SHORT COMMUNICATION

# THE COMPARATIVE METHOD AND THE INFERENCE OF VENOM-DELIVERY SYSTEMS IN FOSSIL MAMMALS

CALEY M. ORR,[*,1,2] LUCAS K. DELEZENE,[1,2] JEREMIAH E. SCOTT,[1,2] MATTHEW W. TOCHERI,[1,3] and GARY T. SCHWARTZ,[1,2]; [1]School of Human Evolution and Social Change, Arizona State University, Tempe, Arizona 85287-2402, U.S.A, caley.orr@asu.edu; [2]Institute of Human Origins, Arizona State University, Tempe, Arizona 85287-4101, U.S.A.; [3]Human Origins Program, Smithsonian National Museum of Natural History, Washington, D.C. 20560, U.S.A.

Reconstructing soft-tissue structure and function from fossilized bones and teeth is rarely straightforward, and the logic of such inference has generated much debate in the paleontological literature (e.g., Thomason, 1995; Rose and Lauder, 1996; Plavcan et al., 2002). Making sound functional inferences from fossil morphology requires careful comparative analysis to determine a clear association between a structure and its hypothesized function (Lauder, 1995). In a widely cited paleoprimatological paper, Kay and Cartmill (1977) described criteria for reconstructing function in fossils. These criteria include (1) the existence of the trait of interest in extant analogue taxa, and (2) the association of the trait and proposed function in all of those taxa. If extant taxa with the structure exist, but lack evidence of the proposed function or phylogenetic history of the function, then efforts to reconstruct function from a fossil structure are undermined. The recent discovery of Paleocene mammals with a dental morphology suggestive of oral venom injection (Fox and Scott, 2005) highlights the difficulties encountered by paleontologists interested in reconstructing function in fossil species.

Fossil canine teeth from the Paleocene of Alberta, Canada, assigned to the pantolestid *Bisonalveus browni* and another, as yet unnamed, mammalian species exhibit gutterlike grooves running along their lengths (Fox and Scott, 2005). In *B. browni*, the groove occurs along the anterior aspect of the maxillary canine, and in the unidentified mammal, it extends along the length of the labial aspect of the mandibular canine (Fox and Scott, 2005). It was suggested that these grooves may have acted to guide venom (presumably exuded from a gland near the base of the tooth) into a bite wound (Fox and Scott, 2005). Moreover, delivering such a wound may have been facilitated by a complex that included shorter mandibular than maxillary canines in *B. browni*, ensuring adequate clearance between the teeth during full gape (Fox and Scott, 2005). The function of such a complex of traits is well documented in colubroid snakes, in which longitudinal grooves extending the length of the fangs are associated with venom injection (Jackson, 2003). This morphology is developed to an extreme degree in snakes of the family Viperidae, in which the fangs are so deeply invaginated that the grooves are closed off, forming a tube, and thus approximating a hypodermic-needle-like configuration (Jackson, 2003).

Within Mammalia, only the shrewlike *Solenodon paradoxus*, the Hispaniolan solenodon (a member of the order Eulipotyphla, a clade comprising hedgehogs, shrews, and moles), has

dental grooves that are thought to function similarly to *B. browni*, although these occur along the lingual aspect of specialized caniniform mandibular incisors (McDowell, 1958). In *S. paradoxus*, a venom gland sits at the base of the tooth, and it is assumed that the deep groove channels venom in a fashion analogous to that of the grooves observed in venomous snakes (McDowell, 1958; Rabb, 1959). Although *Solenodon cubanus*, the Cuban solenodon, exhibits similarly modified grooved incisors and is reasonably assumed to be venomous, venom delivery is not yet documented in this species (Nowak, 1999). A number of other eulipotyphlans, such as the short-tailed shrew (*Blarina brevicauda*), are known to possess toxic saliva, but these species lack specialized anterior teeth for venom delivery (Dufton, 1992).

