

## Earliest hog-nosed skunk, *Conepatus* (Mephitidae, Carnivora), from the early Pliocene of Guanajuato, Mexico and origin of South American skunks

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The hog-nosed skunk, *Conepatus* Gray, 1837, is one of the most widespread carnivorans in the New World, and one of the first to arrive in South America during the Great American Biotic Interchange (GABI). We report a basal hog-nosed skunk, *Conepatus sanmiguelensis* sp. nov., from the early Pliocene San Miguel de Allende Basin, Guanajuato State, central Mexico. The Mexican species greatly extends the first appearance of *Conepatus* from Irvingtonian to early Blancan in North America, more than doubling the time period of previously known appearances. The new species of *Conepatus* is also geographically closer to the Panamanian land bridge than previous records from the United States and northern Mexico, and permits a better sense of the faunal exchange during the early phase of the GABI. The new species is represented by two individuals, including a nearly complete skull and a partial mandible with most of the cheek teeth, as well as a large portion of the skeleton. Such a nearly complete representation of cranial, dental and skeletal materials enables us to conduct a species-level phylogenetic analysis. *C. sanmiguelensis* is characterized by its large size, condyloid foramen confluent with posterior lacerate foramen, presence of a P2, an M1 not very elongated and long trigonid on m1. This combination of primitive and derived characters suggests a phylogenetic position basal to a North American clade [*C. sanmiguelensis* (*C. robustus*, *C. leuconotus*)]. The new phylogenetic reconstruction suggests that Central and South American *Conepatus* form a sister group to the North American clade, and as such, must have equally ancient divergence time that dates back to at least 4–5 Ma. As a result, *C. altiramus* from coastal marine cliffs of Argentina should be seriously reconsidered to be from the Chapadmalal Formation in the early Pliocene, a notion dismissed by some recent authors. If this is correct, South American *Conepatus* represents the first known carnivoran immigrant during the first wave of the GABI. © 2008 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2008, 154, 386–407.

ADDITIONAL KEYWORDS: Carnivora – Mammalia – Mexico – North America – Pliocene – South America – taxonomy.

La zorrillo con nariz de cerdo, *Conepatus* Gray, 1837, es uno de los carnívoros más extensamente distribuidos en el Nuevo Mundo y uno de los primeros en arribar a Sudamérica, durante el Gran Intercambio Biótico Americano (GABI). En este trabajo se reporta la zorrillo con nariz de cerdo *Conepatus sanmiguelensis* sp. nov., del Plioceno temprano de la Cuenca de San Miguel de Allende, Estado de Guanajuato, en la región central de México. La especie mexicana modifica la primera aparición de *Conepatus* del Irvingtoniano, extendiendo su alcance estratigráfico hasta el Blancano temprano de Norte América, duplicando el intervalo de tiempo que anteriormente se conocía para tal aparición. Esta nueva especie de *Conepatus* también está geográficamente más próxima al puente terrestre

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panameño que los registros previos de los Estados Unidos y del norte de México. Así mismo, su presencia permite apreciar mejor el intercambio faunístico durante la etapa temprana del GABI. La nueva especie está representada por dos individuos. Uno de ellos consiste de un cráneo suficientemente completo, el segundo por un fragmento de mandíbula con la dentición casi completa y elementos poscraneales. Tal representación de elementos craneales, dentales y esqueléticos nos permitió realizar un análisis filogenético a nivel de especie. *C. sanmiguelensis* se caracteriza por su gran tamaño; su foramen condiloide al mismo nivel del foramen lacerado posterior; por la presencia de un P2 y un M1 menos alargados y por presentar un trigonoide largo en el m1. Esta combinación de caracteres primitivos y derivados sugiere una posición basal dentro de lo que sería el clado norteamericano [*C. sanmiguelensis* (*C. robustus*, *C. leuconotus*)]. La nueva reconstrucción filogenética sugiere que las especies de *Conepatus* de Centro y Sudamérica forman un grupo hermano del clado norteamericano y como tal, deben tener un tiempo de divergencia que se remonta a hace unos 4–5 Ma. Como resultado, se tiene que *C. altiramus* de los escarpes marinos de Argentina, debería ser reconsiderada seriamente como proveniente de la Formación Chapadmalal del Plioceno temprano, interpretación que tiende a no ser considerada por autores recientes. Si lo anterior es correcto, entonces el *Conepatus* sudamericano representa el primer carnívoro inmigrante conocido durante la primera oleada del GABI.

## INTRODUCTION

The hog-nosed skunk, *Conepatus* Gray, 1837, is one of the most widespread carnivorans in the New World, spanning from the southern United States through much of South America. Possibly as a result of such a wide ranging distribution, it was also one of the earliest to arrive in South America during the early phases of the Great American Biotic Interchange (GABI) when the Isthmus of Panama was first established (Marshall *et al.*, 1982; Flynn *et al.*, 2005b). As such, the fossil history of *Conepatus* on either sides of the Panamanian land bridge is of prime importance in fleshing out a detailed understanding of this mammalian dispersal event.

Despite the success of *Conepatus* in a wide variety of habitats, however, its fossil record is generally rare and most material dates from the middle Pleistocene onward. In North America, it is only found in Irvingtonian or later localities in Florida, Texas, New Mexico and northern Mexico (Schultz & Howard, 1935; Hall, 1960; Ray, Olsen & Gut, 1963; Martin, 1978; Anderson, 1984; Bell *et al.*, 2004). Recent discovery of a nearly complete skull, mandible and skeleton of an undescribed species of *Conepatus* from the early Pliocene of central Mexico thus is of particular significance.

The new species is the earliest and, in many aspects, most primitive form so far known, filling a void in the fossil record of the genus both spatially and temporally. It features a unique combination of primitive and derived morphology that permits insights into the early evolution of the genus. The Mexican form substantially extends the divergence time of *Conepatus* to the early Pliocene. Geographically, it is also much closer to the presumed route of the GABI than previous records. The new species thus affords a rare window of opportunity into the early history of the genus.

## MATERIAL AND METHODS

Comparative materials for living and fossil mephitids 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 leuconotus* (LACM M 53556, 59420, 59423, 59424, 59425, 59626, 59427, 78074; LACM 3946, San Josecito Cave, Mexico); Molina's hog-nosed skunk *C. chinga* (MVZ 114941); striped hog-nosed skunk *C. semistriatus* (LACM M 26686); Patagonian hog-nosed skunk *C. humboldtii* (LACM M 59628); Palawan stink badger *Mydaus marchei* (FMNH 62877); and Javan stink badger *Mydaus javanensis* (FMNH 68731). Other fossil taxa used in the phylogenetic analysis are based on materials listed in Wang, Whistler & Takeuchi (2005a, b).

For character polarity determinations, we chose outgroups that are closest to the initial divergence of the modern skunk clade (common ancestor of *Spilogale* and *Conepatus*), such as *Martinogale* and *Buisnictis*. The holotype of *M. faulli* (LACM 56230) represents the best skull for this purpose (Wang *et al.*, 2005b). For a sense of broader relationships with taxa from Eurasia, we compared the new material with the late Miocene *Promephitis* from China (Wang & Qiu, 2004) and other basal arctoids, such as *Amphicyonodon* and *Amphicticeps* (Wang, McKenna & Dashzeveg, 2005). In PAUP parsimony analysis (Swofford, 1993), all characters are unordered and unweighted.

*Institutional and locality abbreviations:* CPS, Colección Paleontológica Scaglia, Museo Municipal de Ciencias Naturales y Tradicional de Mar del Plata, Argentina; FGS, Florida Geological Survey, Tallahassee, USA; FMNH, Division of Mammals, Field Museum of Natural History, Chicago, USA; GTO, locality from

the State of Guanajuato, Mexico; IGM, Instituto de Geología, Universidad Nacional Autónoma de México, Mexico City, Mexico; JAL TECO, Jalisco-Tecolotlán; LACM, Department of Vertebrate Paleontology, Natural History Museum of Los Angeles County, Los Angeles, USA; LACM CIT, California Institute of Technology Collection, Department of Vertebrate Paleontology, Natural History Museum of Los Angeles County, Los Angeles, USA; LACM M, Department of Mammalogy, Natural History Museum of Los Angeles County, Los Angeles, USA; MPGJ, Museo de Paleontología Geociencias, Juriquilla; MVZ, Museum of Vertebrate Zoology, University of California at Berkeley, Berkeley, USA.

## SYSTEMATIC PALAEOONTOLOGY

ORDER CARNIVORA BOWDICH, 1821

INFRAORDER ARCTOIDEA FLOWER, 1869

FAMILY MEPHITIDAE BONAPARTE, 1845

SUBFAMILY MEPHITINAE BONAPARTE, 1845

CONEPATUS GRAY, 1837

**CONEPATUS SANMIGUELENSIS SP. NOV.**

(FIGS 4–10; TABLE 1)

*Holotype*: IGM 7800, nearly complete cranium with left I1–M1 and right I1–2, I3 alveolus, C, P2 alveolus, and P3–M1; proximal end of left humerus, complete right tibia, one complete and one partial thoracic, complete sacrum, and rib fragments. Collected by Hilda Tronconso and volunteers of the Earth Watch programme in July 2002.

*Type locality and geology*: GTO 75 (MPGJ 272), Coecillos area, Arroyo de Emilio (20°59.97'N 100°45.88'W), San Miguel de Allende Basin, State of Guanajuato, Mexico (Miller & Carranza-Castañeda, 1984; Carranza-Castañeda, 2006). The GTO 75 locality sits on top of a ravine (Fig. 1), and the sediments are thin-bedded, thinly laminated, light grey to light buff coloured mudstones.

*Referred specimens*: IGM 7801, isolated left C and P3–4, right C, P3–M1, partial left dentary with c and p2–m1, partial right dentary with i1–c and p4–m1, 4 partial cervicals, 1 thoracic, 3 caudals, partial right scapular, proximal right humerus and partial left humerus, partial left and right radius–ulna, partial left and right hands with two pathological proximal and middle phalanges, distal right tibia, distal left tibia–fibula, left and right calcanea and astragali, partial left and right feet. From GTO 75 locality, in the same horizon as the holotype (Fig. 2). Collected in 2005.

IGM 7802, right mandible fragment with m1 and m2 alveolus, from locality JAL TECO 9 La Asunción in a deep arroyo located in the Santa Maria village in the southern part of the Tecolotlán basin about 100 km south of Guadalajara City, in Tecolotlán (Jalisco) graben. The associated fauna is of late Hemphillian age and consists of *Dinohippus mexicanus*, *Astrohippus stockii*, *Neohipparion eurystyle*, *Nannippus aztecus*, *Teleoceras fossiger*, *Megatylopus matthewii*, *Hexobelomeryx* sp. and ?*Gomphotherium*.

