Observations of a Grooved Anterior Fang in *Psammodyastes pulverulentus*: Does the Mock Viper Resemble a Protoelapid?

KATE JACKSON*1,2* AND THOMAS H. FRITTS*1*  
*1Department of Zoology, University of Toronto, Toronto, Ontario, Canada, M5S 1A1 and *2National Biological Survey, National Museum of Natural History, Washington, DC 20560, USA.

Greene (1989) presented an analysis of the defensive behaviour and feeding habits of the Asian mock viper, *Psammodyastes pulverulentus*, and reviewed evidence that having enlarged anterior and posterior maxillary teeth were morphological adaptations that facilitated the handling of hard-bodied prey. Greene noted that studies of the mock viper could be important to synthetic considerations of snake evolution, especially in evaluating the hypothesis that protoglyphous snakes (Elapidae) developed venom-conducting fangs from anterior maxillary teeth, rather than from the enlarged, grooved teeth of the posterior maxilla so widespread in colubrid taxa. Greene concluded that in the mock viper, venom was conducted by the enlarged and grooved teeth located at the posterior end of the maxilla.

While examining the teeth of a dried skull of *Psammodyastes pulverulentus*, we detected what appeared to be grooves on the enlarged anterior teeth of the maxilla, and subsequently used scanning electron microscopy to determine details of the tooth morphology. The association of grooves, capable of conducting venom into the tissues of prey, with the enlarged anterior teeth of this species could shed new light on the morphological complex presumed to be adaptive for consuming hard-bodied prey (Savitzky, 1983; Greene, 1989).

The presence of grooves on the anterior teeth of colubrid snakes, capable of conducting venom into prey, or the demonstration of progenitors of such functional grooves, would provide an opportunity to ask whether such grooves appear to be similar in origin to posterior grooved fangs (positional hypothesis), share developmental pathways with grooves and venom canals in protoglyph fangs (protoelapid hypothesis), or are likely to have an origin independent of the opisthoglyphous or protoglyphous tooth (independent hypothesis).

By comparing the grooved anterior fang-like teeth of the mock viper with grooves evident on the fangs
and other maxillary teeth of elapids, as well as with the opisthoglyph fangs of colubrids, and anomalous surface morphologies observed on the teeth of other colubrid specimens, we hope to stimulate other researchers to closely examine the teeth of colubrid snakes in search of proto-fangs.

Specimens were examined using scanning electron microscopy. Maxillary bones were dissected from fluid-preserved specimens, or in the case of one specimen (USNM 134014), a dried skull. In each case, the entire maxilla was mounted on the SEM stub so as to preserve positional data and minimise damage to the teeth.

The maxilla of *Psammodynastes pulcherulentus* is relatively straight and shows no sign of the arched condition reported by Savitzky (1983) (Fig. 1). The maxillary dentition is highly heterodont, with two diastemata, and enlarged teeth in two positions on the maxilla. The enlarged posterior fang is equal in size to the largest anterior maxillary tooth, and approximately three times the length of the smallest anterior maxillary tooth. It is grooved and separated from the teeth anterior to it by a diastema. The labial groove of the posterior fang strongly resembles those of *Boiga*, *Ahaetulla*, *Enhydris*, and *Chrysopelea* in being deep, with rounded sides, well centred on the labial side, and extending the full length of the tooth (Fig. 2). Immediately anterior to the grooved posterior fang is a diastema, preceded by a series of small teeth, several of which were missing in one of the specimens we examined. The average number of small teeth between the large teeth at the anterior and posterior ends of the maxilla is variable (n = 5) (Rasmussen, 1975); we observed nine in USNM 229273. Anterior to these small teeth is a diastema, bounded anteriorly by one or two enlarged teeth, equal in size to the grooved posterior fang (Fig. 3). Immediately anterior to these enlarged teeth are the anterior-most maxillary teeth, which decrease in size anteriorly, are slightly less than half the length of the largest anterior teeth, and are more slender in shape than the small teeth on the middle of the maxilla. With the exception of the grooved fang, the visible ridges of all the maxillary teeth follow the usual pattern of anterior maxillary teeth in colubrids (i.e., a prominent ridge extending along the distal 3/4 of the labial side of the tooth, and a shorter and less prominent ridge occupying an analogous position on the lingual side).

In one specimen from Taiwan (USNM 134014), the enlarged anterior maxillary tooth and the smaller tooth immediately anterior to it were found to be grooved (Fig. 4). These grooves differed from that observed on the grooved posterior fang in that there were several shallow and narrow grooves on each tooth rather than a single, deep labial groove as present in the posterior fangs. The grooves on the anterior teeth were present on all sides of the tooth (lingual, labial, anterior, posterior) (Fig. 5), and were most evident on the central body of the tooth and toward the distal end, rather than extending all the way from the tip to the base. At least five grooves on the lingual and posterior face of the tooth extend to the tooth tip, and as they converge in the narrowest part of the tooth, create a bundled appearance. In contrast, the grooves on the anterior and lingual sides were more obvious. The groove on the anterior face appeared to extend to the tooth tip, although it was shallower and less evident in a short area 1/3 of the tooth’s length from the base. In addition, a groove originating just ventral to the tooth base on the labial surface terminated about 1/3 along the tooth’s length. The ridges observed on the lingual and lingual sides of the anterior maxillary teeth of other specimens were still discernible on the grooved anterior maxillary teeth of this specimen.

