EARLIEST KNOWN CARNIVORAN AUDITORY BULLA AND SUPPORT FOR A RECENT ORIGIN OF CROWN-GROUP CARNIVORA (EUTHERIA, MAMMALIA)

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Abstract: An ossified auditory bulla of a basal carnivoran is described for the first time. Although broken, the bulla of *Viverravus acutus* (Viverravidae, Carnivora) appears to have enclosed the middle ear and to have been composed exclusively of an ectotympanic bone. The structure of the bulla and other basicranial features support the hypothesis that viverravids lie phylogenetically outside crown-group Carnivora and that the last common ancestor of living carnivorans may have existed as recently as 42 million years ago, not 60–70 million years ago as suggested by some authors.

Key words: Carnivora, phylogeny, auditory bulla, *Viverravus*, Eocene, rates of evolution, cytochrome *b*.

EVIDENCE for higher-level phylogenetic relationships within fossil Carnivora relies heavily on the structure of the base of the skull, especially the composition of the bony bulla surrounding the middle ear cavity (Hunt and Tedford 1993; Wesley-Hunt and Flynn 2005). In this paper we describe the first auditory bulla found in a viverravid carnivoran and use it to place the group in a phylogenetic context. Until this discovery, the lack of specimens of early carnivorans in which the bulla and other basicranial structures were preserved made phylogenetic relationships between viverravids and living Carnivora difficult to reconstruct. Viverravids are the earliest carnivorans known in the fossil record, first appearing in the Paleocene of North America about 60 million years ago (Fox and Youzwyshyn 1994), but they are derived in having lost their third molars. Some authors have argued that viverravids belong to the stem-group Carnivora, with no special relationship to any subgroup (Gingerich and Winkler 1985; Wesley-Hunt and Flynn 2005), while others have contended that viverravids were ancestral to aeluroid carnivorans (felids, hyaenids, herpestids and viverrids), because these taxa have all lost the third molars (Flynn and Galiano 1982; Flynn *et al.* 1988; Hunt and Tedford 1993). The phylogenetic position of viverravids is important for determining the age of last common ancestry of living Carnivora. If viverravids are part of the crown group, then the origin of living Carnivora could be as old as the Early Paleocene or Late Cretaceous (Hunt and Tedford 1993), but if they lie outside, the origin could be as young as 42 Ma (Flynn 1996). The discrepancy is critical for quantitative studies, especially for the calibration of carnivoran molecular clocks (Flynn 1996). Many of the characters required to resolve the problem are missing because of the absence of well-preserved basicranial material, especially the auditory bulla. Here we describe the auditory region of *Viverravus acutus*, including the first evidence of an osseous bulla, and use it to reassess the relationship of viverravids to other carnivorans. Rescoring the basicranial characters of *Viverravus* and rerunning the cladistic analysis of deep carnivoran relationships that was recently published by one of us (Wesley-Hunt and Flynn 2005) supports the hypothesis that viverravids lie outside the common ancestry of extant Carnivora.

MATERIAL AND METHODS

Two new specimens of *Viverravus acutus* clarify the anatomy of the basicranium. One skull (UM 67326) is almost complete, with a nearly intact basicranium. No osseous bulla is preserved in this specimen, but the rest of the auditory region is better documented than in any previous specimen. This skull is from the Lower Eocene

Willwood Formation of the Clarks Fork Basin, Wyoming (UM locality SC-148, 2050-m level, Wasatchian NALMA, zone Wa-4, 53·5 Ma; Gingerich 1991; Clyde *et al.* 1994; Polly 1997; Gingerich and Clyde 2001). The second skull (USNM 489122) is crushed, but includes an auditory region partially covered by a broken ectotympanic bulla. This specimen, which was dissolved out of a limestone nodule by one of us (PH), preserves many delicate features, such as the bulla fragment. The USNM specimen is also from the Clarks Fork Basin, but is slightly older than the University of Michigan specimen (Houde Locality 8, which is the same as UM locality SC-004, 1570-m level, Wasatchian zone Wa-1, 54·8 Ma).

X-ray microtomography (XMT) was performed on both specimens using the high-definition scanner at Queen Mary, University of London (Davis and Elliott 2003). This scanner uses a time-delay integration CCD X-ray camera to obtain three-dimensional (3D) images with good contrast resolution that are completely free from ring artefacts. The reconstructed data set for UM 67326 consisted of $1000 \times 1000 \times 1760$ cubic voxels, side length 29 μm. The X-ray generator was set to 120 kV and 0·16 mA, total scan time 62 h. For USNM 489122, the data set was $1600 \times 1600 \times 606$ voxels, 15·29 μm side length, 90 kV and 0·26 mA, total scan time 68 h. Surface renderings and slice-through animations of the specimens were made with Volume Graphics' VGStudio Max volume rendering software.

