Ektopodon, an enigmatic phalangeroid marsupial: its enamel microstructue and mastication pattern

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Abstract

The molars of the Late Oligocene *Ektopodon stirtoni* (Phalageroidea, Marsupialia) have a unique lophodont morphology that differs from all other marsupials and has no parallel in Placentalia. Teeth with a unique morphology often show specific modifications of the enamel. Therefore, the enamel of *Ektopodon* was investigated and compared with the enamel in other Marsupialia. The schmelzmuster of *Ektopodon* is formed mainly by radial enamel with some modifications. A differentiation of the enamel in the leading or trailing edges could not be identified. The distribution of the various enamel types differs among the various marsupial families and is partially diagnostic.

Zusammenfassung

Die Morphologie der lophodonten Molaren des oberoligozänen *Ektopodon stirtoni* (Phalageroidea, Marsupialia) ist einmalig und unterscheidet sich grundlegend von denen andere Marsupialia. Sie hat auch keine Parallele bei den Placentalia. Zähne mit einer stark abweichenden Morphologie zeigen oft auch Sonderbildungen im Schmelz. Deswegen wurde die Mikrostruktur des Schmelzes von *Ektopodon* untersucht und mit dem Schmelz anderer Marsupialia verglichen. Das Schmelzmuster der Molaren von *Ektopodon* wird aber weitgehend von Radialschmelz gebildet, zeigt aber einige Modifizierungen. Eine Differenzierung zwischen dem luvseitigen und leeseitigen Schmelz konnte aber nicht beobachtet werden. Die Verbreitung der Schmelztypen variiert in den verschiedenen Familien der Marsupialia und ist teilweise diagnostisch.

Key-words: *Ektopodon*, Marsupialia, Late Oligocene, enamel microstructure

1. Introduction

Ektopodontidae with the eponymous genus *Ektopodon* are a family within the phalangeroid marsupials from Australia. The fossil record reaches from the upper Oligocene to the Pliocene (Woodburne & Clemens, 1986a, b, Woodburne, 1987, Pledge, 1982, 1986, 2016, Pledge et al., 1999, Rich et al., 2006). Besides their stratigraphic occurrence, Ektopodontidae raised a special interest because of the conspicuous molar dentition. The molars have transverse lophs (Fig. 1A), these lophs, however, are modified into a series of laterally compressed cusps. Such molars have no parallel in metatherian or placental dentitions. The first three upper and lower molars of *Ektopodon* have two or three modified transverse lophs; the lophs are reduced on the fourth molars. In the genus *Ektopodon* the number of cusps per loph varies between 8 and 10 according to the tooth position (Pledge, 2016).

