

CANINE GROOVES: MORPHOLOGY, FUNCTION, AND RELEVANCE TO VENOM

KAILA E. FOLINSBEE,¹ JOHANNES MÜLLER,^{1,†} and ROBERT R. REISZ,^{*,1} ¹Department of Biology, University of Toronto at Mississauga, 3359 Mississauga Road, Mississauga, Ontario L5L 1C6, Canada, kaila.folinsbee@utoronto.ca, rreisz@utm.utoronto.ca

Teeth are staggeringly variable structures, appearing in agnathan fishes before the evolution of jaws and subsequently undergoing a multitude of morphological changes (Smith and Coates, 2000). One major innovation was the development of enlarged canine teeth for prey control and increased oral processing. The appearance in Permian sphenacodontids of this caniniform region represents the very ancient beginnings of heterodonty in vertebrates. Therapsids and cynodonts later developed increasingly heterodont dental patterns, with post-canine teeth differentiating during the Triassic, and later synapsids show a gradual acquisition of the mammalian pattern: incisors, a single canine per quadrant, premolars, and molars. This dental pattern is characterized in mammals by thecodont implantation and a single episode of replacement during an animal's lifespan (Smith, 2000).

Research into the evolution of mammalian teeth has tended to focus on the post-canines and the development of molariform teeth with flattened surfaces and cusps for increased oral processing, but in both living and fossil mammals, canine form can also be extremely variable. Less commonly, some mammals have evolved venom delivery structures as an aid or alternative for subduing prey.

The best known and most highly developed venom systems in vertebrates are present not in mammals, however, but in snakes. Squamate dental morphology is largely homodont, with most taxa in possession of a series of continuously replaced conical teeth. Within colubroid snakes, however, many fossil and extant taxa have enlarged and recurved fangs that are either grooved or hollow (Fig. 1) and capable of ejecting venom under high pressure from modified parotid glands and associated muscles in a highly derived venom-injection system (Kuch et al., 2006). This apparently evolved very early in the clade, and is secondarily lost in non-venomous colubroid snakes.

A recent paper published in *Nature* suggested the presence of a venom-delivery system in an extinct mammal from the late Paleocene of Alberta (Fox and Scott, 2005). Here, we present a reinterpretation of this purportedly venomous mammal and explore the variation within vertebrates of canine grooves and associated structures, with particular emphasis on how they may relate to the prevalence and distribution of venom-delivery systems.

MORPHOLOGY OF CANINE GROOVES

Nydam (2000:292) defines a venom groove as “a narrow slit or infolding in the tooth, at least as deep as it is wide, that runs

nearly the entire length of the tooth.” Although he was applying this definition to helodermatid lizards, it is a good description of venom grooves in other taxa. To identify accurately the presence of a dental venom delivery system in an extinct animal, it will be necessary to differentiate between true venom canals and grooves serving other purposes. In living mammals, the presence of grooved teeth is much more widespread than the presence of venomous salivary secretions.

Synapsids (Including Mammals)—Several recent papers have suggested that the ability to secrete venom may have appeared early in the mammalian lineage (Fox and Scott, 2005; Hurum et al., 2006). Fox and Scott (2005) noted the occurrence of deep grooves on the upper canines of an extinct North American mammal, *Bisonalveus browni*, which, they suggest, implies the presence of a venom delivery system. This interpretation is problematic for several reasons: firstly, canine grooves are present in living mammals from several clades, and are not associated with venom; secondly, *B. browni* shows no evidence of possessing cranial modifications that we would expect to be associated with venom delivery, such as conducting ducts or space for modified glands; and thirdly, there is no phylogenetic support for such an inference (*B. browni* is not related to any mammal known to be venomous).

Canine grooves occur in both living and extinct mammals. In primates, the presence and depth of a canine groove is related to both size (males tend to have more strongly developed grooves) and location (grooves are more prominent on maxillary canines than on mandibular ones). The condition is present in most anthropoids, including some early fossil representatives from the Oligocene Fayum deposits in Egypt (Simons, 2001). Both living and extinct hominoids possess anterior canine grooves. A groove is strongly developed in cercopithecoid monkeys, including the basal extinct catarrhine *Victoriapithecus*, and is also present in colobines (Benefit, 1999).