The new material was used to rescore *Viverravus acutus* in the phylogenetic character matrix of Wesley-Hunt and Flynn (2005). The revised data set was run with a heuristic parsimony search (1000 replicates, random addition sequence option) of 41 taxa and 99 characters using PAUP 4.0b10 (Swofford 1998). Hyaenodontid creodonts *Thinocyon* and *Hyaenondon*, a leptictid eutherian *Lepticits*, and the erinaceomorphan lipotyphlans *Erinaceus* and *Echinosorex* were used as outgroups. In this paper, we concentrate only on the morphology of the viverravid basicranium and its implications for phylogenetic relationships; Wesley-Hunt and Flynn (2005) provided detailed descriptions of the character states and other taxa. The rescored matrix is included here in the Appendix.

Abbreviations. NALMA, North American Land Mammal Age; UM, University of Michigan Museum of Paleontology specimen; USNM, United Stations National Museum of Natural History specimen.

AFFINITIES OF THE NEW MATERIAL

Both skulls belong to the long-lived species *Viverravus acutus* Matthew and Granger, 1915 from the Lower Eocene of North America. The affinity of UM 67326 was determined in a previous revision and phylogenetic analysis of Clarks Fork Basin material (Polly 1997). The USNM specimen can be referred to the same species based on its dentition (and the similarity of the basicranium, which is illustrated below). The teeth were still embedded in limestone matrix so that the crown morphology could not be closely observed (this face of the skull was not scanned, only the auditory region), but the buccal shape and lengths of the cheek teeth were sufficient to refer the specimen to *Viverravus acutus*. The presence of a P^4/M_1 carnassial places the animal within the order Carnivora Bowdich, 1821, the absence of M_3 in combination with its provenance places it within the family Viverravidae Wortman and Matthew, 1899, the small size and non-bulbous, smooth-enamelled teeth place it within the genus *Viverravus* Marsh, 1872, and the size and tooth measurements refer it to *V. acutus* Matthew and Granger, 1915. *Didymictis* is the only viverravid coexisting in the Early Eocene of North America, and it is readily distinguished from *Viverravus* by its much larger size, its proportionally longer P_{3-4}, and the low trigonid on M_2 (Gingerich and Winkler 1985; Polly 1997). Two other *Viverravus* species are known from the Early Eocene: *V. politus* Matthew and Granger, 1915 is larger with a relatively smaller P_3 than *V. acutus*, and *V. rosei* Polly, 1997 is smaller.

DESCRIPTION

Text-figure 1 shows stereopairs of the auditory regions of the two specimens. The images are 3D surface renderings from the XMT scans from which the surface matrix was removed digitally. Supplementary colour slice-through animations of the XMT scans are available on the Palaeontological Association website (http://palass.org). Text-figure 2 shows interpretive line drawings and two XMT slices.

The intact basicranial surface of UM 67326 had a tear-shaped petrosal promontorium and a broad middle ear, or tympanic cavity (Text-fig. 1A). The large cochlear fenestra opened on the caudal surface of the promontorium. A broad groove for the internal carotid artery ran across the ventral surface of the promontorium from its caudomedial corner to the carotid (or middle lacerate) foramen. The carotid foramen pierced the rostrolateral margin of the promontorium (Text-fig. 2A). The petrosal bone appears to have surrounded the carotid opening, but the possibility exists that it was surrounded by a rostral tympanic element that was tightly fused to the petrosal to form the apex of the teardrop-shaped promontorium. This seems unlikely, however, because no sutures were visible on the surface of the specimen or in

the XMT scans. The specimen was immature, as indicated by unfused long bone elements, so a completely obliterated suture would not be expected. A small groove on the caudolateral promontorium ran rostrodorsally to the vestibular fenestra, apparently marking the path of a stapedial artery. The middle ear cavity was wide and shallow rostrally, but narrower and deeper at its caudal end where it received the external acoustic meatus. A deep epitympanic recess for the malleus and incus was located between the opening to the external meatus and the vestibular fenestra.

A low, rounded ridge ran rostrocaudally across the ventral margin of the promontorium along its medial side (Text-fig. 1, arrows). Evidence from the USNM specimen described below suggests that the medial margin of the auditory bulla rested along this ridge, though its surface is not rough in the way that it would be if the suture were a tight one. Caudal to the fenestra cochlea was another low ridge of bone that probably supported the bulla margin at its caudal end. Lateral to that, a curved surface on the mastoid bone also appears to have supported the bulla as it curved laterally around towards the external auditory meatus (visible in Text-fig. 1A). At the rostral end, the bulla probably curved around the wide, flat part of the tympanic cavity just lateral and rostral to the carotid foramen, continuing around the lateral side against the curved vertical wall that runs back towards the external auditory meatus.

An enclosed canal for the facial nerve (CN VII) ran above the tympanic cavity, opening into it just lateral to the vestibular fenestra. This opening can be seen in the XMT slice of the UM specimens in Text-figure 2B. Just caudal to that was the stylomastoid foramen, which provided passage for the nerve caudally out of the tympanic cavity lateral to the cochlear fenestra. The rostral end of the canal curved up towards the brain, opening into the subarcuate fossa on the cranial face of the petrosal.