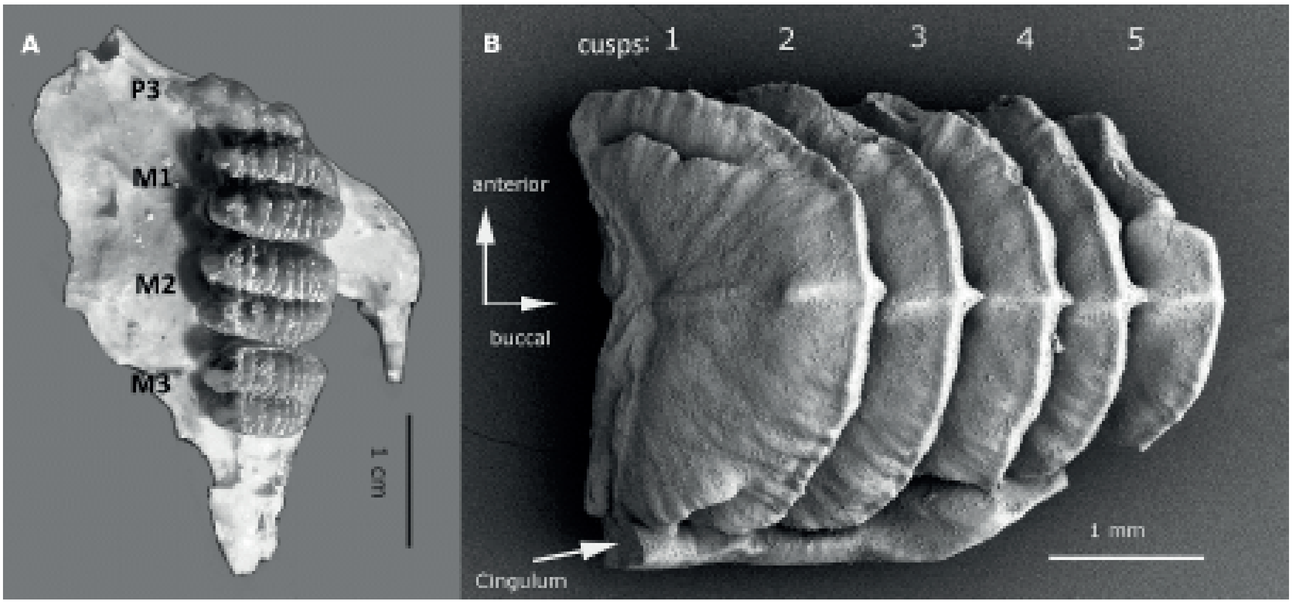

Fig. 1: *Ektopodon stirtoni*, A - Left maxilla with three molars (M1-M3), and alveolus for the fourth (SAM 35309). B – The investigated tooth fragment (KOE 1733), interpreted as a partial metaloph of a left upper molar (?M2).
Both specimens are from Mammalon Hill (SAM locality PL7611; the Type Locality for the species), northwestern shore of Lake Palankarinna, South Australia.

According to the state of art, Ektopodontidae diversified into two genera, *Chunia* with three species (*C. illuminata, C. omega, and C.* sp.) and *Ektopodon* with five species (*E. serratus, E. tommosi, E. stirtoni, E. litolophus, and E. paucicristata*). In most localities only a single species is represented and remains are generally very rare. Pledge (1986, 1991, 2016) actualized the data on Ektopodontidae and completed the earlier monograph edited by Woodburne & Clemens (1986).

Ektopodontidae retained the general morphology of their molars during their time range from the Late Oligocene to Pliocene. The number of cusps per loph on the molars increased only slightly and thus the molars became somewhat larger (Pledge, 2016). So far, no postcranial bones are known, but because of their relation to Phalangeroidea, such as *Phalanger*, an arboreal way of life is very plausible. The body-tail length is estimated 40 cm.

In placental dentitions, teeth with a strongly modified morphology often show a specialized enamel microstructure. Therefore, the aberrant morphology of *Ektopodon* molars is challenging to investigate the schmelzmuster (the three-dimensional arrangement of enamel types within a tooth) in comparison with the enamel microstructure of other marsupials (Koenigswald, 1994).

So far, only a very limited analysis of the enamel has been done by M. Moss, stating some "tubular or fibrous structure", as communicated by Clemens (Woodburne & Clemens, 1986). Neville Pledge generously presented me a small tooth fragment for the destructive investigation of the enamel. The results are discussed here.

The closely arranged cusps on the lophs of the Ektopodon molars show in their grinding function some similarities to elephant molars, and among rodents, to arvicolid molars, having a highly differentiated schmelzmuster (Koenigswald, 1980). Gernot Rabeder, to whom this volume is dedicated, used in his PhD thesis the differentiation of the schmelzmuster in arvicolid molars to shed new light into the systematics of these rodents (Rabeder, 1981)

2. Material and methods

*Ektopodon stirtoni (*Pledge, 1986), molar fragment KOE 1733, Late Oligocene, Mammalon Hill (SAM locality PL7611; the Type Locality for the species), northwestern shore of Lake Palankarinna, South Australia (SAM Adelaide - Neville Pledge)
Phalanger cf. vestitus (Milne-Edwards, 1877), mandible KOE 1693, Recent, Sepik-district, Papua New Guinea (AM Sydney - T. Flannery).
The molar fragment available for the enamel investigation is about 3 mm in width and 4 mm in length. The fragment was assigned as *Ektopodon stirtoni* by Neville Pledge. Because of the inclination of the cusps and a partially preserved cingulum, the fragment was interpreted as a partial metaloph of a left upper molar (M2). The molar fragment is unworn and thus the cusps show their initial enamel surface. The cusps distinctly inclined towards the buccal side. Even if it is unclear if the most lingual cusp is preserved, the remaining cusps are numbered as cusp 1 to 5 for easier identification (Fig. 1B). The profile of each cusp is highly domed in an antero-distal direction. On both sides little struits link the cusps at their highest point (Pledge, 2016), but they do not merge into each other but touch each other on the side. The anterior and posterior crests of the cusps 1 show a bifurcation in its lower part (Fig. 1B). Such additional crests were named precrista and postcrista (Pledge, 1986).

For the interpretation of the enamel microstructure, sections in vertical, transverse, and tangential planes are optimal. All three aspects together – studied at various magnifications - allow a secure reconstruction of the schmelzmuster of a tooth. Isolated photos may show details but provide an incomplete picture. With rare fossils, the number of sections has to be adjusted to the available material. In the case of the tooth fragment of *Ektopodon*, fractioning of the specimen prior to the embedding was a reasonable way to increase the possible number of sections. Cusps 1 and 2 were separated from cusps 3 to 5. That allowed an individual embedment and further treatment of both parts. Cusps 1 and 2 (KOE 1733 A) provided a longitudinal sections in a linguo-buccal direction (Fig. 2A), and cusps 3 to 5 (KOE1733 B) provided a transverse section perpendicular to the growing axis (Fig. 2B).

