

# DESCRIPTION OF A NEW LATE MIOCENE AMERICAN BADGER (TAXIDIINAE) UTILIZING HIGH-RESOLUTION X-RAY COMPUTED TOMOGRAPHY

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**Abstract:** *Chamitataxus avitus* gen. et sp. nov. is a primitive American badger recovered from late Miocene fossil-bearing sediments of the Chamita Formation in northern New Mexico, USA. The holotype and only known specimen is an almost complete skull with left and right I1-M1. Description of *Chamitataxus avitus* is facilitated by high-resolution X-ray computed tomography (HRXCT), which provides non-destructive visualization of the internal morphology. Features such as the hollowing of the mastoid region and the septate and greatly inflated tympanic bulla of *Chamitataxus avitus* are made visible and provide evidence supporting Taxidiinae. The invasion of the nasal bone by a small sinus, the nasosconchal sinus, is documented for the first time in both *Tax-*

*idea taxus* and *Chamitataxus avitus*. The HRXCT data complement information obtained from external and more traditional examination of the skull. The P4 does not exhibit the development of a medial shelf and hypocone observed in *Pliotaxidea* and *Taxidea*. This is evidence for the acquisition of a P4 medial shelf and hypocone by taxidiine badgers independent from that of meline (Eurasian) badgers. The morphological information obtained from this study provides new insight into the evolution and ecomorphology of taxidiine badgers.

**Key words:** badger, Taxidiinae, mustelid, ecomorphology, Miocene, computed tomography.

AMERICAN badgers (Taxidiinae) are medium-sized mustelid carnivorans with a complex dentition and morphological adaptations for excavating fossorial prey. Despite a fair representation in late Cenozoic deposits of North America, the taxidiine badgers do not have an extensive fossil record. Previous to this study, only two genera, the extant *Taxidea* and the extinct *Pliotaxidea*, have been described and included in Taxidiinae. A new high-resolution computed tomographic analysis of previously undescribed material from New Mexico reveals the existence of a primitive species of American badger from the late Miocene.

The oldest *Taxidea* material is about 4.5 myr old and was recovered from the Río Papigochic Valley near Rincon and Yepómera, Chihuahua, Mexico (Drescher 1939; Stock 1948; Lindsay *et al.* 1984). *Taxidea taxus* currently ranges from the western United States, southern British Columbia and northern Alberta, eastward into Ohio and southern Ontario, Canada. Its southern distribution includes Baja California and northern and central Mexico (Long 1972; Hall 1981).

*Pliotaxidea* is restricted to the Hemphillian and includes two species, *P. garberi* and *P. nevadensis*. Its presence is recorded in several western and plains states, including Texas, where it is a member of the type fauna at Coffee Ranch (Dalquest 1969). The earliest recorded appearance of *Pliotaxidea* is early Hemphillian (6.5–6.7 Ma) in the Star Valley local fauna, south-western Idaho (Becker and McDonald 1998).

In 1935 a field party from the Frick Laboratory of the American Museum of Natural History collected the skull of a badger-like mustelid from the Tertiary fossil-bearing sediments of the Santa Fe Group in northern New Mexico. Comparison of this specimen with cranial material of *Pliotaxidea* and *Taxidea* confirms that it is indeed a taxidiine badger and warrants the designation of a new genus and species. The detailed description of the new taxon is facilitated by high-resolution X-ray computed tomography (HRXCT), which provides non-destructive visualization of the internal morphology.

## GEOLOGICAL SETTING AND DETERMINATION OF GEOLOGICAL AGE

### Locality information

The skull was collected from the central Española Basin, near Lyden, Rio Arriba County, New Mexico in 1935 by a Frick Laboratory field party from the American Museum of Natural History. The locality is the Lyden Quarry ('*Osbornoceros* Quarry' of Galusha and Blick 1971, p. 76), Chamita Formation (late Miocene), within the Velarde Graben on the south side of Black Mesa and east of the Rio Grande River (Text-fig. 1).

### Fission-track dating and magnetostratigraphy

Fission-track dates have been obtained from the type section of the Chamita Formation. MacFadden and Manley (1976) obtained a zircon fission-track age of  $5.6 \pm 0.9$  Ma from a pumice layer near the top of the 'Upper Tuffaceous Zone'. The Lyden Quarry, unlike the AMNH quarries (San Juan and Rak Camel) located within the base of the tuffaceous zone, is some distance from the type section of the Chamita Formation worked by MacFadden (1977), yet magnetostratigraphic data from the 'Upper

Tuffaceous Zone' suggest a possible age estimate for the Lyden Quarry deposits. This zone was previously correlated with Chron 6 of the Geomagnetic Polarity Time Scale (GPTS, calibrated by Berggren *et al.* 1985), between 6.7 and 6.5 Ma (Tedford and Barghoorn 1993). Utilizing the revised calibration of the GPTS by Cande and Kent (1992, 1995), the 'Upper Tuffaceous Zone' may be correlated with C3Br, with an estimated age between 7.1 and 7.3 Ma.

### Mammalian biochronology

The local fauna from the San Juan and Rak Camel quarries is late Hemphillian, with several forms typical of the age (MacFadden 1977). Taxa include: *Plesiogulo* sp. (extinct wolverine); the equids *Astrohippus ansae* and *Dinohippus interpolatus*; the camelids *Hemiauchenia* sp. and *Megatylopus matthewi*; the antilocaprids *Ilingoceros* and cf. *Plioceros*; *Dipoides williamsi* (beaver), '*Canis*' *davisi* (canid) and *Pliotaxidea garberi*. The presence of *Pliotaxidea* introduces the interesting possibility of sympatry with the new taxidiine.

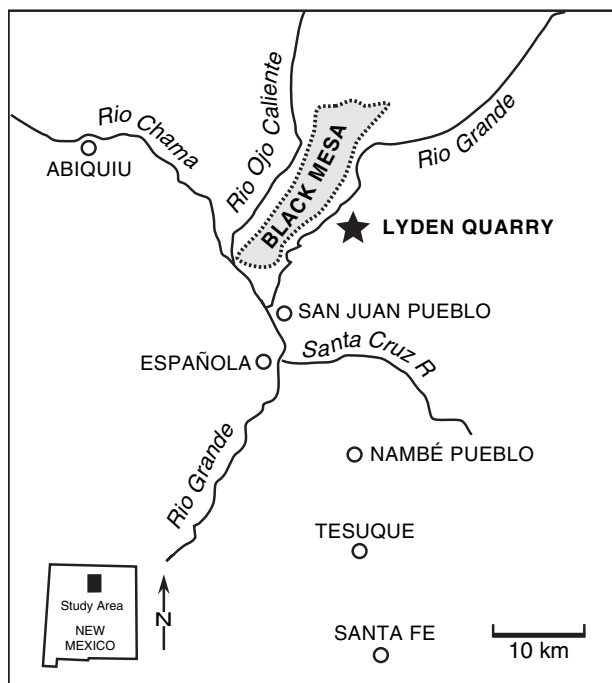
Associated with the new taxidiine at the Lyden Quarry are the antilocaprids *Osbornoceros osborni* and *Plioceros blicki*; the canids *Vulpes stenognathus*, *Osteoborus secundus* and *Canis* sp.; and the giant camel *Megatylopus*. This local fauna may be equated with the late Hemphillian local fauna of the 'Upper Tuffaceous Zone' (Tedford and Barghoorn 1993). However, *Osbornoceros* has not been reliably identified from the type section of the Chamita Formation (Tedford, pers. comm. 1998).

