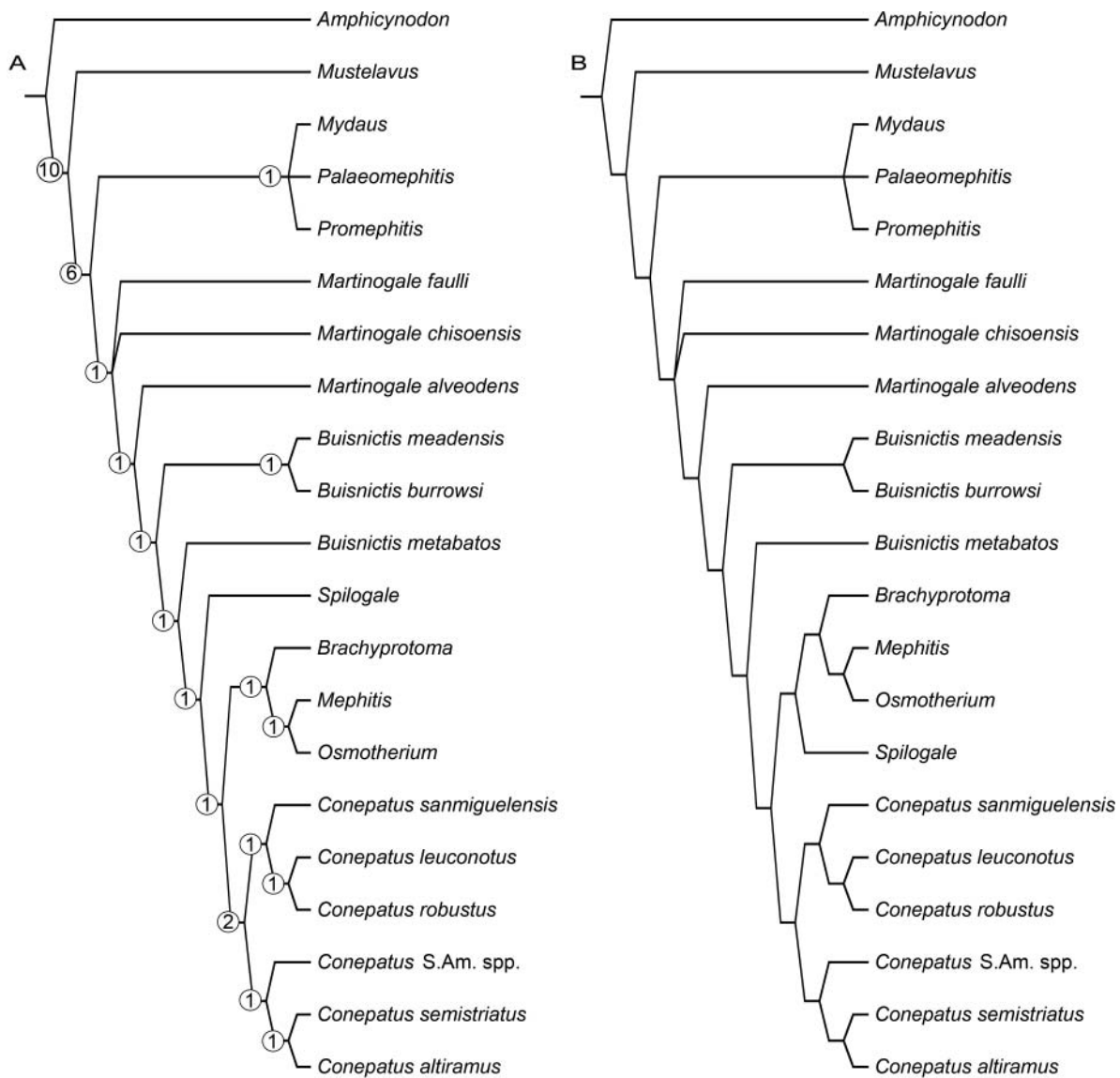


Figure 8. **A**, shortest tree found by 'implicit enumeration' in TNT (Goloboff *et al.* 2008) on a 39 character by 21 taxa matrix (Online Supplementary Material Tables 2 and 3), numbers in circles indicating Bremer supports (from 1667 trees); **B**, manually forced topology found in most molecular-based studies, which is seven steps longer than the shortest morphological tree, indicating considerable homoplasies among morphological characters.

routine in TNT, which yielded a single tree of 72 steps (Consistency Index = 0.667; Retention Index = 0.809) (Fig. 8A).

Our new phylogeny places *Buisnictis metabatos* at a transitional position between previous known species of *Buisnictis* and *Spilogale*. Only one derived character (broadened P4 protocone crest) separates *B. metabatos* from the *B. meadensis*–*burrowsi* clade. On the more derived side, *B. metabatos* is also not far from the living crown clade – only the less anteroposteriorly broadened M1 separates it from the more derived clade. Such a short morphological distance on either side suggests that our fossil records are closing previous gaps.

In contrast to the morphological tree, recent molecular phylogenies of New World mephitines generally place *Spilogale* and *Mephitis* as sister taxa to the exclusion of *Conepatus* (Dragoo *et al.* 1993; Dragoo & Honeycutt 1997; Flynn *et al.* 2005; Fulton & Strobeck 2006; Eizirik *et al.* 2010), although most (except Dragoo *et al.* 1993) have a very limited taxon sampling (a single species for each genus). In a bootstrap analysis, Bryant *et al.* (1993, fig. 6) arrived at a similar local topology in his morphological tree, even though his data matrix contains no shared derived character for a *Spilogale*–*Mephitis* clade to the exclusion of *Conepatus*. Not surprisingly, the molecular arrangement is also largely reflected in a supertree of Carnivora

(Bininda-Emonds *et al.* 1999) because no alternative tree had been proposed up to then.