The routine preparation of the two fragments includes an embedding into an artificial resin (epoxy) because such delicate teeth neither can be sectioned or ground. The resin blocks are cut with a saw in the direction of the desired section, but outside of the tooth fragments. Using this cut surface, further grinding was done on sand paper until the desired section was nearly reached. Grinding was continued with grinding powder (1000 grid) on a piece of glass. After washing in an ultrasonic device, the dried surface was etched with 10% hydrochloric acid (HCl) for about 3 seconds. After sputter-coating the enamel was investigated under the SEM.
The process of grinding with sandpaper, grinding powder and the subsequent etching and sputter coating was repeated several times in order to correct a poor preparation, such as scratches or an unsuitable etching. The repeated grinding allows to study the enamel in various different levels in the height of the tooth.

Enamel can be investigated at different levels of complexity (Koenigswald & Clemens, 1992). The investigation concentrated on two levels, the occurring types of enamel and their arrangement in the schmelzmuster. Enamel types are characterized by the orientation of the prisms (P) and the interprismatic matrix (IPM). The schmelzmuster describes the distribution of the enamel types in the architecture of the tooth. Because only a molar fragment was investigated, potential differences in the enamel on the dentition level, such as differences between molars and incisors, remain unknown.
Different enamel types are mostly arranged more or less parallel to the enamel dentin junction (EDJ). If different enamel types are separated by a sharp border, they are described as layers. If there is a more gentle transition the term zones is used.
The schmelzmuster of various genera of different marsupials was surveyed earlier (Koenigswald, 1994, 1995), providing the background for characterizing the enamel of *Ektopodon*.

2.1 Used abbreviations

AM	Australian Museum, Sidney
EDJ	enamel dentin junction
IPM	interprimatix matrix
KOE	Enamel collection at Institut für Geowissenschaften (Paläontologie), Universität Bonn
OES	outer enamel surface
P	prism
PLEX	prism less external enamel

SAM South Australian Museum, Adelaide

SEM Scanning electron microscope

A glossary of the terminology used for the enamel description was provided by KOENIGSWALD & SANDER (1997a).

