

Dental macro- and microwear in *Carinodens belgicus*, a small mosasaur from the type Maastrichtian

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Abstract

Teeth of the small durophagous mosasaur *Carinodens belgicus* are known from Maastrichtian Atlantic-Tethyan deposits worldwide. The peculiar dentition of *Carinodens* inspired debate and speculation on its dietary niche ever since its first description. In this contribution, we describe the macro- and microwear pattern in five well-preserved isolated teeth, allowing further and independent evaluation of aspects of feeding behaviour and diet. Macroscopically, wear is concentrated on the apex and mesiodistal sides. Microwear was mapped using Scanning Electron Microscopy at several magnifications and can be characterised as scratches and pits. Coarse scratches were found to be the most common and pits were found to be the least common feature. Scratch orientation is primarily along the mesiodistal plane or in the labiolingual plane with an angle of ~130°. These microwear features can be explained either by oral processing or passive abrasion by sediments or food. As scratch width only indicates the minimum width of the abrading particle, the material causing the wear here could have ranged from silica-based silts to larger abrasives. However, in this case, abrasion by sediments might not explain this wear because of the biocalcarenic nature of the type Maastrichtian sediments; siliciclastics are virtually absent. Therefore it is more likely that hard food particles, such as benthic organisms with hard exoskeletons, caused the wear on the enamel of *Carinodens*, or *Carinodens* ventured out to more sandy areas to forage as well. The mesiodistal and labiolingual direction of the microwear scratches might suggest that *Carinodens* showed more complexity in the use of its teeth than simple grasping, and that a gripping and pulling motion during feeding similar to that employed by modern varanids may have been the cause.

Keywords: mosasaurs, dental microwear, Cretaceous, Maastrichtian, diet, *Carinodens*

Introduction

Almost a century after its first description (Dollo, 1913), the diminutive mosasaur *Carinodens* was still poorly known, and even considered ‘enigmatic’ (Schulp et al., 2006: p. 175). Only recently, new material allowed for further elaboration on aspects of its morphology (Kaddumi, 2009; Schulp et al., 2010), distribution (Schulp et al., 2013 and references therein), diving behaviour (Schulp & Vonnhof, 2010, Schulp et al., 2013) and diet (Schulp, 2005).

Already in 1913, Dollo speculated on the dietary preferences of this small, presumably durophagous mosasaur, based on the unusual morphology of its teeth. The presence of an associated fragment of a sea urchin combined with the bulbous tooth morphology led Dollo to suggest *Carinodens* could have fed on sea urchins. Lingham-Soliar (1999) addressed the feeding preferences of *Carinodens*, considering the “[...] apical cusps on the posterior teeth [...] suited to crushing and shedding the thin shells of invertebrates such as *Nautilus* and some forms of crustaceans and echinoids rather than piercing.” Biting experiments

using a reconstructed jaw allowed the feeding options of *Carinodens* to be narrowed down (Schulp, 2005; Schulp et al., 2010). Stable isotope analysis of tooth enamel (Schulp & Vonhof, 2010; Schulp et al., 2013) suggests *Carinodens* to have exploited a shallow marine / nearshore niche. Fossil stomach contents are not known in *Carinodens*, and no work has been done yet on finite element analysis of *Carinodens* in assessing its potential bite force and feeding behaviour either.

In addition to the approaches outlined above, dental macro- and microwear analysis can help provide answers on diet and feeding behaviour in non-mammalian amniotes (Rybczynski & Reisz, 2001; Goswami et al., 2005; Schubert & Ungar, 2005; Williams et al., 2009; Varriale, 2011; Whitlock, 2011; Young et al., 2012). Unlike morphology, in which virtually every adaptation is still an inherited trait (except for poorly understood epigenetic features), microwear is a direct record of a physical interaction of the animal with the environment. And unlike isotope studies, which record a chemical interaction from a section of time during the tooth's development before it was ever used, the environmental interaction measured in microwear is a direct physical one that occurred at a time when the tooth was being used. In this way, microwear may be the most direct evidence of physical interactions of a fossil organism with its environment.