*Osbornoceros* is also associated with a transitional Clarendonian–Hemphillian fauna in the Gabaldon Badlands of the southern Albuquerque Basin (Lozinsky and Tedford 1991). Tedford (pers. comm. 1998) has suggested that perhaps the Lyden Quarry may lie below the strata in the type Chamita Formation. Based upon the combined biochronological and magnetostratigraphical data, the age of the new taxidiine may be safely estimated as being no younger than 7.3 Ma.

## MATERIAL AND METHODS

### High-resolution X-ray computed tomography (HRXCT)

**Data acquisition.** In addition to a more traditional approach to the description of the skull of the new taxidiine (Text-fig. 2), I have incorporated images of the skull generated by high-resolution computed tomography. The scans were obtained using an industrial-grade scanner equipped with an 'Ultra High-Resolution Image Intensifier System' with a microfocal X-ray



**TEXT-FIG. 1.** Map of the central Española Basin, northern New Mexico, USA, showing the type locality for *Chamitatus avitus*, F:AM 27458.

source at The University of Texas High-Resolution X-ray Computed Tomography Facility (for a description of the facility and techniques, see Ketcham and Carlson 2001). Exported scan data were adjusted and digitally 're-sliced' to create images in all three slice planes (coronal, sagittal, horizontal). Details pertaining to the scan parameters and data processing are included with the slice animations in supplemental data files on the Palaeontological Association website (<http://palass.org>).

*Labels and anatomical abbreviations.* The following label colour and abbreviation style conventions were followed for labelling the slice images in the animations: (1) red/abbreviation in upper case for bones; (2) yellow/abbreviation in lower case for foramina, processes, sulci and other structures; and (3) white/abbreviation in mixed case for dentition and dental structures. A slash (/) between two labels indicates an equivocal identification (e.g. bone in the region of the approximated suture between the alisphenoid and the orbitosphenoid is labelled AS/OS).

All but a few of the abbreviated anatomical terms are found in their Latin form in the fourth edition of *Nomina Anatomica Veterinaria* (Frewein *et al.* 1994). New terms of my creation are so noted in the description. A list of anatomical features, synonyms, and the abbreviations used on the HRXCT images is provided in the supplemental data files on the Palaeontological Association website. A shortened explanation of abbreviations is given below. Within the following description of the new taxidiine, referral to images in each of the three slice planes includes a letter descriptor for the plane (i.e. C for coronal, S for sagittal and H for horizontal) followed by the slice number (found in the upper left-hand corner of each slice image).

*Three-dimensional volume renderings.* The original scan data were volume-rendered to produce three-dimensional reconstructions of the fossil. These reconstructions are in the form of animations that rotate along each of three planes. The animations may be found on the Palaeontological Association website under supplemental data; they present more detailed views of the specimen than those provided by traditional illustrations.

#### *Anatomical comparisons*

A skull of a subadult extant American badger, *Taxidea taxus* (MVZ 52125), was also scanned using HRXCT and the generated data set has been of incomparable value for identification of complex internal structures in the new taxidiine. Ontogenetic changes in the skull of

*Taxidea taxus* include the fusion of cranial sutures, which is complete in individuals several years in age (Long 1974). The advantage of using a subadult *Taxidea* for comparison with an adult fossil taxidiine is in having an essentially full grown individual with unworn permanent dentition and cranial sutures that are not completely obliterated. I estimated the relative positions of the cranial sutures in the new taxidiine to assist in the labelling of computed tomographic images of the skull. Full-size animations of the *Taxidea* data set may be found in the supplemental data on the Palaeontological Association website. The crania of other mustelids, including *Pliotaxidea*, *Arctonyx* (hog badger) and *Meles* (Eurasian badger), were also examined. A list of catalogued specimens studied may be found in Owen (2000).

*Institutional abbreviations.* AMNH, American Museum of Natural History, New York; FAM, Frick American Museum Collection, American Museum of Natural History, New York; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley, California; all USA.

*Anatomical abbreviations for cranial bones labelled on the HRXCT images.* AS, alisphenoid; BO, basioccipital; BS, basisphenoid; ECT, ectotympanic; ENT, entotympanic (no differentiation between rostral and caudal); ET, ethmoid; EO, exoccipital; FR, frontal; IN, incus; JU, jugal; LA, lacrimal; ML, malleus; MT, maxilloturbinate; MX, maxilla; NA, nasal; OC, occipital = fused exoccipitals, basioccipital and supraoccipital; OS, orbitosphenoid; PA, parietal; PE, petrosal; PL, palatine; PRS, presphenoid; PMX, premaxilla; PT, pterygoid; SO, supraoccipital; SQ, squamosal; TB, tympanic bulla; VO, vomer.

*Anatomical abbreviations for processes, foramina and other features labelled on the HRXCT images.* acf, anterior carotid foramen; cc, cranial cavity; cg, crista galli (of the ethmoid); chg, chiasmatic groove; co, cochlea; coc, condyloid canal; cp, cribriform plate of the ethmoid bone; cpf, caudal palatine foramen; crc, crista conchalis; cw, cochlear window; dnm, dorsal nasal meatus; ds, dorsum sellae; eacc, external aperture of carotid canal; eam, external auditory meatus; ec, ectoturbinate (undifferentiated) of the ethmoid; ec 1, ectoturbinate 1 of the ethmoid; efm, ethmoid foramen; en, endoturbinate (undifferentiated) of the ethmoid bone; en I, endoturbinate I; ena, external nares; eoc, external occipital crest; eop, external occipital protuberance; et, undifferentiated endo and ectoturbinate; etr, epitympanic recess; fc, facial canal; fmg, foramen magnum; fmov, fossa for m. obliquus ventralis of the eye; fo, foramen ovale; fr, foramen rotundum; fs, frontal sinus; gf, glenoid fossa; hf, hypoglossal foramen; hyf, hypophyseal fossa; iam, internal auditory meatus; icc, internal carotid canal; ioc, infraorbital canal; iof, infraorbital foramen; ipf, internal plate of the frontal; ina, internal nares; jf, jugular foramen; jp, jugular process; ldc, lambdoidal crest; lf, lacrimal foramen; lfs, lacrimal fossa; lis, lamella(e) intrasinuales; mbs, minor bullar septum; mp, mastoid process; mpf, major palatine foramen; mr, maxillary recess;

