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Sonitictis moralesi, gen. et sp. nov, a new hypercarnivorous and durophagous mustelid from middle Miocene Tunggur Formation, Inner Mongolia, China and its functional morphology

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ABSTRACT

We name a rare, hypercarnivorous and durophagous mustelid *Sonitictis moralesi*, new genus and species, in honour of Jorge Morales for his contributions to carnivore palaeontology. *Sonitictis moralesi* is from the middle Miocene Tunggur Formation of Inner Mongolia, China (Tunggurian Land Mammal age). *S. moralesi* has a short and robust jaw that deepens slightly behind the m1 and possesses a shallow groove at its ventral surface. Dentally, it has robust premolars and highly hypercarnivorous m1 that has lost the metaconid and a trenchant talonid. Known by three jaw fragments, knowledge of this new mustelid is still poor and its relationship uncertain. However, based on its possession of a ventral groove, robust premolars and hypercarnivorous first molar, we tentatively place it in the subfamily Mellivorinae, which includes modern *Mellivora capensis* (honey badger) and extinct species of *Eomellivora*, plus others. We conducted mandibular force profile analyses on one *S. moralesi* specimen and compared bite force estimates to several specimens of *E. piveteaui, E. wimani* and *M. capensis*. The results suggest that *Sonitictis* likely was a more capable predator and consumer of vertebrate prey than the extant *Mellivora*, reaching the low end of the bite force estimates for the larger and more robust *Eomellivora*.

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Mustelidae; middle Miocene; Tunggur Formation; Inner Mongolia

Introduction

The middle Miocene Tunggur Formation in Inner Mongolia is a classic deposit with rich records of fossil mammals since its initial discovery by the Central Asiatic Expeditions of the American Museum Natural History (Spock 1929; Osborn and Granger 1931). Most of the materials were later described in a series of papers by Colbert (1934a, 1934b, 1934c, 1936a, 1936b, 1939a, 1939b, 1940), Stirton (1934) and Dawson (1961). A Sino-USSR expedition in 1959 (Chow and Rozhdestvensky 1960) yielded two additional taxa (Li 1963; Zhai 1964). Continued explorations by the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) and other international institutions since the 1980s have greatly enriched the small mammal records (Qiu and Wang 1999; Qiu et al. 2006, 2013a). A diverse array of large and small mammals is now known in the Tunggur Formation (Wang et al. 2003; Qiu et al. 2013a), which forms the basis of the middle Miocene Chinese Tunggurian Land Mammal age (Wang et al. 2013; Qiu et al. 2013b). Given this importance, the Tunggur Formation continues to receive palaeontological attention during the past 30 years and new taxa or better specimens are occasionally found, especially from the relatively poorly explored Tairum Nor exposures (Wang 2004; Tseng et al. 2009).

We report another rare mustelid from the Tunggur Formation that has not previously been described. The new mustelid combines a hypercarnivorous dentition with robust premolars and strong jaws, presumably adapted to a durophagous diet. Such a combination of dental and mandibular features has not been seen in the middle Miocene of Asia. Despite it being represented by only three fragmentary lower jaws and teeth so far, we take this opportunity to celebrate Jorge Morales's palaeontological career and to describe a new genus and species, *Sonitictis moralesi*. The robust jaw and teeth also offer an opportunity to explore its functional morphology.

Materials and methods

The fossil materials were collected for this study by the authors as well as many other field participants during the past 25 years. Where possible, individual specimens were attributed to collectors (see Referred Specimens). All described materials are deposited in the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing.

Institutional abbreviations

AMNH: American Museum of Natural History, New York, USA; **Bat-3**: Batallones-3 fossil collection in the Museo Nacional de Ciencias Naturales, Madrid, Spain; **IVPP**: Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **LACM**: 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; **MVZ**: Museum of Vertebrate Zoology, University of California, Berkeley, USA.

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Supplemental data for this article can be accessed here.

3D Models

A 3D model of the mandible of *Sonitictis moralesi* (IVPP V28317, holotype) was created using the photogrammetry software Agisoft Metashape (version 1.7.3), which can be downloaded from MorphoSource (https://www.morphosource.org/concern/media/000385228?locale=en). For the purpose of the mandibular force profile analysis, the posterior portion of the mandible was reconstructed using *Mellivora capensis* (see below) as a template (Figure 1S in Supplemental data.

A left jaw of *Eomellivora wimani* (LACM 162957, cast, likely from the late Miocene of Linxia Basin, China; original repatriated to IVPP) was scanned using a NextEngine laser scanner (model 2020i) in combination with ScanStudio software (version 2.0.2), downloadable at MorphoSource (https://www.morphosource.org/concern/media/000387259?locale=en). The scanner is set in the highest resolution possible in the 'wide' range setting. Two orthogonal sets of 360° scans (at intervals of 22.5°) were obtained, and manually aligned and fused into a single model. Final mesh results are saved in the PLY format that preserves texture information and manipulated in MeshLab software (version 2020.07). Size scale (in mm) is captured by build-in calibrations of the NextEngine scanner.

Jaw measurements of *Eomellivora* specimens from Batallones-3 were taken from 3D PDFs published by Valenciano et al. (2015). *Mellivora capensis* mandible 3D models were created using LACM 28121, downloadable at MorphoSource (https://www.morphosource.org/concern/media/000385235?locale=en) or CT-scanned (MVZ 184107) using a GE Phoenix Nanotom M 180 (Functional Anatomy and Vertebrate Evolution Laboratory, University of California, Berkeley) at 63.46-micron voxel size with a voltage of 150 kV and current of 90 mA and then reconstructed as 16 bit TIFF images and segmented in 3D Slicer (segment editor module; Slicer version 4.11.20210226), downloadable at MorphoSource (https://www.morphosource.org/concern/media/000386215?locale=en).

Linear measurements taken in the mandibular force profile analysis were measured on 3D models using Geomagic Wrap (version 2020, 3D Systems) except those from Batallones, which were measured within the respective 3D PDFs. Digital model measurements were taken to the nearest 0.01 mm. See supplemental information for 3D mesh files.

