



Enamel microstructure of the Late Cretaceous multituberculate mammal *Kogaionon*

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Cretaceous multituberculate mammals of Europe are poorly known, as a rule represented by isolated teeth. The only exception is the Late Cretaceous (Maastrichtian) monotypic genus *Kogaionon* Rădulescu & Samson, 1996 from Romania, represented by a single skull, without dentaries, assigned to Kogaionidae Rădulescu & Samson, 1996. Another kogaionid genus is *Hainina* Vianey-Liaud, 1979, represented by several isolated teeth from the Paleocene of Belgium and Spain, and from the Maastrichtian of Romania. The skull of *Kogaionon* is roughly rectangular in palatal view, resembling superficially that of Paleocene *Taeniolabis* (except for having a strongly elongated snout), but the upper dentition differentiates the Kogaionidae from all other multituberculates. In this paper we studied the enamel microstructure of *Kogaionon* and demonstrate that it is of gigantoprismatic type.

In recent decades, mammalian systematists have recognized the utility of characteristics of enamel microstructure in phylogenetic interpretation, particularly among multituberculates (e.g., Carlson & Krause 1985; Fosse *et al.* 1985; Krause & Carlson 1986, 1987; Simmons 1993; see also papers in Koenigswald & Sander 1997, and a summary by Kielan-Jaworowska & Hurum 2001). Sloan & Van Valen (1965) divided advanced Multituberculata (subsequently referred to by McKenna 1975 as Cimolodonta) into two suborders Taeniolabidoidea and Ptilodontoidea. This division is now not valid. Kielan-Jaworowska & Hurum (2001, but see McKenna & Bell 1997 for an alternative classification) divided the order Multituberculata into a paraphyletic suborder 'Plagiaulacida' and a suborder of derived multituberculates Cimolodonta McKenna, 1975. Cimolodonta in turn are subdivided into superfamilies; the previous suborder Taeniolabidoidea has been restricted to a single family Taeniolabididae (see also Fox 1999). As, however, Sloan & Van Valen's (1965) division of derived Multituberculata was valid when the basic studies on multituberculate enamel microstructure were performed, we use the name 'Taeniolabidoidea' *sensu* Sloan & Van Valen (1965) in quotation marks, and we retain the name Ptilodontoidea, used now as a superfamily.

In studies on human enamel a model was developed describing numerical density and distribution of enamel prisms (Fosse 1968a). These parameters equal density and distribution of ameloblasts in human tooth germs. The model was also valid for canine and feline enamels and tooth germs (Fosse 1968b). A preliminary study of enamels in Late Cretaceous multituberculates showed an important difference between two major groups recognized at that time: 'Taeniolabidoidea' have large, widely separated and discrete enamel prisms (designated gigantoprismatic enamel), whereas the prisms are smaller and more densely packed in Ptilodontoidea (Fosse *et al.* 1978). Subsequent, more detailed studies by Carlson & Krause (1985) and Fosse *et*

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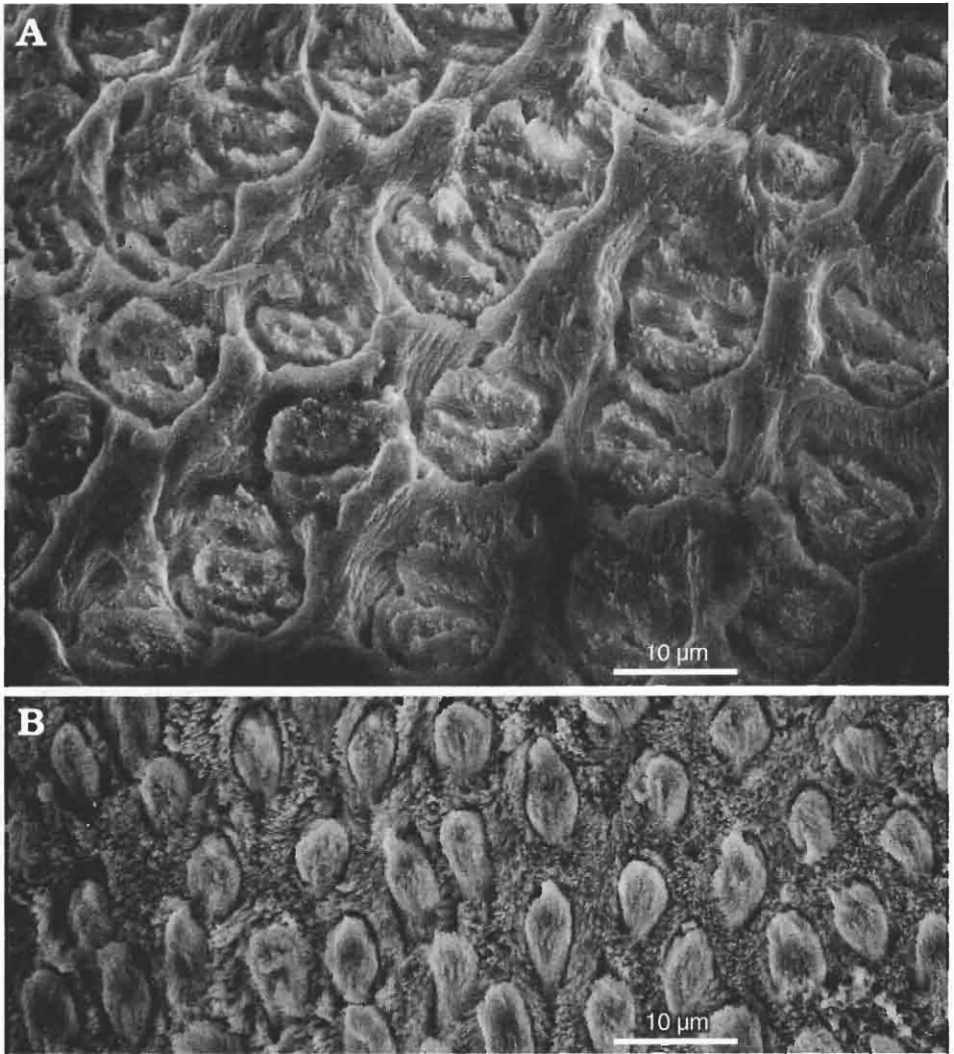