mss, mastoid sinus; mtc, musculotubular canal; mxp, maxillary process of premaxilla; ncs, nasoconchal sinus; npm, nasopharyngeal meatus; obs, oblique bullar septum; occ, occipital condyle; of, orbital fissure; opc, optic canal; opf, optic foramen; ot, osseous tentorium; pac, parasagittal crest; pc, petrosal crest; pcf, posterior carotid foramen; pclp, posterior clinoid process; pcp, paroccipital process; pf, palatal fissure; pgf, postglenoid foramen; pgg, postglenoid process; plf, posterior lacerate foramen; plp, palatine process of the premaxilla; pop, postorbital process of the frontal; pp, perpendicular plate of the ethmoid bone; pr, promontorium of petrosal; sds, sulcus for dorsal sagittal sinus; sdps, sulcus for dorsal petrosal sinus; smf, stylomastoid foramen; spf, sphenopalatine foramen; spn, septal process of the nasal; ss, sphenoidal sinus; ssc, semicircular canal; ssf, frontal sinus septum; ssg, sulcus for the sigmoid sinus; sst, sulcus for the transverse sinus; svps, sulcus for ventral petrosal sinus; tbs, transverse bullar septum; tc, temporal canal; tm, temporal meatus; ts, tuberculum sellae; tsc, transverse sinus canal; ves, vestibule; vnm, ventral nasal meatus; vps, vagina processus styloidei (pit for tympanohyal); zps, zygomatic process of the squamosal.

*Anatomical abbreviations for dentition and dental structures labelled on the HRXCT images.* C, upper canine; Cr, root of upper canine; I1, upper 1st incisor; I1r, root of upper 1st incisor; I2, upper 2nd incisor; I2r, root of upper 2nd incisor; I3, upper 3rd incisor; I3r, root of upper 3rd incisor; M1, upper 1st molar; M1mc, metacone of upper 1st molar; M1pa, paracone of upper 1st molar; M1ps, parastyle of upper 1st molar; M1rab, anterior buccal (labial) root of upper 1st molar; M1rli lingual root of the upper 1st molar; P2, upper 2nd premolar; P2ra, anterior root of upper 2nd premolar; P2rp, posterior root of upper 2nd premolar; P3, upper 3rd premolar; P3ra, anterior root of upper 3rd premolar; P3rp, posterior root of upper 3rd premolar; P4, upper 4th premolar; P4mc, metacone of upper 4th premolar; P4ms, metastyle of upper 4th premolar; P4pa, paracone of upper 4th premolar; P4pr, protocone of upper 4th premolar; P4ps, parastyle of upper 4th premolar; P4rab, anterior buccal (labial) root of upper 4th premolar; P4rli, lingual root of upper 4th premolar.

## SYSTEMATIC PALAEOLOGY

CARNIVORA Bowdich, 1821

CANIFORMIA Kretzoi, 1945

ARCTOIDEA Flower, 1869

MUSTELIDAE Fischer von Waldheim, 1817

TAXIDIINAE Pocock, 1920

Genus CHAMITATAXUS gen. nov.

*Derivation of name.* Spanish, *Chamita*, little Chama, in reference to the formation from which the fossil was recovered, and Latin, *Taxus*, badger.

*Type and only known species.* *Chamitataxus avitus* sp. nov.

*Diagnosis.* As for *Chamitataxus avitus* gen. et sp. nov., below.

*Chamitataxus avitus* sp. nov.

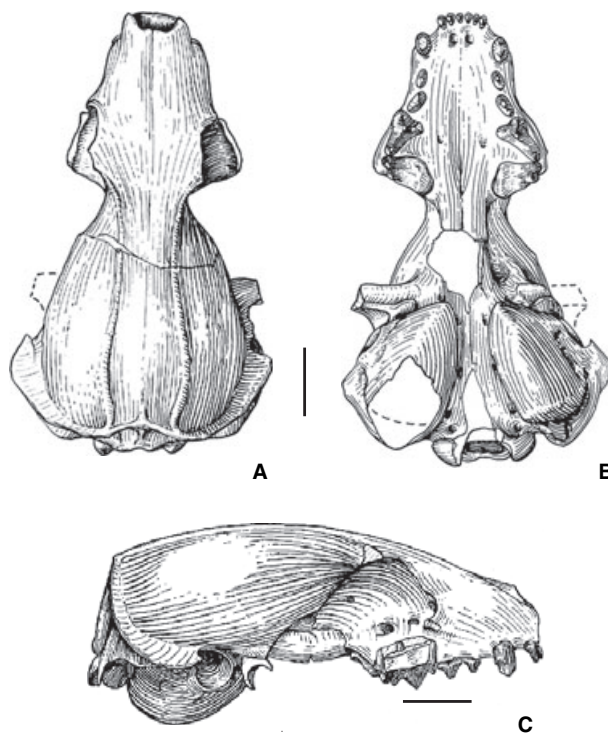
Text-figures 2–5

*Derivation of name.* Latin, *avitus*, ancient.

*Material.* Holotype and only specimen, F:AM 27458: an almost complete skull with left and right I1-M1.

*Locality and horizon.* Frick Laboratory (AMNH) locality ESP. 251-535, Lyden Quarry (= *Osbornoceros* Quarry), central Española Basin, south side of Black Mesa, east of the Rio Grande River, Rio Arriba County, New Mexico; Chamita Formation of the Santa Fe Group (late Miocene).

*Diagnosis.* Differs from other members of Taxidiinae *Pliotaxidea* and *Taxidea* in its small adult size, small calibre of the infraorbital canal, occiput (supraoccipital shield) not broadened laterally, P4 without a medial shelf and hypocone, M1 with a less expansive posterolingual cingulum (such that M1 is less triangular in shape), palatal fissures circular in outline, and raised parasagittal crests on the skull.



**TEXT-FIG. 2.** *Chamitataxus avitus* gen. et sp. nov., F:AM 27458, holotype. A, dorsal, B, ventral, and C, right-lateral views of the skull. Scale bars represent 10 mm.

## Description

### General consideration of the skull

The greatest length of the skull (rostral border of the premaxilla to the caudal edge of occipital condyle) is 72.30 mm (Text-fig. 2). The greatest breadth (as measured across the mastoid processes of the petrosal) is 42.93 mm. Because this is the only known specimen of this species, the size range of this taxon is unknown. However, this individual was an adult at time of death, as indicated by fully erupted and heavily worn M1s (Text-fig. 3) and a lack of visible cranial sutures. Several cranio-dental measurements were taken with digital calipers (to the nearest 0.01 mm) and are given in Table 1.

The external surface of the skull is completely free of matrix. The nasal, cranial and bullar cavities are completely infilled with a light brown fine-grained sandy siltstone matrix. The skull has undergone some minor torsion and has been slightly crushed during preservation. It exhibits two post-mortem fractures (one at the right maxilla and the other encircling the rostral border of the cranium). Those measurements affected by the above are flagged. Features of the skull most relevant for understanding badger ecomorphology and phylogenetic relationships are presented in the following sections.