Non-mammalian amniotes are not 'supposed to' masticate their food, but a few exceptions can be found among living squamates (Dalrymple, 1979) and many more exceptions have been identified among fossil taxa, especially archosaurs (Buckley et al., 2000; Ōsi & Weishampel, 2009; O'Connor et al., 2010). Most often this is because the foods require being fractured before they can be digested, and this includes plant foods as well as hard-shelled animals such as molluscs, crustaceans, and echinoderms. When any food item is too large to swallow whole, though, it needs to be reduced in size, and many non-mammalian amniotes employ teeth specialised for cutting tough materials like meat (Purslow, 1991). The most notable are the many types of theropod dinosaurs that have elaborate denticles on their carinae and show wear patterns typical of animals that eat large prey items, such as *Tyrannosaurus* (Schubert & Ungar, 2005). Fewer marine reptiles have been identified so far specifically with these specialisations, though recent work is identifying dental specialisations for macrophagy and hypercarnivory in some Metriorhynchoidea (Young et al., 2012). Multiple marine reptiles have been identified that have globular teeth and are presumed to be durophagous, such as some ichthyosaurs (Motani, 2005) and placodonts (Mazin & Pinna, 1993; Rieppel, 2002), but nothing concerning dental wear patterns, macroscopic or microscopic, has been worked out, except one study comparing microwear with assumed feeding types in marine reptiles (Poynter, 2011). In all of these situations, a combination of macroscopic observations of dental wear, as well as studies of dental microwear, are useful in assessing the mechanical use of teeth in the animals' interactions with the environment.

Here we present an analysis of dental macroscopic wear and microwear as preserved on five isolated *Carinodens* teeth from the type Maastrichtian, and evaluate whether this line of evidence does support earlier hypotheses on *Carinodens* exploiting a durophagous niche in the type Maastrichtian ecosystem. This small sample does not allow the type of comparison of microwear data in which counts of features are compared to other similar extant taxa that can permit further information on feeding ecology due to comparison and statistical strength. Counts of pits and scratches in a quantitative statistical measure may not be relevant without extensive further testing of similar animals, which is outside the scope of this study. Because there was only one observer (FH), interobserver error issues at least are not an issue (Grine et al., 2002; Purnell et al., 2006; Mihlbachler et al., 2012). So, our study here will focus on patterns of wear observed in *Carinodens*, limited to comments on what it informs us about food processing patterns and dietary abrasives.

Material & Methods

Teeth

Five isolated teeth were studied. All teeth are from the Natuurhistorisch Museum Maastricht (NHMM) collection, and all teeth come (if known) from the Maastricht Formation in the type Maastrichtian area (see, e.g., Schiøler et al., 1997 for details on stratigraphy). NHMM 1873 is from Geulhem; no stratigraphical details were recorded by the collector; NHMM MK1910 comes from the (now disused) Curfs quarry near Geulhem; stratigraphic provenance is top Meerssen-base Geulhem Member. NHMM 1980 006 is also from the Curfs quarry, but no stratigraphic details are known from this specimen. NHMM (ex Museum Natura Docet Denekamp De Heer collection) K.19.03.083 is from the nearby Ankerpoort / Sibelco 't Rooth quarry, again with no precise stratigraphic details. For the three teeth without further stratigraphic details, the minimum age can be considered Nekum Member and Valkenburg Member (both Maastricht Formation), as those are the deepest levels exposed at Curfs and 't Rooth quarries, respectively. The fifth specimen, NHMM 1982 199, ex collection Casselli, was discovered around 1915 in the nearby Valkenburg area, and entered the NHMM collections without further details on stratigraphic provenance. The morphology of the five teeth studied here all matches the mid-posterior part of the dentary or maxilla, corresponding to tooth position #8-#13 (see Schulp et al., 2010).

Imaging

All SEM photos were acquired using an FEI Phenom table top scanning electron microscope. Most images were acquired in 'topographic A' setting rather than default backscatter mode, so as to accentuate the depth profile of the microwear scratches.