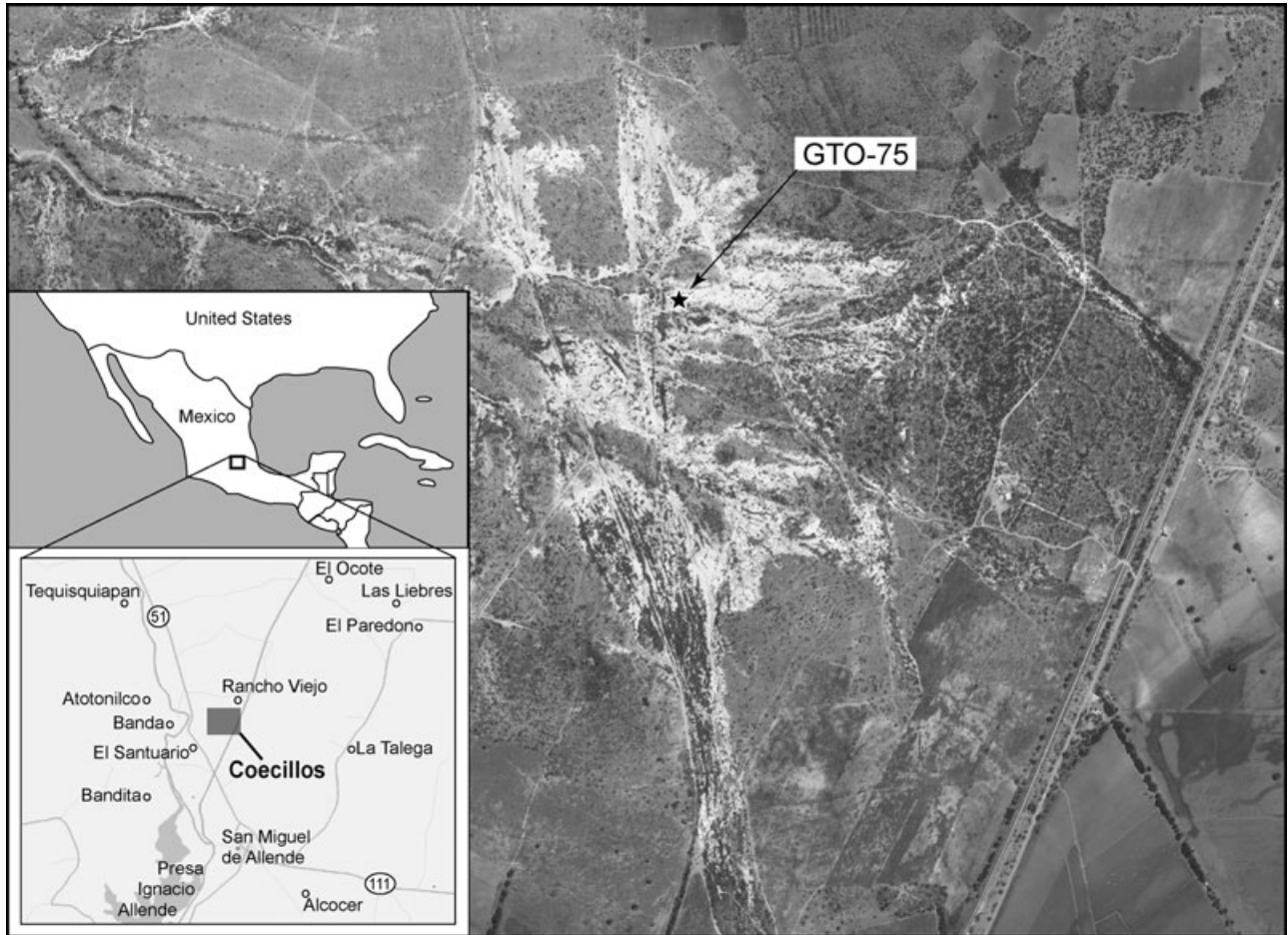
*Fauna, strata, and age*: The Coecillos area (GTO 30) is an extensive area in San Miguel de Allende basin, where abundant Hemphillian fossil material was discovered. It is located in the middle of a small valley surrounded by small hills of andesitic basalt. Continued search in the well-exposed badlands allowed the discoveries of additional localities with Hemphillian, Irvingtonian and, recently in a small hill in the north-east of the area, Blancan faunas. The oldest fossils discovered in this area were *Calippus* (*Grammohippus*) *hondurensis* and *Dinohippus interpolatus* in La Presa locality (GTO 44), and we assign an age of earliest late Hemphillian. Typical Hemphillian fossils have been collected from the GTO 30 locality, including *Astrohippus stockii*, *Dinohippus mexicanus*, *Neohipparion eurystyle*, *Nannippus aztecus*, *Teleoceras fossiger*, *Machairodus* sp., *Notolagus velox*, *Hypolagus* sp. and *Paenemarmota* cf. *P. barbouri*, as well as *Catagonus* cf. *C. brachydontus*, *Megatylopus* cf. *M. matthewi*, *Texoceros* sp. and *Hexobelomeryx fricki* (Fig. 3).

One of the important localities discovered in recent years in the middle of this area is GTO 75 Arroyo de Emilio (type locality of *Conepatus sanmiguelensis*). It is a small ravine where Hemphillian fossils were collected. The lower layer of the stratigraphic sequence is a deposit of about 40–60 cm of grey volcanic ash. Above this, the sediment is composed of laminated sandy clay with abundant irregular concretions of calcium carbonate (Fig. 3). The thickness of this layer is variable from 2 to 5 m. Almost all of the fossil materials known from this site were collected in the top of this layer, including *Dinohippus mexicanus*, *Astrohippus stockii*, *Catagonus brachydontus*, *Paenemarmota* cf. *P. barbouri* and *Hexobelomeryx fricki*, (Carranza-Castañeda, 2006: 53). This layer is covered by light-yellow clay, when exposed to weathering, but has a brownish colour when freshly exposed. The thickness of this layer is about 0.75–1.50 m. It is in this layer where the skunk material was collected, associated with *Paenemarmota* cf. *P. barbouri*, as well as some isolated teeth of *Dinohippus mexicanus* and other materials.

In erosional unconformity, all of the Hemphillian sequence is covered by a very fine clay of grey colour when freshly exposed. The thickness of this layer is

**Table 1.** Cranial and dental measurements (inmm) of *Conepatussanmiguelensis*, *sp nov.*, and other species of the genus. Sources of measurements include Reig (1952), Churcher & Van Zyll de Jong (1965), and Martin (1978), and those for extant species are our own

	<i>C. sanmiguelensis</i>		<i>C. leuconotus</i>		<i>C. robustus</i>		<i>C. semistriatus</i>		<i>C. altiramus</i>		<i>C. talarae</i>		<i>C. chinga</i>		<i>C. humboldtii</i>	
	IGM 7800	IGM 7801	IGM 7802	Mean	Mean	Mean	LACM M 26686	MCN 173	Mean	MVZ 114941	LACM M 59628					
Condylobasal length	82.5			72.74	94.00	77.6				76.5			69.6			
Basilar length	75.7			65.05	78.00	70.9				69.5			63.9			
C1-M1 length (alv.)	26.5			22.80	27.80	23.8				22.9			22.0			
Width across canines	20.7			17.82	24.50	18.3				18.6			17.5			
Width across P4s/M1s	32.0			28.34		29.7				30.0			27.9			
C1 length	4.7	5.1		4.31	7.10	5.0				4.5			4.8			
C1 width	3.9	3.7		3.17		3.8				3.0			3.5			
P2 length	1.7															
P2 width	1.1															
P3 length	4.8	4.9		3.63		4.0				4.4			3.5			
P3 width	3.1	3.6		2.75		2.7				3.2			2.5			
P4 length	7.8	8.3		6.97	9.30	7.6		6.51		7.4			7.1			
P4 width	5.3	5.9		5.01	6.45	5.9		5.24		5.8			5.2			
M1 length	8.3	8.9		8.52	10.65	9.1		6.92		7.9			7.1			
M1 width	8.3	8.8		7.85	10.20	8.5		8.83		8.7			8.2			
c1 length		5.1		4.72		5.9		4.07		4.7			5.3			
c1 width		3.8		3.28		4.1				3.3			3.5			
p2 length		3.3		2.52		3.1				3.0			2.3			
p2 width		2.4		2.07		2.5				2.2			2.1			
p3 length		4.2		3.52		3.8				3.8			3.5			
p3 width		3.3		2.69		2.9				2.7			2.6			
p4 length		5.1		4.17		4.7		4.10		4.6			4.3			
p4 width		3.8		3.32		3.5		3.53		3.9			3.2			
m1 length		11.5	9.4	10.05	12.30	10.4		8.4		10.1			9.0			
m1 width		6.0	4.5	5.43	7.00	5.4		4.7		6.1			4.9			
m1 trigonid length		6.4	4.2	5.14	6.15	5.3		3.8		4.6			4.2			



**Figure 1.** Map and satellite image of the locality GTO 75, north of San Miguel de Allende Basin, Guanajuato State, Mexico.



**Figure 2.** Photograph of locality GTO 75 in the Coecillos area, San Miguel de Allende Basin, Guanajuato State, Mexico. Arrow indicates sites where IGM 7800 (middle) and IGM 7801 (far right) were collected. White vertical bar indicates the layer where associated fauna was found. Black horizontal lines (middle and far right) mark the lower boundary of Pleistocene deposits that cap the Tertiary exposures. Photo by X. Wang, 2 June 2006.

variable, 1–2 m. In this layer a *Glyptotherium* shield with an associated jaw was collected, a site named GTO 78 Arroyo de Emilio-Gliptodon. In the same layer at different sites, a jaw, one fragment of a skull and several isolated teeth of *Equus* were collected, in addition to *Thomomys* and *Hypolagus* sp. This fauna is assigned to the Irvingtonian based on the horse material and the presence of *Thomomys* sp.

The stratigraphy of the JAL TECO 9 Santa Maria area consists of layers of oxidized clay with reddish colour, sandy clay and several palaeochannels with sandy gravels. The *Conepatus* specimen (IGM 7802) was collected in a clay layer towards the top of this sequence. All of the fossiliferous sediments are covered by lacustrine sandy layers that crop out in almost all the Santa Maria area. Above the lacustrine sediments is an important clay-bed sequence that contains volcanic ash dated at  $4.89 \pm 0.16$  Ma by the  $^{40}\text{Ar}/^{39}\text{Ar}$  method (Kowallis *et al.*, 1998).