While the presence of grooves in the teeth of colubroid snakes and *Solenodon* supports Fox and Scott's (2005) hypothesis that the fossil specimens from Alberta represent mammals that possessed venom-delivery systems, the analysis is incomplete because it did not consider the distribution of such grooves in other mammalian taxa. We used the comparative method to further test the hypothesis that canine/incisor grooves are exclusively an adaptation for venom delivery in mammals. For this hypothesis to be supported, grooved anterior teeth should not be present in any nonvenomous species. If grooved incisors or canines do occur in multiple nonvenomous mammals, then the hypothesis should be considered unsupported.

## MATERIALS AND METHODS

We surveyed representative species from all eutherian orders using specimens housed at the Smithsonian National Museum of Natural History and in the comparative zoology collections at Arizona State University. Further data were gathered from the literature when appropriate. For each species sampled, we examined at least one specimen and typically up to ten. In cases where a groove was evident, between five and ten specimens were examined in order to confirm that the specimen was representative of the species.

Our analysis of canine/incisor morphology should not be considered exhaustive—we report only on those taxa found to exhibit grooves on the incisors or canines similar to those of *B. browni* and the unidentified fossil mammal. The goal of the study was to confirm the absence of the groove in nonvenomous taxa to test the hypothesis that such grooves are uniquely associated with the function of venom delivery. Because *Solenodon* is the only extant mammal reported to possess dental morphology associated with oral venom injection, the hypothesized link between canine/incisor grooves and venom delivery can only be

*Corresponding author: School of Human Evolution and Social Change, Arizona State University, PO Box 872402, Tempe, AZ 85287-2402 USA

weakened if other mammals possess such grooves. That is, more comprehensive sampling can only document further instances of nonvenomous mammals with grooved canines or incisors, unless another mammal is shown to be venomous and characterized by the morphology in question. Additionally, we found no intraspecific variation in groove presence/absence, and thus such variation is not reported in detail here. Regardless, nonvenomous species that are polymorphic for this feature still constitute evidence against the hypothesized link.

## RESULTS

We observed pronounced gutterlike grooves in the canines of several nonvenomous mammalian species from three eutherian orders. Many primates exhibit some expression of a longitudinal canine groove on the maxillary canine. In strepsirrhine primates, there is often no canine groove, and in species in which grooves are present (mostly of the families Lemuridae, Lepilemuridae, and Indridae), they are often very shallow (see Swindler, 2002; Whitehead et al., 2005). However, the trait is well expressed in anthropoids, with most taxa exhibiting gutter-like maxillary canine grooves. Likewise, the mandibular canines of coatis (both *Nasua* and the smaller *Nasuella*) and the maxillary canines of many species of pteropodid bats exhibit grooves. Figure 1 illustrates this feature in the maxillary canines of three representative anthropoid primates—a baboon (genus *Papio*; Fig. 1A), a mandrill (genus *Mandrillus*; Fig. 1B), and a howler monkey (genus *Alouatta*; Fig. 1C)—and a representative pteropodid chiropteran, the large flying fox (genus *Pteropus*; Fig. 1D); in the coatis

(Fig. 1E), the groove is on the mandibular canine. For comparison, the mandibular caniniform incisor of *Solenodon* (Fig. 1F) is shown along with the maxillary canine of *B. browni* (Fig. 1G) and the mandibular canine of the unidentified fossil mammal (Fig. 1H) (see also Fox and Scott, 2005).

The anthropoid canines are particularly illustrative (Fig. 1A–C): these teeth possess a longitudinal groove that changes in outline, from V-shaped near the tooth's apex to a wider, C-shaped contour toward the base, similar to that of *B. browni* (Fig. 1G); however, in the primates, the groove extends to the tip of the canine root. As in *B. browni* (Fox and Scott, 2005), the groove is non-occlusal, fully enameled, and does not result from wear (Zingeser, 1968). Furthermore, primate maxillary canines are typically taller than mandibular canines. For example, in large-bodied male papionins, the height of the mandibular canine averages 69% that of the maxillary canine (n = 89 individuals; data from Plavcan, 1990), contributing to the substantial clearance between the canines at maximum gape. The groove is never fully obstructed by the mandibular canine, despite the fact that this tooth hones on the maxillary canine during occlusion. A similar configuration in *B. browni* was argued to facilitate an adequate gape for piercing and allowing venom to flow through the unobstructed groove (Fox and Scott, 2005).