None of the specimens have been coated or treated otherwise prior to scanning, other than gentle cleaning.

Macroscopic wear

Wear facets were observed visually. The specimens described here were isolated teeth, with the narrow breadth being labiolingual (lateral to medial, see Fig. 1), and longer breadth mesiodistal (anterior to posterior, Smith & Dodson, 2003; see Fig. 1). Tooth geometry makes it difficult to determine which side is mesial and which is distal. This necessitates referring to wear facets as either labiolingual, mesiodistal, or apical (toward the crown tip).

Microwear

Scratches were measured digitally from the SEM photos using Adobe Illustrator. Because the images do not have the same scale, the method of selecting ‘measuring boxes’ as done in Sereno et al. (2007) is not applicable here. Instead the entire image has been measured for microwear, which is categorised here as coarse scratches, fine scratches and pits. Coarse scratches are defined as scratches with a width $\geq 0.3 \mu\text{m}$, whereas fine scratches are defined as having width of $< 0.3 \mu\text{m}$, based on mean scratch width. This method will increase the risk of bias in measurements since scale and magnification differ between some of the SEM images. Therefore it was chosen not to establish scratch size standards for this dental microwear, and only to simply count scratches and pits, and to measure scratch orientation along the mesiodistal axis. Future statistical quantification of the microwear on teeth of *Carinodens* will require more intensive analysis as well as comparison with microwear data from other species.

Results

Macroscopic wear patterns

The *Carinodens* teeth display wear facets of similar shape and location; one located at the apex of the teeth (apical nubbin),

and a wear facet at one (or occasionally both) mesiodistal sides (Fig. 2). Some specimens appear to have polishing on their labiolingual sides, though this is not universal and only minor in comparison to the distinct apical and mesiodistal facets. Tooth morphology suggests that they are positioned in such a way that upper and lower teeth are staggered in position (Schulp et al., 2004), and this naturally would cause close contact of the teeth to lead to wear at oblique angles on the mesiodistal faces of opposing teeth. The apices of teeth are not likely to have met another tooth in occlusion, as they would face the interdental space of opposing teeth during occlusion.

Microwear

Microwear patterns include a larger number of scratches than pits (Fig. 3). Coarse scratches are more common than fine scratches, although this might be a result affected by the ability to discriminate such fine details. Imaging resolution limits one’s abilities to reliably recognise microwear because microwear features are not uniform in shape and the way they are visually interpreted (Mihlbachler & Beatty, 2012), whether by SEM or light microscopy methods. The entire worn surface is, by its very nature, an accumulation of fractured surfaces of various scales. Even the relatively smooth surfaces in between distinct scratches and pits are covered in smaller, imperceptible scratches and pits (at the given resolution). Thus, we acknowledge that our counts of microwear features are a measure of the relative proportion of features of a size perceptible at the scale we are observing.

The specimens observed have a distinct wear facet with microwear scratches in various directions. These scratches can be divided into (relatively) broader grooves and (relatively) narrower grooves. The scratches and grooves can be divided into roughly two directions: in the mesiodistal plane and in the labiolingual plane with an angle of $\sim 130^\circ$ (Fig.3). Some pits can be observed, however these are very few compared to the number of scratches and grooves. Coarse scratches can occasionally be found that are extremely broad and coupled with multiple parallel scratches, most likely the result of a single, irregular, large object being dragged across the surface.