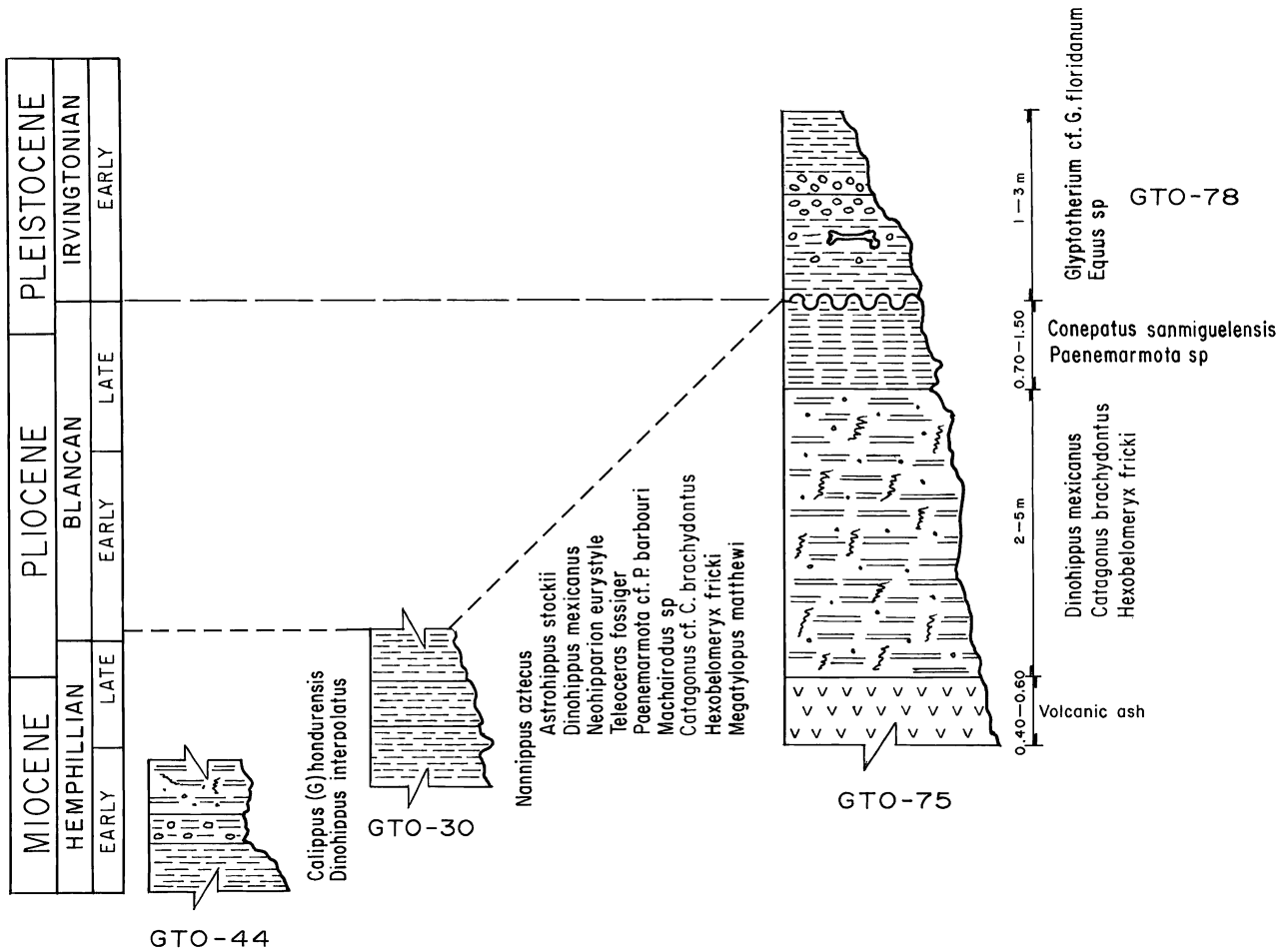


Figure 3. Stratigraphic columns and faunal compositions of GTO 75 and related localities.

Fossils associated with the skunk jaw fragment (IGM 7802) in the JAL TECO 9 locality are isolated teeth and plates of *Crocodylus* sp., *Megalonyx* sp., abundant horse material belonging to *Dinohippus mexicanus*, *Neohipparion eurystyle* and *Nannippus aztecus*, a few isolated upper teeth of *Astrohippus stockii*, *Teleoceras fossiger*, *Machairodus* cf. *M. coloradensis*, *Canis ferox*, *Rhynchotherium* sp., *Megatylopus matthewi* and *Hexobelomeryx fricki*.

*Etymology*: Referring to the San Miguel de Allende Basin, from where the holotype was collected.

*Diagnosis*: Among genera of mephitids, *Conepatus sanmiguelensis* possesses the following derived characters to indicate membership within the *Conepatus* clade: retracted external nasal opening (presence of a 'hog-nose'), loss of condyloid canal, elongation of M1, high-crowned P4 and m1 talonid equal or longer than trigonid. *C. sanmiguelensis* is distinguished from South American species (*C. talarae*, *C. chinga*

and *C. humboldtii*) in its large size, condyloid foramen merged within the posterior lacerate foramen, presence of a P2, more quadrate M1 (antero-posterior length = transverse width) and more elongated M1 relatively to P4. In contrast to North American species (*C. leuconotus* and *C. robustus*), *C. sanmiguelensis* is distinct in the following primitive characters: frontal sinuses less inflated, paroccipital process horizontally orientated, P2 present, P4 shearing blade less high-crowned and more dorsally curved, M1 protocone low-crowned and M1 lingual cingulum lacking a ridge connecting to postprotocrista. *C. sanmiguelensis* is distinguishable from the Central American *C. semistriatus* plus the extinct South American *C. altiramus* in the lack of an entoconulid on m1 and in the presence of a P2.

DESCRIPTION

The following description of *Conepatus sanmiguelensis* is based mainly on material from San Miguel de

Allande Basin. A single jaw fragment from the Tecolotlán basin is too poorly preserved to offer significant morphological insight. Both specimens from San Miguel, IGM 7800 and 7801, are generally well preserved, but have suffered from various degrees of fracturing. The two specimens complement each other in preserved elements such that a nearly complete composite skeleton is preserved. The palate and pterygoid regions on IGM 7800 were separated from the dorsal half of the skull and were later restored in the laboratory.

#### Skull (Fig. 4)

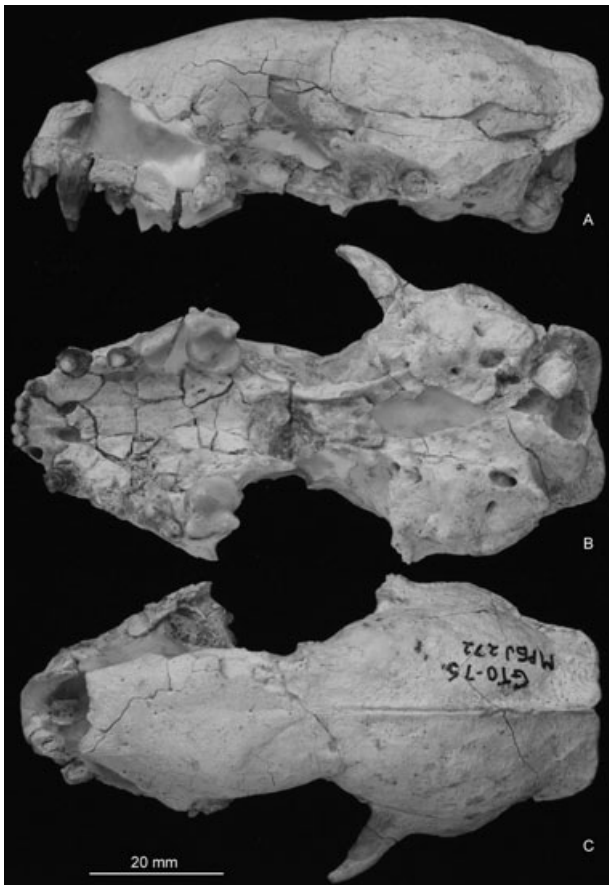
The nasal is completely fused with the frontal and maxillary and no suture is visible. The anterior tips of the nasals display a nearly transverse edge with a slight curve bending posteriorly. Such a gentle curve is similar to those in living species of *Conepatus* and thus suggests that the anterior edge of the nasals is essentially intact. On the internal surface of the nasal, the root of the nasal turbinate can be seen to taper toward

the anterior edge of the nasal, as can be seen in skulls of living hog-nosed skunks, further evidence of an intact nasal in IGM 7800. However, a small, anterior protrusion along the medial contact of the left and right nasals, commonly seen in extant *Conepatus*, is broken off. Other than this damage, we judge the nasal to be essentially intact and show the true extent of its anterior edge. If this is the case, then the nasal displays the retraction of the external naris in hog-nosed skunks. In lateral view, the anterior edge is at the same level as the posterior edge of the upper canines, a stage of retraction more advanced than in *C. humboldtii* but similar to that in *C. leuconotus*.

The frontal area is gently domed, but not as inflated as in extant species of *Conepatus*. In dorsal view, a postorbital process of the frontal is barely visible, common for most species of *Conepatus*, although the temporal crest leading from the postorbital process is elevated enough to indicate the position of the postorbital process. The distance between the postorbital process and postorbital constriction is fairly long (12 mm) among known species of *Conepatus*. A discrete central (single) sagittal crest is low (shallow) and becomes slightly deeper near the posterior end. A nuchal crest is well developed, which projects posteriorly beyond the posterior margin of the occipital condyles. The zygomatic arch is only partially preserved on the left side, and it exhibits the typically slender, rod-like structure in all extant mephitids.

In ventral view, the palate is extensively fractured, although its overall dimension is more or less intact. The premaxillary–maxillary suture is fully fused, and it is not possible to ascertain the position of this suture, a character useful for species identification in *Conepatus*. The posterior border of the palatine is nearly at the same level as the posterior edge of the M1, a primitive condition as in *C. humboldtii* in contrast to a more posteriorly positioned border in more advanced species of *Conepatus*, such as *C. leuconotus*.

In the basicranium area, the bulla is strongly fused to the surrounding regions. A long tube for the external auditory meatus is also heavily fused to the postglenoid process. The area surrounding the mastoid process is inflated, as is typical of all mephitids. The paroccipital process is short and directed posteriorly. A concave fossa is present on the broad tip of the paroccipital process. This fossa is the largest in IGM 7800 among all species of *Conepatus* that we have examined, and the paroccipital process is largely horizontally orientated (with the above fossa facing essentially ventrally) in contrast to a more vertically orientated process in all other species. The condyloid foramen opens on the posterior rim of the posterior lacerate foramen, i.e. the former merges with the latter to open into the same pit as the posterior lacerate



**Figure 4.** *Conepatus sanmiguelensis* sp. nov., IGM 7800, holotype: A, lateral, B, ventral and C, dorsal views of the skull.

foramen, a condition seen in *C. leuconotus* but not in southern species such as *C. humboldtii* and *C. chinga*. The condyloid canal is absent from the internal surface of the occipital condyle.