### Bones of the cranium, including the otic region

*Occipital.* The occiput in dorsal view is triangular in form, as is characteristic of taxidiine badgers. The supraoccipital shield is pentagonal in shape, not low and laterally broadened as in *Taxidea* and *Pliotaxidea*. The lambdoidal crest is robust (Text-fig. 4A) and extends rostrolaterally onto the mastoid portion of the petrosal. The degree of development of the lambdoidal crest

equals or surpasses that of *Taxidea*; thus, fossorial capabilities may be inferred, given the importance of the lambdoidal crest and mastoid as attachment sites for pectoral limb and neck-activating musculature. Additionally, on either side of the external occipital crest are deep pockets, which may have served to anchor head and neck-activating musculature; see Hall (1927) and Quaife (1978) for descriptions of the musculature of *Taxidea*.

The osseous tentorium (C 31–89; S 55–195; H 36–75; Text-figs 4A, 5), which is visible only in the HRXCT images, projects obliquely toward the rostrum from the internal wall of the supraoccipital to separate the cerebral and cerebellar fossae. The dorsal contact of the tentorium is at the internal occipital protuberance, a thickened region of the internal lamina of the supraoccipital. This contact is higher in position than that exhibited by the tentorium of *Taxidea*, which contacts the internal lamina of the supraoccipital level with the midpoint between the lambdoidal crest and the dorsal margin of the foramen magnum (Text-fig. 6A).

HRXCT images in the horizontal plane illuminate the walls of both jugular foramina and one can trace their path into the sulcus for the sigmoid sinus (C 40–45; H 108–114). The jugular foramen and posterior lacerate foramen are confluent (Text-fig. 4B), not separate, as exhibited by *Taxidea* (Text-fig. 6B), the meline badgers *Arctonyx* and *Meles*, and the ratel, *Mellivora*. *Pliotaxidea* possesses a confluent foramen (Owen 2000) and there is some variation in the degree of separation in *Arctonyx* and *Meles* (Bryant *et al.* 1993).

*Parietal.* An external sagittal crest, which marks the extent of the origin of the primary jaw-closing muscle, the m. temporalis, is not present at the dorsal midline. However, commencing at

**TABLE 1.** Measurements of *Chamitataxus avitus* gen. et sp. nov. (F:AM 27458).

Morphometric variable	Measurement (mm)
Greatest length of the skull (anterior premaxillary to caudal edge of occipital condyle)	72.30
Length from mid-alveolus of the upper canine to the occipital condyle	65.77
Breadth across the rostrum above the canines	16.95
Breadth across the postorbital processes	18.04*
Breadth across the postorbital constriction	12.91
Length of the palate as measured from anterior premaxilla to posterior border of palate	35.52*
Palatal width at canines	9.52
Palatal width at M1	9.04*
Length of the canine as measured from mesial to distal borders of the alveolus	4.20 (r)
Width of the canine as measured from buccal to lingual borders of the alveolus	3.17 (r)
Length of the maxillary tooth row	26.05 (l); 25.95 (r)
Length of cheek teeth (P2 mesial border to M1 distal alveolar border)	20.93 (l)
P4 length as measured on buccal side	8.20 (l); 7.80* (r)
Width of the P4 protocone (buccal border to the edge of the protocone)	5.20 (l)
Greatest transverse width of M1	7.60 (l); 7.70 (r)
Greatest mesial–distal length of the lingual lobe of M1	6.60 (l); 6.40 (r)
Greatest mesial–distal length of the buccal lobe of M1	4.20 (l); 4.10 (r)
Occipital breadth as measured across mastoid processes	42.93
Occipital depth (measured from dorsal lambdoidal crest to ventral border of foramen magnum)	19.94
Breadth across occipital condyles	16.43
Greatest anterior–posterior length of tympanic bulla	21.45 (l)

\* Approximate; (l), measurement taken on left; (r), measurement taken on right.

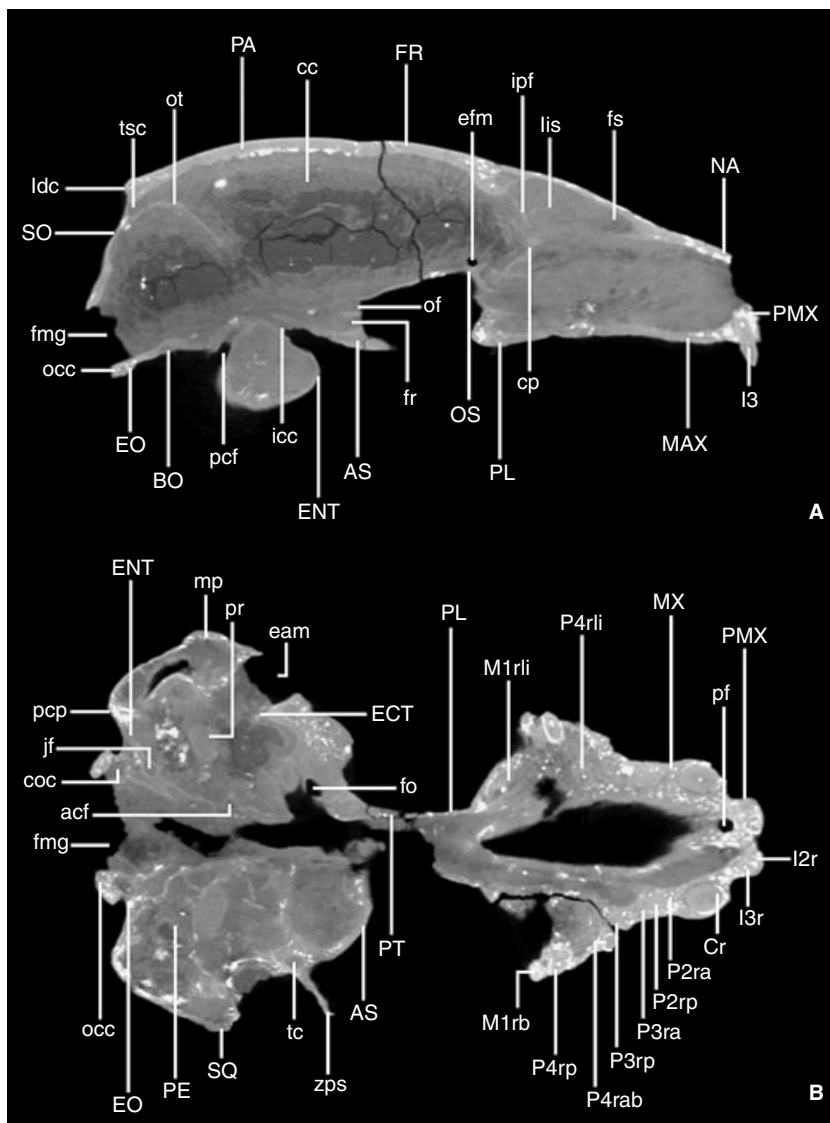


**TEXT-FIG. 3.** *Chamitataxus avitus* gen. et sp. nov., F:AM 27458, holotype; occlusal view of the upper right dentition. Scale bar represents 10 mm.