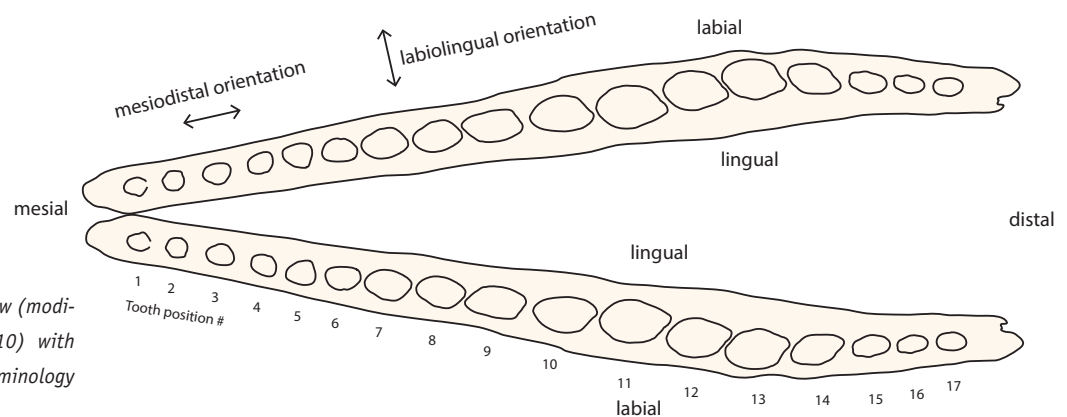


Fig. 1. Schematic mosasaur jaw (modified after Schulp et al., 2010) with general dental orientation terminology after Smith & Dodson (2003).