Systematic palaeontology

Class Mammalia Linnaeus, 1758

Order Carnivora Bowdich, 1821

Family Mustelidae Fischer von Waldheim, 1817

Subfamily Mellivorinae Gray, 1865

Sonitictis new genus

Type species

Sonitictis moralesi, new genus and species.

Included species

Type species only.

Diagnosis

Sonitictis has the following hypercarnivorous characters that match best with mellivorines: short and robust horizontal ramus of lower jaw, with laterally flared cheek teeth, deep symphysis, a weak groove around the ventrolateral aspect (mostly below m1) of the ramus and a slight chin; a lower cheek teeth dental formula of p1-4 and m1-2; premolars are broad and strongly built, posterior accessory cusps small; m1 short relative to p4, m1 hypercarnivorous with complete loss or a remnant of metaconid and talonid dominated by a single, centrally located hypoconid; m2 reduced. *Sonitictis* differs from hyaenids in short jaws, relatively small premolars with incipient accessory cusps and trenchant talonid.

Sonitictis moralesi new genus and species

Aelurocyon (?) sp. Wang et al. (2003):24.

Holotype

IVPP V28317, partial left dentary with p4-m1 and alveoli of c-p3 and m2 (Figures 3 and 4; 3D model in MorphoSource.org, see Data deposition section), collected by Meng Jin on 1 October 1994.

Type Locality

The lower part of the middle channel sandstone, near '346 locality' (346 refers to a previous kilometre mark along the highway in the 1990s, which has since been renumbered), approximately 1 km east of Highway intersection with Tairum Nor exposure, Sonit You Qi, Inner Mongolia Autonomous Region, China.

Referred specimen

IVPP V28316, partial right lower jaw with p2 alveolus and p3-m1 (Figures 4 and 5), field number IM1705-16, collected from 'north of Aletexire' by Wang Hongjiang on 1 May 2017; IVPP V25334, left partial jaw with p2-3 alveoli, p4 and m1-2 alveoli (Figure 6), from IVPP 86026 locality, collected by IVPP 1986 expedition.

Diagnosis

As for genus.

Etymology

Genus name, *Sonit*, Mongolian, night; Sonit refers to the Mongol geographic region that includes both Left (Zuo) and Right (You) Banners (Qi, or County) that encompass the Tunggur Formation; *ictis*, Latin, weasel. Species name is in honour of Jorge Morales for his contribution to the understanding of carnivoran evolution in Europe and Africa, as well as his works in other fossil mammals in the Cenozoic. English translation: 'Morales' Sonit weasel.'

History of collection, stratigraphy and age

Discovered by the American Museum of Natural History Third Central Asian expeditions in 1928 (Spock 1929), the Tunggur Formation has attained significance because of its rich vertebrate fossils. The success of the AMNH expeditions at amassing an impressive assemblage of fossil mammals, dominated by the iconic shovel-tusked elephant, *Platybelodon* (Osborn and Granger 1931, 1932), ensures that the Tunggur fauna has become the basis of Chinese Tunggurian Land Mammal age/stage. Following this early success in the 1920–1930s, a Sino-Russian expedition was organised in 1959 (Chow and Rozhdestvensky 1960) and a 1986 expedition by the Institute of Vertebrate Paleontology and Paleoanthropology led by Qiu et al. (1988).

The long hiatus between AMNH and IVPP expeditions, coupled with a lack of access to archives, resulted in some later inconsistencies in the interpretation of AMNH localities by the IVPP 1986 expeditions. With access to AMNH archives, Wang et al. (2003) were able to reconcile some of these discrepancies (Figure 1). Although most of the AMNH and IVPP localities were satisfactorily relocated by matching AMNH field photos or Chinese topographic maps, the IVPP 1986 *Platybelodon* (86021) and IVPP 1986 Moergen II (86020) localities were not positively relocated and georeferenced until 2005 and 2009, respectively.

Despite the above progress, however, there are still significant uncertainties in the stratigraphic positions in two of the three specimens described. IVPP V28317, the holotype, has the most accurate stratigraphic information because the senior author was present in the field team, even though no GPS device was available at the time.

IVPP V25334 was collected during the IVPP 1986 expeditions and the only record of the IVPP loc 86026 is a plot on the 1:100,000 topographic map (Sharutala Dadui quadrangle) on the 1,000-metre contour line. Although precise stratigraphic position is unavailable, it seems safe to assume that IVPP V25334 was collected from the top 20 m of the local section (Figure 1), i.e. the upper section along the rim of the Tunggur Tableland (Figure 2).

Although IVPP V28316 was the most recently collected (2017), it lacks a GPS but was referred to as from 'north of Aletexire'. The lower section at Aletexire (the lower 22 m of the section in Figure 2), about 1.3 km northwest of IVPP loc 86026, is not visible standing at the rim of the Tunggur Tableland and we assume that both AMNH and IVPP 1986 expeditions probably did not visit this section (Wang et al. 2003). Fossils are most abundant on top of a sandstone bench at top of the local section (Figure 2), which is assumed to be the horizon where IVPP V28316 came from.

As first envisioned by Wang et al. (2003), the Aletexire-86026 section, with a total thickness of well over 70 m (Figure 2), can potentially serve as a bridge in the vexing problem of correlating most of the sections along northern and western margins of the Tunggur Tableland with the Tairum Nor section to the south.