Caudal to the promontorium in UM 67326 was a large jugular, or posterior lacerate foramen that opened directly into the cranial cavity (Text-fig. 2A). Rostral to that was an opening for the inferior petrosal sinus. XMT showed that the sinus travelled rostrally from the opening through a completely enclosed bony canal lying between the petrosal and basioccipital (Text-fig. 2B). The canal ran the length of the promontorium before opening into the cranial cavity. The sinus opened into the cranial cavity in a position demonstrably distinct from the carotid foramen, indicating unambiguously that the canal carried the sinus rather than the internal carotid artery. On the right side of the specimen the canal is intact, but on the left side shifting of the petrosal and related breakage have exposed it ventrally (see supplementary slice-through animation files of the UM specimen). The new specimen makes it clear that the ventral exposure of the sinus in the previously described specimen of *Viverravus politus* (= *Protictis schaffi*; Gingerich and Winkler 1985) was due

to the same sort of post-mortem breakage. The canal makes the bone along the medial margin of the promontorium thin and delicate, easily broken by post-mortem crushing or preparation. It is likely that many carnivoran specimens that have been described as having a fissure between the promontorium and basioccipital had an enclosed bony canal in life.

The middle ear cavity was floored by a broad ectotympanic bulla, the anterior fragment of which was preserved in USNM 489122 (Text-fig. 1B). The bulla in this speci-men was displaced medially off the promontorium post mortem, but was lying close to life position covering the rostral portion of the cavity. The bulla was broken, with its caudal end missing. The extent and structure of the bulla fragment, combined with the morphology of the promontorial ridge that supported it, imply that much if not all of the bulla was composed of a ventrally rounded ectotympanic bone. No sutures, thickenings or septa were visible in preserved fragment, even with XMT. A crista tympani, or tympanic annulus, ran parallel to the external

TEXT-FIG. 2. A, line drawing of the right auditory region of *Viverravus acutus*, UM 67326 in ventral view. The light grey shading shows the extent of the middle ear cavity and the dark grey shows the petrosal prominence. The dashed line shows the plane of section of B. B, XMT slice through UM 67326 showing the canal for the inferior petrosal sinus. Ventral is to the top, lateral to the left and dorsal to the bottom. C, line drawing of the right auditory region of USNM 489122. Shading as in A. D, XMT slice through USNM 489122. Orientation and scale are identical to C. The slice was taken parallel to the view of C, just below the surface of the bulla fragment, which is the structure at the top of the slice. The crista tympani (*ct*) can be seen. Abbreviations: *CN VII*, canal for the facial nerve; *cf*, carotid foramen; *coch*, cochlea; *ct*, crista tympani; *eam*, external auditory meatus; *er*, epitympanic recess; *fc*, fenestra cochleae; *ips*, inferior petrosal sinus; *jf*, jugular foramen; *mec*, middle ear cavity; *pgf*, postglenoid foramen; *pr*, promontorium; *sfp*, stylomastoid foramen primitivum.

auditory meatus, just inside the lateral margin of the fragment on its dorsal side (Text-fig. 2D). This crista provides convincing evidence that the bone is not a displaced fragment of the alisphenoid or basioccipital because neither has a ridge on its dorsal side that can been seen in the XMT scans of the intact UM specimen. The bone extending lateral to the annulus indicated that *Viverravus* possessed a bony meatal tube of at least short length. The rostromedial margin of the bulla element lay along the rostral part of the promontorial ridge, confirming that the ridge supported the bulla in life (Text-fig. 1B). The bulla was crushed rostrally and laterally, making its margins difficult to define. The caudal part of the bulla was missing, making it impossible to know whether it extended all the way to the back of the tympanic cavity, though the morphology of the UM specimen suggested that it may have. The ectotympanic would necessarily have to have extended caudally behind the external auditory meatus (the crista tympanica supports the tympanic membrane, or eardrum), which was near the back of the tympanic cavity (Text-fig. 2A, C). Any contribution to the bulla by a caudal entotympanic in *Viverravus* would therefore have been quite small and uninflated, because that element, if present, would have been limited to the small area between the external auditory meatus and the ridge caudal to the cochlear fenestra. Some living carnivorans, notably *Nandinia binotata*, have a cartilaginous posterior bulla, the part covered by a caudal entotympanic in other carnivorans (Hunt 1974, 1987, 1989). It is impossible to know whether the caudal wall of the bulla was osseous or cartilaginous in *Viverravus*, but that area would not have been inflated as it is in *Nandinia* or in aeluroids with a caudal ectotympanic. The carotid artery would have pierced the bulla or passed between it and the promontorium at the caudal end medial to the cochlear fenestra.

In USNM 489122, an unattached, broken peg-like bone lay under the bulla rostral to the external meatus in the vicinity of the tympanic annulus (see supplementary slice-through animations). This structure may be part of the hyoid apparatus that was displaced post mortem, but is more likely the tympanic process of the malleus.