#### Mandible (Figs 5, 8)

The mandible has strong and thick (mediolaterally) horizontal rami, as is typical of *Conepatus*. A mental foramen is visible at the level of the anterior root of the p4. A blunt and deep angular process has an enlarged fossa for the inferior ramus of the medial pterygoid muscle at the expense of the fossa for

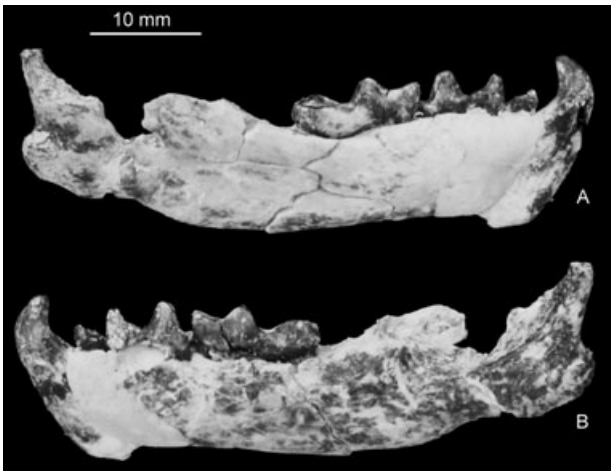
the superior ramus of the same muscle, a character shared by *Mephitis* and *Conepatus*.

#### Teeth (Figs 6–8)

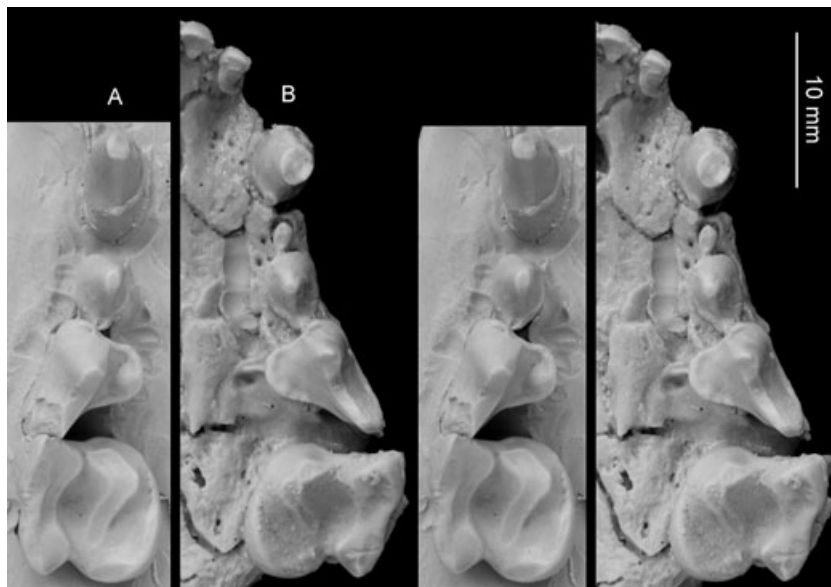
Dentally, *Conepatus sanmiguelensis* possesses a combination of primitive and derived characters for a transitional species. Apart from the right I3 and right P2, all other upper teeth are preserved. The incisors sustained little wear and the enamels on the occlusal surface are still intact. I1–2 show no sign of cuspules on either sides of the main cusp, and I3 has a basal, longitudinally orientated ridge on the lingual side. The canines are strong and straight. The enamel surface has no ornamentation but there is a weak cingulum on the lingual side.

A residual P2 in IGM 7800 is present on the left side and that on the right side is lost. This tiny P2 is so small, measuring  $1.7 \times 1.1 \times 0.9$  mm (length vs. width vs. crown height), that it probably does not occlude with the lower premolars. However, the P2 is not crowded to the lingual side of the P3, as is the case in a similar stage of P2 reduction in *Promephitis* (Wang & Qiu, 2004), i.e. it maintains a space for itself between the C1 and P3, in contrast to a closed space in extant species of *Conepatus* that have lost the P2.

P3 is well preserved in both specimens. It has a single, high-crowned main cusp and lacks a posterior accessory cusp. A very weak anterior ridge leads down toward the tip of the main cusp, whereas a more distinct posterior ridge trails behind the main cusp. A lingual cingulum is well developed, especially along the posterior half of the tooth.



**Figure 5.** *Conepatus sanmiguelensis* sp. nov., IGM 7801, referred specimen: A, medial and B, lateral views.

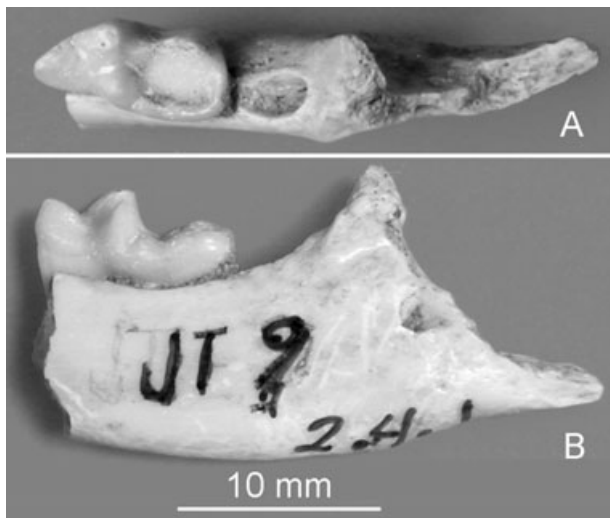


**Figure 6.** *Conepatus sanmiguelensis* sp. nov., Stereophotos of polyester casts of upper teeth. Occlusal views of A, IGM 7801, referred specimen, and B, IGM 7800, holotype.





**Figure 7.** *Conepatus sanmiguelensis* sp. nov., IGM 7801, referred specimen. Stereophotos of polyester casts of lower teeth. Occlusal views of A, right jaw, and B, left jaw. The p2–3 were collected as isolated teeth, and their position and imbrications on the left jaw are reconstructions based on the orientation of the p4, which is preserved *in situ*. This type of imbrication (clockwise rotation) is less common among *Conepatus*, and the more common type is an anticlockwise rotation on the left jaws.



**Figure 8.** *Conepatus sanmiguelensis* sp. nov., IGM 7802, referred specimen from JAL TECO 9: A, occlusal, and B, lingual views.

Both P4s are preserved in IGM 7800 and 7801. The shearing blade of P4, particularly the posterior half, is higher-crowned than in *Mephitis*, about the same crown height as in *Conepatus humboldtii*, but not as high as in *C. leuconotus*. In *C. leuconotus* it has lost the sharp bend in lateral view around the area where the

carnassial notch should be (all mephitids have lost the notch). The protocone is crest-like on IGM 7800 but shows signs of initial development of a low cusp on IGM 7801, and is posterior to the anterior edge of the paracone. The protocone crest is also relatively low-crowned compared with that in *C. leuconotus*.

Both M1s on IGM 7800 and the right M1 on IGM 7801 are well preserved and suffered little wear. The outline of the M1 is quadrate with its length/width ratio is approximately 1. The lingual cingulum is expanded posteriorly, but not as much as in *Conepatus leuconotus*. The protocone is also not as crowded toward the paracone as in the latter. The protocone is relatively low crowned compared with that in *C. leuconotus*. There is no ridge connecting the posterior end of the postprotocrista and lingual cingulum, a structure present in *C. leuconotus*.

The i1–i3 are preserved on IGM 7801. The roots of the lower incisors are imbricated with that of the i2 shifted lingually relative to those of the i1 and i3. The crown size increases from i1 to i3, and the tips of the crowns are too worn to discern cusp morphology. The lower canine is strongly curved, more so than seen in other species of *Conepatus*. There is a very weak lingual and posterior cingulum.

Only the left p2–3 are preserved and both have double roots. Both of these premolars are less reduced, relative to p4, than in living *C. leuconotus*.

The p2 main cusp is very low and the posterior end of the tooth is broad. The p3 main cusp is also low, and there is a ridge along its posterolingual side. A prominent posterior cingulum is present in p3. Both p4–m1s are well preserved in IGM 7801. The p4 is high crowned and is higher than the tip of m1 paraconid. The main cusp is weakly ridged on the anterior surface and a slightly more distinct posterior ridge, as well as a lingual ridge, is present. The lingual ridge extends down toward the posterior root and forms a bulge at the base of the crown. There is a small, but distinct, anterior cingular cusp and a larger posterior cingular cusp. A weak anterior cingulum and more distinct posterior cingulum are present.

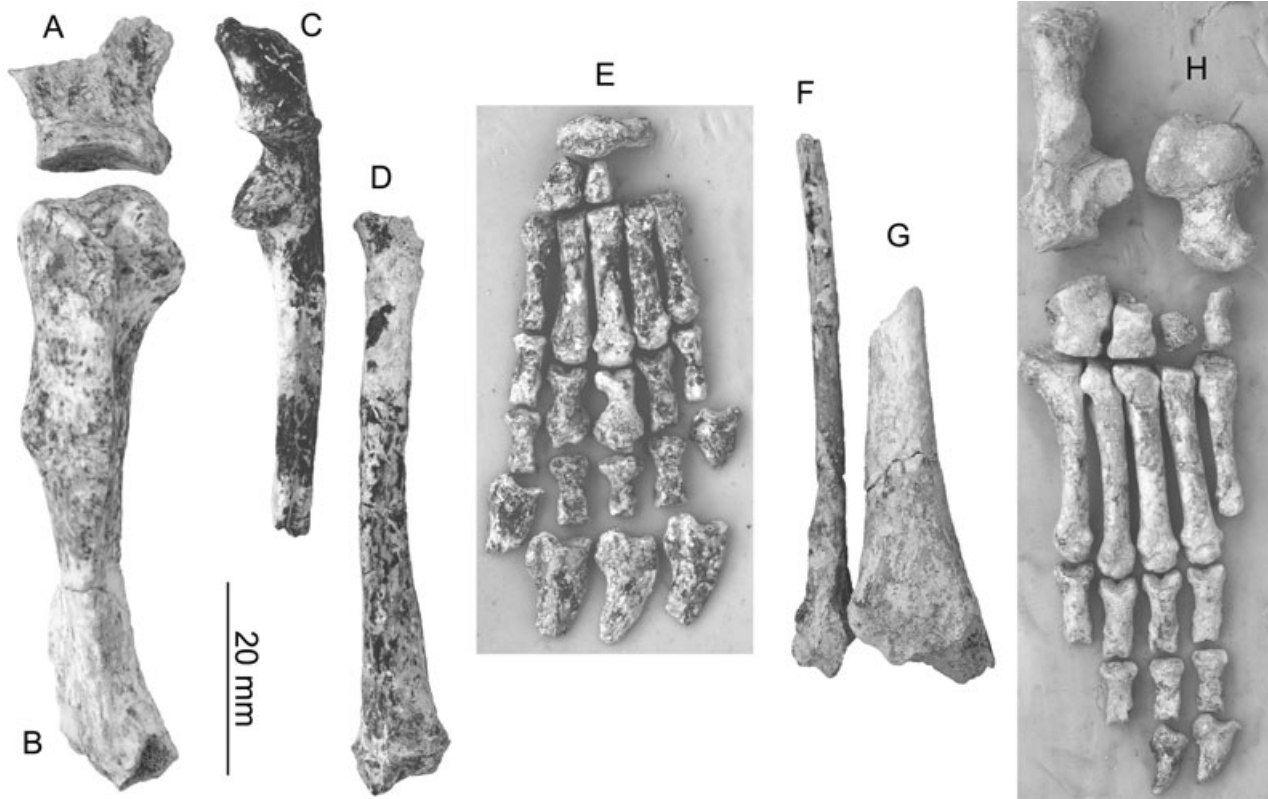
The m1s are moderately worn, although most cusp shapes are still readily distinguishable. The lengths of trigonid and talonid are approximately equal (Figs 7, 8; Table 1). The shearing blade (labial edge of the paraconid–metaconid) of the trigonid is the longest and most longitudinally orientated among all known species of *Conepatus*. Such a long trigonid also gives it a more open appearance, i.e. the paraconid is more anteriorly positioned. A weak ridge is present on the