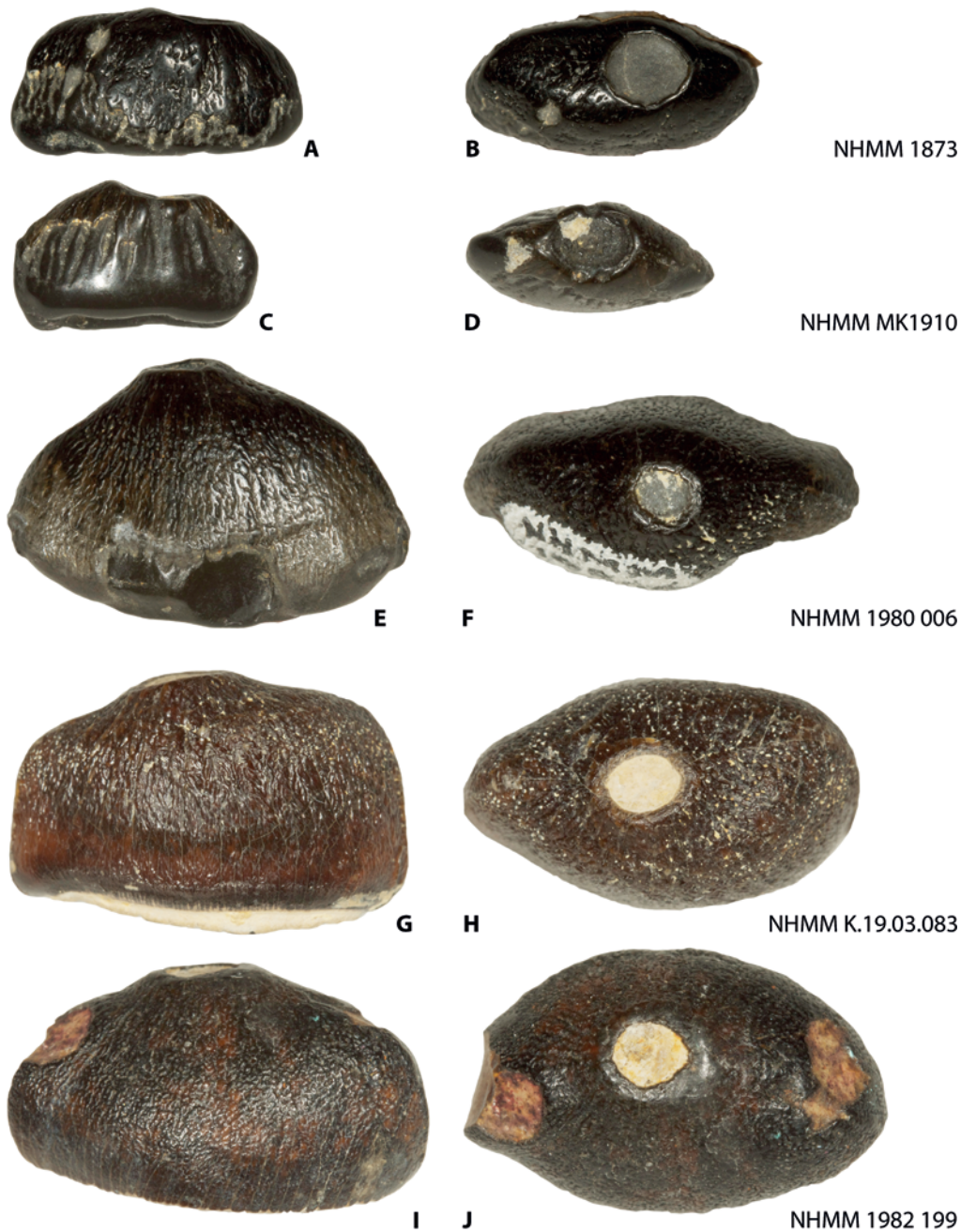


Fig. 2. Carinodens tooth specimens in lateral view (left) and apical view with wearfacets (right).

Discussion

In an ideal world, tooth wear data could be simply entered into an equation that immediately identifies an animal's diet. But tooth wear is only interpretable in context, limited to small samples and often lacking comparable extant animal forms. We are limited to informed speculation about what wear patterns really tell us. But these new data on macro- and microwear provides two pieces of information: 1) we can see that abrasives were moved across the occlusal surfaces of *Carinodens* teeth; and 2) that these abrasives were moved across these teeth in multiple directions, often perpendicular to the plane of simple orthal occlusion. What could this mean?

Mastication

The most obvious conclusion from these data is one about the movements of the jaws during feeding, an established type of method for which microwear can be used (Gordon, 1984). Though it is not yet established directly how the orientation of microwear features relate to jaw movements in non-mammalian amniotes, it appears sensible to infer that they relate to the movement of abrasive particles across a tooth surface either passively or during some sort of oral processing (crushing, not necessarily mastication in the mammalian sense). In this data it can be seen that the abrasives pushed across the teeth of *Carinodens* were being pushed in directions either mesiodistally or at angles nearly perpendicular to the long axis of the tooth