PHYLOGENY AND COMPARISONS

Prior to specimen USNM 489122, no bulla had been recovered from either of the earliest carnivoran groups Viverravidae or Miacidae (we use Miacidae informally because it is now recognized to be a paraphyletic grouping). Lack of direct evidence for an ossified bulla in these early groups prevented them from being easily referred to any of the major carnivoran clades and left open the question of whether the ossified bulla in living Carnivora is homologous (*sensu* Patterson 1982). Recent cladistic

analyses have either been forced into the uneasy assumption that the bulla was ossified in these early taxa (which have had important consequences for character scoring and interpretation of polarities) or been forced to disregard bulla characters, scoring them either as unknown or omitting them altogether (Flynn *et al.* 1988; Wyss and Flynn 1993; Wang and Tedford 1994; Wesley-Hunt and Flynn 2005). All of these solutions were problematic, as the inclusion of bullar characters forced viverravids into a potentially erroneous plesiomorphic condition, but their exclusion ignored phylogenetically informative characters. Wesley-Hunt and Flynn (2005) used peribullar characters to convey the phylogenetic information that would have been contained in bullar traits had they been present. Our new material vindicates that approach, as they confirm that viverravids had an ossified ectotympanic bulla attached to the skull.

To place the primitive bulla in an evolutionary context we reanalysed Wesley-Hunt and Flynn's (2005) data matrix using the data provided by the new specimens. The tree topology was not changed and viverravids remained phylogenetically outside crown-group Carnivora plus miacids (Text-fig. 3). The parsimony analysis found 45 shortest trees, each requiring 443 steps, with a consistency index (excluding uninformative characters) of 0·315 and a retention index of 0·664, respectively. Placement of stem-group taxa was virtually the same as in the previously published tree, with discrepant placement and homoplasy mostly confined to the crown-group taxa (not shown). Viverravids were well resolved in the strict consensus with respect to one another and to other taxa.

TEXT-FIG. 3. Phylogenetic tree showing the relationships of *Viverravus acutus* to other Carnivora. Basicranial and bulla characters support the exclusion of *V. acutus* and other viverravids from crown-group Carnivora and hypotheses of a more recent origin of the latter. This tree is based on a strict-consensus cladogram of 45 most parsimonious trees based on 41 taxa and 99 characters (consistency index, 0·315; retention index, 0·664).

The bulla of *Viverravus acutus* differed from all extant Carnivora in three important ways: it was relatively wider at the rostral end, it did not extend much caudal to the petrosal prominence, and it was, most probably, composed entirely of an ectotympanic element. *Viverravus* is further differentiated from aeluroid carnivorans, the crown-group clade to which it has previously been considered ancestral, in that it had no ventral process on the promontorium (Hunt 1989) and no posterior inflation of the tympanic cavity. However, both *Viverravus* and aeluroid carnivorans share a condition in which the ectotympanic bulla contacts the promontorium just rostral to the cochlear fenestra. But the morphology of the contact differs. In the aeluroids the contact appears as a flattened facet on the surface of the promontorium, as if the ectotympanic pressed into the promontory surface. This is in contrast to the condition observed in *Viverravus* in which contact is along a rounded bony ridge along the medial margin of the promontorium. It is important to note that a flattened facet on the promontorium (as described by Hunt 1989) is not present in all aeluroid carnivorans; it is lost in many modern taxa, and while there is contact between the bulla and promontorium in fossil aeluroids, no contact is present in *Nandinia*, which is considered a very basal aeluroid. Viverravids did not possess the deep fossa for the tensor tympani muscle in the roof of the middle ear nor the rostrally rounded promontorium that unite crown-group carnivorans with one another and with many miacids. Among carnivorans whose tympanic region and bullae have been described, *Viverravus* most closely resembled the Oligocene amphicyonid *Paradaphoenus cuspigerus* (Hunt 2001) in that the tympanic cavity of both was broad anteriorly and floored by an exclusively ectotympanic bulla. But *Paradaphoenus* differed from *Viverravus* in that the promontorium of the former was not teardrop-shaped, in that the inferior petrosal sinus opened directly into the posterior lacerate foramen, in having a bulla that was inflated rostrally against the postglenoid process, and in having a bulla inflated caudally behind the prominence. The preserved bulla is not anteriorly inflated, nor does *Viverravus* have concavities on the squamosal or alisphenoid to indicate inflation. These depressions were clearly seen in early taxa such as *Prohesperocyon* and *Miacis sylvestris* (Miacidae), suggesting that an anteriorly inflated bulla was shared by these other taxa and crown-group Carnivora. In *Viverravus*, the caudal ridge for attachment of the posterior bulla lies immediately behind the fenestra cochleae, allowing little room for a posteriorly expanded chamber. The earliest taxon thought to have a posteriorly inflated bulla was the Late Eocene *Tapocyon* (Miacidae). The bulla of *Viverravus* was also not expanded medial to the prominence, a condition seen in some Feliformia, where it was derived several times independently (Wesley-Hunt and Flynn 2005). The

viverravid *Didymictis* probably did have some medial inflation to its bulla as attested by the shape of the basioccipital lateral to the promontorium. *Viverravus* (and Viverravidae) also differed from more derived carnivorans in the apparent lack of a rostral entotympanic. No rostral element was observed in our two specimens, nor does any viverravid have a roughened surface of the rostromedial promontorium or lateral basisphenoid that would indicate the presence of such an element. Evidence of a rostral entotympanic first appears in *Oödectes* (Miacidae).