posterior face of the trigonid, as is typical for all New World skunks (Wang *et al.*, 2005b). The talonid is slightly wider than the trigonid. The hypoconid occupies about two-thirds of the talonid and the entoconid takes up the lingual one-third of the talonid. The hypoconid is also significantly higher than the entoconid, and the two cusps enclose a longitudinally orientated talonid basin, which is enclosed posteriorly by a rim formed by the merging of these two cusps. A shallow notch is present at the anterior end of the entoconid, where no sign of an entoconulid is present. The m2s are lost in both jaws. That on the left side left a single-rooted alveolus (4.8 mm in anteroposterior dimension).

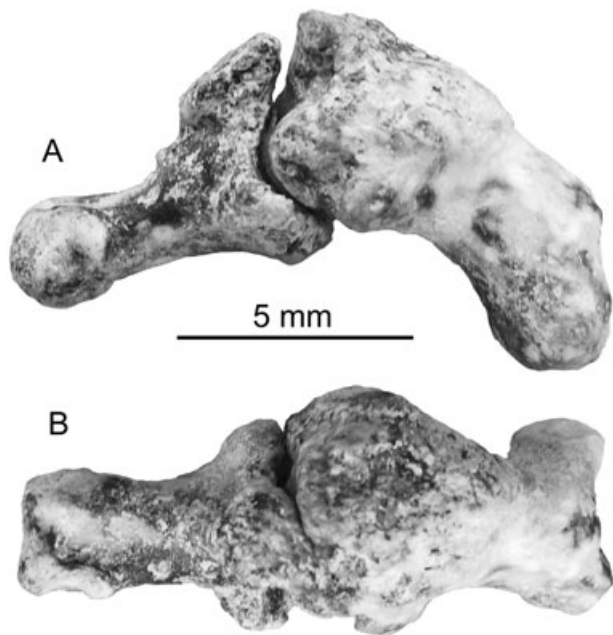
#### *Skeleton* (Figs 9, 10)

For anatomical terminologies, we use those in Evans & Christensen (1979). We have access to one skeleton for each extant genera of North American skunk (*Spilogale*, *Mephitis*, *Conepatus*), and the following descriptions thus concentrate on generic comparisons.

Four partial cervicals are preserved. Three are mostly centrum, and only one is essentially complete.



**Figure 9.** *Conepatus sanmiguelensis* sp. nov., IGM 7801, referred specimen: A, lateral view of right proximal scapula; B, anterior view of proximal humerus; C, anterior view of left ulna; D, anterior view of left radius; E, dorsal view of right hand (terminal phalanges shown in lateral view); F, anterior view of left distal fibula; G, anterior view of left distal tibia; and H, dorsal view of left foot (terminal phalanges shown in medial view).



**Figure 10.** *Conepatus sanmiguelensis* sp. nov., IGM 7801, referred specimen. Pathological proximal and medial phalanges. A, medial, and B, dorsal views.

The centra in all four cervicals are relatively long compared with that of *Conepatus chinga* (MVZ 114941), suggesting a long neck for *C. sanmiguelensis*. A single thoracic from IGM 7801 is probably near the region of T3–5, with the dorsal (spinous) process mostly missing. It has well-developed, rugose transverse process. Another thoracic is associated with IGM 7800 and judging by its lack (or very weak) caudal costal fovea and its elongated, posteriorly projecting transverse process, it is probably near the posterior region (last or penultimate) of the thoracic series. It has a strong and erect dorsal process. Two sacral vertebrae from IGM 7800 are well fused, as in living hog-nosed skunks. The suture surface with the pelvic is very rugose. Two caudals are preserved in IGM 7801. Their long centra suggest a long tail.

Only the articulation fossa is preserved for the right scapula in IGM 7801. It has a much stronger coracoid process than in *C. chinga*. A proximal humerus in IGM 7801 has a relatively large greater tubercle, a character shared with *Mephitis* but is in contrast to a smaller tubercle in *Spilogale*. The head is also more convex in anterior view than a more rounded profile in *Spilogale*. The tuberosity for teres major is more prominent than in *C. chinga*. Between the left and right partial radio-ulna on IGM 7801, the entire anatomy of these two bones can be observed. As in living hog-nosed skunks, the ulna shaft is bowed and the olecranon slanted toward the medial side, characters of a non-cursorial limb. The styloid process

of the radius has a posterior ridge that is absent in living *C. chinga*. Nearly the entire left and right hands are preserved in IGM 7801. Metacarpal V is reduced and much thinner than the remaining metacarpals. Two proximal (probably III and IV; these were not preserved in original articulation) and one medial phalange show clear signs of pathological conditions. The distal ends of the proximal phalanges are enlarged, probably due to injuries, and movements are severely restricted due to extra growth (Fig. 10). Front limb terminal phalanges are much longer and deeper than those in the hindlimbs among living skunks, presumably a fossorial adaptation. This is also true for *C. sanmiguelensis*.

Only a left head (IGM 7800) and two distal condyle fragments (IGM 7801) are preserved for the femur. A complete right tibia in IGM 7800 and partial left and right tibiae in IGM 7801 are available. Beside being larger in size (maximum length 88.8 mm), the tibia is very similar in overall morphology to that in *C. chinga* (length 73.3 mm). Both calcanea and astragali are present in IGM 7801. The astragalar trochlear has a similarly shallow groove as in *C. chinga*, and the shortness of the trochlear and presence of an astragalar foramen suggests little rotation with regard to tibia articulation. A plantar tendinal groove (Wang, 1993: fig. 5) is distinct and is in contrast to its absence in *C. chinga*. The posterior articular surface of the calcaneum and its corresponding posterior calcaneal process of the astragalus are relatively flat as compared with a more curved articulation surface in *C. chinga*. Both feet in IGM 7801 are preserved. As in the hands, metatarsal V shows a similar degree of reduction compared with the other digits. The terminal phalanges are significantly shorter and shallower than those in the hands.

#### COMPARISON

*Conepatus* is morphologically distinctive and generally not easily confused with other genera of skunks. By its large size and advanced cranial and dental morphology, *Conepatus* is far removed from basal North American skunks such as *Martinogale*, *Buisnictis* and *Spilogale* (see Phylogeny for a list of derived characters in *Conepatus* that distinguish the latter from the basal forms). The Pleistocene *Brachyprotoma* has a short rostrum as in *Conepatus*, but the former is like *Spilogale* in size and has a swollen, conical P4 protocone, a character that suggests a relationship with *Mephitis* (Wang *et al.*, 2005b). Another North American Pleistocene genus, *Osmotherium*, is poorly known and generally shows a stage of evolution equivalent to *Mephitis*. The Guanajuato species shares with *Conepatus* the following derived characters: retracted external nasal opening, high-crowned P4 and m1 talonid

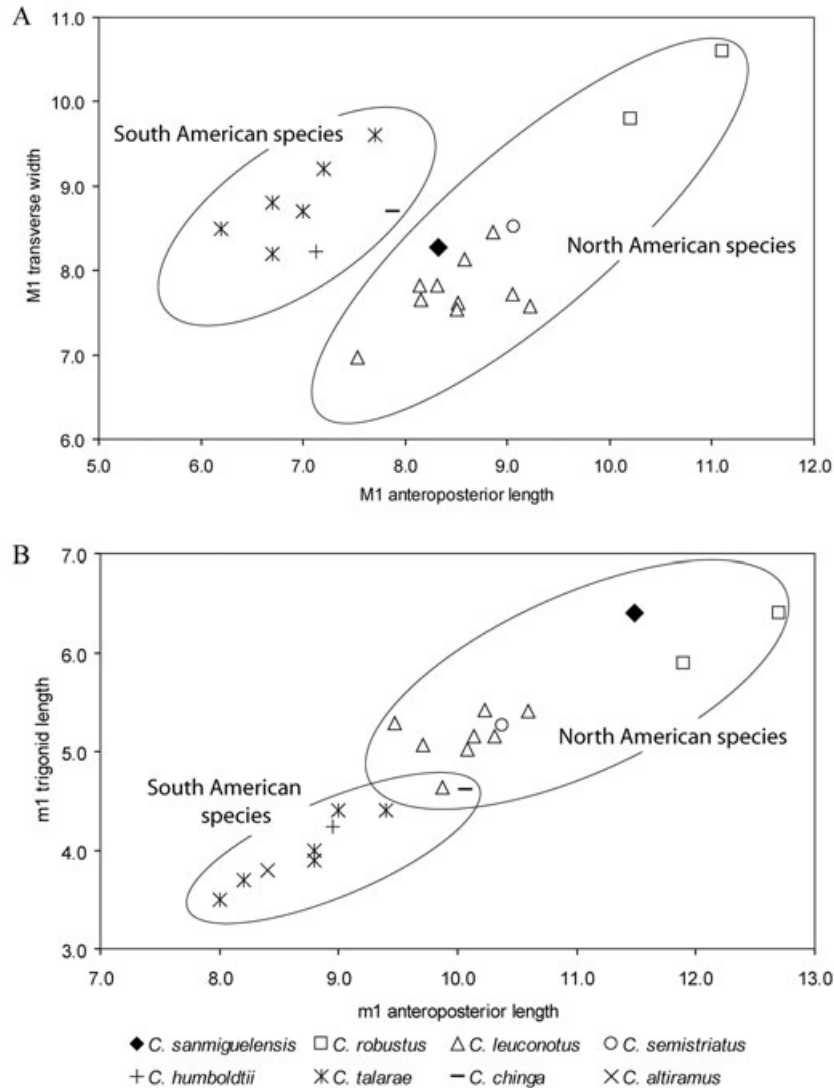
equal to or longer than trigonid. Its membership within *Conepatus* is thus secure.