In the upper canine of the fossil baboon *Papio angusticeps*, for instance, the groove runs along the anteromesial face and extends along the entire length of the root (Fig. 2A). The groove tends to be widest at the thickest point of the tooth (the base), then narrows slightly as it approaches the apex. There is frequently apical wear on the mesial side of the canine, incurred from occlusion with the distal edge of the mandibular canine, and occasionally there is wear on the margins of the groove from this cause. The groove occurs on the opposite side from the shearing distal edge, which is worn through occlusion with the lower third premolar (Fig. 2B). This shearing edge extends along the length of the canine.

In the lower canine, there is a less pronounced mesial groove along the edge of the tooth. This may occasionally demonstrate occlusal wear from the upper second incisor. The groove is directly opposite the distal occlusal surface with the upper canine.

*Corresponding author.

†Current address: Humboldt-Universität, Museum für Naturkunde, 10099 Berlin, Germany, Johannes.Mueller@MUSEUM.HU-Berlin.de.

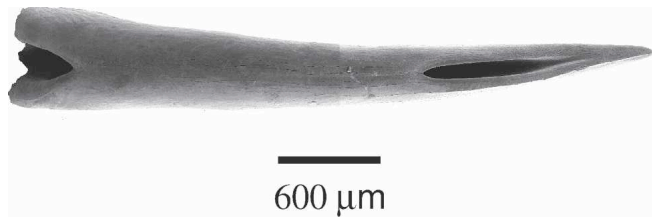


FIGURE 1. SEM image of early Miocene (MN 2) viper fang from the Mainz Basin, Germany with enclosed venom groove (anterior view). Venom is discharged from the aperture at the apex of the hollow, tubular tooth (from Kuch et al., 2006).

This pattern also occurs in hippos and suiforms. Pickford (1986; 1988) noted the presence of a deep groove on the distal edge of the upper canine in hippopotamuses and peccaries. We observed grooves on the anterior or anteromesial faces of the upper canines in suids and hippos, with one or more grooves on the posterior faces of the canines. These were variable in number and depth, but were visible in all observed specimens. In suids and tayassuids, the lower canine is sharpened against the upper canine, with slight differences in exact occlusal morphology between pigs and peccaries (Herring, 1972). There is also variable grooving with corresponding occlusal facets in the lower canines in these taxa. In hippos and suids, the upper canine sits behind the lower when the jaws are closed, and occlusion occurs along the mesial edge of the upper and the distal edge of the lower. In both these groups where large canines are honed on the opposing tooth, there is a groove present on the opposing side from the shearing wear. This observation could suggest that the groove in the canine may function to support the structural integrity of the canine or tusk.

Canine grooves in these taxa do not appear to be correlated with any particular dietary strategy; primates and suids are omnivorous, eating both plant and animal material, while hippos are herbivorous.

Despite the suggestion of an early initial appearance of venom and venom-producing structures, the occurrence of venom in living mammals is rare. The only known mammals with a venom delivery system are members of the Eulipotyphla, shrews and *Solenodon paradoxus*. The Caribbean *Solenodon* has enlarged and modified lower second incisors with a deep channel on the anteromesial surface. This channel is distinct from a groove; the enamel of the tooth wraps around a hollow duct, forming a tubular structure that opens and widens at the base. Inferior to the base of the tooth along the anterior portion of the mandible, is a pocket where the venom gland lies. Toxic saliva travels up through a duct from this submaxillary gland along the channel. We could find no evidence for wear facets on the canines in *Solenodon*.

Blarina brevicauda, the short tailed shrew, has modified salivary glands that produce venomous saliva and five, sharp, unicuspid, puncturing lower incisors that push the venom into its prey during a bite (Pournelle, 1968; Nowak, 1999). These incisors do not possess channels or ducts, but retain a concave inner surface; there does not appear to be any enlargement of the modified glands in the mandible. Likewise, *Neomys fodiens*, the European water shrew, has an elongated lower first incisor and concave lower incisors that connect to a submaxillary venom gland (Pournelle, 1968).

One of us (R.R.) has seen the new specimen of *B. browni*, and noted in detail the size and position of occlusal wear facets on the surface of the canine that were reported by Fox and Scott (2005). We believe the position of the wear facets indicates they did in fact serve a mechanical function during normal chewing. The posterior wear facet on the lower canine (UALVP 43114) defi-