Fig. 1. SEM micrographs of etched and gold coated planed enamel surfaces, taken at the same magnifications. **A.** Gigantoprismatic enamel in P2 of *Kogaionon unguereanui* (SPT 001). **B.** Microprismatic enamel in P4 of a ptilodontoid *Mesodma* sp., PMO 169.283.

al. (1985), undertaken independently, showed the same pattern, based on much larger samples: Ptilodontoidea are characterized by small, circular, densely packed enamel prisms (referred to afterwards by Hahn & Hahn 1999 as microprismatic enamel), while 'Taeniolabidoidea' have large, arcuate-shaped prisms (see Koenigswald & Sander 1997 for definition of prisms and other microstructures of mammalian enamel). No other extinct or recent mammalian enamels are gigantoprismatic (Fosse *et al.* 1978; Fosse *et al.* 1985).

Gigantoprismatic enamel has been suggested by Krause & Carlson (1987) to be the plesiomorphic type. Wood & Stearn (1997) suggested that, contrary to the generally accepted opinion, the small prisms may be plesiomorphic for multituberculates and 'giant' derived. This conclusion, however, has not been supported by phylogenetic analyses (see Kielan-Jaworowska & Hurum 2001 for review). These considerations are of special interest because of the highly un-

certain relationships among derived multituberculates, including both 'Taeniolabidoidea' and Ptilodontoidea. Unfortunately, published investigations of enamel structure in more plesiomorphic and geologically older multituberculates, the 'Plagiaulacida', are preliminary and results are equivocal (Fosse *et al.* 1991).

Kogaionon is the only skull among a few multituberculates known from the Late Cretaceous of Europe (Rădulescu & Samson 1996; Csiki & Grigorescu 2000). So far, only preliminary results of *Kogaionon* craniodental morphology were published (Rădulescu & Samson 1996). In this context, any new information on its structure is a welcome addition to our knowledge.

Enamel microstructure of *Kogaionon*

Kogaionon Rădulescu & Samson, 1996 is a monotypic multituberculate genus assigned to the cimolodontan family Kogaionidae Rădulescu & Samson, 1996, placed by Kielan-Jaworowska and Hurum (2001) in a superfamily *incertae sedis*. *K. unguireanui* Rădulescu & Samson, 1996 is based on the holotype and the only known specimen (which is the complete skull with dentition, but without the dentaries) housed at the Institute of Speleology in Bucharest (abbreviated SPT). The skull derives from the Maastrichtian Sânpetru Formation, locality of Dealul Tămășel near Sânpetru, in Hațeg Basin, Romania. Of the holotype skull we studied right P2, which has been broken and brought to the Paleontological Museum, University of Oslo, where it was examined under SEM by the first author. For comparison the P4 of *Mesodma* sp. (a typical ptilodontoid), housed at the Paleontological Museum in Oslo, Norway (abbreviated PMO), from the Early Paleocene of Saskatchewan, Canada was treated in the same way and micrographed in a similar enamel location for comparison.

Method. — Each tooth was mounted on an aluminium stub with the buccal cuspal enamel on top, planed slightly with 1000 grit abrasive paper, etched 5 secs. with 5% nitric acid, rinsed in running water, gold-coated and micrographed in a Jeol, JSM-5200 microscope.

The mean prism central distance in the *Kogaionon* enamel is 15.16 μm yielding 5024 prisms per square mm. In the ptilodontoid *Mesodma* enamel the mean central distance was only 7.33 μm yielding 21491 prisms per square mm. The enamel of this *Mesodma* sp. was in the upper range regarding prism central distances. For comparisons with other taeniolabidoid and ptilodontoid enamels, see table 1, p. 440 in Fosse *et al.* (1985).

Conclusion. — Kielan-Jaworowska & Hurum (2001), stated that the superfamily assignment of the aberrant Late Cretaceous–Paleocene European family Kogaionidae cannot be resolved. Although in skull shape (known only in *Kogaionon*) the Kogaionidae show some similarity to that of the Taeniolabididae, the upper dentition differentiates them from all other multituberculates. The finding of gigantoprismatic enamel in *Kogaionon* does not cast light on the relationships of the Kogaionidae, however, it supports the idea of relationships between *Kogaionon* and *Hainina*. This latter European Paleocene–Cretaceous genus (Vianey-Liaud 1979, 1986; Csiki & Grigorescu 2000; Peláez-Campomanes *et al.* 2000) has, as demonstrated by Carlson & Krause (1985) gigantoprismatic enamel. Our paper thus gives additional argument for assignment of *Hainina* to the Kogaionidae, as suggested by Kielan-Jaworowska & Hurum (2001).

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