In the Chiroptera, longitudinal grooves are present in the maxillary canines of all species of the genera *Acerodon* and *Pteropus* (Fig. 1E), as well as in those of other pteropodid bats (Jones and Kunz, 2000; Kunz and Jones, 2000; see data published online by Giannini and Simmons, 2005). As in the primates, the groove narrows apically, but it is more "ampoule-shaped" near the base
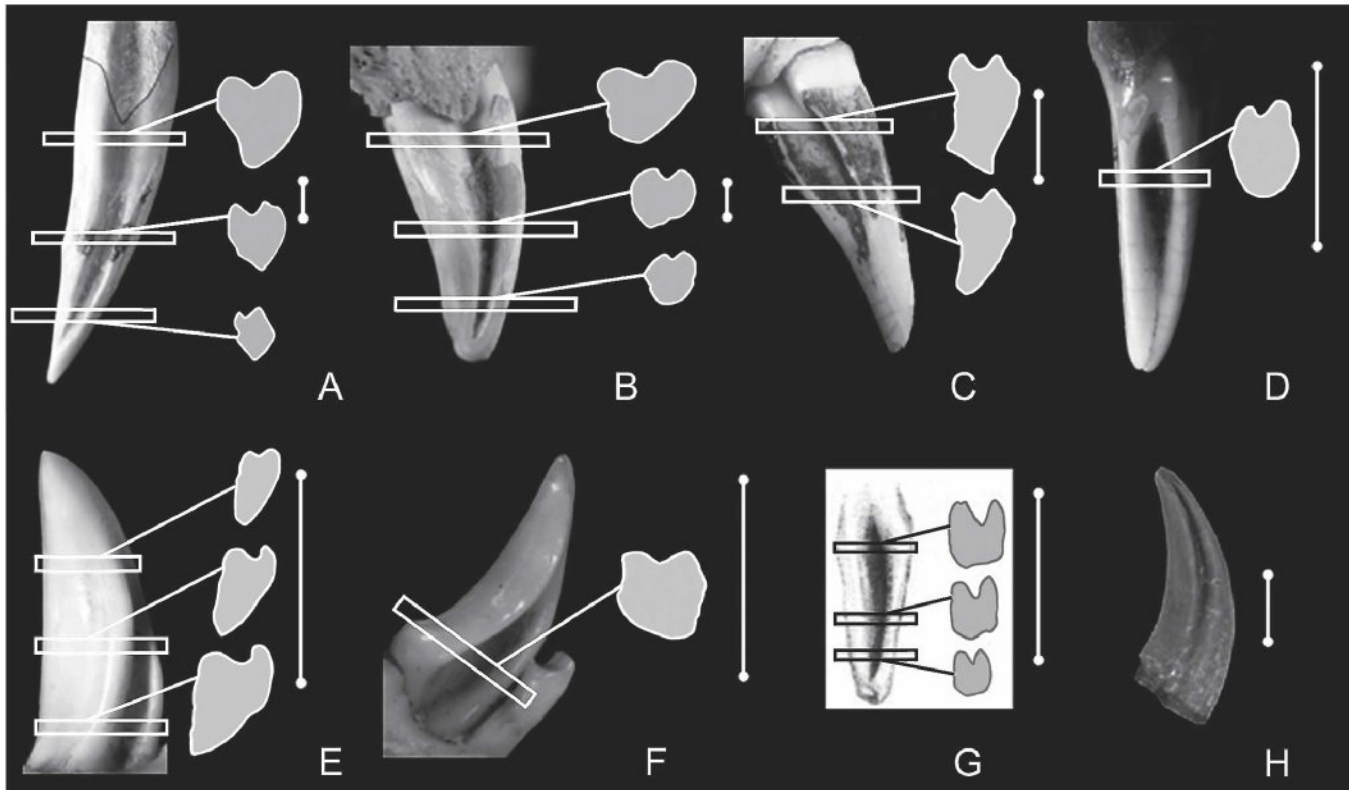