Systematic screening for small mammals at the Tairum Nor section did not start until the 1990s. Qiu and Wang (1999) first proposed the Tairum Nor Fauna largely based on small mammals,

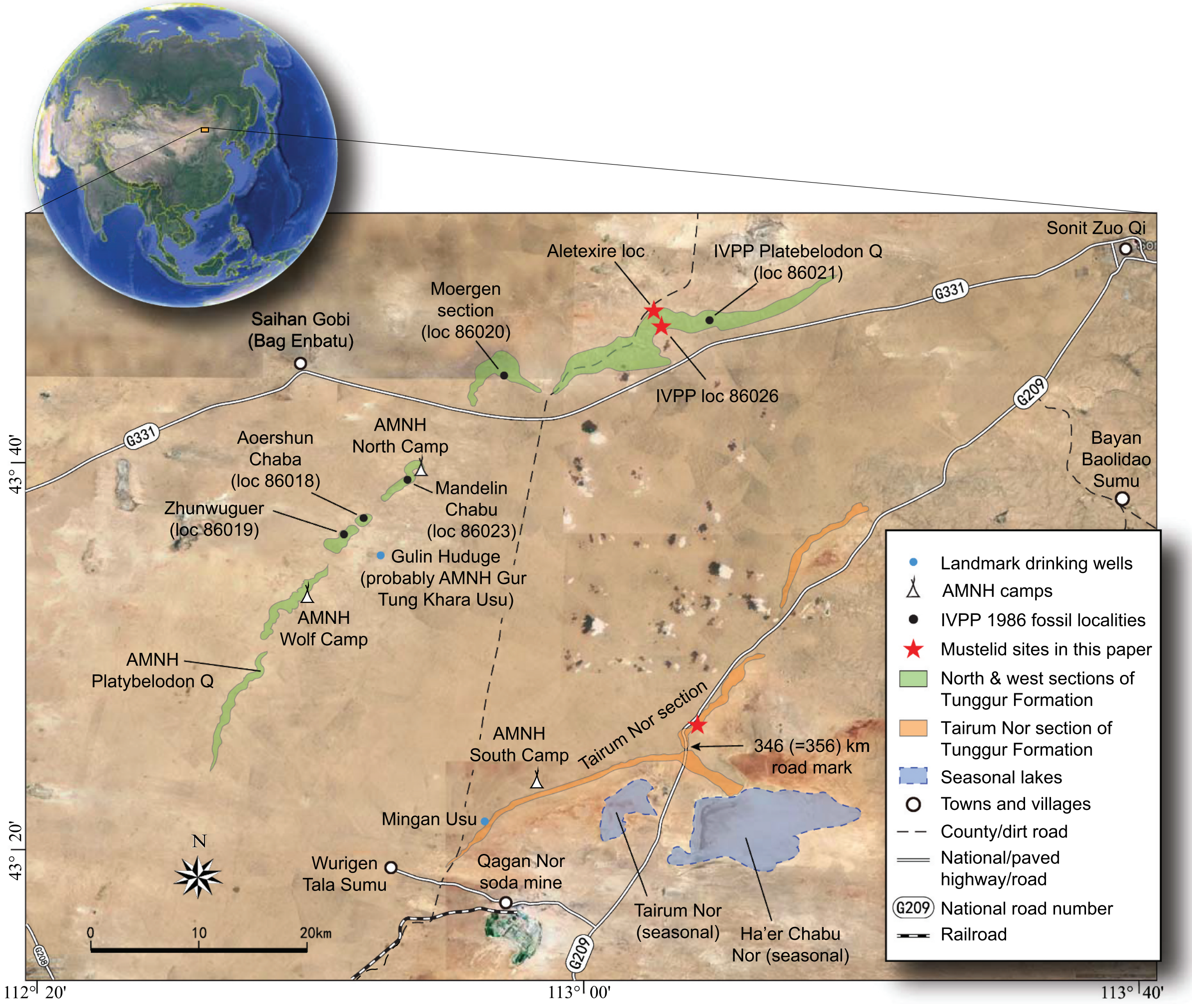

Figure 1. Distribution of Tunggur Formation and relationships of AMNH 1928–1930 and IVPP 1986 localities. AMNH localities were based on archival studies by Wang et al. (2003) and IVPP 1986 localities were based on plots in IVPP topographic maps and Qiu et al. (1988). Satellite photos by Google Earth Pro (Version 7.3.3.7786) (2020) was downloaded on 21 May 2021.