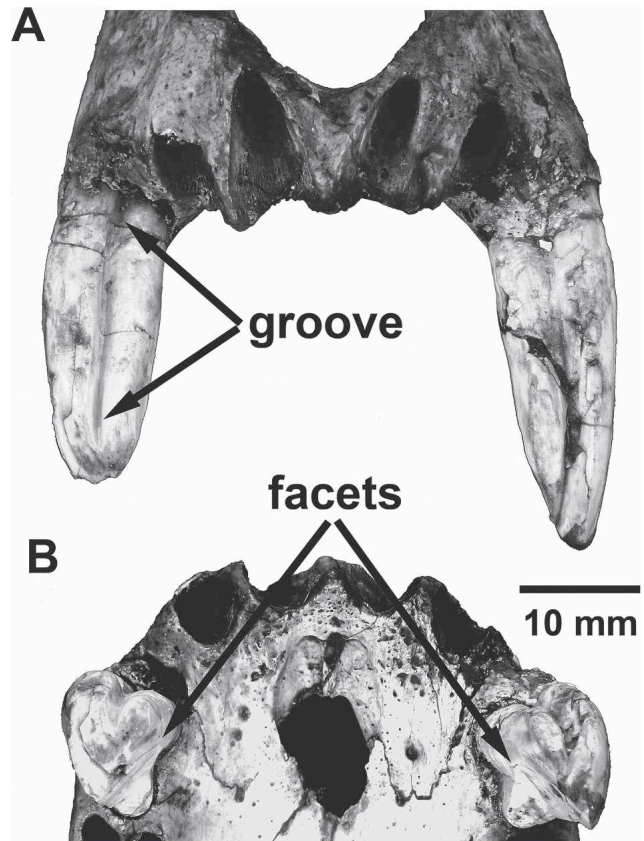


FIGURE 2. Adult male *Papio angusticeps* (Co100), a Pleistocene papionin from Coopers Cave, South Africa, showing deep anteromesial grooves in upper canines. **A**, anterior view of muzzle (maxilla and premaxilla). **B**, palatal view. The posterolingual shearing crest (**sc**) of the upper canine is located opposite to the deep anteromesial groove. This facet is created by occlusion with the mandibular third premolar (which shows a corresponding shearing crest). The canine is expanded on the anterior edge, and narrows to a crest distally; it wear occurs continuously, and the canine decreases in length over the animal's lifespan.

nately occluded with the upper, and did so along the length of the mesial edge of the groove on the anterior side of the upper canine. There is also a shorter wear facet on the lateral edge of the groove. Fox and Scott (2005) suggested the lower canine did not fit into the groove; however, we observe that they were in close occlusion. There is a wear facet at the tip of the upper canine as well, and a small anterior groove near the broken tip of the lower canine. This is similar to the situation in some primates, where the distal face of the lower canine may occlude with the groove on the anterior face of the upper canine.

The root of the canine in *B. browni* is very long (approximately twice as long as the crown of the tooth), and unlike in cercopithecoids and hippos, the groove does not extend into the root, but tapers out near the base of the crown. There is no posterior wear facet, only wear on the anterior (grooved) side, as in some primates. We cannot support an inference of functional homology to the grooves seen in cercopithecoids, suids, and hippos. However, the occlusal wear on the edges of the groove suggests to us that it would not have made an effective venom delivery structure. The morphology of the grooves in *Solenodon* is very different. In *Solenodon*, the groove is tubular and almost completely enclosed, and flared laterally towards the base for the entry of the venom duct. In *B. browni*, the groove is more open, and becomes shallower at the base, much more like the situation in a primate canine.

We did not see any evidence for pocketing within the maxilla of this specimen, although it is possible that modified venom glands could have existed in the maxillae and mandibulae of *B. browni* and other extinct animals without requiring any modification of the bone. However, the specimen is lacking in any diagnostic features that would unambiguously indicate venomousness.

There are two examples of fossil (non-squamate) taxa for which an inference of venom delivery is fairly well supported. The enigmatic *Euchambersia*, a Late Permian therocephalian from South Africa (of which there are only two known specimens) possesses a deep maxillary fossa that communicates with a canine groove (Hotton, 1991; Sues, 1996; Rubidge and Sidor, 2001). Hotton (1991) implied that this morphology indicates the presence of a venom gland with associated canine modification for delivery. There is a groove on the upper canine that is pinched towards the base, creating an almost hollow, tubular, snake-like tooth. *Euchambersia* also possesses several unique features that may be suggestive of modified glandular structures. The snout is unusually wide, formed by broadly expanded premaxillae. The snout is emarginated anterior to the maxillary canine, with a deep pocket pinched in immediately in front of the tooth. There is a distinct groove in the maxillary bone leading from this emarginated area directly to the groove in the upper canine (R. Reisz, pers. obs.; Mendrez, 1975). This structure, in conjunction with the canine groove, supports the suggestion that *Euchambersia* may have been capable of delivering venom.