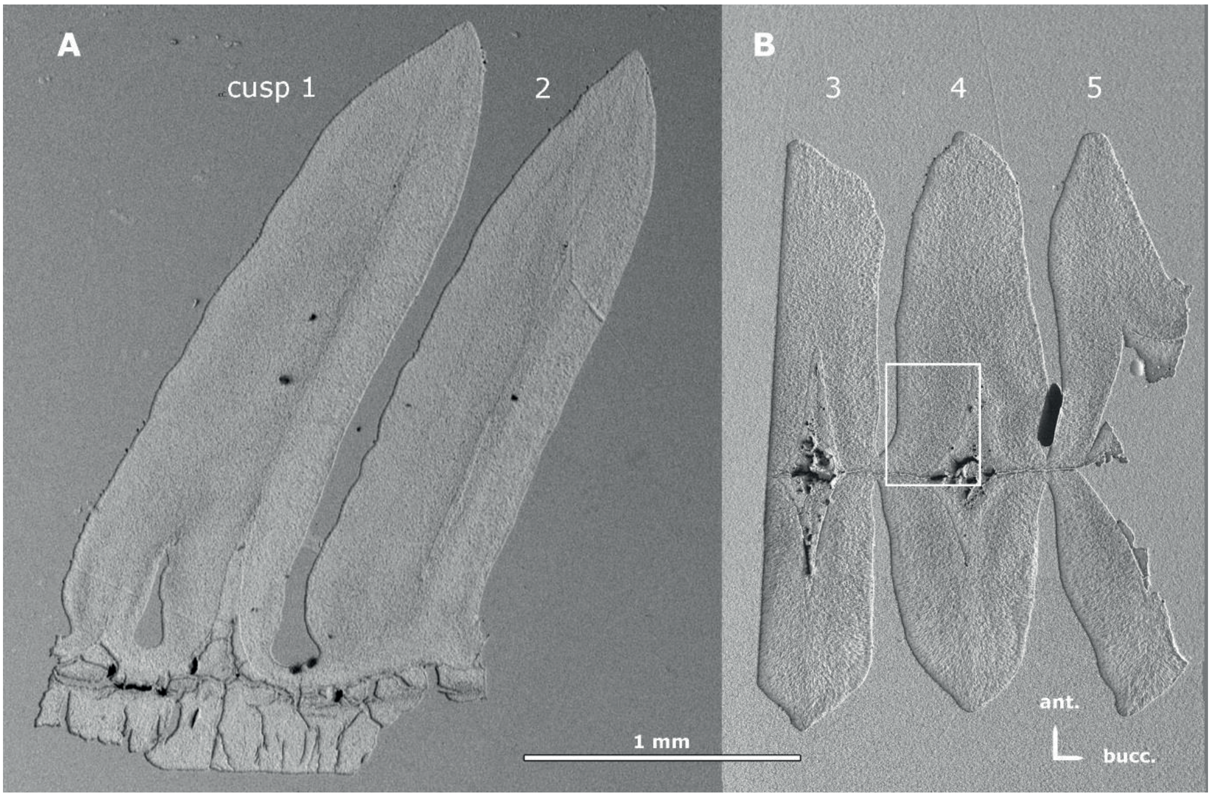

Fig. 2: *Ektopodon stirtoni*, A, vertical section of cusps 1 and 2 (KOE 1733A) showing the deep separation of the cusps. B, transverse section of cusps 3 to 5 (KOE 1733B) at a depth where the dentine core is met and the cusps are just beginning to fuse. The frame indicates the position of Figure 3.

3. Results

The schmelzmuster of *Ektopodon* is dominated by radial enamel that can be divided into three zones between EDJ and OES. The inner and the middle layer zones have a prismatic enamel, whereas the thin outer zone is formed by prism-less enamel (PLEX).
The thickness of these three zones varies and their separation is vague. Therefore, they are described as zones, whereas layers are separated more sharply.

The inner and the middle zone are made of radial enamel, with prisms generally arising from the EDJ towards the OES. The two zones differ distinctly in the orientation of the IPM.
In the inner zone, close to the EDJ, prisms are arranged in radial rows separated by thin sheets of IPM.