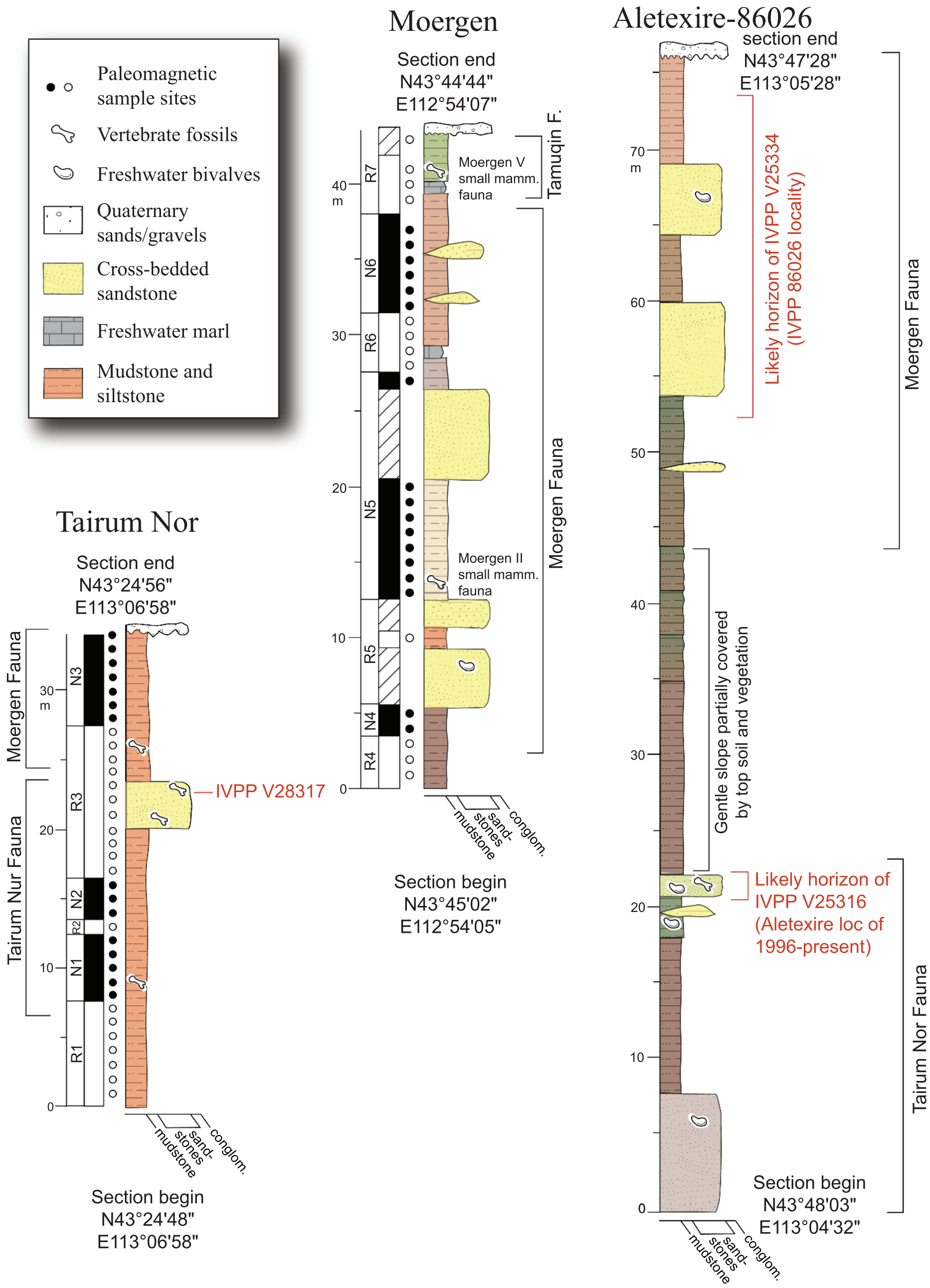

Figure 2. Three main stratigraphic sections in Tunggur Formation. The Moergen and Tairum Nor sections are modified from Qiu et al. (2013a:Fig. 5.3), which also forms the basis for faunal (chronological) interpretations in this chart. See also Qiu et al. (2013a) for magnetostratigraphic correlations.

and remarked that small mammals from the red beds in Tairum Nor section are somewhat more primitive than the Moergen Fauna. More recent updates maintain a similar view (Qiu et al. 2006, 2013a) and further singled out the Dingjiaergou Fauna in Tongxin, Ningxia as a possible faunal equivalent that may correlate to the European MN 6.

Due to relatively short sections with coarse-grained sandstones, correlations of the magnetostratigraphy in the Tunggur Formation have been difficult and controversial (Wang et al. 2003; Qiu et al. 2013a). Unfortunately, the Aletexire section still lacks magnetic study, except for a test run of the lower-most 5 m (Liddicoat et al. 2007). If the upper red beds in the Tairum Nor section really have faunas that are correlative to the Moergen Fauna (Qiu and Wang 1999; Qiu et al. 2006, 2013a), then the Aletexire section has the potential to demonstrate superpositional relationship of the Moergen and Tairum Nor faunas, as is presently assumed (Figure 2).

Despite the fact that the Chinese Tunggurian Land Mammal age has long been established based on the Tunggur faunal assemblages (Li et al. 1984; Qiu 1989; Qiu and Qiu 1995; Qiu et al. 2013b), the geochronology of the Tunggur Formation is still not fully resolved. Magnetostratigraphy currently offers the only means for a numerical age, but widespread, isolated sections and relatively thin strata interrupted by coarse sandstone render a secure correlation a major challenge (Wang et al. 2003). Given the above discussion, *Sonitictis* seems to span much of the Tunggur Formation.

Figure 3. *Sonitictis moralesi* new genus and species, holotype, IVPP V28317, left dentary with p4-m1, from Tairum Nor, Tunggur Formation. A, lingual view; B, labial view.

Based on the palaeomagnetic framework in Qiu et al. (2013a), *Sonitictis moralesi* can be as young as 12–13.5 Ma but possibly as old as 15 Ma.

Age and geographic distribution

So far known in middle Miocene of Inner Mongolia only.

Description (Figures 3–6; Table 1; 3D model in MorphoSource.org)

The mandibular ramus is short, deep and robust. The exposed distance of p1 root to m2 root is 52 mm in the holotype. The depth of jaw at m1 is 26 mm. In lateral view, the anterior end of the horizontal ramus is deeper in all three specimens, with the rest of the ramus tapering towards posterior end. This deep symphysis creates a slight 'chin' on the lower border of the ramus. The lower border of the horizontal ramus also lowers towards the posterior end and associated with this deepening of ramus is a weak groove on the ventrolateral aspect of the jaw (much of the posterior parts of the jaws are missing in all three specimens and the full extent of ventral deepening is unknown), reminiscent of that in *Eomellivora* and *Mellivora*. A small mental foramen is located between the roots of p3. Much of the premolar row is displaced labially, as is typically the case for bone-crushing carnivorans, such as in borophagine canids (Wang et al. 1999). The lower jaw thus suggests an animal with a short and broad rostrum, consistent with a durophagous diet.

Only the distal alveolar surface of the lower canine root is preserved. This alveolar remnant does indicate that the lower canine is relatively lingually positioned relative to the premolars. As in the canine alveolus, only the lingual side of the p1 root is preserved, which indicates a single-rooted tooth with a very reduced p1. The p1 is probably less than half as long as the p2 and probably measures no more than 3 mm in anteroposterior length in the holotype, indicating a sudden reduction relatively to the p2. The p2 alveoli are partially (IVPP V28316) or completely (holotype and IVPP V25334) preserved. The p2 is double-rooted with the posterior root substantially larger than the anterior root. The maximum alveolar length of the p2 in holotype is 7.3 mm. The p3 is preserved on IVPP V28316. It is a robust tooth with crown height similar to that of p4 and m1 paraconid. The occlusal outline of the p3 is concave on the lingual side and convex on the labial side. The main cusp is strong with a straight anterior face free of a cingular cusp. A small posterior accessory cusp is present, which is shifted slightly towards the lingual side of the main cusp. A posterior and lingual cingulum is present in the p3. The p4 is slightly larger than the p3 but is otherwise similar to the latter except having a more distinct posterior accessory cusp and posterior cingulum.