Our morphological assessments, based on fossil and extant taxa, consistently place *Spilogale* at the base of the living New World skunk clade (Fig. 8A) (Wang *et al.* 2005; Wang & Carranza-Castañeda 2008). Characters in support of such an arrangement include loss of P2 related to the shortening of jaws, squaring and posterior expansion of M1, doming of forehead and reduction of postorbital process of frontal, reduction or loss of condyloid canal, and enlargement of inferior ramus of angular process. Dragoo *et al.* (1993) remarked that external morphologies in the three living genera of North American skunks also seemingly support such an arrangement. If the molecular relationship is correct, this implies parallel developments of the above derived cranial and dental characters. Indeed, if the single shortest tree based on morphological characters is forced by Mesquite to a topology of the relationships based on molecular phylogenies (Fig. 8B), seven extra steps (total tree length = 79) would be required (a rerun of our matrix with the constraints option, by placing the mtDNA hypothesis of (*Conepatus* (*Spilogale*, *Mephitis*)) as monophyletic, resulted in four new trees of 79 steps). In our morphological tree, which often delineates individual taxa by 1–3 characters in the transitional region, seven extra steps represent a considerable number of homoplasies.

Furthermore, a recent molecular estimate of divergence time for living *Conepatus* was placed at 9.2 Ma (Eizirik *et al.* 2010), almost twice as old as the earliest fossil record of the genus (Wang & Carranza-Castañeda 2008). If the molecular estimate is correct, this implies a long cryptic history (ghost lineage) of *Conepatus*, presumably in a low latitude refugium that is yet to be discovered.

Zoogeography

Crustal extension around the Gulf of California began as early as ~12 million years ago (Lizarralde *et al.* 2007; e.g. Stock & Hodges 1989) and sea floor spreading at the Alarcón Rise, near the mouth of the gulf, occurred at 3.7 Ma (Castillo *et al.* 2002). An episode of marine transgression in the San José del Cabo Basin began in the Middle Miocene and probably recorded sea level change and syndepositional extension (McCloy 1984; Martínez-Gutiérrez & Sethi 1997). Regression, shoaling and continental deposition in the Miraflores area began in the Early Pliocene. With a single record of *Buisnictis metabatos* in Baja California Sur, it is impossible to know to what extent this Early Pliocene species was isolated from mainland Mexico by the Gulf of California. However, it is probably fair to assume that the distribution of *B. metabatos* was contiguous with the mainland through connection to the north, as is attested by fossils collected at the localities of La Goleta (Carranza-Castañeda 1991), Arrastracaballos

(Carranza-Castañeda & Miller 1996) and Miraflores. Prior to the formation of the gulf, both Baja California and continental Mexico shared the same or similar faunas (Miller 1980; Carranza-Castañeda *et al.* 2010).

As small predators, skunks are some of the most wide-ranging carnivorans. In North America they range from east to west coasts as well as spanning a large range of latitudes. Nevertheless, tropical and subtropical regions have served as refugia for skunks, and this is the case for both Old World and New World lineages. In his monograph on *Spilogale* taxonomy, Van Gelder (1959) proposed that the present distribution of spotted skunks is the result of post-glacial recolonization of ancestral populations in southern USA and Mexico. Mexico thus served as a refugium for both eastern and western spotted skunks (Van Gelder 1959, fig. 5). Van Gelder (1959) and Mead (1989) also remarked that spotted skunks are more diverse in Central America and Mexico. Van Gelder further speculated that the pygmy spotted skunk, *Spilogale pygmaea*, is probably the most primitive, based on its coat colour patterns, less inflated mastoids, lack of crests on the skull, and narrow interorbital and postorbital regions, and may have given rise to the living eastern and western spotted skunks.

For the hog-nosed skunks, *Conepatus*, we have documented a basal species, *C. sanmiguelensis*, from the Early Pliocene San Miguel de Allende Basin, Guanajuato State, central Mexico (Wang & Carranza-Castañeda 2008). Central Mexico thus appears to have played a crucial role in the origin of the *Conepatus* clade. The hog-nosed skunks have a relatively more southern distribution in North America compared to both *Spilogale* and *Mephitis*. It is perhaps not surprising that of the three living genera of skunks, only *Conepatus* made it to South America during the Great American Biotic Interchange.

There are two living species of *Mephitis*. The hooded skunk, *M. macroura*, has a southern distribution ranging in southern USA, through Mexico, to several Central American countries (Hwang & Larivière 2001). This is in contrast to the striped skunk, *M. mephitis*, whose more northerly distribution is in Canada, through the USA, to northern Mexico (Wade-Smith & Verts 1982). In addition to being smaller in size, the hooded skunks are also less divergent in allozyme variation compared to those of striped skunks, although samples analysed for *M. macroura* (two specimens, both from New Mexico, the northernmost extent of its distribution) are substantially smaller than those for *M. mephitis* (eight specimens) (Dragoo *et al.* 1993, table 1). Being the most cold-tolerant genus by far, *Mephitis* may be the only exception to the rule of southern refugium. In this connection, we note that the earliest *Mephitis* was found in the Pliocene of Kansas (Hibbard 1952).

Our present documentation of yet another transitional skunk basal to the living crown clade further strengthens the impression that southern North America and Central America probably played an important role as a refugium for

skunks. More basal skunks, such as all species of *Martinogale* and two previously known species of *Buisnictis*, are known in the mid-latitude of the USA. It seems reasonable to assume that early species of *Martinogale* must have been adapted to relatively cold climates in Beringia in order for them to immigrate to North America. By the Early Pliocene, however, skunks have become well adapted to subtropical habitats in central Mexico, which has since acted as a refugium for New World skunks.

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Supplementary material

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