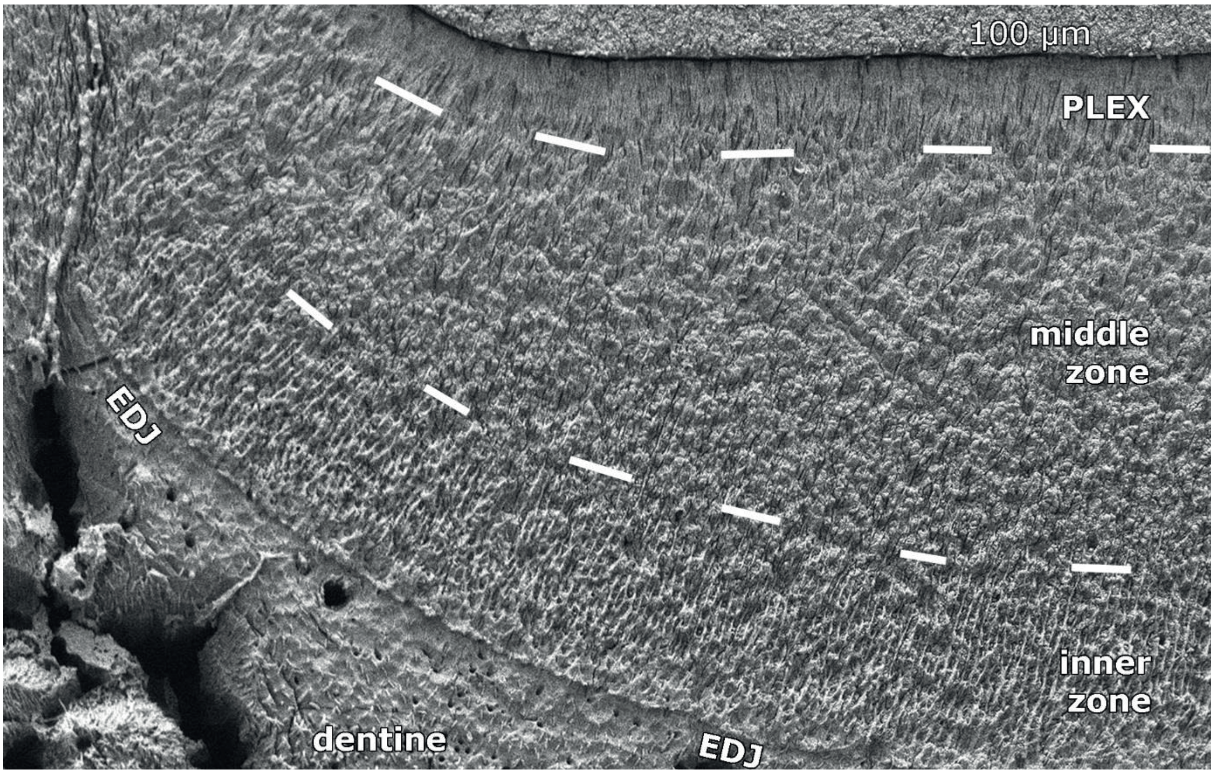

Fig. 3: Transverse section of the central part in cusp 4 in *Ektopodon stirtoni*. The inner zone is marked by sheets of IPM between radial rows of prisms. In the middle zone the IPM is less organized. The outer zone is formed by PLEX. EDJ - enamel dentine junction, PLEX - prism less external enamel.

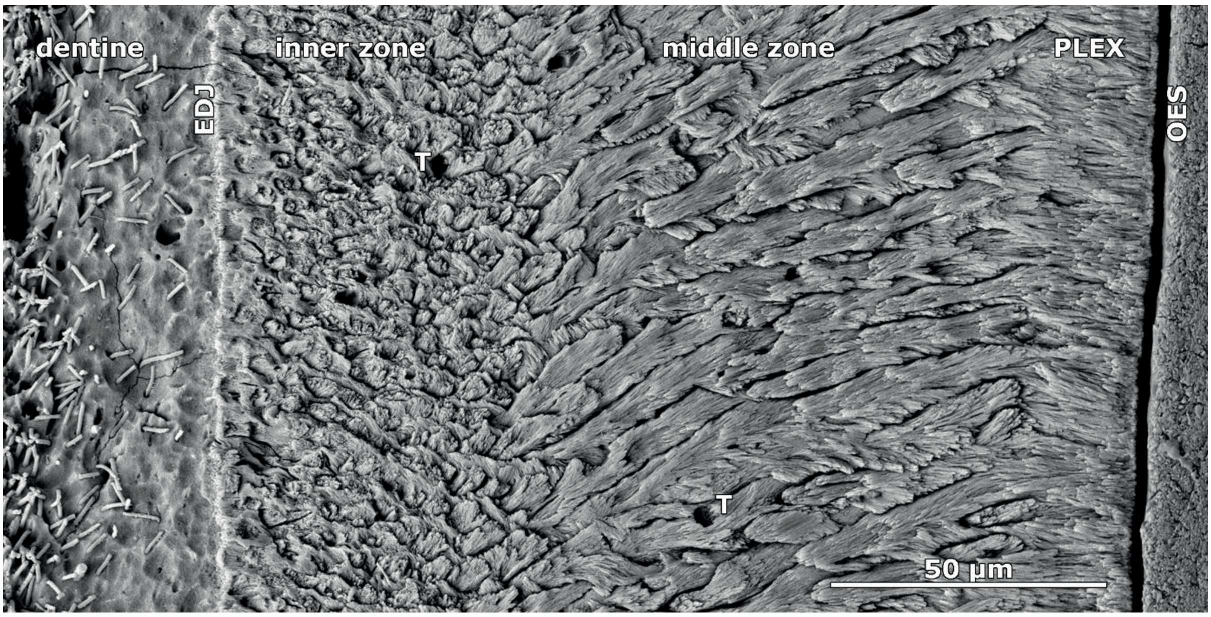

Fig. 4: Vertical section of one side of the cusp 2 in *Ektopodon stirtoni*. The dentine is on the left side. The enamel can be differentiated into three zones parallel to the EDJ. The inner zone and the middle zone are formed by radial enamel, whereas the outer zone is a PLEX. Abbreviations: EDJ - enamel dentine junction, PLEX - prism less external enamel, T - tubuli.

In the transverse section (Fig. 3), close to the EDJ, the IPM is visible as light lines between the prisms that are seen in cross-section. This specific modification was described as radial enamel with inter-row sheets (REIS) occurring in Eulipotyphla, especially in Soricinae (Koenigswald & Reumer, in press). In the lophs of *Ektopodon*, the thickness of this inner zone varies.

In the studied transverse section, the REIS is thickest and seen best in the middle of the cusps, and gets thinner towards the anterior and posterior margins. In the vertical sections, the REIS of the inner zone is less obvious, because the section was in an angle to the rows of prisms and not parallel (Fig. 4). A more detailed view (Fig. 5), however, shows the large angle between the IPM and the prisms. The prisms are rising from the EDJ at about 45° and the IPM is oriented perpendicularly.