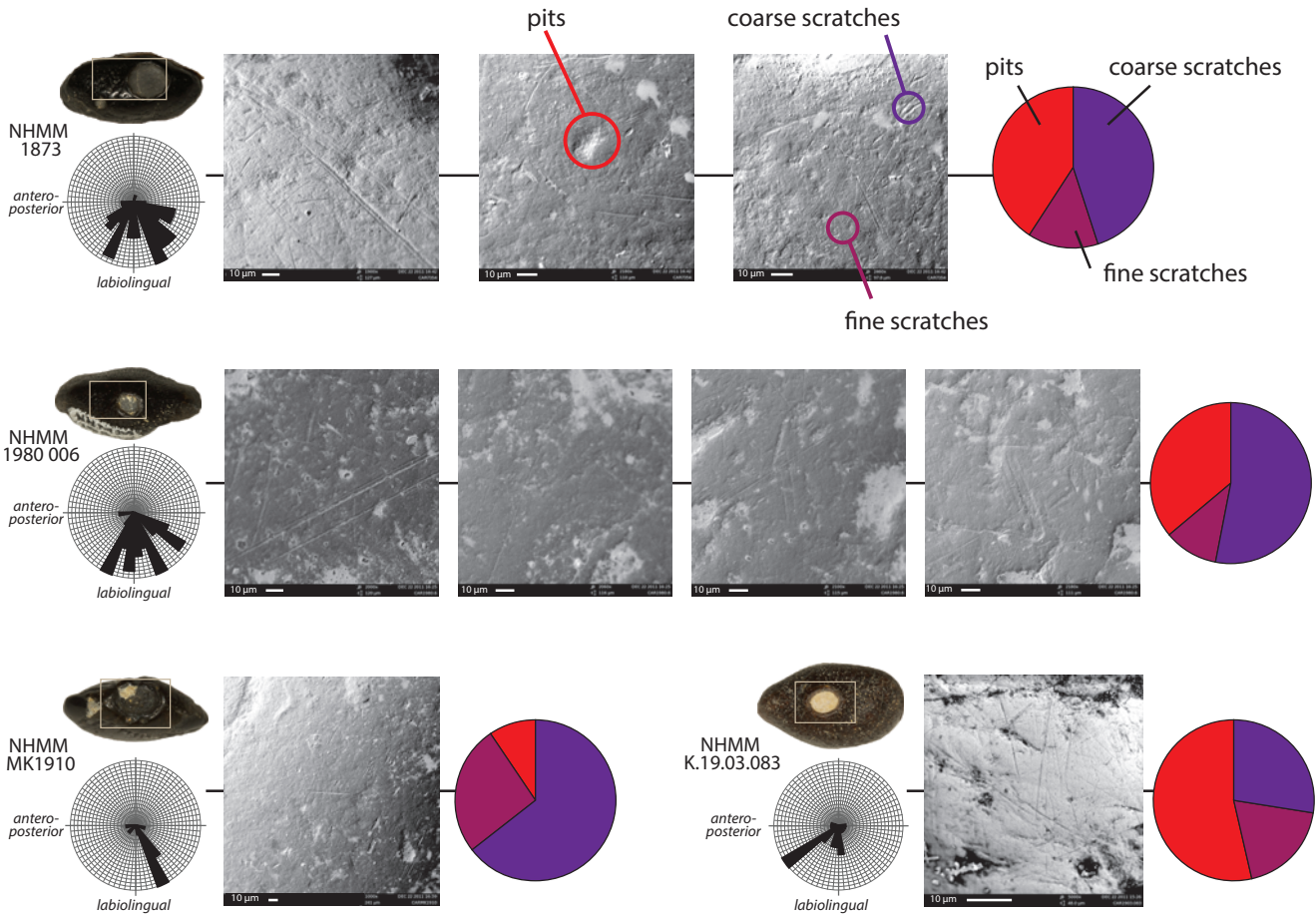


Fig. 3. SEM images of microwear features with quantitative results (scale bars shown in images, squares show studied wearfacet area) paired with rose diagrams depicting scratch directions on the mesiodistal plane.

row. These teeth are not completely flat, so the fact that abrasives may have slipped in multiple directions as the teeth were being brought closer to each other during jaw closing. But the directions observed are not merely random, but oriented almost exclusively mesiodistally or labiolingually. As teeth overlapped or interdigitated, it makes sense that abrasives could be pushed mesiodistally across them. But for wear to be found in labiolingual directions, these abrasives would have had to be pushed across the teeth either in a translational movement or during a clenched bite followed by a pulling motion. Modern *Varanus* has been observed cutting large prey items by grasping and then pulling on the prey item by retracting and laterally shifting their necks (Auffenberg, 1988). This appears to relate well to cranial mechanics in varanids (Moreno et al., 2008), and may also have been a behaviour of *Carinodens* and other mosasaurs. Mosasaurs are considered by many to be sister taxa to varanid lizards, and have skull architectures very similar to them. This relatedness and similarity in structure makes the assumption of similar feeding behaviour the most parsimonious to infer. If so, this would also possibly explain the mesiodistal microwear orientations, and possibly the labiolingual ones as well.

Abrasives

Regarding abrasives, it is important to recognise that the formation of microwear features is an indentation event that results from a balance of force, particle size, and material hardness of the tissues and materials involved (Atkins, 1982; Fischer-Cripps, 2007; Lucas, 2004). Most animals avoid bite forces that could lead to tooth fracture, as food consumption – and therefore a reasonably functional dentition – is an obvious necessity of life. Enamel microstructure in mammals is complex, which helps to avoid such fractures (Darvell, 2009; Lawn et al., 2009; Lee et al., 2011), but non-mammalian amniotes tend to have thin enamel that is mostly uniform in thickness (Beatty & Heckert, 2009; Sander, 1999) and aprismatic (Sander, 1999) and most likely more prone to fracture. Interestingly, the enamel in *Carinodens* (and most globidensine mosasaurs in general) does show a marked increase in thickness towards the apex. But, an animal may not avoid the oral processing activities that lead to microscopic fractures of teeth in the form of microwear because they tend not to be sensed easily if small enough. Bite force in squamates is known to be modulated in cycles similar, but not exactly the same as in mammals (Ross et al., 2007).