CONCLUSION

The ear and basicranium of *Viverravus* had a morphology unlike that of any crown-group carnivoran. The auditory bulla of *Viverravus* was a broad, convexly rounded structure composed, most probably, of a single ectotympanic element. The middle ear cavity was large and shallow, extending rostral and lateral alongside the promontorium, rather than caudally as in many living carnivorans. This new material provides convincing evidence that viverravids lie phylogenetically outside crown-group Carnivora, confirming the hypothesis that crown-group taxa possess derived features that unite them with other Palaeogene taxa to the exclusion of viverravids (Gingerich and Winkler 1985; Wyss and Flynn 1993; Wesley-Hunt and Flynn 2005). The previous hypothesis that viverravids are allied to the aeluroid carnivorans within the crown group (Flynn and Galiano 1982; Hunt and Tedford 1993) is not supported by the new material. By extension, these data also support a younger divergence of around 42 Ma for crown-group Carnivora (Text-fig. 3), not an older divergence of 55–70 Ma.

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Supplemental file captions

Supplemental-file 1. Slice-through animation of the basicranium of *Viverravus acutus*, UM 67326. Specimen is positioned in ventral view with rostral to the top. See Text-figures 1 and 2 for scale, orientation and labelling.

Supplemental-file 2. Slice-through animation of the basicranium of *Viverravus acutus*, USNM 489122. Specimen is positioned in ventral view with rostral to the top left. See Text-figures 1 and 2 for scale, orientation and labelling.