The middle zone differs in the transverse and the vertical sections (Figs 3 and 4) distinctly from the inner zone. The inter-row sheets are missing and the prisms are less arranged in rows. The prisms continue to rise towards the OES but at a lower angle. In the transverse their cross-section appears to be stretched. The vertical section shows that the prisms reduce their inclination after leaving the inner zone and point towards the OES almost perpendicularly. In the same way, the IPM reduces its angle with the prisms (Fig. 4) and continues in the outer zone. The middle zone is two or three times as thick as the inner zone. In the anterior and posterior loops of the enamel it covers the entire thickness of the enamel except the thin outer zone.

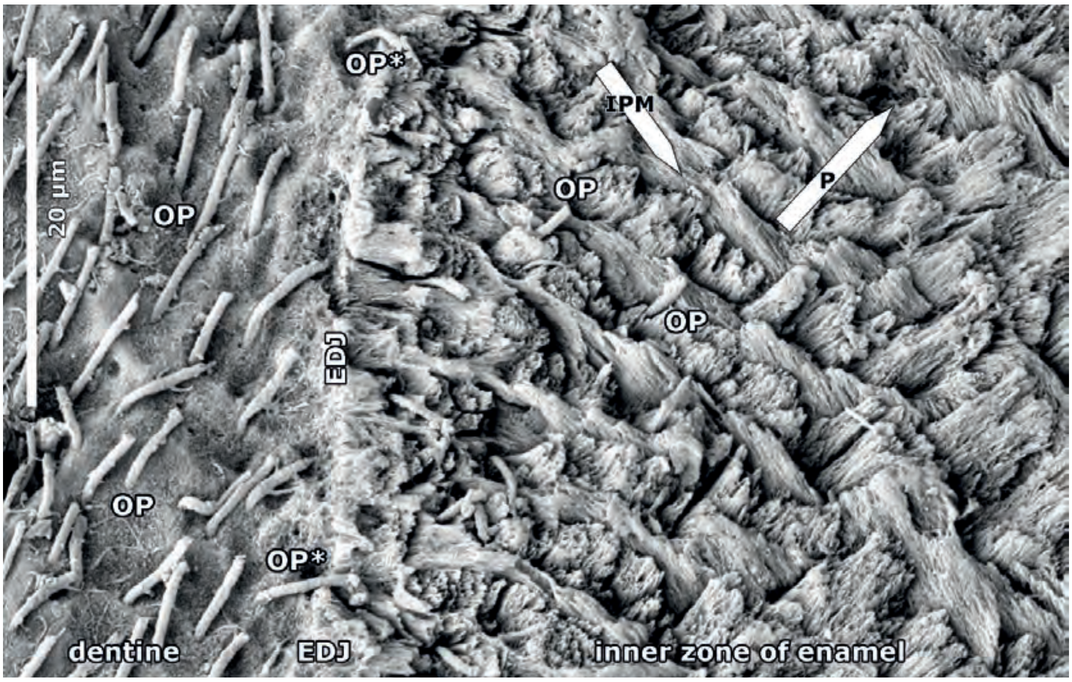

Fig. 5: Enamel and dentine in *Ektopodon stirtoni*. The dentine (left side) shows odontoblastic processes with ramifications. Some of the odontoblastic processes cross (OP*) the EDJ and occur within the enamel. There, they are seen parallel to the prisms of the inner zone of the enamel. Abbreviations: EDJ - enamel dentine junction, IPM - direction of the interprismatic matrix, OP - odontoblastic processes, P - prism direction.

The thin outer zone formed by a prism-less enamel is formed by crystallites driving from the prism and the IPM. The prism sheath surrounding the prisms in the middle vanishes, and thus its crystallites are not discernable from those of the IPM anymore. All crystallites are parallel and perpendicularly to the OES. The thickness of the outer zone is variable.
The described enamel schmelzmuster is somewhat generalized and does not include possible differentiations on the very base of the tooth cusps. Similarly the extent of the inner zone may be different in basal part. However, the available material did not allow a more comprehensive investigation, but the observed results allow a comparison with other marsupial animals.
One specialty of marsupial enamel is the occurrence of tubules within the mineralized tissue (e.g. GILKESON, 1997). The tubules are visible as holes in the sections (Fig. 4). They are containing odontoblastic processes. The odontoblastic processes are well seen in the dentine (Fig. 5) and show some ramification. The main axes are similar in thickness, slightly less than 0.5 μm. The applied etching during preparation was relatively mild and preserved the mineralized odontoblastic processes, while the surrounding dentine was removed. Most probably, the mineralization of the odontoblastic processes occurred during fossilization. Similarly mineralized odontoblastic processes within the dentine have been observed in several Eutheria (e.g. KALTHOFF et al., 2011).