Within *Conepatus*, *C. sanmiguelensis* is distinct from all known species, fossil or extant, by its primitive possession of a small P2. The single skull from Guanajuato does not permit an assessment of variations in the reduction or loss of the P2. However, a similar stage of P2 reduction is seen in the Eurasian *Promephitis*. In a large series of *Promephitis* skulls from Hezheng, Gansu Province, China, a tiny P2 is consistently present when this area of the skull is preserved (Wang & Qiu, 2004). Therefore, it seems likely that the small P2 on IGM 7800 is a consistent character and represents a transitional stage of tooth reduction. In addition, its quadrate M1 is also a transitional feature for species of *Conepatus* (Fig. 11). With the exception of

the Rancholabrean *C. robustus* (see discussion below), *C. sanmiguelensis* is the largest among all fossil and living species of *Conepatus*. The m1 shearing blade (trigonid) in *C. sanmiguelensis* is also the longest among all known species of the genus.

The m1 in IGM 7802 is 22% smaller than those in IGM 7891 (Table 1). Its trigonid is also slightly shorter than in the latter. Given the limited materials at hand, we cannot determine if these differences are due to morphological or chronological variations. We tentatively place IGM 7802 in *Conepatus sanmiguelensis* pending better material from the Tecolotlán graben.

The above combination of characters (most of them primitive conditions for *Conepatus*) allows clear contrast between *C. sanmiguelensis* and other known species. That *C. sanmiguelensis* represents the earli-



**Figure 11.** Plots of fossil and extant species showing relationship of A, M1 lengths vs. widths; and B, m1 length vs. m1 trigonid length. See text for explanations.

est representative of *Conepatus* distinct enough from other species seems to be readily born out by the above comparisons. In the phylogeny section below, we further demonstrate that *C. sanmiguelensis* is also a basal species in a North American *Conepatus* clade.

#### PHYLOGENY

The phylogenetic position of the skunks is traditionally regarded as a clade within the Family Mustelidae based on such commonly recognized characters as anal glands, reduced dental formula and loss of a carnassial notch on the P4 (e.g. Muizon, 1982; Bryant, Russell & Fitch, 1993; Wyss & Flynn, 1993; Baskin, 1998; Wolsan, 1999). This position has been increasingly challenged by recent molecular studies that place the skunks outside the clade formed by the living members of Procyonidae and Mustelidae and thus advocate a distinct family (Mephitidae) (Wayne, Benveniste & Janczewski, 1989; Vrana *et al.*, 1994; Ledje & Arnason, 1996a, b; Dragoo & Honeycutt, 1997; Flynn *et al.*, 2000, 2005a; Marmi, López-Giráldez & Domingo-Roura, 2004; Sato *et al.*, 2004, 2006); Delisle & Strobeck, 2005; Fulton & Strobeck, 2006). The above controversies aside, however, both traditional (morphological and palaeontological) and molecular approaches agree that skunks originated from Eurasia sometime in the early Miocene (possibly earlier if their deep split from other arctoids is true) and immigrated to North America during the late Miocene.

The earliest and most primitive skunk in North America is *Martinogale* Hall, 1930 in the late Clarendonian (see Wang *et al.*, 2005b for a recent summary). Through a transitional genus, *Buisnictis* Hibbard, 1950, the living North American skunk clade began to emerge, which includes *Spilogale* Gray, 1865, *Mephitis* Geoffroy Saint-Hilaire & Cuvier, 1795, and *Conepatus* Gray, 1837; as well as two fossil genera in the Pleistocene, *Brachyprotoma* Brown, 1908 and *Osmotherium* Cope, 1896, that are nested within the extant clade (Wang *et al.*, 2005b).

By comparison with such outgroups as *Martinogale* and *Buisnictis*, *Conepatus* is morphologically the most derived, both cranially and dentally, and tends to be the largest in size among extant genera of North American skunks (Wang *et al.*, 2005b). Various DNA sequence studies, however, are either consistent with such an assessment (Dragoo, Honeycutt & Schmidly, 2003) or suggest a more basal position for *Conepatus* among extant mephitids (Dragoo & Honeycutt, 1997; Flynn *et al.*, 2005a). If the latter is true, then some of the derived dental characters must have been acquired independently.

The well-preserved material of *Conepatus sanmiguelensis* offers a unique opportunity to evaluate character polarities among species of the genus. We scored a

data matrix using a combination of a previous framework for early North American mephitids (Wang *et al.*, 2005b) and a species-level analysis of *Conepatus* by examining extant osteological collections and previously described fossil taxa. Our matrix, 19 taxa by 38 characters, includes all living species plus fossil species that are well preserved and described in sufficient detail (Table 2 and Appendix 1). We treat all South American species (*C. chinga*, *C. humboldtii*, *C. primaevus*, and *C. talarae*) as a group of small-sized skunks with a mediolaterally widened M1 and shortened m1 trigonid (we do not have a sufficiently large series of living South American samples to evaluate variations; nor do we have access to the two fossil species). However, we individually coded the Argentinean *C. altiramus* because of its shared character (presence of an entoconulid on m1) with *C. semistriatus* and its possible special status as the first South American immigrant (see Zoogeography below). Parsimony analysis results in six shortest trees, a strict consensus of which is shown in Figure 12. Species relationship within *Conepatus* is fully resolved (except the South American clade).

#### DISCUSSION

Based on our phylogeny above, the living hog-nosed skunks can be divided into three groups: a North American group (*Conepatus sanmiguelensis*, *C. robustus*, *C. leuconotus*), a Central American and northern South American transitional group (*C. semistriatus*, plus the extinct Argentinean *C. altiramus*), and a South American group (*C. chinga*, *C. humboldtii*, *C. primaevus*, *C. talarae* and possibly other fossil species).

In North America, two extant species, the eastern hog-nosed skunk *Conepatus leuconotus* (Lichtenstein, 1832) and the common hog-nosed skunk *Conepatus mesoleucus* (Lichtenstein, 1832), are traditionally recognized, the former being somewhat larger in size. However, an analysis of morphology and mitochondrial DNA by Dragoo *et al.* (2003) suggests that they are conspecific, and that only *C. leuconotus* should be recognized, a conclusion followed herein. Fossils typical of *C. leuconotus* begin to appear in Irvingtonian–Rancholabrean sites, such as the Irvingtonian Williston IIIA and Haile VIIA localities in Alachua and Levy counties, Florida (Ray *et al.*, 1963), Rancholabrean San Josecito Cave (LACM locality no. 192), Nuevo Leon Province, Mexico (Hall, 1960), and Rancholabrean Burnet Cave, Eddy County, New Mexico (Schultz & Howard, 1935). The Florida materials (jaw fragments and teeth) tend to fall within the higher end of most measurements of extant *C. leuconotus*, whereas the Mexican materials [a nearly complete skull with all cheek teeth, LACM CIT 3946, was cited by Hall (1960), although numerous other

**Table 2.** A 19 taxa by 38 characters data matrix used in the PAUP analysis. Character numbers correspond to those listed in Appendix 1. Characters 1–34 are adopted from Wang *et al.* (2005b) and characters 35–38 are coded to specifically resolve relationships within *Conepatus*

Taxa	Character																																										
	1										2										3																						
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38					
<i>Amphicynodon</i>	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	0	0	0	0	0	0	0	0			
<i>Mustelavus</i>	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	0	0	0	0	0	0	0	0	0			
<i>Mydaus</i>	1	1	1	1	1	1	1	1	0	0	1	0	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0		
<i>Palaeomephitis</i>	?	?	1	1	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?			
<i>Promephitis</i>	1	1	1	1	1	1	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	0	0	0			
<i>Martinogale faulli</i>	1	1	1	1	1	1	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	0	0	0			
<i>Martinogale chisoensis</i>	1	1	1	1	1	1	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	0	0	0			
<i>Martinogale alveodens</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?			
<i>Buisnictis</i>	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?			
<i>Brachyrotoma</i>	1	1	1	1	1	1	1	1	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?		
<i>Spilogale</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
<i>Mephitis</i>	1	1	1	1	1	1	1	1	0	0	1	2	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
<i>Osmotherium</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?		
<i>C. sanmiguelensis</i>	1	1	1	1	1	1	1	1	0	0	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
<i>C. leuconotus</i>	1	1	1	1	1	1	1	1	0	0	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>C. robustus</i>	1	1	1	1	1	1	1	1	0	0	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>C. semistriatus</i>	1	1	1	1	1	1	1	1	0	0	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>C. altiramus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
S. Am. <i>Conepatus</i> species	1	1	1	1	1	1	1	1	0	0	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	