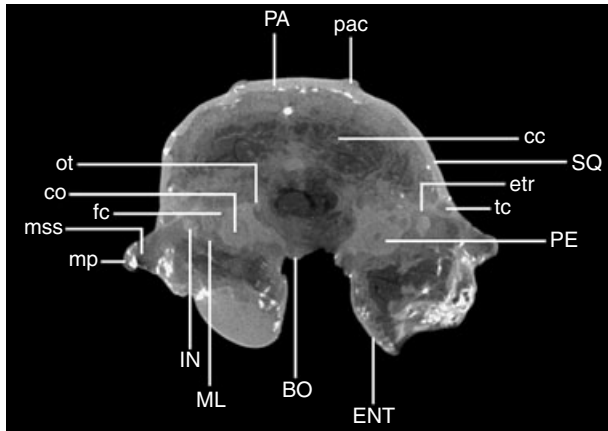
the lambdoidal crest, two parasagittal crests extend rostrally over the parietal and onto the frontal, where they continue to the postorbital process of the frontal (Text-figs 2A, 5). The parasagittal crests are similar to those exhibited by *Melogale* (ferret badger) and the Oligocene mustelid *Plesictis genettoïdes* (Helbing

1930, pl. 1; pers. obs. on *Melogale*). They are unlike the low ridges exhibited by subadult and some adult *Taxidea* and the type of *Pliotaxidea garberi* described by Wagner (1976). The crests are roughly parallel, slightly bowing midway along the rostral-caudal length of the parietal and extending caudally to intersect the lambdoidal crest at near right angles. Those exhibited by *Taxidea* and *Pliotaxidea garberi* diverge caudally to merge into the lambdoidal crest. The crests are thick, with distinct medial and lateral walls, the lateral being the most vertical. They do not, however, reach the tall, robust state of the parallel crests exhibited by the extinct mustelid, *Leptarctus*.

*Frontal.* Within the rostral half of each frontal bone are the frontal sinuses (C 239–322; S 68–158; H 19–59), which appear to be separated into three major compartments as in *Taxidea* (see S 106–111; Text-fig. 6A). The three sinuses do not appear to communicate, but all open into the nasal cavity. The sinuses are subdivided by a ‘honeycomb’ of osseous plates (lamellae intrasinuales) that create blind cavities.



**TEXT-FIG. 4.** *Chamitataxus avitus* gen. et sp. nov., F:AM 27458, holotype. A, sagittal slice 105 from the HRXCT data set, illustrating the observed morphology in the sagittal plane at the level of the left I3. B, horizontal slice 115 from the HRXCT data set, illustrating the observed morphology in the horizontal plane at the level of the palate. For explanation of abbreviations, see text; for detailed list, see supplemental data files on the Palaeontological Association website (<http://palass.org>).



**TEXT-FIG. 5.** *Chamitataxus avitus* gen. et sp. nov., F:AM 27458, holotype; coronal slice 085 from the HRXCT data set, illustrating the observed morphology in the coronal plane at the level of the otic region. For explanation of abbreviations, see text and supplemental data files on the Palaeontological Association website (<http://palass.org>).

Ectoturbinate may invade the sinuses as in *Taxidea*, but the HRXCT data do not provide enough resolution to be certain.

**Ethmoid.** The ethmoid is visible only in the HRXCT images. The cribriform plate (C 236–245; S 105–146; H 40–85) is perforated by numerous foramina, which transmitted the olfactory nerve bundles. Discrete foramina cannot be readily identified in the scan images, but the mesh-like appearance created by the foramina and the attachments of the ethmoturbinate are evident. On the caudal surface of the cribriform plate the crista galli (slice C 235–238) thinly separates the two ethmoidal fossae, into which the olfactory bulbs of the brain were lodged. The margins of the fossae are weakly discernible, but the olfactory bulbs must have been of good size, based on the convex shape of the floor of the frontal sinuses in C 238–240 and the dorsal margins seen in H 40. The fossae appear to maximize the space in the postorbital constriction for large olfactory bulbs. The weak nature of the crista galli and relatively large size of ethmoidal fossae in most carnivores indicate the relative importance of the olfactory capabilities in these mammals (Negus 1958; Evans 1993).

The ethmoturbinate, being of such a delicate nature, are not well preserved. Given the minimal density contrast between the matrix and the ethmoturbinate within the nasal cavity, the actual intricacy of the elements preserved is not evident in the HRXCT images. Thus, information on the extent and complexity of the ethmoturbinate is not available. Specific ethmoturbinate, endoturbinate I and ectoturbinate 1, are described under ‘Nasal conchae’.

**Squamosal.** The postglenoid process (S 48–75, 180–195) is well developed bilaterally, curling rostrally to create the caudomedial portion of the glenoid fossa (S 55–75, 180–222). The configura-

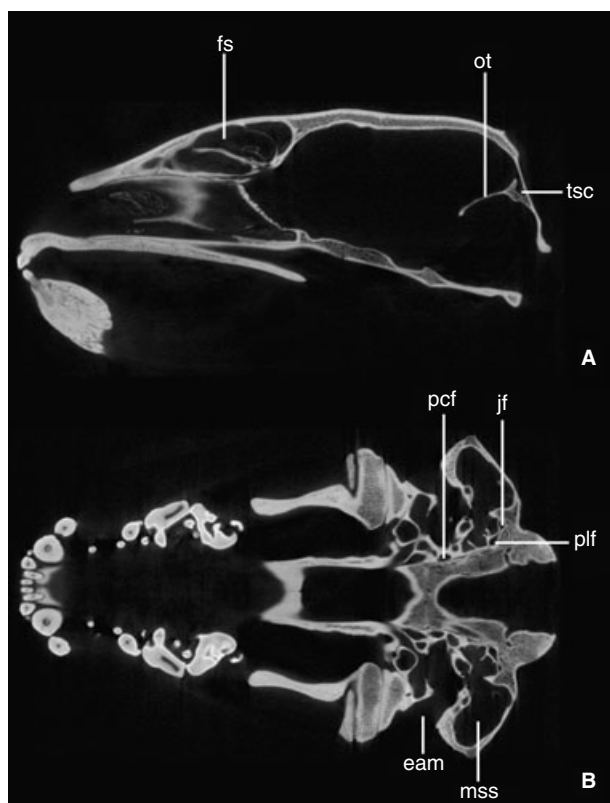
tion of the glenoid region is typical of many mustelids of advanced ontogenetic age, creating an articulation with the condylar process of the dentary that restricts lateral movement within the joint. The development of a narrow glenoid with a pronounced rostral lip is characteristic of *Taxidea*, providing a means to preserve an effective bite when the head is lowered and the chin is pressed against the substrate, as when *Taxidea* captures prey within a burrow (Long 1965). The killing bite employed by *Taxidea* on ground squirrels is a single controlled grasping bite to the thoracic region (Michener and Iwaniuk 2001). The restricted lateral movement of the dentaries certainly must contribute to the effectiveness of the bite.