The m1 is short relative to that of the p4, as seems also the case in oligobunines. As in the premolars, the occlusal outline of the m1 is concave lingually and convex labially. The protoconid is taller than paraconid. The protoconid-paraconid forms a strong cutting blade, bending slightly lingually towards the anterior end. The metaconid is either completely lost (holotype) or indicated by a tiny cusp at the base of protoconid on IVPP V28316. On the holotype, in place of the metaconid is an indistinct ridge running along the lingual aspect of the protoconid. The talonid is less than one-third total

Figure 4. *Sonitictis moralesi* new genus and species, left and right dentaries, Tunggur Formation, A, IVPP V28317, holotype; B, IVPP V28316, referred specimen. Stereo photos of occlusal view.

length of the tooth. The talonid is trenchant and dominated by a single, centrally located hypoconid. The entoconid is absent. A reduced, single-rooted m2 is indicated by the holotype (maximum anteroposterior alveolar length 2.9 mm) and IVPP V25334.

Comparison and taxonomic remarks

It is difficult to determine the higher-level relationship of *Sonitictis* due to a lack of upper teeth and relatively high degree of hypercarnivory from a relatively early deposit. Wang et al. (2003) initially identified the holotype as '*Aelurocyon* (?) sp.' (a junior synonym of *Megalictis*), drawing on hypercarnivorous characters from the North American oligobunines. The Tunggur mustelid indeed shares a number of similarities with the North American oligobunines, primarily in the robust, durophagous premolars, relatively short m1, extreme reduction or loss of m1 metaconid, and highly trenchant talonid. However, *Sonitictis* differs from North American oligobunines in its lack of a large posterior accessory cusp on premolars, despite that this character can often equally be applied to the mellivorines (see below).

One key feature of the oligobunines is its possession of a carnassial notch on P4, as well as a small M2, primitive characters for some basal musteloids that define a (possibly paraphyletic) 'paleomustelid' (roughly equivalent to oligobunine) (Baskin 1998). Lacking an upper carnassial, we are unable to confirm if the carnassial notch is present in *Sonitictis*. However, the North American *Megalictis* is mostly early Miocene (late Arikareean) in age, about 22.7–18.5 Ma (Valenciano et al. 2016a), although less specialised species of oligobunines are present in the middle Miocene of North America, such as *Brachypsalis* (Baskin 1998). A dispersal from North America, showing up in the Tunggur Formation of Inner Mongolia, would represent an immigrant many millions of years later than its North American counterparts.

Wang et al. (1998) mentioned a right dentary fragment (IVPP V11053) from Tieersihabahe in Junggar Basin under '*Oligobunis*? sp.' However, as in the case of *Sonitictis moralesi*, the Junggar Basin specimen is too poorly preserved (lacking an upper carnassial) to be positively identified as a North American oligobunine. The case for an Old World presence of the New World paleomustelids is still far from certain. We note that *S. moralesi* is substantially larger than the Junggar form and also has slightly better development of accessory cusps on premolars.

Within the 'neomustelids', the robust jaw and premolars and hypercarnivorous m1s in *Sonitictis* are somewhat similar to those of *Plesiogulo* in the subfamily of Guloninae. However, the lower premolars in all species of *Plesiogulo* lack a posterior accessory cusp, a condition quite different from those in mellivorines (Zdansky 1924; Teilhard de Chardin 1945; Kurtén 1970). It is thus likely that their hypercarnivorous m1s are convergently acquired.

Another highly hypercarnivorous mustelid from the Tunggur Formation is *Sthenictis neimenguensis* (Tseng et al. 2009). However, besides the hypercarnivory of its lower carnassial (reduced metaconid and entoconid), there is nothing else that resembles *Sonitictis*

Figure 5. *Sonitictis moralesi* new genus and species, right dentary, IVPP V28316, from Aletexire area, Tunggur Formation, A, labial view; B, lingual view.

the jaw of *Sthenictis neimenguensis* being long and slender and its premolars being likewise much more gracile. Therefore, the highly trenchant m1 in *Sthenictis neimenguensis* must be a character convergent with *Sonitictis*, as hypercarnivory has evolved numerous times in Carnivora, particularly in mustelids.

Among Eurasian middle Miocene mustelids, *Hoplictis* comes closest to *Sonitictis*. The genus *Hoplictis* was initially named as a subgenus of *Ischyrictis* by Ginsburg (1961), while describing carnivorans from the French Sansan locality. Its type species is *Ischyrictis* (*Hoplictis*) *florancei* (Mayet 1908) from the French locality of Pontlevoy-Thenay. Ginsburg and Morales (1992) later elevated it to genus and considered it to converge to cat-like adaptations. Ginsburg and Morales thought it related to *Ischyrictis*, *Laphictis*, *Eomellivora* and *Gulo*. Valenciano et al. (2019) is the latest to summarise about *Hoplictis*, and in addition to the type species, they recognised five additional species: *H. noueli* from the French Artenay locality (MN4) (Mayet 1908), *H. anatolicus* of Çandir (MN6), Turkey (Schmidt-Kittler 1976), *H. baihu* from the Halamagai Formation (Tunggurian) in Junggar Basin, Xinjiang, China (Valenciano et al. 2019), *H. helbingi* from La Grive (MN7-8) of France (Viret 1951) and *H. grangerensis* of Granger Clay Pit (Clarendonian) of United States (Bryant 1968). Most recently, Valenciano et al. (2020) placed *Hoplictis* in a cladistic framework, positioning it at the base of his Mellivorinae clade. However, their cladogram places modern *Mustela putorius* between *Hoplictis* and the rest of their mellivorine clade. Such a peculiar arrangement of placing a highly derived *Mustela* within mellivorine calls into question of the cohesion of their mellivorine clade.

Sonitictis is both geographically and chronologically closest to *Hoplictis baihu* from Chinese middle Miocene of Xinjiang Autonomous Region (another referred species from Xinjiang, *H.* cf. *H. helbingi* (Valenciano et al. 2019), is not discussed here because the referred lower jaw lacks teeth). Indeed, species of *Hoplictis* share with *Sonitictis* a highly hypercarnivorous lower carnassial, ranging from presence of a small, remnant metaconid in *H. baihu* to complete loss of metaconid and entoconid in *H. florancei*, *H. noueli* and *H. helbingi* (Valenciano et al. 2019). However, the form of the jaws and premolars in *Hoplictis* shows a different pattern from that in *Sonitictis* in the former's relatively slender and elongated horizontal rami and similarly long and tall-crowned premolars with a large p4 posterior accessory cusp. A similar kind of resemblance is also seen in *Namibictis senuti* of early-middle Miocene of Namibia (Valenciano et al. 2019:Fig. 5). Therefore, the lack of bone-crushing jaw and premolars in *Hoplictis* sets it apart from *Sonitictis*.