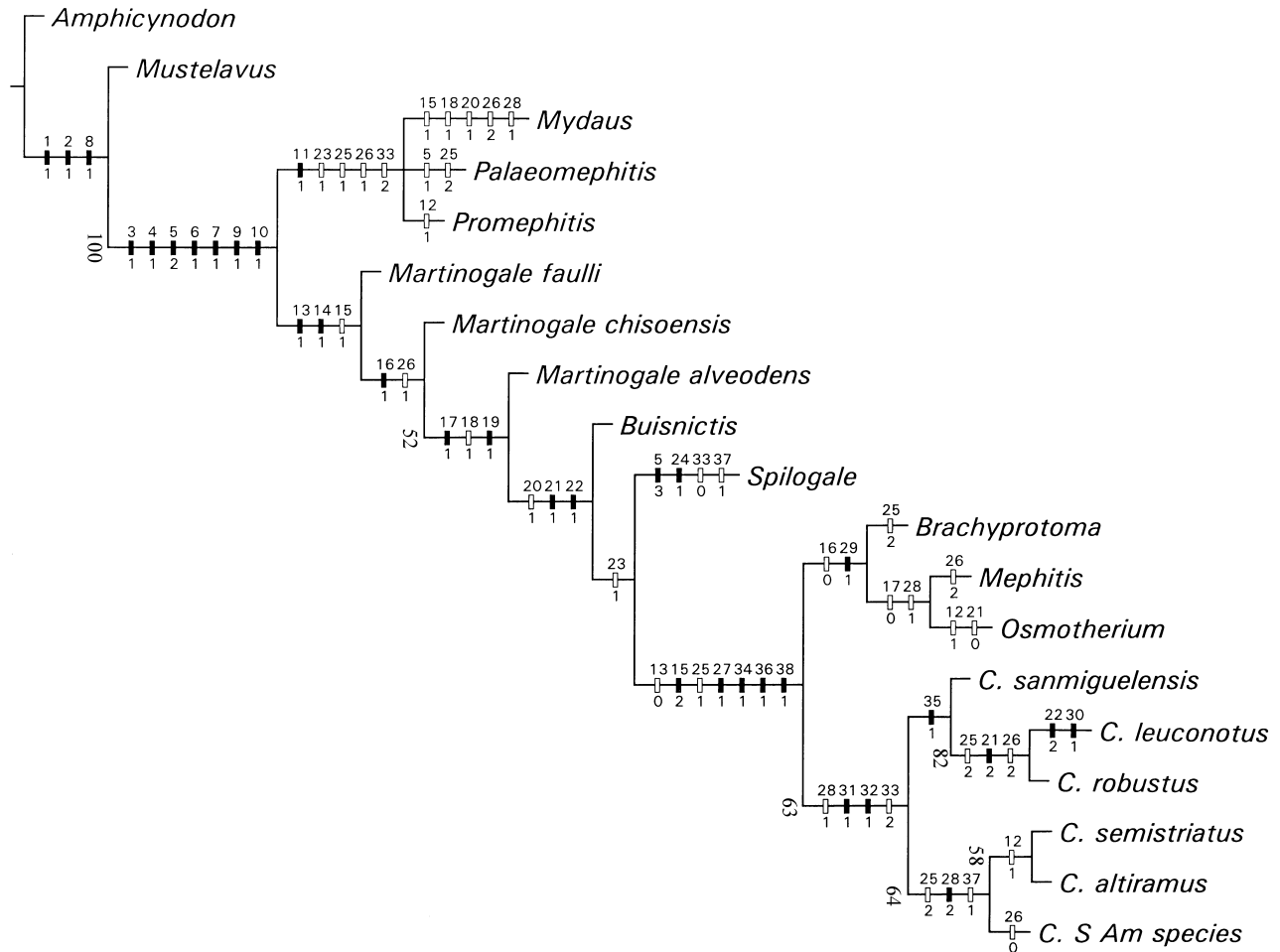
specimens are also available] readily fall within the range of living species. Although an isolated P4 (FGS V-5855A) has almost identical dimensions (7.8 by 5.9 mm in length and width) as those of *C. sanmiguelensis*, an isolated M1 (FGS V-5855B) is of a much larger size (9.8 by 8.9 mm for length and width) than that of IGM 7800. This enlargement of the M1 relative to P4 and a more elongated M1 signal the more derived status of the Florida materials (close to *C. leuconotus*) than *C. sanmiguelensis*.

Martin (1978) erected a late Pleistocene (Rancholabrean) species, *Conepatus robustus*, from the Haile XIVB locality in Alachua County, Florida. In most measurements, *C. robustus* represents the largest species of the genus. Its P4 length is on average 19% larger than *C. sanmiguelensis*, whereas the M1 length is even larger (29%). Such a relative enlargement of the M1 vs. P4 is a common trend among North American species of *Conepatus* and is consistent with a relatively late form for *C. robustus*. The combined characters of large size, enlargement and elongation of M1, loss of P2, and a deep notch between m1 entoconid and metaconid (Martin, 1978: fig. 1) in *C. robustus* clearly suggest a close relationship to the extant *C. leuconotus* and make the Florida Pleistocene species easily distinguishable from *C. sanmiguelensis*.

Compared with the North American species, *Conepatus sanmiguelensis* is primitive in its possession

of a P2, a horizontally orientated paroccipital process and a quadrate M1 (not anteroposteriorly elongated). However, *C. sanmiguelensis* shares with the North American clade a condyloid foramen confluent with the posterior lacerate foramen. This character appears to be restricted to the North American species and suggests a common origin for all North American forms.

In Central America and northern South America, the extant *Conepatus semistriatus* (Boddaert, 1785) seems to belong to a transitional species both geographically and morphologically. *C. semistriatus* features intermediate proportions in its M1s and m1s (Fig. 11), but also possesses an entoconulid at the anterior end of the entoconid crest. The latter character is shared by an Argentinean Pliocene species, *C. altiramus* Reig, 1952. Two dentaries with cheek teeth were illustrated (Reig, 1952: figs 1, 2): CPS 173, the holotype, is a left dentary with p4–m2 and CPS 172 is a right dentary with c–m2. Two morphological details are apparent from the figures: (1) both m1s possess a distinct entoconulid, i.e. a small cusplule between the metaconid and entoconid, a character seen only in extant *C. semistriatus*; and (2) both m1s have a relatively unshortened trigonid, a primitive feature particularly prominent in *C. sanmiguelensis*. At 8.4 mm in length, the m1 of *C. altiramus* (Reig, 1952: table of measurements), however, is much smaller than those of *C. sanmiguelensis* and extant *C. semi-*



**Figure 12.** Strict consensus of six shortest trees of North American skunks found by Branch and Bound option of the PAUP program. Solid bars indicate synapomorphies and open bars indicate homoplasies and reversals. Numbers to the left of the bars are character numbers that correspond to those in Appendix 1 and Table 2, and numbers to the right of the bars are character states. Numbers at nodes are bootstrap values (> 50%, 100 replications). Tree length = 67, consistency index = 0.7, retention index = 0.82. Character 25 (loss of P2) is optimized as independently occurring in the *C. leuconotus*–*robustus* clade and in the *C. semistriatus*–South American clade, rather than a single occurrence at *Conepatus* and then reversals.

*striatus*, and is comparable with that of the extant *C. humboldtii* (Churcher & Van Zyll de Jong, 1965: fig. 7). The presence of an entoconulid in *C. altiramus* is highlighted by the phylogenetic analysis (Fig. 12), although this species is still too poorly known to be sure that it truly has a close relationship with *C. semistriatus* (see additional discussion in Zoogeography).

Species that are completely restricted to South America (south of northern Peru) include two living forms, *C. humboldtii* Gray, 1837 and *C. chinga* (Molina, 1782), as well as some fossil taxa, such as *C. primaevus* (Burmeister, 1879), *C. praecursor* Rusconi, 1932, *C. altiramus* Reig, 1952, and *C. talarae* Churcher & Van Zyll de Jong, 1965. Compared with

the North American clade, this group is small in size and generally has more primitive cranial and dental morphology, e.g. nasal less retreated posteriorly, condyloid foramen outside posterior lacerate foramen, P4 relatively long and less high crowned, although their transversely widened M1 may be a derived character for the South American group. We refrain from calling the South American group a clade (even though such is depicted in our cladogram) because a rigorous analysis of their phylogenetic status is not possible based on available comparative materials. Nonetheless, we offer the following comments on selected fossil species.

Burmeister (1879) erected *Conepatus primaevus* from the Ensenadan of Buenos Aires Province,

Argentina. Recently, Forasiepi (2003) referred more complete materials to this species and confirmed its validity as a distinct species. In particular, an accessory cusp posterolingual of the M1 metacone is present in *C. primaevus*, a character also found in *C. altiramus* but not in other species of *Conepatus*.

Rusconi (1932) named a new subspecies, *Conepatus mercedensis praecursor*, from Buenos Aires Province, Argentina, and dated it as Ensenadan. Reig (1952) raised it to full species status (*C. praecursor*). Its holotype consists of a dentary fragment with m1–2, and its carnassial, 9.0 mm in length, falls in the upper end of variation in *C. talarae* (see below). The status of this taxon remains uncertain due to its poor state of preservation.

Churcher & Van Zyll de Jong (1965) named a species, *Conepatus talarae*, from the late Pleistocene Talara tar-seeps deposits in north-western Peru. A substantial sample of 59 specimens representing at least seven individuals form the hypodigm of this species, and as in *C. altiramus* above, it represents a small form about the same size as extant *C. humboldtii*. On average, the anteroposterior length of M1 in *C. talarae* is 20% shorter than that in *C. sanmiguelensis*. In addition, the M1s in *C. talarae* have a transversely widened proportion, which is characteristic of the extant *C. chinga* and *C. humboldtii*. Finally, *C. talarae* appears to have an m1 entoconulid anterior to the entoconid (Churcher & Van Zyll de Jong, 1965: fig. 2b), a character shared with *C. semistriatus* and *C. altiramus*.

Other reports of South American Pleistocene *Conepatus* include a record of *C. chinga* from the Tarija Basin, southern Bolivia (Hoffstetter, 1963). Most of the historical collections of the rich mammal fossils from the Tarija Basin lack detailed stratigraphic documentation, but the Tarija mammals represent a typical Ensenadan assemblage, and the fossil-producing beds have been palaeomagnetically constrained to ~0.6–1.0 Ma (MacFadden *et al.*, 1983). This would extend the geological range of *C. chinga* to the middle Pleistocene.

## ZOOGEOGRAPHY

If the recent molecular phylogenetic studies are correct regarding a basal position for *Conepatus* among extant North American skunks (Dragoo & Honeycutt, 1997; Flynn *et al.*, 2005a), then it follows that the genus must have a much longer divergence time than is suggested by previous fossil records. For example, early *Spilogale* can be traced to early to late Blancan Rexroad (Kansas), Mt. Blanco (Texas), and Beck Ranch (Texas) localities, and that for *Mephitis* to early Blancan Broadwater (Nebraska) and Rexroad (Kansas) localities (Anderson, 1984; Baskin, 1998).

This seems to imply that *Conepatus* may have an equally ancient divergence.

Equally interestingly, *Conepatus* occupies one of the largest geographical ranges of any living terrestrial mammal in the New World (Van Gelder, 1968). Its four extant species span from southern Colorado to southern Argentina (Wozencraft, 1993). Before this report, fossil records of *Conepatus* on either side of the Isthmus of Panama gave the appearance of a nearly simultaneous emergence of this genus during the middle Pleistocene (Woodburne, Cione & Tonni, 2006). On the North American side, the earliest record is from the Irvingtonian of Florida (Anderson, 1984; Bell *et al.*, 2004), whereas on the South American side, the first record belongs to the Ensenadan of Argentina (Tonni, Bargo & Prado, 1988; Cione & Tonni, 1995; Woodburne *et al.*, 2006). Such apparent coeval records gave the appearance of rapid expansion of ranges when the genus first evolved.

Our new record from central Mexico suggests a more complex history that was previously hidden from view. It is now clear that known North American records from Florida, Texas and New Mexico are biased because of the relatively poor representation from Mexico. The new species from central Mexico suggests that ancestral lineages of *Conepatus* must have centred on southern North America and Central America, and that *Conepatus* probably arrived at South America earlier than previously thought.