FIGURE 1. Canine/incisor grooves in venomous and nonvenomous mammals. The photographs of the extant taxa were taken with the specimens oriented so as to best highlight the groove. All cross sections are oriented so that the groove is facing toward the top of the figure. **A**, anterior view of the left maxillary canine of *Papio*, unnumbered ASU osteological specimen; **B**, anterior view of the left maxillary canine of *Mandrillus*, unnumbered ASU osteological specimen; **C**, anterior view of the left maxillary canine of *Alouatta*, NMNH 518232; **D**, anterior view of the left maxillary canine of *Pteropus*, NMNH 112596; **E**, lingual view of the left mandibular canine of *Nasua*, NMNH 108310; **F**, lingual view of the left mandibular incisors of *Solenodon*, NMNH 2230-1395—note that the larger, caniniform tooth (left) possesses the groove of interest; **G**, anterior view of the left maxillary canine of *B. browni*, UALVP 43115 (modified from Fox and Scott, 2005); **H**, labial view of the right mandibular canine of the unnamed fossil mammal, UALVP 43116 (modified from Fox and Scott, 2005). Scale bars equal 5 mm.

of the tooth, as in *B. browni* (Fox and Scott, 2005). The groove is fully enameled, but does not extend onto the root, being restricted exclusively to the tooth crown, as in *B. browni* (Fox and Scott, 2005).

The mandibular canine groove in coatis is situated along the mesiolingual aspect of the tooth. The distolingual side of the daggerlike canine is straight with a sharp edge, while the mesiolingual aspect is slightly recurved. The gutterlike groove is fully enameled and follows the curved course of the tooth; although we observed some intraspecific variation in its depth, it is often very deep. In overall appearance, the coati canines (Fig. 1D) are superficially similar in appearance to that of the unidentified mammalian fossil (Fig. 1H; Fox and Scott, 2005). Unlike *B. browni* and anthropoid primates, the mandibular and maxillary canines of the coatis are approximately equal in height. Nevertheless, with a gape (measured as the distance between maxillary and mandibular canine tips) that averages six times the height of the canines (Christiansen and Adolfssen, 2005), coatis have substantial clearance of these teeth at maximum mandibular depression.

## DISCUSSION

The inference of function in fossils always involves an element of uncertainty, as the fossil taxon may be an exception to a pattern established in an extant comparative sample. Nevertheless, the existence of a strong correlation between structure and function in the analogue taxa can provide a reasonable degree of confidence. However, in cases where there is little or no correlation between a particular form and a particular function (i.e., some extant taxa with the structure exhibit the function and some do not), evidence for the hypothesized function in the fossil record is equivocal at best. It is also important to take into account the number of independent evolutionary origins of a structure and its function. For example, if 100 species have a structure-function complex, but that complex was inherited from a common ancestor, then those 100 species should be treated analytically as a single instance of the association. A form-function relationship can only be strengthened by documenting evolutionarily independent acquisitions of the complex.

Our survey demonstrates that grooved canines appear to have evolved independently at least three times in nonvenomous mammals (at least once in pteropodid bats, once in the *Nasua-Nasuella* clade, and at least once in primates; see Fig. 2), and thus there is no clear correlation between canine/incisor grooves and a venom-delivery system (VDS) within Eutheria. Other features of the VDS complex, such as longer maxillary than mandibular canines (Fox and Scott, 2005), also appear in nonvenomous animals that exhibit longitudinal canine grooves. The fact that the venomous *Solenodon* has a longitudinal groove on an incisor rather than the canine does not necessarily render it an inappropriate analogue for reconstructing the function of canine grooves in fossil taxa. However, the latter taxon represents only a single instance of the association between canine/incisor grooves and venom delivery within Eutheria.