Appendix. *Phylogenetic character matrix*

	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	39	40	41	42	43	44	45	46	47	48	49
Tapocyon	1	0	1	0	0	1	?	0	0	0	0	0	1	0	0	1	0	1	1	2	1	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	?	2	0	1	1	1	0	0	1	1
Vulpavus ovatus	1	1	1	1	1	1	1	0	0	0	0	0	1	0	0	0	1	1	0	1	1	0	0	1	1	0	0	1	0	1	0	0	?	0	0	0	0	0	1	1	1	1	0	1	0	0	0	0	1
Vulpavus profectus	1	1	1	0	1	1	?	1	0	0	0	0	1	0	0	0	1	0	1	0	0	1	0	0	1	0	0	1	0	1	0	0	0	0	0	0	1	0	1	1	1	1	0	0	0	0	0	1	1
Miacis parvivorus	?	0	1	1	?	?	?	?	?	0	0	0	1	3	?	?	0	1	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	?	0	1	0	1	0	1	0	0	0	0	1	1	0
Prohesperocyon wilsoni	1	?	1	0	?	0	0	0	0	0	0	0	1	1	1	1	0	1	1	?	1	?	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1	0	1	0	1	1	0	0	0	1	1
Miacis cf M. sylvestris	?	?	0	0	1	?	?	0	0	0	0	0	1	1	0	1	0	1	0	2	1	0	0	0	2	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	1
Miacis cognitus	1	0	1	0	0	1	1	0	0	0	0	0	1	3	1	1	0	0	2	2	0	0	1	0	2	0	0	1	0	1	0	0	0	2	1	0	0	1	0	1	0	2	1	0	0	0	0	1	0
Oodectes herpestoides	1	0	1	1	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	2	1	0	1	0	2	0	0	3	0	1	1	0	0	2	0	1	1	1	0	0	2	0	0	0	1	0	0	1	1
Hesperocyon gregarius	1	0	1	1	1	1	?	1	0	0	0	0	1	2	1	1	0	1	0	2	1	?	1	0	2	2	0	3	3	0	1	0	?	2	2	1	1	1	1	0	2	0	1	0	1	0	0	1	0
Otarocyon	1	0	1	0	1	1	1	0	0	0	0	0	1	0	1	1	0	0	2	2	0	?	2	0	2	2	0	3	0	1	1	0	?	2	2	1	0	1	1	0	2	0	0	0	1	0	0	1	1
Canis latrans	1	0	0	1	1	1	1	1	0	0	0	0	1	1	0	1	0	1	1	2	1	?	2	0	1	1	0	1	0	1	1	1	0	2	2	1	0	1	1	0	2	1	1	1	1	0	0	1	1
Daphoenus/Amphicyonid	1	0	0	1	1	0	0	1	0	0	0	0	1	3	1	1	1	1	1	2	0	1	0	?	1	0	1	1	0	2	2	0	2	2	0	1	1	?	1	0	1	0	1	1	0	0	0	0	0
Protictis schaffi	?	1	0	1	0	1	?	1	1	1	0	0	0	0	0	?	0	0	1	2	0	0	0	0	?	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	?	0	0	2
Viverravus minutus	?	?	1	0	1	?	1	1	1	0	1	0	0	0	0	0	0	0	0	2	0	?	0	0	0	1	2	0	0	0	2	0	2	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0	2
Viverravus cf V. gracilis	?	?	1	?	0	?	?	1	0	0	1	?	1	0	0	0	0	0	?	?	?	?	0	0	0	1	2	0	0	0	1	0	0	1	0	0	0	1	0	1	0	1	0	1	0	1	0	0	2
Viverravus acutus	?	0	1	0	0	1	?	1	1	0	1	0	1	0	0	0	0	0	?	2	1	0	1	0	0	0	1	0	0	0	0	0	?	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0
Didymictis vancleveae	?	?	?	?	0	?	?	1	1	0	0	0	0	2	0	?	0	0	?	?	1	0	0	0	0	0	0	?	0	1	1	0	?	0	0	0	1	2	0	0	0	0	1	0	1	0	0	1	1
Zodiolestes diamonelixensis	1	0	?	0	1	0	1	0	1	0	0	0	1	1	1	1	0	2	2	2	1	?	0	2	1	1	1	3	0	1	1	1	2	2	2	1	1	2	1	1	2	0	1	1	0	0	1	1	2