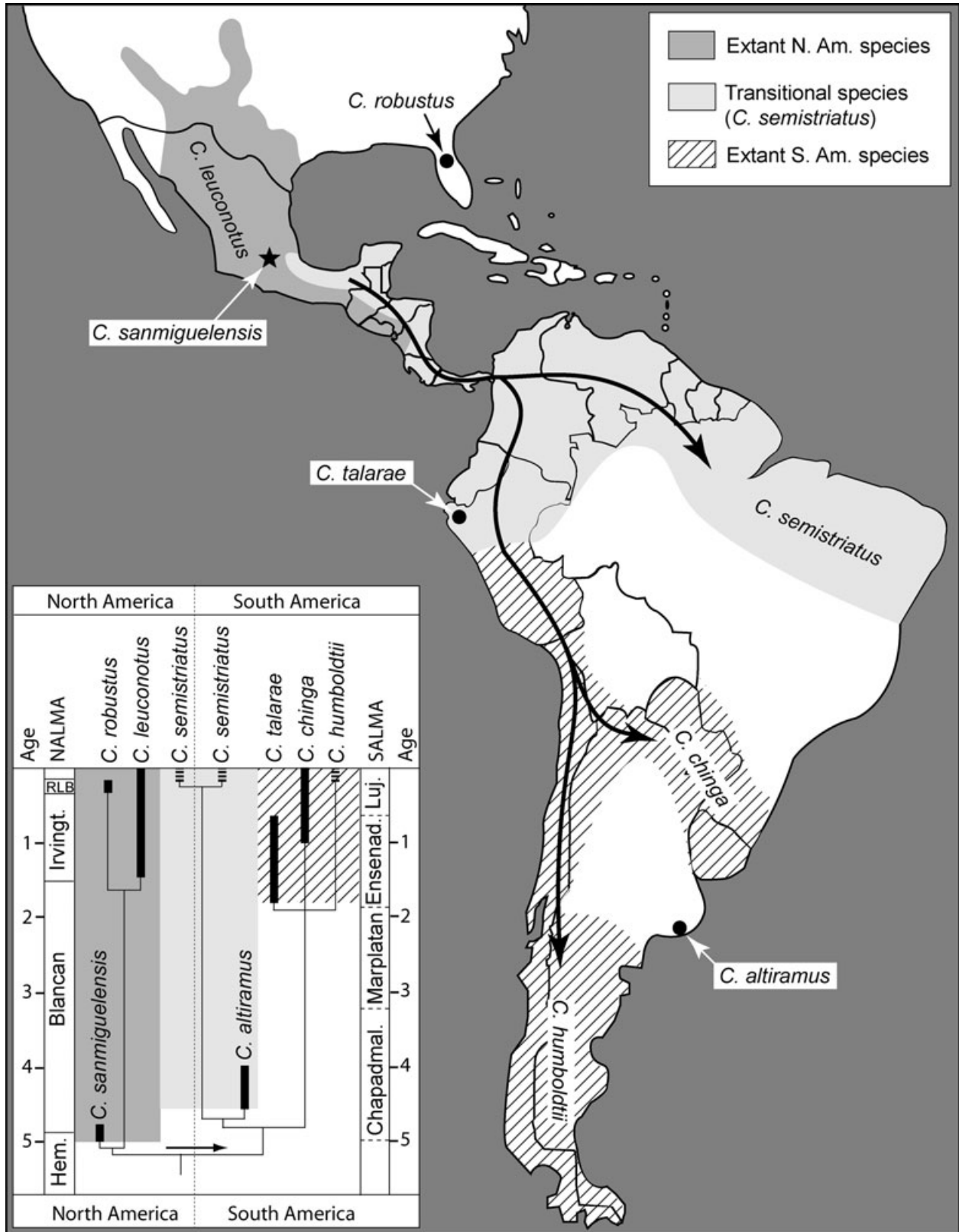
## FIRST APPEARANCE OF NORTH AMERICAN *CONEPATUS*

*Conepatus sanmiguelensis* is the earliest known record of the genus (Fig. 13). As our phylogeny indicates, the Guanajuato form falls within the North American clade (*C. sanmiguelensis*, *C. robustus*, *C. leuconotus*), and thus it is also the earliest record for that clade. With the Guanajuato record (early Pliocene, about 4.8 Ma) and the referred Tecolotlán material (> 4.89 Ma), *Conepatus* is now pushed back 3 millions years earlier than previous thought. Such an early occurrence also implies that its sister clade, *C. semistriatus* plus all other South American species, must have originated just as early if not earlier. This raises the question of the earliest record of *Conepatus* in South America, an issue we briefly explore below.

## ZOOGEOGRAPHY OF NORTH AMERICAN *CONEPATUS*

As one of the morphologically most derived species of the genus, the extant *Conepatus leuconotus* (including *C. mesoleucus*) ranges from south-western United States (Arizona, New Mexico, Texas and southern Colorado), through Mexico, to some Central American countries (as far south as Nicaragua). The presence of





**Figure 13.** Map of distribution of living hog-nosed skunks and selected fossil species. Species ranges, phyletic relationships and immigration scenario are depicted in the box on the lower left side. Distributions of North American species are based on Hall (1981) and those for the South American species on Eisenberg (1989), Redford & Eisenberg (1992) and Eisenberg & Redford (1999). Abbreviations for North and South American Land Mammal ages: Chapadmal., Chapadmalalan; Ensenad., Ensenadan; Hem., Hemphillian; Irvingt., Irvingtonian; Luj., Lujanian; RLB, Rancholabrean.

*C. sanmiguelensis* in central Mexico, as well as Pleistocene records in Florida, suggests that ancestral species of this clade have occupied the same general region in southern North America since about the early Blancan. This also implies that a Plio-Pleistocene Central American lineage, presently represented by the extant *C. semistriatus*, must have been the main source that gave rise to the South American species of *Conepatus*. Unfortunately, this presumed ancestral Central American lineage is still hidden from view because of a lack of fossil records.

#### FIRST APPEARANCE DATUM OF SOUTH AMERICAN *CONEPATUS*

*Conepatus altiramus* Reig, 1952 is a matter of some importance both because of its transitional morphology comparable with that of *C. semistriatus* (see Phylogeny above) and because of its status as possibly the earliest immigrant skunk in South America. *C. altiramus* is from 'Barranca de Los Lobos' between Mar del Plata and Miramar in Buenos Aires Province, along the Atlantic coast of Argentina. According to Reig (1952), the holotype (CPS 173) was collected from layers 3–5 in the lower part of the Chapadmalal Formation, which was divided into 15 layers by Kraglievich (1952). Marshall & Sempere (1993: 361) listed *Conepatus* and *Platygonus*, along with four cricetid rodents, from the Chapadmalal Formation as the first documented North American immigrants in the Pliocene and their presence in South America marked the initial wave of the GABI.

Cione & Tonni (1995: 147–148), however, casted doubt about the occurrence of the hog-nosed skunk in the Chapadmalal Formation: '... this record is based on a unique specimen of *Conepatus* (Mustelidae) collected in 1936 by L. and G. Scaglia. At that time, all the rocks at the base of the cliffs were assigned to the Chapadmalalan. Reig (1958) stated that the material came from the Chapadmalalan, but in 1957 he had assigned it to the Barranca de los Lobos? "Formation." No other specimen has been recorded in pre-Ensenadan beds.' Recent workers generally follow this opinion (but see Hunt, 1996) and placed the first occurrence of *Conepatus* in the Ensenadan (Soibelzon & Prevosti, 2007; Woodburne *et al.*, 2006). It appears that Cione and Tonni's reservations about the Chapadmalalan record of *Conepatus* are mainly because of a lack of corroborating pre-Ensenadan records else-

where in South America and because of the apparent Irvingtonian first appearance of *Conepatus* in North America (Anderson, 1984; Bell *et al.*, 2004; Woodburne *et al.*, 2006). It is perhaps revealing that, of the six Chapadmalalan immigrant taxa listed by Marshall & Sempere (1993), only *Conepatus* was singled out as a spurious record (Woodburne *et al.*, 2006). By dismissing the Chapadmalalan record, a simultaneous appearance of *Conepatus* in the early Pleistocene of North and South America becomes a satisfying biochronological scenario.

Our present documentation of an early Blancan *Conepatus* in Mexico calls for a re-evaluation of above scenario. It is now possible, even likely, that *Conepatus* entered South America in pre-Ensenadan time. Whereas the presence of the skunk in the Chapadmalal Formation remains to be verified by further collecting along the coastal marine cliffs of Argentina, a case can be made to accept the face value of *C. altiramus* in the Chapadmalalan South American Land Mammal Age (SALMA). Woodburne *et al.* (2006: appendix I) suggested that Chapadmalalan SALMA spans approximately 3.3–5.0 Ma, although they acknowledged that its lower boundary is not calibrated. If *C. altiramus* is truly from the lower part of the Chapadmalal Formation, as originally claimed by Reig (1952), then an early Chapadmalalan occurrence for *C. altiramus* is likely, an age that is consistent with its North American counterpart (i.e. *C. sanmiguelensis*). This would, again, place skunks as one of the earliest immigrants to South America in the early stage of the GABI, and as such, has important ramifications for the first invaders of the South American continent.

#### REPLACEMENT OF TRANSITIONAL SPECIES IN SOUTH AMERICA

Our preliminary phylogeny suggests that *Conepatus altiramus* belongs to the transitional species clade (mostly consisting of the extant *C. semistriatus*). If this is correct, then the transitional clade, as represented by *C. altiramus* from the Chapadmalalan of Argentina, had spread, almost from the very beginning, to much of southern South America, areas that are presently occupied by the more advanced *C. chinga* and *C. humboldtii*. *C. talarae* appears to be the earliest record of the *C. chinga-humboldtii* clade. Its presence in northern Peru, near the current

species boundary of *C. semistriatus* and *C. chinga* (Fig. 13), indicates that, by Ensenadan time, the present pattern of species distribution in South America may have taken shape, i.e. the *talarae-chinga-humboldtii* had replaced the transitional species (*C. altiramus*) by the Ensenadan.

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## APPENDIX 1

Definitions of characters and their states used in compiling the data matrix for phylogenetic analysis. Character numbers and character state numbers correspond to those in Table 2 and Figure 12.

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. Extra roots on m1: 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 (entoconulid) on anterior segment of m1 entoconid crest: absent (0); present (1).
13. P4 parastyle: absent (0); present (1).
14. Talonid cusps of m1: hypoconid approximately equal in height to entoconid (0); hypoconid dominant over entoconid (1).
15. M1 lingual cingulum: surrounding protocone lingually (0); posteriorly 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. Crown height of p4: 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. Entoconid crest of m1: fully enclosed on lingual side (0); notch on anterior end of entoconid crest (1); deeply notched (2).
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: transverse width nearly twice anteroposterior length (0); transverse width less than twice anteroposterior length (1); approximately equal length and width; 3, anteroposteriorly elongated (2).
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. Condylod canal: present (0); extremely reduced or absent (1).
35. Condylod foramen: outside of posterior lacerate foramen (0); confluent with posterior lacerate foramen (1).
36. Postorbital process of frontal: present (0); extremely reduced or absent (1).
37. Infraorbital foramen: one foramen (0); two or more foramina (1).
38. Angular process: small inferior ramus for medial pterygoid muscle (0); enlarged inferior ramus.