Of the primates, only the slow loris (*Nycticebus coucang*) makes use of an adaptation similar to venom injection, using a toxin secreted from a gland in the elbow for defense (Alterman, 1995). These primates lick the gland, allowing them to administer a toxic bite. It has been hypothesized that the mandibular tooth comb (a row of needlelike procumbent incisors and canines) of these animals may help channel the toxin into bite wounds (Alterman, 1995). However, given that the tooth comb is ubiquitous in the Strepsirrhini, and that no other primates of this clade are known to use toxins for defense, this structure most likely did not evolve for the function of toxin delivery, but may have been exapted for this purpose (sensu Gould and Vrba, 1982). In any case, the use of a toxin by *Nycticebus* is unlikely to suggest a
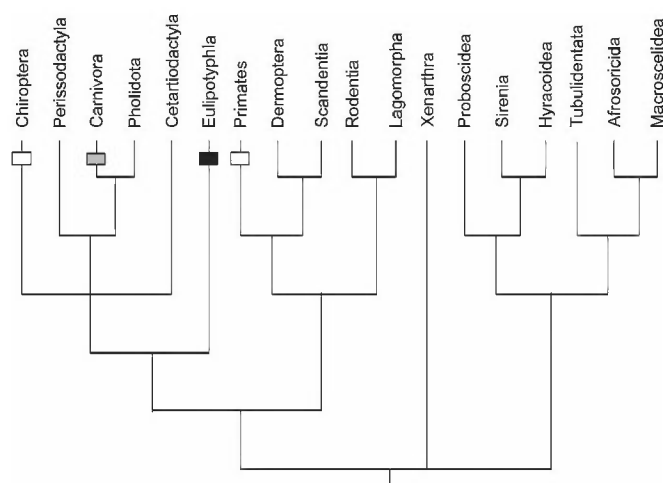


FIGURE 2. Phylogenetic relationships of extant eutherian orders (after Armine-Madsen et al., 2003; de Jong et al., 2003; Springer et al., 2004; Gibson et al., 2005; Kriegs et al., 2006; Nishimura et al., 2006) and the evolution of canine/incisor grooves and venom delivery. White rectangles indicate the presence of grooved maxillary canines in the absence of venom delivery in species within the orders Chiroptera and Primates (note that not all species within these clades possess the grooved morphology). The gray rectangle indicates the presence of grooved mandibular canines in the *Nasua-Nasuella* clade in the absence of venom delivery within Carnivora. The black rectangle shows the position of *Solenodon*, the only mammal known to have grooved anterior teeth (incisors) in association with venom injection; there are other venomous eulipotyphlans (shrews), but they do not exhibit dental adaptations for venom delivery. Thus, there are at least three independent evolutionary origins of grooved anterior teeth in nonvenomous species, whereas there is only one in a venomous species.

phylogenetic history of venom injection as an explanation for the presence of canine grooves in primates because *Nycticebus* does not exhibit such grooves in either the maxillary or mandibular canines, whereas such morphology does appear in strepsirrhines (Swindler, 2002; Whitehead et al., 2005) for which there is no evidence of toxin use.

The full distribution and degree of expression in Strepsirrhini is not yet clear, but the trait does not appear to be as well expressed as it is in anthropoids. Because many strepsirrhines and tarsiers lack deep, well-defined, and gutterlike maxillary canine grooves, such morphology may be an anthropoid synapomorphy. Anthropoids commonly use their canines as weapons during intraspecific agonistic encounters, especially among males (e.g., Plavcan, 2001). It is possible that longitudinal grooves (or the margins that define the grooves) act to increase the structural integrity of the canine in some fashion. It may be that the 'groove' is in fact the secondary consequence of two ridges built up to act as longitudinal struts, such that the ridges are actually the features of interest. This hypothesis may warrant further investigation, particularly given Plavcan and Ruff's (2006) conclusion that selection has favored strong canines in male anthropoids.

Within the Microchiroptera, vampire bats (*Desmodus rotundus*) secrete a powerful anticoagulant in their saliva (Hawkey, 1966), which might be delivered in a fashion analogous to venom. However, the canines of vampire bats are highly specialized as a part of their feeding strategy and do not exhibit longitudinal grooves (see also Greenhall, 1972). Most other microchiropterans also lack pronounced grooves, although there is substantial variation in the development of longitudinal ridges within this clade. These ridges occasionally produce shallow indentations along the length of the tooth (Freeman, 1992).

Because pteropodid bats and their successive outgroups are not venomous (Fig. 2), a phylogenetic history of such a function in this clade is improbable. Pteropodids are almost entirely frugivorous (Courts, 1998; Stier and Mildenstein, 2005), generally squeezing juice from fruit pulp with their teeth and spitting out the pulp and seeds (Nowak, 1999), but there are only limited descriptions of how they use their canines (e.g., Dumont and O'Neal, 2004). Thus, there is no indication of what function (if any) canine grooves might serve in these bats.