Dinictis/Nimravidae	1	0	1	0	1	2	1	0	1	0	1	0	1	0	1	0	0	1	?	?	?	?	0	?	?	1	0	2	1	1	?	1	2	2	1	0	?	0	?	1	0	0	1	1	0	1	1	1	2
Hoplophoneus	1	?	1	1	1	2	1	0	1	0	1	0	1	1	0	1	0	1	1	1	1	?	1	0	?	1	0	2	1	1	1	0	2	2	1	0	?	0	1	?	0	0	1	1	?	1	1	0	2
Palaeoprionodon lam.	2	0	1	2	1	1	1	1	0	2	?	1	2	3	2	1	1	0	0	1	0	1	0	0	1	2	1	2	0	0	1	1	1	2	2	0	0	2	2	2	1	0	1	1	?	0	0	0	2
Stenogale julieni	2	?	1	0	0	2	0	1	0	1	?	?	1	1	1	1	0	0	?	2	1	?	0	0	2	2	2	2	1	1	0	2	2	2	1	0	0	1	3	3	0	1	1	1	0	1	0	1	?
Proailurus lem.	?	0	1	0	0	2	?	?	0	1	0	1	1	3	1	1	0	?	2	2	1	?	0	0	1	2	2	2	0	1	0	2	2	2	1	0	1	0	3	3	1	0	1	1	0	0	0	1	2
Herpestid	1	0	0	0	0	2	1	0	1	2	0	0	2	3	2	1	1	0	2	2	1	?	0	1	2	2	2	2	1	0	1	0	2	2	0	1	?	2	1	3	0	1	1	1	1	0	0	0	2
Herpestides antiquus	2	0	1	0	0	0	2	0	0	0	2	0	1	3	1	1	0	1	2	2	1	0	0	1	1	2	1	2	0	1	1	0	2	2	2	0	0	0	1	2	2	1	1	1	1	0	0	1	2
Viverrid	2	0	1	2	1	1	2	1	1	0	2	0	2	3	2	1	0	1	2	2	1	?	0	0	2	2	2	2	1	1	1	1	2	2	1	0	0	1	2	2	1	1	1	1	1	0	0	1	1
Felis	2	0	0	0	0	1	1	0	0	2	0	0	0	1	2	1	0	1	2	2	1	?	0	0	2	2	0	2	0	1	1	1	2	1	1	0	0	1	3	3	0	1	1	1	1	0	0	0	2
Hyaenid	2	0	0	0	0	2	1	0	0	2	?	1	2	3	2	1	1	0	0	2	1	?	0	0	2	2	2	2	2	0	1	1	2	2	1	1	?	0	3	3	0	0	1	1	1	0	0	0	2
Nandinia binotata	2	0	1	0	0	2	1	0	0	1	0	1	1	3	0	1	0	0	2	2	2	?	0	0	2	1	1	2	2	1	0	1	2	2	2	0	0	0	2	2	2	1	1	1	1	0	0	0	3
Pteronarctos	2	0	1	2	?	0	2	2	1	1	0	0	2	2	0	1	1	?	2	0	2	?	?	0	2	?	0	?	0	?	1	1	1	0	1	0	?	1	0	1	?	?	?	1	1	0	?	1	2
Gulo	2	0	1	1	0	1	1	1	1	0	0	0	0	0	0	1	0	0	2	2	1	1	0	2	1	2	0	3	0	1	0	1	2	2	0	0	0	1	1	1	1	1	1	0	1	0	1	0	2
Ailurus	3	0	1	2	0	1	?	1	0	0	0	0	1	2	0	1	0	2	1	1	1	?	0	1	2	2	2	3	0	1	1	1	1	2	2	0	0	1	1	2	1	0	1	1	2	0	1	0	3
Ursid	3	0	0	2	0	1	1	1	0	0	0	0	1	2	1	0	0	0	2	1	1	1	1	0	2	1	0	3	0	1	1	?	0	2	2	0	0	1	1	1	1	0	1	0	2	0	1	0	2
Mephitis	1	0	1	2	1	2	1	1	1	0	0	0	0	2	0	0	1	0	1	2	1	1	0	2	2	0	1	3	0	1	0	1	1	1	0	0	1	1	1	1	2	1	0	1	1	0	1	0	2
Procyon lotor	2	0	1	2	0	2	0	1	1	0	0	0	1	3	0	1	0	2	2	2	1	?	0	2	2	1	0	3	0	1	1	1	0	2	0	0	0	1	2	0	1	1	1	1	2	0	1	0	3
Otariidae	2	0	1	2	0	2	2	1	3	?	1	1	3	0	1	0	?	0	0	2	1	?	0	0	2	1	0	?	0	1	1	0	0	2	2	0	?	2	1	0	1	?	?	0	0	0	?	0	?
Lepticitis	1	1	?	?	?	1	0	0	1	1	0	0	0	1	0	1	0	0	2	?	1	1	0	0	0	0	0	3	?	0	0	0	1	0	1	1	0	0	1	2	1	0	0	0	0	0	1	?	0
Erinaceus	0	1	0	1	0	1	0	0	1	0	0	0	1	0	1	0	?	?	?	1	1	0	?	0	1	0	0	0	1	0	0	1	1	1	0	0	0	1	0	0	2	0	0	0	0	0	0	0	2
Hyaenodon	0	0	?	0	0	0	0	?	?	0	0	0	0	1	0	0	0	?	?	?	0	?	0	0	0	0	0	0	0	0	?	?	3	0	0	0	?	0	0	0	0	0	?	?	?	0	0	0	2
Thinocyon	0	?	2	0	0	0	?	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
Echinosorex	1	1	1	2	0	2	2	1	1	0	0	0	0	2	0	0	0	0	0	2	1	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	1