The mastoid is inflated and the sinus created within (C 25–92; S 21–60; H 84–111) is connected to the middle ear cavity through the caudal bullar cavity (Text-fig. 5). The inflation of the mastoid is not the same as that exhibited by Mephitidae (skunks), in which the middle ear cavity invades the caudolateral portion of the mastoid and squamosal via an opening in the epi-tympanic recess (Pocock 1921; Segall 1943; de Muizon 1982; Bryant *et al.* 1993; pers. obs. on *Conepatus* and *Mephitis*). The caudal expansion of the middle ear cavity into the mastoid and paroccipital processes is as extreme as that exhibited by *Taxidea* (Text-fig. 6B) and *Pliotaxidea*. The extant African mustelids *Ictonyx* (zorilla; includes *Poecilictis*, North African striped weasel) and *Mellivora* (ratel) exhibit a similar hollowing of the mastoid (Pocock 1921; pers. obs. on *Mellivora*), but not to the extent observed in taxidiine badgers.

**Tympanic bulla.** The tympanic region is notable in taxidiine badgers by virtue of its inflated and septate bullae. When viewed ventrally, the bullae are markedly large, encompassing 30 per cent of the total rostrocaudal length of the skull. As in *Taxidea*, the rostral inflation of the tympanic bulla almost obscures from view the external opening of the foramen ovale (H 109–115; Text-fig. 4B) and the opening to the musculotubular canal.

Both tympanic bullae have suffered some minor compressional damage and the right bulla is broken caudally, exposing an infilling of matrix (Text-figs 2B, 5). The caudal entotympanic is the primary element involved in the inflation of the bulla in non-otter mustelids (the ‘Type B’ bulla of Hunt 1974). The ectotympanic forms the floor and walls of a very short tube, as seen in *Taxidea* and *Pliotaxidea*, but unlike the long tube exhibited by the meline badgers, including the fossil forms *Melodon* and *Parataxidea*.

As characteristic of taxidiine badgers, the tympanic bulla is highly septate. Minor bullar septae (e.g. S 150; H 110) radiate from the promontory of the petrosal to contact the bullar wall. A large oblique bullar septum (C 103–107; S 79–89, S 172–183; H 123–134) commences at the anterior wall of the bulla and extends caudolaterally to form a plate, essentially dividing the rostral two-thirds of the bullar cavity into dorsal and ventral chambers. A caudal transverse bullar septum (C 29–41, 60–66; H 123–134) extends from the internal border of the external auditory meatal tube to the medial wall of the bulla, creating a small caudal cavity and a larger rostral cavity. As in *Taxidea*, the transverse septum does not completely close off the bulla behind the promontorium, as there appears to be an airspace connec-



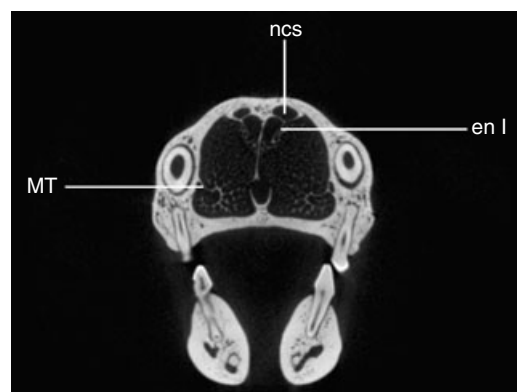
**TEXT-FIG. 6.** Skull of Recent *Taxidea taxus* (MVZ 52125). A, sagittal slice from the HRXCT data set, illustrating the observed cranial morphology at the level of the right II. B, horizontal slice from the HRXCT data set, illustrating the observed morphology at the level of the basisphenoid-basioccipital suture. For explanation of abbreviations, see text and supplemental data files on the Palaeontological Association website (<http://palass.org>).

tion between both the rostral and caudal chambers and the mastoid sinus.

#### *Bones of the rostrum and palate*

**Nasal.** A sinus associated with the rostral continuation of endoturbinate I opens in the caudal portion of each nasal (C 324–338; S 130–131) in a similar fashion to that of *Taxidea*. I have applied the name ‘nasoconchal sinus’ to this opening instead of the less positionally informative ‘sinus I’ of Paulli (1900). The rostral extent of the nasoconchal sinus is seen in the right nasal, at the level of the P2 in coronal section (C 338). The thin ventral floors are difficult, but not impossible, to discern as is the endoturbinate I (see description under ‘Nasal conchae’). The sinuses are bounded medially by the relatively thick and pentagonal-shaped septal processes and should not be confused with the dorsal nasal meatuses, passages medial to endoturbinate I. The nasoconchal sinuses appear at the level of the P2–P3 in coronal views (HRXCT data) of *Taxidea* (Text-fig. 7).

**Maxilla.** The left maxilla bears an incomplete infraorbital canal (C 302–311; S 60–72) because of preservational loss of most of



**TEXT-FIG. 7.** Skull of Recent *Taxidea taxus* (MVZ 52125). Coronal slice from the HRXCT data set, illustrating the observed morphology of the nasal region at the level of the P3. For explanation of abbreviations, see text and supplemental data files on the Palaeontological Association website (<http://palass.org>).

the jugal. However, enough of the canal is present to indicate that it is of relatively small calibre, much like that of most caniforms, but unlike the medium-sized canal exhibited by *Taxidea*, and the large canal exhibited by *Meles*, *Arctonyx* and otters.

A maxillary recess (C 297–308; H 78–97), which housed the lateral nasal gland (of thermoregulatory importance in carnivores; see Blatt *et al.* 1972), lies caudal to the crista conchalis. It is a shallow pocket in the maxilla and adjacent lacrimal, palatine and frontal bones. It is impossible to discern from the scan data whether the maxillary recess is devoid of ethmoturbinates, but if similar to the condition in *Taxidea*, the recess should be open.

**Premaxilla.** Caudal to the incisor row on the palatal surface, each premaxilla bears a palatal fissure (C 374–384; S 113–121, 128–137; H 113–121) that is circular in outline. Those of *Taxidea* and *Pliotaxidea* are oval in shape with caudal margins that are directed in a somewhat lateral direction. Other mustelids have elongate or oval palatal fissure margins.

**Palatine.** The caudal border of the ventral portion of the palatine has suffered some damage, but it clearly extends caudal to the M1 as in other mustelids. This arrangement extends the length of the hard palate and nasopharyngeal meatus. In mature taxidiine badgers, the suture between the palatine and frontal is obscured by the ventral orbital crest demarcating the extent of the jaw-closing muscle, m. pterygoideus medialis.

**Nasal conchae.** The HRXCT images providing views of the nasal cavity did not yield much detail on the complexity and arrangement of the nasal conchae (maxilloturbinate, endoturbinates and ectoturbinates) because of poor resolution.