Within the mellivorines, the largest and most durophagous is the extinct Eurasian and North American *Eomellivora* and possibly related *Ekorus* from Africa (Werdelin 2003; Valenciano and Govender 2020). Initially based on materials from Chinese late Miocene Baode (locality 31), Shanxi Province and Xin'an (locality 12), Henan Province, Zdansky (1924) erected the type species *E. wimani*. This species is now known in several late Miocene sites in north and south China (Teilhard de Chardin 1945; Zong 1997; Qi 2006). Similar forms have been reported elsewhere in Eurasia (Kretzoi 1942; Orlov 1947a, 1947b, 1948; Ozansoy 1965;

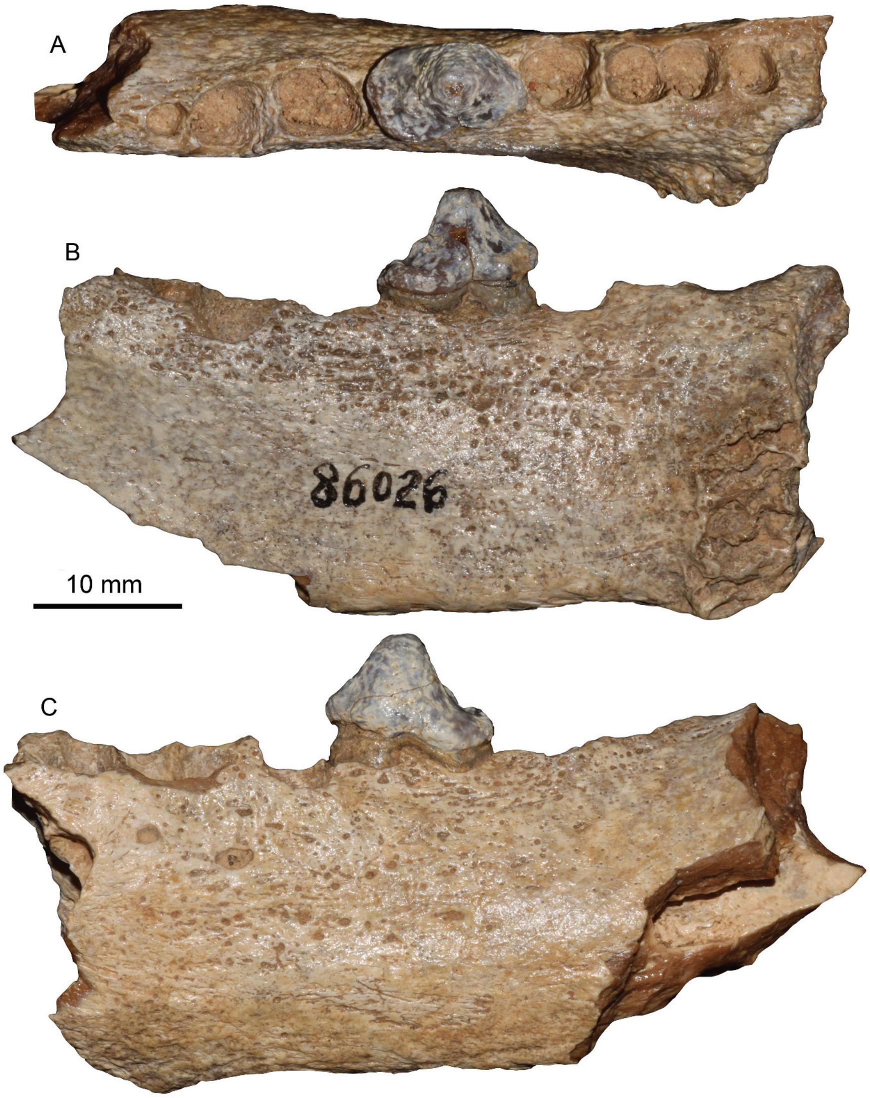

Figure 6. *Sonitictis moralesi* new genus and species, left dentary, IVPP V25334, from IVPP loc. 86,026, Tunggur Formation, A, occlusal view; B, lingual view; C, labial view.

Table 1. Dental measurements (in mm) of *Sonitictis moralesi* new genus and species. * Indicates an estimate.

	p3			p4			m1			
Specimen	length	width	height	length	width	height	length	trig width	trig length	tal width
IVPP V28316	11.14	6.44	7.84	12.12	6.96	8.88	13.54	6.34	10.52	5.72
IVPP V28317				11.91	7.19	8.4*	14.67	7.38	10.99	5.88
IVPP V25334				11.42	6.96	8.40				

Crusafont-Pairó and Ginsburg 1973; Wolsan and Semenov 1996; Vangengeim and Tesakov 2013; Alba et al. 2021), Africa (Morales and Pickford 2005) and North America (Stock and Hall 1933). Valenciano et al. (2015); (2017)) redescribed some western Eurasian materials and recognised five species: *E. wimani, E. ursogulo, E. hungarica, E. piveteaui* and *E. fricki*, in contrast to a more conservative approach of lumping them into a single species by Wolsan and Semenov (1996). Alba et al. (2021) added another species, *E. moralesi*, from the latest middle Miocene Vallès-Penedès Basin of Spain, as the basal-most species of *Eomellivora*.

Eomellivora has certainly reached or exceeded *Sonitictis* in body size, robust jaws, bone-crushing premolars and hypercarnivorous lower carnassials, but perhaps not the shortening of the jaw/rostrum. In addition, *Eomellivora* also has a slight 'chin' due to a deepening of the symphysis, which is present in the earliest and most primitive species, *E. moralesi*. The earliest species of *Eomellivora* is *E. tugenensis* (Morales and Pickford 2005) from late middle Miocene Ngorora Formation of Kenya, which is roughly equivalent in age to the Tunggur Formation. *E. tugenensis*, however, is based on rostral part of a skull. Alba et al. (2021), however, expressed doubts about its membership within *Eomellivora* and Valenciano and Govender (2020) placed it within their Mellivorini. While upper teeth of the *E. tugenensis* cannot be directly compared with the Tunggur materials, the locations of its P2 and P3 roots seem to suggest that *E. tugenensis* has not developed a broadened rostrum (which is correlated to a laterally flared anterior tooth row in the lower jaw) as is present in all known late Miocene forms have (Valenciano et al. 2015).