In *Ektopodon* (Fig. 5), as typical for marsupials, these odontoblastic processes can be observed crossing the EDJ and penetrating into the enamel. Within the enamel the processes occur always with the same orientation as the prisms. This strengthens the idea that they are bound to the prisms. According to the observed, tubuli might extend into the middle zone.

4. Discussion

4.1 Comparison of the enamel microstructure

A survey of the enamel microstructure on the schmelzmuster level was given by KOENIGSWALD (1994) for recent and fossil marsupials from Australia. Observations on various fossil marsupials from Australia, South America and Antarctica were added (KOENIGSWALD & GOIN, 2000, GOIN et al., 2006). Thus a general outline of the enamel microstructure in marsupials is known, although some dentitions may provide additional specializations. Despite similarities some basic differences separate marsupial enamel from placental enamel (KOENIGSWALD, 1995).

The enamel of *Ektopodon* shows a schmelzmuster with three zones. Two zones are formed by two modifications of radial enamel. The outer zone is a PLEX. The combination of different enamel types in the schmelzmuster occurs in placentals as well as marsupials, although such a differentiation might have evolved independently. Both groups include taxa with a simpler schmelzmuster.

The radial enamel dominating the schmelzmuster of *Ektopodon* is regarded as the basal enamel type of prismatic enamel in theria. The two modifications are present in both groups as well.
The radial enamel with inter-row sheets occurs in various marsupial families (Tab. 1). This enamel type was found in placental mammals and described as REIS, for example in Soricinae (KOENIGSWALD & REUMER, in press).

Marsupial family	Tooth type	Radial enamel	Inter-row sheets	Simultaneous turn of prisms	HSB	Zipper enamel	Borderline	Irregular enamel
Didelphidae	M	●●						
Dasyuridae	M C	●● ●●						(●)
Thylacinidae	M C	●● ●●						●● ●●
Peramelidae	M	●●	●●					
Phascolarctidae	M I	●● ●●					●●	
Diprotodontidae	M I	●● ●●	●●	●●		●●		 ●●
Vombatidae	M I	●● ●●			●● ●●			
Thylacoleonidae	P I	●● ●●	●●	●●				(●) ●●
Phalangeridae	M I	●● ●●	●●	●●			(●)	
Ektopodontidae	M	●●	●●	●			●	
Potoroidae	M I	●● ●●	●● ●●	●● ●●		●● ●●		
Macropodidae	M I	●● ●●	●● ●●	●● ●●		●● ●●		(●)
Pseudocheiridae	M I	●● ●●	●● ●●	●● ●●			(●)	
Petauridae	M I	●● ●●	●● ●●	●● ●●				
Acrobatidae	M I	●● ●●						

Tab. 1: The occurrence of specific characters of the enamel in the marsupial families (modified from Koenigswald 1994). C - canines, I - incisors, M - molars.

One characteristic of the marsupial enamel is the dominance of parallel prisms without decussation. The crystallites of the IPM, forming inter-row sheets or anastomosing between prisms, are often oriented at a large angle to the prisms and thus providing a decussating structure, basically different from the decussating layers of prisms in Placentalia. Such decussating layers of prisms, called Hunter-Schreger bands, occur in Marsupialia only sporadically (e.g. in *Vombatidae*).
A unique kind of prism decussation in marsupials, called zipper enamel, has been found in the crests of molars and incisors, e.g. in Macropodidae. Two fields of radial enamel meet at the crest. The prisms

of both fields interfinger in vertical layers for a short distances. This enamel type was called zipper enamel. Special attention was paid to the crests of enamel in *Ektopodon* but no zipper enamel was identified. In placentals a zipper enamel was never found. There the enamel surrounds even sharp edges of the dentine.

In the marsupial enamel prisms may perform simultaneous turns without decussating. Such simultaneous turns may occur repeatedly several times between the EDJ and the OES, but without any decussation of the prisms.

In some marsupial teeth a distinct structure between fields of radial enamel was detected, e.g., in Phascolarctidae, and called borderline (Koenigswald, 1994). It described the contact between two fields of enamel. In *Ektopodon* no typical borderlines were observed, but that might be due to the limited number of sections. One suspect structure occurs where the two fields of radial enamel meet in the crests of the cusps. But the available sections do not provide enough details. Another unusual structure is the line in the enamel between the anterior and the posterior half of the cusps. The wavy structure reminds strongly of the borderline found in *Phascolarctos* (Koenigswald, 1994, Figs. 28 & 29). A borderline structure similar to the zipper enamel has never been seen in placental enamel. Obviously, placental enamel surrounds sharp edges of the dentine core with fewer problems.