Two fossil soricines were recently reported from the Pleistocene of Spain; these share both phylogenetic proximity and some degree of morphological similarity to *Solenodon* (Cuenca-Bescós and Rofes, 2007). The indeterminate soricine has a groove along the mesial face of the lower incisor, and a fossa in the mandibular symphysis. *Beremendia fissidens* has a different morphology, with a shallower groove along the mesial edge of the incisor (mandibular morphology, including presence or absence of fossa, is not figured or discussed for this taxon). There is no evidence of occlusal facets on these teeth (Cuenca-Bescós and Rofes, 2007). We disagree with Cuenca-Bescós and Rofes' assumption that these fossil soricines support Fox and Scott's hypothesis, but we find their interpretation of an 'envenomation apparatus' more credible in these fossil taxa than in *Bisonalveus browni*.

In the absence of similar associated skeletal evidence of palatal or mandibular fossae for the proposed venomous glands, the interpretation of canine grooves as a venom delivery system in *Bisonalveus browni* remains highly speculative. If *B. browni* could be shown to be phylogenetically proximal to the Eulipotyphla, it would more strongly support the contention of venomousness through phylogenetic proximity. However, *B. browni* is a pantolestid, distant from the Eulipotyphla and more closely related to carnivores (Fox and Scott, 2005) and therefore, phylogenetic optimization for an inference of venom is not supported.

It is not surprising that mechanisms utilizing toxic salivary secretions for immobilizing prey are rare among terrestrial vertebrates; the sophisticated mammalian masticatory apparatus has led to a wide range of feeding strategies without requiring the use of venom.

Reptiles—There is a significant amount of variation in the structure of venom teeth within the living and extinct Reptilia. Sues (1991) described teeth from a Triassic reptile with two deeply infolded, enamel-lined grooves along the labial and lingual surfaces of the tooth. The grooves become shallow at the apex. Other teeth from a slightly younger locality show similar morphology (Sues, 1996), but the grooves are enclosed, forming complete tubes that run through the center of the tooth on the labial and lingual sides. Other than the presence of these

grooves, the teeth are identical to normal squamate teeth (re-curved, with cutting edges on the mesial and distal edges).

Reynoso (2005) described a Jurassic sphenodontian that may share convergent cranial and dental morphology with colubroids and helodermatid lizards, suggestive of the presence of venom in this taxon. The fangs of this sphenodontian show grooves on their anteromedial surface, and Reynoso asserted that the gape would have been wider and weaker than in other sphenodontians because the postcoronoid end of the jaw is relatively reduced in length. We find this interpretation as problematic as that for *B. browni*. The simple fangs are not very specialized, nor are the grooves apparently particularly deep; these grooves appear on two caniniform teeth at the anterior right jaw, which would imply venom delivery through both of these teeth. The broken postcoronoid portion of the jaw does appear to be shorter than that of other sphenodontians; however, no cranial elements are known for this taxon, and therefore reconstruction of the gape and bite morphology cannot therefore be conclusive.

The best known venomous vertebrates, snakes, represent a special case in vertebrate evolution because they have evolved alternative feeding techniques such as constriction or envenomation in association with the lightly built, highly kinetic ophidian skull.

Only two extant lizards possess venom: the Gila monster and the Mexican beaded lizard, both members of the Helodermatidae. Unlike snakes, the paired venom glands of these lizards occur in the lower jaw anterior to the bone of the dentary, and venom is delivered via ducts leading to grooved lower teeth (Beck, 2005). The glands are not directly connected to these teeth; therefore, unlike snakes, the bite is inflicted and then bathed in venom that is brought up through the venom duct via capillary action. The largest teeth are in the lower jaw and have two grooves, a deep anterior one surrounded by cutting flanges and a shallower, posterior groove (Beck, 2005). When discussing the question of venom grooves in a fossil monstrosaur lizard, *Primaderma nessovi*, Nydam (2000) suggested that despite phylogenetic proximity and morphological similarity, the grooves in the teeth of this taxon do not correspond to venomous capabilities. Instead, he suggested that the blade-like structure may be more suited to shearing, unlike the more cylindrical venom teeth of *Heloderma*.

Canine morphology in both living and fossil vertebrates is extremely variable, as is the morphology of the groove when it is present. Because of the variability of this structure and the inconclusiveness of the evidence for venom even if a groove is present, we feel it is unwarranted to postulate a wide distribution of venom in the fossil record.