Compared to *Eomellivora* (using *E. wimani* and *E. piveteaui* as examples, and to a lesser extent *Mellivora*), *Sonitictis* seems to share with *Eomellivora* posteriorly deepening jaw (this is more easily seen in the holotype, although breakage at this point makes it difficult to judge how much deepening) with a groove near the ventral surface of the horizontal ramus. In *Eomellivora* and *Mellivora*, a distinctly downwardly protruding lower border shortly behind the m2 (below masseteric fossa) is visible in lateral view (Valenciano et al. 2015:Fig. 3) (see also 3D models in the online supplemental material of this paper). Perhaps not coincidentally, this downward protrusion is also associated with a groove and roughened area along ventral border, presumably for attachment of digastric muscles. Such a morphology is also seen in the extinct durophagous otter (Wang et al. 2017) and presumably of functional significance (Tseng et al. 2017). If our identification of a groove plus downward deepening in *Sonitictis* is correct (to be confirmed in better preserved specimens), this may offer the strongest character for a mellivorine relationship. In both *Eomellivora* and *Mellivora*, the posterior horizontal ramus is also laterally bent, which is especially pronounced in the latter. The functional significance of this lateral bend is not clear. In *Sonitictis*, breakage on the posterior jaw does not permit secure observation of this feature, but the preserved segment seems to suggest that this bend is also present.

Dentally, *Sonitictis* lacks the prominent anterior and posterior accessory cusps seen on the p3-4 of *Eomellivora*, which are also more labially displaced than seen in the former. The lower carnassials of *Sonitictis* and *Eomellivora* are highly convergent and exhibit remarkable similarity, although the latter shows more concavity along lingual border and lacks a ridge where the metaconid is (present in *Sonitictis*). In addition, the m1 protoconid in *Eomellivora* is relatively low-crowned, likely a derived condition.

Given the above comparisons and other zoogeographical and chronological considerations, we think it more likely that *Sonitictis* falls in the mellivorine clade, although probably forming an early divergence from other mellivorines, now recognised as forming two clades, the tribes Eomellivorini and Mellivorini (Valenciano and Govender 2020). We, therefore, conduct our functional analysis with this framework in mind.

Functional morphology

To contextualise the functional morphology of *Sonitictis* given its mandibular morphology, we conducted mandibular force profile analyses on one specimen of *S. moralesi* (IVPP V28317) and compared bite force estimates to several specimens of *Eomellivora, Mellivora capensis* and *Canis lupus*. All measurements and estimates follow Therrien et al. (2016) and were derived from their ‘solid mandible’ approach, which has been demonstrated to yield identical comparative patterns of bite force estimates as fully 3D, CT-based approaches, a method also applied to a Spanish amphicyonid (Morales et al. 2021). We measured mandible depth, width and distance to the articular process from the left hemimandible at the p3-p4, p4-m1 and post-m1 interdental gaps or positions (Table 2). Section modulus around the mediolateral axis (Zx) was estimated for each position on each specimen as Zx at a given position = π*(mandible width at position/2)*(mandible depth at position/2)^2/4 (Therrien et al. 2016). Relative bite force magnitude was then calculated as Zx/L, where L is the out-lever arm distance (from interdental gap location to most posterior edge of articular process).

Relative bite force profiles from p3 to post-m1 positions show that *Sonitictis* is closest to *Eomellivora* in both magnitude and shape of the force profiles (Figure 7). In both *Eomellivora* and *Sonitictis*, bite force increases gradually from p3-p4 to p4-m1, then shows a distinct jump from p4-m1 to post-m1 positions. The force profile of extant *Mellivora* shows less of an abrupt change from p3 to post-m1 (Figure 7). In contrast, a *Canis lupus* specimen included for comparison shows a pattern distinct from the mellivorines: there is a larger jump in bite force from p3-p4 to p4-m1 than from p4-m1 to post-m1 positions. It is interesting to note that the bite force estimates for both *Eomellivora* and *Sonitictis* are higher than in *Canis lupus*, whereas extant *Mellivora* shows lower bite forces than *C. lupus* (Table 2). Using a previously reported actual bite force magnitude of 2,000 N at the m1/post-m1 position in *C. lupus* (Therrien et al. 2016), we extrapolated bite force estimates using relative bite force magnitude % differences between the mellivorines and *C. lupus. Eomellivora* range from 2,150 N to 5,674 N in bite force and in *Mellivora* it is 771–805 N. *Sonitictis* has an estimated bite force of 2,238 N at the m1/post-m1 position (Table 2). The results of these analyses suggest that *Sonitictis* likely was a more

Table 2. Linear measurements and section modulus estimates of select mustelids and canids. L, lever arm length; Zx, section modulus in mediolateral axis; Zy section modulus in mediolateral axis.