The enamel of *Ektopodon* has typical elements occurring in Marsupialia. In a premolar and molar of *Phalanger* cf. *vestitu*s, a representative of the nearest related extant group, an inner zone of REIS superimposed by a thicker zone of radial enamel and a variable PLEX near the OES were recognized. Thus the basis agreement with Phalangeridae is confirmed (Tab. 1). The schmelzmuster alone, however, would not allow the exclusion of several other marsupials.

4.2 The mastication pattern

Pledge (2016) postulated a transverse jaw movement in *Ektopodon*, because the lophs and the valleys of upper and lower molars are oriented transversely. During the power stroke the mandible is moved in bucco-lingual direction. The inclination of the cusps strengthens this reconstructed direction during the mastication process. In upper and lower molars, the cusps are inclined towards the moving antagonist. In such a lateral movement is combined with an alternative occlusion of only one side at a time, the left or the right jaws. The power stroke, which in primitive mammals consist of two phases separated by a central occlusion (Hiiemäe & Kay, 1972, Kay & Hiiemäe, 1974), is in *Ektopodon* continuous. Phase 1 and 2 cannot be discerned because there is not central occlusion. Such a perfect alignment of phases I and II in direction and inclination is a derived pattern that occurs in various herbivorous mammals (Koenigswald et al., 2013).

The concluded jaw movement is only possible, if the lophids of the lower jaw and the lophs of the uppers are oriented parallel. In the reconstruction of the palatine (Pledge, 1986, Plate 3.3 D and E) the lophs of the upper molars are directed almost perpendicular to the sagittal axis whereas those of the lower molars are much more angled in mesial direction. This discrepancy is unlikely, because it would hinder a smooth function. Only more complete material will correct this discrepancy.

A transverse jaw movement of *Ektopodon* is not common in marsupials but occurs, for instance, in *Vombatus*. The transverse jaw movement is indicated there by the position of the enamel. It covers only the trailing sides of upper and lower molars. Striations in the dentine core confirm the transverse movements.

In contrast, the lophodont molars of *Macropus* occlude in a very different way. The lower jaw is moved upwards and slightly forward, so that the shearing crests of the transverse lophs cut against each other during phase 1 of the power stroke. The weak longitudinal crests show slight facets that indicate a transverse movement during phase 2. But this lateral movement is distinctly less important than the proal movement during phase 1. In placental mammals similar lophodont dentitions with transverse cutting edges are seen in various unrelated taxa, e.g. in *Deinotherium, Pyrotherium*, and *Tapir*. The main function happens similarly during phase 1, whereas phase 2 in these dentitions is insignificant or missing.

4.3 Leading and trailing edges

The unusual morphology of *Ektopodon* molars led to the expectation that the enamel might show a differentiation of the enamel between leading and trailing edges in the conspicuous transverse lophs. Such differentiations were observed in various molars of placental mammals (Koenigswald & Sander, 1997b). In the molars of the rodent *Otomys*, for instance, the transverse lophs are strongly inclined comparable to those of *Ektopodon*. In each loph the enamel is much thicker on the trailing side, which functions as a crest, whereas the enamel of the leading side is very thin but nevertheless of a more complex schmelzmuster (Koenigswald, 1980). The trailing side is so thin that it does not reach the occlusal surface. In arvicolid molars the half-lophs are more or less vertical and both sides, the leading and the trailing side are functioning. Nevertheless the schmelzmuster is characterized by different enamel types on both sides (Koenigswald, 1980, Rabeder, 1981).

In the molar enamel of *Ektopodon*, however, no differentiation between the lingual and the buccal sides of the cusps could be detected. In *Ektopodon* the problem is solved in a different way. The dentine core is surprisingly small and the main height of the tooth is formed by the enamel cap. Thus the dentine is exposed only in a late stage of the life history. Neither the leading side nor the trailing side are thickened, but both together have to withstand the stress during mastication. Therefore a differentiation of the enamel was not necessary. It is difficult to estimate the stress because the kind of diet is not known. The occlusal stress, however, may have been limited, because most of the teeth figured by PLEDGE (2016) are fresh. The valley between the lophs never seems to be intensively worn or flattened. That indicates that the enamel of *Ektopodon* teeth was not specialized for an abrasive diet.

5. Summary

The schmelzmuster of the *Ektopodon* molars is dominated by radial enamel but separated into three zones. The inner one shows a radial enamel with inter-row sheets (REIS), the middle one is thickest and has unspecialized radial enamel. The outer zone is formed by PLEX of varying thickness. This pattern is typical for marsupials and occurs in the *Phalanger* as well. The expectation of a differentiation between the enamels of the leading and the trailing edges was not fulfilled. The different extent of the dentine cores in the lophs may be provide an explanation.

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