Endoturbinate I is not visible in the scans throughout its length, but it is the longest turbinal element within the nasal cavity. It originates from the dorsal half of the cribriform plate of the ethmoid and extends rostrally to attach to the crista ethmoidalis of the nasal bone (e.g. S 113–116; H 64–71). Its attachment to the ventral floor of the nasoconchal sinus is faintly

visible in coronal section (C 330–337), but is more apparent just rostral to the cribriform plate (C 268–275).

The maxilloturbinate in *Taxidea* is very large with numerous branches and scrolls (Text-fig. 7). In the new taxidiine the base and a few branches of the maxilloturbinate are visible in coronal section at the level of P2–3 (C 330–339). The base of the maxilloturbinate attaches to the crista conchalis of the maxilla (e.g. C 355).

Only one ectoturbinate, number 1, may be positively identified in the HRXCT images. Ectoturbinate 1 arises from the cribriform plate of the ethmoid and continues rostrally, attached to the septum of the frontal bone. In coronal section, it appears as a small branch dorsal to endoturbinate I (e.g. C 270).

#### Dentition

*Incisors.* The incisors, three in each premaxilla, increase in relative size laterally. I1–2 are somewhat peg-like, while I3 is more robust. The lingual surfaces exhibit wear, giving the occlusal surface a distinctive bevelled appearance. The right I2 is damaged.

*Canine.* The canine is recurved and deep-rooted, the root extending into the maxilla such that it is visible dorsal to the P2 in coronal section (e.g. C 345). Both canines have broken tips, so the maximum length is not known.

*Premolars.* Three upper premolars are present in the maxilla (Text-fig. 3). P1 is absent as in other taxidiine badgers. P2 and P3 are unicuspid and each has an anterior and posterior root. The anterior half is deflected lingually, such that the tooth is not aligned with the anterior–posterior axis of the canine. The posterior half of P2 exhibits a weak posterior cingulum. P3, larger in size than P2, has a distinct posterior cingulum. The P4 is three-rooted (see H 115), the anterior and posterior labial roots externally exposed. It has a well-developed parastyle and an elongate, but worn metastylar blade that lacks a carnassial notch. The protocone is of moderate size and is separated from the more posteriorly placed paracone by a thick neck. Although worn, the P4 protocone is larger than that of *Martes* (marten), but not as large as those of *Taxidea* and *Pliotaxidea*. It is preserved on the left P4, but is broken on the right P4. The posterior face of the metacone abuts the M1 paracone. Unlike the P4s of *Taxidea*, *Pliotaxidea* and meline badgers, the P4 lacks a medial shelf and hypocone (Text-fig. 3).

*Molar.* The M1 has a large lingual root (see H 110) and a single buccal root (see H 115). There is no evidence of a third root as exhibited by the M1 of *Taxidea*. The parastyle is small. The lingual two-thirds of the occlusal surface of both left and right M1s is heavily worn (Text-fig. 3). When viewed posteriorly, the M1 is concave, with the parastyle as the highest point. The posterolingual cingulum, despite wear, is expanded. It imparts a shape to the M1 that is more triangular than those of most mustelids, although not to the extent demonstrated by *Pliotaxidea* and *Taxidea*. The M1 certainly does not exhibit the classic ‘dumb-bell’ morphology of *Martes* and *Mustela* (weasels). The right M1 retains the worn base of the protocone. Based on its position, it is likely that it was at the terminus of a preprotocrista that extended lingually instead of posterolingually (as in *Martes*, *Mustela* and

meline badgers). Unfortunately, the occlusal surface wear is so extreme that it is not known if the preprotocrista was composed of distinct cusps between the paracone and the protocone. Posterolingual to the metacone of the right M1 is a small accessory cusp, which is common to both taxidiine and meline badgers.

## DISCUSSION

### *Importance of the middle ear and nasal regions*

The utilization of HRXCT data for the description of *Chamitataxus avitus* contributes greatly to our understanding of the evolution of taxidiine badgers. The middle ear and nasal regions are particularly informative, providing characters for phylogenetic studies and investigations of ecomorphological evolution.

Within the bulla of many mustelids is a crest-like septum, termed the ‘posterior rafter’ by Pocock (1921). This transversely orientated septum, also identified by Segall (1943), divides the bullar cavity into a small rostral and a larger caudal chamber. It is present in the bullar cavity of taxidiine badgers *Chamitataxus*, *Pliotaxidea* and *Taxidea* as well as in *Galictis* (grison), *Gulo* (wolverine), *Ictonyx*, *Martes*, *Meles* and *Mellivora*. The development of the transverse septum in *Melogale* is so extreme that only a notch caudal to the promontorium allows communication between the chambers (Pocock 1921).

The presence of ‘partial transverse septa’ in *Taxidea* and other mustelids was first noted by Flower (1869). In his description of variation within the tympanic bulla in mustelids, Pocock (1921) elaborated on the observations presented by Flower (1869) by differentiating the large anterior and posterior ‘rafters’ and other septal structures. These other structures, or minor septae, vary in number and may be connected by spongy bone.

The arrangement of septae may be a difficult character to use in phylogenetic analyses of taxa within Arctoidea (Ivanoff 2001), but appear to be informative within Mustelidae. Taxidiine badgers have the most septate bullae.

In the bullae of arctoid carnivorans, inflation of several elements creates ‘transbullar sinuses’ (Ivanoff 2001), increasing the hypotympanic space. Large middle ear spaces in mammals have increased compliance, increasing sensitivity to low-frequency sound (Fleischer 1978; Relkin 1988). The mastoid sinus in *Chamitataxus*, *Pliotaxidea* and *Taxidea* is large, and inflation of the mastoid is visible externally. Its connection to the tympanic bulla must play a significant auditory role in these badgers.

The chambered inflated bulla in *Chamitataxus* must have increased sensitivity to the resonant frequencies within the ear. Mammals of small body size requiring low-frequency hearing are thought to have developed inflated bullae (Webster 1962; Webster and Webster 1975;

Fleischer 1978). Low-frequency hearing is of importance to mammals living in open habitats because low frequencies travel over long distances without losing informational content (Fleischer 1978). Consideration should be given to the relationships of bullar morphology and open environments when considering predatory style of taxidiine badgers.

Mammalian predators appear to be under strong selective pressure to localize sounds accurately (Heffner and Heffner 1984, 1987), which would be important for hunting prey in open habitats. Hall (1944) suggested that the bullae of *Pliotaxidea* and *Taxidea* amplified sounds to aid in detection of insect prey. However, fossorial rodents, not insects, are the primary component of the diet of *Taxidea* (Lampe 1976). Observations made by Lampe (1976) of the predatory behaviour of *Taxidea* indicate more attentiveness to auditory stimuli above ground than when digging.

Mammals with small heads and close-set ears are better able to hear high-frequency sounds (Heffner and Heffner 1985). *Mustela nivalis* (least weasel) is a small mustelid capable of hearing low-frequency sounds as well as high-frequency sounds (Heffner and Heffner 1985). These weasels typically hunt for small mice and microtine rodents, often in underground burrows (Sheffield and King 1994). *Mustela nivalis*, markedly smaller in body size than the taxidiine badgers, has inflated bullae filled with air cells, also exhibited by other species in *Mustela* (Pocock 1921; Owen 2000). The bullae of taxidiine and musteline mustelids represent two different, yet functionally similar adaptations for increasing auditory sensitivity.