Specimen	Specimen Number	Interdental Gap	Depth (mm)	Width (mm)	L (outlever)(mm)	Zx (cm3)	Zy (cm3)	Zx/L (=bite force)	% cf. *C. lupus*
Canis_lupus	*LACM (M) 23,010*	p3-p4	20.08	11.19	123.95	442.66	246.66	3.57	100.00%
Canis_lupus	*LACM (M) 23,010*	p4-m1	30.88	13.20	103.29	1236.02	528.47	11.97	100.00%
Canis_lupus	*LACM (M) 23,010*	Post-m1	29.50	13.58	76.34	1160.29	534.00	15.20	100.00%
Eomellivora wimani	*LACM 162957*	p3-p4	30.00	12.20	108.65	1077.89	438.36	9.92	277.79%
Eomellivora wimani	*LACM 162957*	p4-m1	30.44	14.40	90.48	1310.56	620.02	14.48	121.04%
Eomellivora wimani	*LACM 162957*	Post-m1	43.44	15.40	66.19	2853.75	1011.75	43.12	283.68%
Eomellivora_piveteaui	*Bat-3’08.526*	p3-p4	24.21	10.51	88.93	604.67	262.43	6.80	190.39%
Eomellivora_piveteaui	*Bat-3’08.526*	p4-m1	22.94	12.95	74.05	668.66	377.43	9.03	75.46%
Eomellivora_piveteaui	*Bat-3’08.526*	Post-m1	31.28	8.58	50.42	823.74	225.82	16.34	107.48%
Eomellivora_piveteaui	*Bat-3’09.1000*	p3-p4	26.84	14.38	91.42	1017.15	544.81	11.13	311.56%
Eomellivora_piveteaui	*Bat-3’09.1000*	p4-m1	28.19	12.90	73.00	1006.50	460.53	13.79	115.22%
Eomellivora_piveteaui	*Bat-3’09.1000*	Post-m1	34.78	12.12	55.83	1439.44	501.83	25.78	169.63%
Mellivora_capensis	*LACM (M) 28,121*	p3-p4	15.17	7.66	59.51	173.04	87.35	2.91	81.42%
Mellivora_capensis	*LACM (M) 28,121*	p4-m1	15.03	8.01	50.96	177.55	94.60	3.48	29.11%
Mellivora_capensis	*LACM (M) 28,121*	Post-m1	17.60	7.62	37.87	231.63	100.21	6.12	40.24%
Mellivora_capensis	*MVZ 184107*	p3-p4	15.10	7.91	59.85	176.95	92.69	2.96	82.79%
Mellivora_capensis	*MVZ 184107*	p4-m1	14.25	7.96	50.41	158.77	88.73	3.15	26.32%
Mellivora_capensis	*MVZ 184107*	Post-m1	17.88	6.90	36.99	216.63	83.64	5.86	38.53%
Sonitictis moralesi	*IVPP V28317*	p3-p4	25.13	10.43	78.49	646.59	268.34	8.24	230.67%
Sonitictis moralesi	*IVPP V28317*	p4-m1	26.03	10.67	66.55	709.73	291.02	10.66	89.12%
Sonitictis moralesi	*IVPP V28317*	Post-m1	28.19	11.55	52.98	901.10	369.20	17.01	111.90%

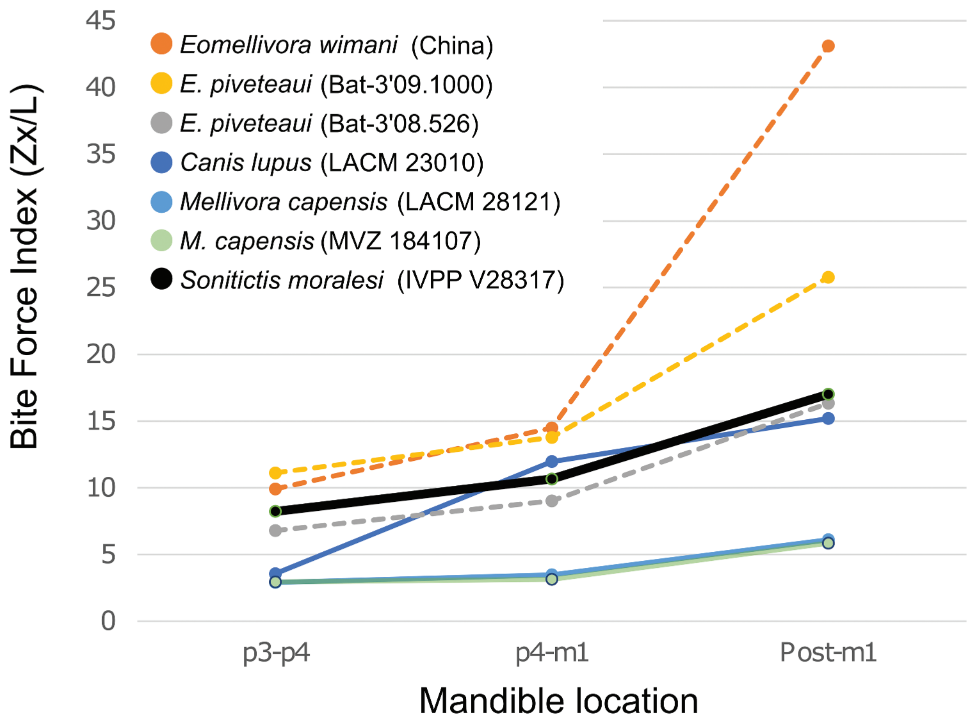

Figure 7. Bite force indices of *Sonitictis moralesi* and several extant and extinct badger species. Dorsoventral mandibular forces (Zx/L; section modulus about the mediolateral axis/lever arm length) at interdental gaps between p3, p4, m1, and at the post-m1 positions, respectively.

capable predator and decimator of vertebrate prey than the extant *Mellivora*, reaching the low end of the bite force estimates for the larger and more robust *Eomellivora*. In turn, these two fossil honey badgers were capable of bite force magnitudes that rival living top predators such as *Canis lupus*, as also shown in other extinct mustelids (Valenciano et al. 2016b).

The general interpretations of *Sonitictis* functional morphology from mandibular profile analysis are consistent with those inferred from dental and mandibular characteristics (see specimen descriptions above), although our reconstruction of its missing ascending ramus based on modern *Mellivora capensis* is speculative (Fig. S1) and can only be verified by future discoveries of better materials. Additionally, the shortened jaw of *Sonitictis* relative to *Eomellivora* may represent further differentiation of feeding strategy in the former, but will require larger sample sizes to tease out the significance of such morphological differences for jaw biomechanics.

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Data availability statement

3D models for the holotype of *Sonitictis moralesi*, two lower jaws of *Mellivora capensis* (LACM (M) 23010 and MVZ 184107), one lower jaw of *Eomellivora wimani* (LACM 162597) and one lower jaw of *Canis lupus* (LACM (M) 23010) in the functional morphology analysis are deposited at MorphoSource (https://www.morphosource.org/dashboard/collections/000385219/edit?locale=en&). See also Materials and Methods section for weblinks of individual specimens.

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