Within Procyonidae, the coatis are monophyletic (Beninda-Emonds et al., 1999), and the grooved morphology is presumably homologous in *Nasua* and *Nasuella*. Such grooves are absent in other procyonids, such as raccoons (*Procyon*), ring-tailed cats (*Bassariscus*), and kinkajous (*Potos*), as well as in all other carnivorans sampled, indicating that a grooved mandibular canine is a synapomorphy of the *Nasua-Nasuella* clade. Furthermore, as is the case for anthropoids and chiropterans, there is no evidence of venom delivery in any extant carnivoran, and thus a phylogenetic history of such a function for the groove in coatis is also highly unlikely. Coatis are omnivorous, subsisting on fruit, invertebrates, and sometimes large rodents (Smythe, 1970). Socially, coatis live in moderately sized multifemale groups, but males older than two years of age tend to be solitary (Kaufmann, 1962; Russell, 1981; Gompper and Krinsley, 1992). As in anthropoid primates, fighting among males is common, and the canines are employed as weapons during these agonistic encounters (Gompper and Krinsley, 1992). Canine breakage is fairly common, probably as a result of using the tooth for combat (Gompper and Krinsley, 1992). This may indicate that male coatis are under selection for increased canine strength (as in male anthropoid primates), which further suggests that the grooves (or the defining ridges) may act as structural supports.

Given that grooved anterior teeth are found in these diverse lineages with no clear common function, canine/incisor grooves cannot be tied specifically to venom delivery—within Eutheria, grooved anterior teeth evolved independently at least three

times in nonvenomous species (Fig. 2), but only once in a venomous context (i.e., *Solenodon*). However, it is possible that further study could reveal finer distinctions between the canine/incisor morphology of venomous and nonvenomous animals. For example, the grooves in primate canines, while pronounced, appear to be somewhat shallower than in *B. browni*, such that they are not as steeply walled or as deeply invaginated into the tooth. These differences may be functionally significant. However, in *Solenodon*, the steepness of the groove walls approximates that of the nonvenomous taxa, and the groove is not invaginated more deeply into the tooth (Fig. 1F). Furthermore, in colubroid snakes, the depth of the venom-delivery groove is highly variable across taxa, ranging from a shallow groove to a tubular structure (Jackson, 2003), suggesting that groove depth may not be a reliable indicator of the presence of a VDS.

In addition to dimensions of the groove, other morphological or physiological criteria for distinguishing dental specializations for venom delivery might be established. One possibility is that canine/incisor grooves might have a different function in animals of different body sizes due to an allometric effect on venom efficacy. That is, it may be inefficient for large-bodied animals to use venom because their large prey cannot be incapacitated quickly enough by such means. Thus, grooved canines or incisors in small animals may be indicative of venom injection, whereas in larger animals, these grooves may reflect a different adaptation. However, the problem of applying a body-mass threshold for inferring the presence of a VDS is that several of the nonvenomous taxa with grooved canines overlap the venomous *Solenodon* in body mass (Table 1). Thus, there does not appear to be a simple relationship between body mass, venom delivery, and the presence of canine/incisor grooves.

Unfortunately, using the comparative method to define further criteria for distinguishing adaptations to venom delivery may be difficult given that species of *Solenodon* are the only extant venomous mammals that exhibit grooved anterior teeth. If *Solenodon cubanus* is confirmed to be venomous, venom de-

TABLE 1. Body mass data for selected nonvenomous and venomous mammals.