The diversity of form and arrangement of nasal conchae is important for understanding relationships among the Carnivora, and has been an integral part of several studies of extinct and extant taxa (e.g. Anthony and Iliesco 1926; Joeckel and Stavas 1996; Joeckel *et al.* 2002). The delicate nature of these turbinate bones makes them excellent candidates for non-destructive analysis via computed tomography, as first demonstrated by Joeckel and Stavas (1996). Unfortunately nasal conchae in most fossil carnivorans do not preserve well (as in the case of *Chamitataxus*) or may be damaged in preparation, and thus much of the information is lost. However, the shapes of the frontal sinuses (which are invaded by ectoturbinate in *Taxidea*) and nasal cavity in *Chamitataxus* are similar to those of *Taxidea*, and may indicate a similar arrangement of internal structures.

The invasion of the nasal bone by a small sinus, the nasoconchal sinus, is documented for the first time in both *Taxidea* and *Chamitataxus*. The function of this sinus is not known, but perhaps serves as some kind of structural support or increased area for olfactory purposes. Joeckel (1998) utilized CT data to document the caudally elongate frontal sinus in hyaenine hyaenas and suggested

that it serves to provide increased resistance to muscular loading during biting. The nasoconchal sinus of taxidiines may also be related to an aspect of predatory behaviour. While digging in pursuit of prey, *Taxidea* often thrusts its nose into the hole as it is excavating, and uses its nose during search or investigative behaviour, keeping it near to the ground as the head is slowly swung side to side (Lampe 1976). *Taxidea* is able to detect hibernating subterranean prey as well as relocate cached prey (Michener 2000). Both behaviours require keen olfactory capabilities.

#### *Evolution of Taxidiinae and badger ecomorphology*

Long before the advent of modern phylogenetic analysis, Pocock (1920, p. 423) expressed a belief that the badgers *Meles* and *Taxidea* are not closely related and that 'likenesses between them are superficial, adaptive, and due to similarity of habits'. He described the anatomical features of badgers and other mustelids in detail and thus placed *Taxidea* in Taxidiinae (Pocock 1920). This arrangement was not widely accepted for some time, even with consideration of fossil taxa. The extinct Eurasian badgers *Melodon*, *Parataxidea* and *Promeles* were included in Melinae by Pilgrim (1932), with *Parataxidea* and *Taxidea* hypothesized as being most closely related. In his classification of mammals, Simpson (1945, p. 227) stated that 'Further separation of the badgers into different natural groups seems to me impossible or at least premature now.'

The examination of dental and tympanic characters in fossil and extant badger taxa by Petter (1971) led her to conclude that Melinae was not a 'natural unit' but an 'etho-ecological' grouping. This observation was a step in the right direction toward understanding badger phylogeny and ecomorphology, but Petter only separated badger taxa into smaller Linnaean tribes, including 'Melini' (includes *Arctonyx*, *Meles*, *Melodon* and *Parataxidea*) and 'Taxidini' (includes *Pliotaxidea* and *Taxidea*). Although Petter considered these groups as separate lineages, they were retained within 'Melinae'.

Upon consideration of craniodental data (including characters he considered convergent) and Petter's (1971) hypotheses, Long (1981) placed *Arctonyx*, *Meles*, *Melogale* and *Parataxidea* in 'Melini' and *Taxidea* and *Pliotaxidea* in 'Taxidiini'. Yet, the inclusion of *Taxidea* within Melinae was historically accepted (see Simpson 1945) for some time based on fossorial adaptations and possession of a P4 with a medial shelf and hypocone. The Simpsonian subfamilies were evaluated by Bryant *et al.* (1993) in their phylogenetic analysis of the morphology of extant mustelids. Melinae was found to be polyphyletic, with *Melogale* as the most basal mustelid, *Arctonyx* and *Meles* sister taxa, and the positions of *Mellivora* and *Taxidea* equivocal.

Analyses of dental characters in badgers (including several fossil taxa: *Arctomeles*, *Dehmictis*, *Iranictis*, *Pliotaxidea*, *Rhodanictis* and *Taxodon*) conducted by Ginsburg and Morales (2000) resulted in a hypothesized sister-taxon relationship of *Parataxidea* to *Pliotaxidea* + *Taxidea* based solely on the possession of a large P4 hypocone. *Chamitataxus avitus* provides evidence that the P4 hypocone evolved in taxidiine badgers independently from meline badgers, and supports the non-monophyly of badgers and independent ecomorphological evolution proposed by Bryant *et al.* (1993).

The late Miocene was the time of highest diversity for both taxidiine and meline badgers. By the latest Hemphillian, Taxidiinae was represented by three genera in North America, *Chamitataxus avitus* being the most primitive. Diversification of taxidiine badgers and their ecomorphological evolution was concurrent with significant environmental change. Data from palaeosol carbonates and fossil mammalian tooth enamel indicate that C<sub>3</sub> ecosystems (in reference to plants primarily using the Calvin photosynthetic cycle) were predominant in western North America before 7.5 Ma (Cerling *et al.* 1993, 1998b). The expansion of plants utilizing a C<sub>4</sub> photosynthetic pathway (e.g. warm-season grasses) was expeditious and synchronous in Asia, Africa and the Americas between 8 and 5 Ma (Cerling *et al.* 1993, 1997, 1998a). Modern C<sub>4</sub> ecosystems, including savannas, temperate grasslands, steppes and semi-desert scrublands, were essentially established by the Pliocene (Cerling *et al.* 1998b). At this time taxidiine badgers were able exploit new food resources (rodents exhibited marked diversification at this time; see Potts *et al.* 1992), their specialized morphology not only advantageous for excavating prey but also for setting up den sites within open habitats.

## CONCLUDING REMARKS

The craniodental data presented here establish *Chamitataxus avitus* as a taxidiine badger. Unfortunately, the specimen does not include the lower dentition or any postcranial material. It is unknown whether *Chamitataxus avitus* was fossorial, although the robust nature of the lambdoidal crest and the nature of the occipital infer powerful musculature that is comparable with that of *Taxidea taxus*. Features of the middle ear and nasal cavity certainly suggest adaptations for a predatory style similar to that of *Taxidea*.

We now know taxidiine badgers were more diverse in the late Miocene than previously understood. Discerning the timing and patterns of ecomorphological evolution is integral to elucidating the phylogenetic relationships of badgers to other mustelids. The utilization of information from the skull of *Chamitataxus avitus*, especially that

obtained by HRXCT, will be critical for identifying early branching events and patterns of convergence. The morphological features revealed by this study are relevant to understanding the ecomorphology and phylogeny of this important specimen, and relevant to understanding mustelid comparative anatomy and evolution.

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