This could be responsible for an animal like *Carinodens* to feed while doing microscopic damage to its teeth.

Damage of the sort observed as microwear can be done by particles of many sizes, and the only limit is that particles responsible could not have been smaller in diameter than the maximum width of microwear features observed. Many of the coarse scratches observed here are between 2 and 4 µm wide, which could have been done by particles of coarse silt size or greater. Fine scratches may be as small as 0.5 µm wide, which could be done by grains of fine silt size or greater. It is important to consider here that a minimum size is pointed out, not a maximum size. The abrasives that could have made those marks on the teeth could be silt-sized, or much larger. The relative breadth of an indentation by a round particle cannot be greater than the width of the particle, but it can be narrower if the force applied to it is small. Therefore, this does not exclude benthic materials or large food items from possible causes of these microwear features, it only establishes that the microwear features were caused by something no smaller than 2–4 µm in width.

The material composition of these grains of silt size or greater may be more relevant. Though bite forces can allow materials of lesser hardness to indent a harder solid, this is far less likely a cause than indentation by materials of greater or equal material hardness. The hardness of squamate enamel is not yet known, but the likely value of its hardness is somewhere between that of pure apatite (Dietrich, 1969) and mammalian enamel (Cuy et al., 2002; Xu et al., 1998), and may be similar to that of estimates made for the enamel of some archosaurs (Erickson et al., 2012). Mosasaur enamel is known to have a structure that may allow some specialisations to avoid fracture such as modifications to its thickness (Sander, 1999), but it is not prismatic like mammalian enamel and may not be as resistant to indentation and more prone to fracture. This appears to be a shared feature between marginal and pterygoid teeth of mosasaurs (Pellegrini & Beatty, 2011). If somewhere in between the hardness of apatite and mammalian enamel, then the abrasives that are most likely to result in indentations to *Carinodens* enamel would have been silica-based grains, such as quartz silts and sands.

Mulder et al. (2013) summarise the sedimentological setting of all known *Carinodens* occurrences. The sedimentary context ranges from exclusively biocalcarenic (type Maastrichtian occurrences, see Mulder et al., 2013) to more clastic (sandy) facies, such as with material from Ukraine. The occurrences from Russia, Morocco, Brazil and Jordan are all (to some degree) phosphatic, and glauconite is reported from the Ukraine, USA and Bulgarian occurrences.

Calcium carbonate grains are typically too soft to indent enamel, and recent work on other marine vertebrate tooth wear patterns seems to suggest that when comparing animals with similar diets but exposure to siliciclastics versus carbonates, those animals feeding amid carbonate substrate exhibit

significantly less dental wear than those feeding amid siliciclastics (Beatty, 2007; Beatty et al., 2011). So, the causes of this wear may be either by attrition (tooth-tooth wear) from the occluding tooth, or by some other abrasive. Although foraging in siliciclastic dominated sediments cannot be excluded, this does not seem likely given that the nearest potential source of more siliciclastic-rich sediment would be the Brabant Massif or the Eifel, which is a long distance away from the Maastricht localities. This also excludes the role of taphonomic processes in the application of the dental wear.

If siliciclastics from substrate are not the abrasive involved, perhaps hard prey objects are. This brings us back to the idea of durophagy, and what potential prey items may have been causing these coarse scratches. Plenty of marine invertebrates have hard body parts, and the complex structure of nacre may allow it to reach the hardness of enamel (Ashby et al., 1995; Currey, 1980; Currey et al., 2001; Jackson et al., 1988; Katti et al., 2005; Meyers et al., 2008). Schulp (2005) evaluated a variety of (extant) potential prey items using a reconstructed jaw model, which allowed to bracket the potential prey items of *Carinodens* to (the Cretaceous equivalents of) small oysters, gastropods, arthropods and echinoderms (see also Schulp et al., 2010, for a re-evaluation). The macro- and microwear data presented here is not in disagreement with these feeding options.

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