Appendix. Continued.

	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99
Tapocyon	0	2	1	0	1	0	1	1	0	1	?	0	?	?	?	0	0	0	0	0	?	0	0	?	?	?	?	?	0	0	0	0	1	0	0	0	1	0	0	?	0	?	0	0	?	?	?	?	?	1
Vulpavus ovatus	0	1	0	0	1	2	0	0	2	?	0	?	?	?	0	0	0	0	0	0	?	0	0	?	?	?	?	?	0	0	0	0	1	0	0	0	1	0	0	?	0	?	0	0	?	?	?	?	?	1
Vulpavus profectus	1	1	0	0	1	2	0	0	2	1	0	?	?	0	0	0	0	0	0	0	?	0	0	?	?	?	?	?	0	0	0	0	0	0	0	0	1	1	1	0	0	?	0	0	?	?	?	?	?	1
Miacis parvivorus	0	1	0	0	1	0	1	1	2	1	?	?	?	0	0	0	?	0	0	0	?	0	0	?	?	?	?	?	0	0	0	0	1	0	0	0	1	0	0	0	0	?	0	0	?	?	?	?	?	1
Prohesperocyon wilsoni	0	1	0	0	1	0	1	1	1	?	?	?	?	?	0	0	?	0	0	0	?	0	0	?	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	?	0	?	0	0	?	?	?	?	?	1
Miacis cf M. sylvestris	0	1	0	0	1	0	1	1	2	?	?	?	?	0	0	0	0	0	0	0	?	0	0	?	?	?	?	?	0	0	0	0	1	0	0	0	1	0	0	0	0	?	0	0	?	?	?	?	?	1
Miacis cognitus	2	1	0	0	1	0	1	1	2	?	0	?	?	0	0	?	0	0	0	0	?	0	0	?	?	?	?	?	0	0	0	0	1	0	0	0	1	0	0	?	0	?	0	0	?	?	?	?	?	1
Oodectes herpestoides	0	1	0	0	1	0	0	0	2	1	0	0	0	0	0	0	0	1	0	0	?	0	0	?	?	?	?	?	0	0	0	1	0	1	0	0	0	0	0	?	0	?	0	0	?	?	?	?	?	?
Hesperocyon gregarious	2	0	0	1	1	0	1	0	1	1	0	0	0	0	0	?	0	0	1	1	?	0	0	?	?	?	?	?	0	0	0	0	0	0	0	?	0	0	0	0	0	?	0	0	0	?	?	?	?	1
Otarocyon	2	0	0	1	2	1	0	1	0	1	1	0	1	0	0	?	0	1	0	0	?	0	0	?	?	0	?	?	0	0	0	0	0	0	1	0	0	0	0	0	0	?	0	0	1	?	?	?	?	2
Canis latrans	2	0	0	1	1	0	1	0	1	0	0	1	0	1	0	0	1	0	1	0	?	0	0	?	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	1	0	0	0	0	1
Daphoenus/Amphicyonid	2	1	0	1	0	1	0	0	0	?	1	1	1	0	0	1	1	1	?	1	?	0	0	?	?	1	?	?	0	0	0	0	1	1	1	1	0	1	1	0	0	?	1	0	1	?	?	?	?	1
Protictis schaffi	0	1	0	1	0	0	1	0	1	0	1	1	1	0	0	0	1	1	0	1	0	0	0	?	?	0	?	?	0	0	0	1	0	1	0	0	1	1	?	?	1	1	?	1	?	0	?	?	?	1
Viverravus minutus	0	?	0	1	0	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	?	?	?	?	?	?	1
Viverravus cf V. gracilis	0	2	0	0	1	0	1	0	1	0	0	0	?	0	0	0	0	0	0	0	?	0	0	?	?	?	?	?	0	?	0	0	0	0	0	0	1	1	1	?	1	?	0	?	?	?	?	?	?	1
Viverravus acutus	0	1	0	1	0	1	0	1	0	1	0	0	1	0	0	?	0	0	0	0	0	0	0	?	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	?	0	?	0	?	0	?	?	?	?	1
Didymictis vancleveae	0	1	0	1	0	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	?	?	?	?	1
Zodiolestes diamonelixensis	0	1	1	1	0	1	?	1	2	1	0	1	?	0	0	0	1	2	1	0	0	0	0	?	0	0	0	?	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	?	?	?	2
Dinictis/Nimravidae	2	2	1	1	1	0	1	1	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	?	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	1	0	1	0	1	0	0	0	0	1
Hoplophoneus	2	2	1	1	1	0	1	1	?	?	1	?	0	0	0	0	1	0	1	1	0	0	0	?	0	0	?	?	0	0	0	0	1	1	1	1	1	0	0	0	1	0	1	0	1	0	0	0	0	1
Palaeoprionodon lam.	?	?	1	1	2	1	1	?	1	1	0	0	0	0	?	0	0	3	0	0	?	0	0	?	1	1	?	0	0	1	1	0	0	1	0	1	1	1	0	?	1	1	0	0	1	?	?	?	1	1
Stenogale julieni	0	1	2	1	1	0	1	?	2	1	0	0	?	0	0	0	0	3	0	0	?	0	0	?	0	0	1	?	1	0	0	1	0	0	0	0	1	0	1	?	0	0	0	?	0	?	?	?	1	1
Proailurus lem.	0	1	2	1	1	0	1	0	1	1	0	0	?	0	?	?	0	3	0	0	?	0	0	?	0	0	1	?	1	0	0	0	0	1	0	0	1	1	0	?	0	0	0	?	0	?	?	?	1	1
Herpestid	0	2	1	1	1	0	1	0	0	1	0	1	0	0	0	0	1	2	1	1	1	0	0	1	0	1	0	1	0	1	1	1	1	1	0	0	0	0	0	0	1	1	0	?	1	1	0	1	0	1
Herpestides antiquus	0	1	1	1	0	1	?	0	2	?	?	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	?	0	0	0	0	1	0	0	0	1	0	0	?	1	?	0	?	1	?	?	?	0	1
Viverrid	0	1	0	1	1	1	0	1	0	1	0	0	0	0	0	0	1	3	1	0	1	0	0	1	0	1	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	1
Felis	0	1	2	1	1	1	1	0	3	0	0	0	0	0	0	0	1	3	1	1	1	0	0	1	0	1	2	0	0	1	0	1	0	1	1	0	1	0	0	0	1	0	1	0	1	0	0	0	0	1
Hyaenid	0	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	1	3	1	1	0	0	0	0	1	1	2	0	0	0	0	0	1	1	0	1	0	?	0	0	1	1	0	0	1	0	1	0	0	1
Nandinia binotata	0	1	1	1	1	0	1	1	2	2	1	0	0	0	1	0	1	3	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	0	1	0	0	0	1	?	1	0	1	0	1	0	1	0	0	1
Peronarctos	0	1	1	1	0	1	0	2	2	0	0	?	2	0	?	1	1	1	0	1	1	0	1	?	1	1	0	1	0	1	0	?	?	1	?	?	1	0	1	?	?	1	0	1	0	?	?	?	?	?
Gulo	0	1	2	1	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	1	0	0	0	1	0	1	0	0	1	0	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Ailurus	1	0	0	1	1	0	0	0	2	1	0	0	0	0	0	0	0	1	1	1	0	0	0	1	1	0	0	0	1	1	1	1	1	1	1	0	1	1	1	1	0	1	0	1	0	0	0	0	0	1
Ursid	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1
Mephitis	0	1	2	1	0	0	1	2	1	1	1	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0
Procyon lotor	1	0	0	0	1	0	0	0	2	0	0	1	0	0	0	0	1	2	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	1	1	1	0	0	0	1	0	1	0	0	0	1	1
Otariidae	?	?	0	1	?	?	?	?	2	2	1	0	?	0	2	0	0	1	0	1	0	0	0	1	0	0	1	1	0	0	?	?	?	1	1	?	0	0	0	?	0	1	0	1	0	?	?	?	?	?
Lepticitis	0	0	0	0	0	0	0	0	0	0	0	1	?	1	1	1	0	1	1	0	0	1	0	?	0	0	?	1	1	0	0	?	1	0	0	?	0	?	1	0	1	0	1	0	1	?	?	?	?	?
Erinaceus	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	1	0	0	0	0	1	0	?
Hyaenodon	0	0	0	1	0	1	0	0	0	?	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	1	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0
Thinocyon	0	0	0	1	0	0	1	0	0	0	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
Echinosorex	1	0	0	0	0	0	0	0	2	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	1	1	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	?