| Taxon | Body mass (kg)* | | |
| --- | --- | --- | --- |
| | Combined Sex | Male | Female |
| Nonvenomous taxa with canine grooves | | | |
|   Carnivora | | | |
|     *Nasua narica* | 4.05 | | |
|     *Nasuella olivacea* | 1.38 | | |
|   Chiroptera† | | | |
|     *Acerodon jubatus* | 0.90–1.25 | | |
|     *Pteropus dasymallus* | 0.55 | | |
|     *Pteropus giganteus* | 1.30–1.60 | | |
|     *Pteropus hypomelanus* | 0.43–0.45 | | |
|     *Pteropus scapulatus* | 0.36 | | |
|     *Pteropus vampyrus* | 0.65–1.10 | | |
|   Primates† | | | |
|     *Alouatta palliata* | | 7.15 | 5.35 |
|     *Mandrillus sphinx* | | 31.60 | 12.90 |
|     *Miopithecus talapoin* | | 1.38 | 1.12 |
|     *Papio hamadryas cynocephalus* | | 21.80 | 12.30 |
|     *Pongo pygmaeus pygmaeus* | | 78.50 | 35.80 |
|     *Saimiri sciureus* | | 0.78 | 0.66 |
| Venomous taxa | | | |
|   Eulipotyphla | | | |
|     *Blarina brevicauda* (no groove) | 0.017 (0.010–0.024) | | |
|     *Solenodon paradoxus* (grooved mandibular incisor) | 0.90 | | |

*Body-mass data are from Silva and Downing (1995), except for primates (data are from Smith and Jungers, 1997) and the coatis (data are from Diniz-Filho and Tôrres, 2002). Silva and Downing compiled means or ranges from many different sources. Where more than one value was reported for a taxon, the value listed here is the average of those listed in Silva and Downing, with the range in parentheses. Where Silva and Downing list only ranges for a taxon, that range is reported. Separate male and female body masses were not available for most of the nonprimate taxa, so are not reported. Such data are available for primates, and because anthropoid primates tend to be quite sexually dimorphic, the data are divided by sex.
†Pteropid bats other than *Pteropus* and *Acerodon* and most anthropoid primates possess a grooved maxillary canine. We only list representatives of different body masses in order to convey the range of body-size variation in these two clades.

livery is almost certainly homologous between this taxon and *S. paradoxus*, rendering the sample size for comparative study of mammals that deliver venom via a dental groove to a single evolutionary event. As noted, robust application of the comparative method requires multiple cases of a form-function complex evolving for a particular biological role. Thus, drawing a correlation between particular features and venom delivery in mammals may be difficult or impossible given the paucity of extant analogues available for comparison.

Because venom injection is rare in Mammalia, and because nonvenomous mammals with canine grooves are fairly common, we consider the conclusion that *B. browni* and the unidentified mammalian taxon were venomous to be unsupported, or the evidence to be equivocal at best. Our survey included mammals of widely different lineages, body masses, dietary habits, and social behavior, indicating that no simple correlation can be drawn between the presence of longitudinal grooves of the anterior dentition and any particular function. Consequently, although the inference of venom-delivery adaptation in the fossil material from the Paleocene of Alberta may be correct (Fox and Scott, 2005), it is not supported by analogy with extant mammals that possess canine/incisor grooves.

Alternative hypotheses to explain the evolution of grooves in the anterior dentition should be considered. We have suggested that perhaps such grooves increase the strength of the tooth in some way, especially in animals in which the canines are frequently used as weapons in intraspecific agonistic encounters. Perhaps the function of the groove (or more likely the ridges that define the groove) in *Solenodon* is to strengthen the tooth so that it can be used effectively for piercing, rather than serving a primary function as a gutter for venom delivery (or perhaps both explanations are correct). Detailed allometric studies and data on the development of canines, coupled with methods such as finite-element analysis to compare closely related taxa with and without the groove may help test such structural hypotheses. However, one piece of evidence against this alternative hypothesis is that carnivorans (other than coatis) that use their canines for prey capture should be expected to exhibit a similar feature, which is not the case. Alternatively, longitudinal dental grooves may simply be a functionless nonaptation (sensu Gould and Vrba, 1982) that has evolved through some other mechanism—for example, as a pleiotropic effect of some more primary morphological change.

CONCLUSION

A survey of mammalian anterior dentitions indicates that there is no clear correlation between longitudinal canine grooves and venom delivery. Most anthropoid primates, some bats, and the coatis exhibit similar grooves with no evidence of venom delivery or phylogenetic histories of such a function; thus, this feature is not reliable for reconstructing such a function in fossil mammals. The available evidence is equivocal at best regarding the existence of venom-delivery systems in *B. browni* and the unidentified fossil mammal from the Paleocene of Alberta.

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