ALTERNATE HYPOTHESES

Snakes use venom to stun their prey long enough for ingestion. Their lightly built skulls, homodont dentition, and lack of limbs for grasping effectively requires dependence on an alternate form of prey control. Mammals, on the other hand, have forelimbs with which to grasp prey while inflicting bites, much sturdier skulls capable of holding and tearing prey, and large chewing muscles and muscular attachments on both the jaws and skull. In the case of small venomous mammals, mild venom may serve to stun prey that might otherwise evade capture. The small venomous water shrew (*Neomys fodiens*) needs to eat its own weight in food (fish, frogs and invertebrates) in a 24-hour period to maintain a high metabolic rate (Pournelle, 1968). Presumably, they use venom to stun prey quickly for rapid ingestion and to reduce prey escapes. *Blarina brevicauda* is terrestrial, and primarily consumes insects and molluscs; venom may help a small animal capture prey more easily. A behavioural study investigating whether the presence of venom significantly increases rate and/or number of captures by *Blarina* vs. a non-venomous sister

species would be an interesting addition to this field to address the question of the adaptive value of venom in insectivorous mammals.

It is difficult to explain the evolution of venom in *Solenodon paradoxus*, when it is uncommon in other lipotyphlans. This species is large (500 mm including tail), has powerful claws for digging, and is known to eat primarily insects (Pournelle, 1968). Freiberg and Walls (1984) suggested that intraspecific competition may be a factor because solenodons are not immune to their own venom (but similarly, neither are venomous snakes). Perhaps earlier in their evolutionary history they fed on larger prey that required more subduing, and they never lost the trait. Mebs (2002) states that until now, no definite reason has been presented as to why these mammals use venom. He also suggests that other mammals, including humans, have an enzyme in their saliva that lowers blood pressure, and speculates that 'a certain venomousness' might have been a plesiomorphic trait in mammals, and ancestrally may have served as a defence against predators. Superficially, this suggestion would seem to support the Fox and Scott hypothesis, however but it is one thing to observe that the potential for venomous saliva exists, and quite another to demonstrate the morphological and physiological changes required for such an innovation.

We can suggest equally plausible alternative hypotheses for the presence of canine grooves in suids, hippos, primates, and the fossil *Bisonalveus browni*, that are not contingent on venom. Grooves may increase the structural strength of a slender canine by providing more surface area for enamel (which is harder than dentine). In both primates and suids, the groove is located directly opposite the shearing edge of the canine on which it is located. The P3 lies almost parallel to the mandible, with much of the root exposed. The upper canines scrape against this exposed enamel surface, creating a shearing crest on the distal edge of the upper canine as both teeth wear down over time. The groove is directly opposite to the sharpened edge of the upper canines, and may therefore be related to increasing the structural stability of the tooth as it is continuously sharpened and worn down. In hippos and suiforms, the groove-occlusion morphology is more variable, with occlusion often occurring on the distal face of the lower tooth along the lateral edge of the groove. In *B. browni* as well, occlusion occurs on the edge of the groove, but in that case, the groove is on the anterior side of the canine. The hypothesis that the groove functions to buttress a tooth could be tested experimentally, or by modelling the system using the different existing groove structures.

Komodo dragons possess grooves that store bacteria, allowing them to inflict vicious infectious bites (Auffenberg, 1981). After it has been bitten, a prey animal sickens and dies within days or hours. We find this explanation less persuasive, but the grooves in the fossil *B. browni* may have had a similar function, harbouring bacteria that poisoned its prey. Freedman (1957) suggested that the groove in primate canines may have permitted rapid penetration during the bite and easier withdrawal of the teeth during fights. To support this, we would need evidence that the canines are used in fights, and the groove functions in that way. These hypotheses are merely potential functional explanations, and need to be tested to determine the best interpretation of the morphology.

CONCLUSION

The ability to secrete and inject venom into prey is rare, yet has evolved in multiple clades and in different anatomical areas. It is most widespread and specialized in colubroid snakes, which are dependent on venom for prey acquisition. Dental grooves are much more widespread both across and between clades. This is unsurprising since they occur on teeth, which are known to be developmentally and evolutionarily plastic. We advocate caution

when inferring the existence of venom in fossil taxa; evidence for such a rare and complex physiological system cannot be solely based on dental features that show structural plasticity. Further work needs to be done to test the hypotheses presented herein to better understand the function and evolution of the canine groove in mammals.

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