Our observations and those of others suggest that the teeth of some snakes of distantly related genera have grooves that result from variations of the usual surface morphology of the teeth and are not present in all members of the species (as presently understood). The presence of grooves on the enlarged maxillary teeth of heterodont opisthoglyphs has occasionally been reported in individual specimens of *Ahaetulla* and *Psammophis* (Anthony, 1955), but this condition is apparently the exception rather than the rule in these genera, as appears to be the case in *Psammodynastes pulcherulentus* as presently defined. The presence of grooves on maxillary teeth anterior to the posterior fangs has been reported in *Oxybelis* (Underwood, 1967). These grooves, however, are not invariably restricted to the labial surfaces of the maxillary teeth. Grooves have been reported on the lingual surfaces of the maxillary teeth of some specimens of the African genus *Aparallactus* (Boulenger, 1889, fide Anthony, 1955). Using scanning electron microscopy, we have observed shallow grooves on the enlarged palatine as well as maxillary teeth of some specimens of *Boiga cynodon*, the dog-toothed cat snake. In addition, shallow grooves occur on maxillary teeth other than the fang in various elapids (e.g., *Notechis*...
Fig. 2. *Psammodynastes pulverulentus* (USNM 120180): Grooved posterior fang of right maxilla, labial view.

Fig. 3. *Psammodynastes pulverulentus* (USNM 120180): Enlarged (ungrooved) anterior tooth of right maxilla, labial view.
and Ogmodon; Underwood, 1967). These may represent venom canals which have not developed to the same degree as in the primary fang. We have observed such grooves on the anterior surfaces of the second and third maxillary teeth of *Notechis scutatus*, with grooves extending from the base to two-thirds of the length of the tooth, along the anterior surface. The maxillary teeth posterior to the fangs of *Ogmodon vitatus*, a presumably basal elapid, are similar to those of *Notechis* in having narrow grooves sometimes connected to concavities at the base of the tooth, extending along the anterior face of the tooth shaft. Like the elapids examined, the *Psmmodynastes* specimen had the most conspicuous groove on the anterior surface of the tooth.

Our observations of the surface morphology of the grooved posterior fangs of many colubrid species suggest that the grooved anterior fang of *Psmmodynastes pulserulentus* is not homologous to the grooved posterior fang found in many colubrid species. The posterior maxillary teeth of colubrines are usually distinguishable from the anterior maxillary teeth by the presence of ridges on the anterior and posterior surfaces of the tooth rather than the labial and lingual surfaces. In species in which the posterior fang is grooved, the lingual surface of the tooth is smooth, with the ridges sometimes faintly visible on the anterior surface of the tooth and on the posterior edge of the groove (Jackson and Fritts, 1995). On the grooved anterior fang of *Psmmodynastes pulserulentus* (USNM 134014), by contrast, ridges are still visible on the labial and lingual surfaces of the tooth.

We have not demonstrated the association of the grooves seen on the anterior enlarged teeth of the mock viper with the conduction of venom into the tissue bitten. In *Lycophidion* and *Mehelya*, the duct from Duvernoy's gland appears to empty in the region of the enlarged anterior maxillary teeth (Savitzky, 1981). If the duct from Duvernoy's gland is closely positioned in *Psmmodynastes*, it seems possible that enlarged, grooved anterior maxillary teeth may act as venom-conducting fangs.

Our dissection of the cephalic glands of *Psmmodynastes pulserulentus* (USNM 291828 from Taiwan) was not definitive. Duvernoy's gland is large and extends from the level of the posterior margin of the orbit to the angle of the jaw, and is bounded dorsally at about the middle of the orbit by a lobate, anteriorly-dorsally oriented muscle mass, and anteriorly by an elongate supralabial gland which continues posteriorly, ventral to Duvernoy's gland. The central mass of Duvernoy's gland is positioned at the base of the enlarged and grooved rear fangs, and the base of these teeth occupy a convexity on the medial surface of the gland. However, no central duct was apparent to us. The supralabial gland is positioned dorsal to the remainder of the maxillary teeth, extending as far anteriorly as the enlarged anterior teeth. A ridge of white tissue extends anterior to Duvernoy's gland along the dorsal surface of the supralabial gland to the level of the enlarged anterior teeth, but confirmation of this structure as a duct from the Duvernoy's gland will require histological study, which we have not attempted. Regardless of whether or not the mock viper has any relationship with elapid origins, an anatomical search for the position of the venom ducts relative to the anterior teeth of the mock viper is relevant to evaluating this component of an effective venom-delivery mechanism. Greene (1989) concluded that the venom of the mock viper was important in subduing prey, but did not consider the anterior teeth as a means of introducing the venom.

These results suggest that grooved fangs, potentially capable of conducting venom, may evolve independently of opisthophyphous fangs, so that the hypothesis that proteroglyph denticity arose from an opisthophyphous precursor by means of a shortening of the maxilla and loss of anterior maxillary teeth may not be the most parsimonious evolutionary scenario. One alternative is the enlargement of anterior teeth in association with preferences for hard-bodied prey, and subsequent development of a venom-conducting tooth morphology facilitating prey handling and digestion.

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**Fig. 4.** *Psmmodynastes pulserulentus* (USNM 134014): Enlarged (grooved) anterior tooth of right maxilla, labial view.

**Fig. 5.** *Psmmodynastes pulserulentus* (USNM 134014): Enlarged (grooved) anterior tooth of right maxilla, posterolingual view.