

# Dental microwear of a Late Triassic dinosauriform, *Silesaurus opolensis*

TAI KUBO and MUGINO O. KUBO



Kubo, T. and Kubo, M.O. 2014. Dental microwear of a Late Triassic dinosauriform, *Silesaurus opolensis*. *Acta Palaeontologica Polonica* 59 (2): 305–312.

*Silesaurus opolensis* belongs to Silesauridae, the closest sister group to dinosaurs. The present study analyzed the dental microwear patterns of *Silesaurus opolensis*. Low pit-to-scratch ratios imply they did not feed on hard objects. Unimodal distributions of both wear-facet and non-facet scratch orientations indicate simple orthal jaw movement. Scratch orientation and density differ between microscopic regions in *Silesaurus*, and unlike hadrosaurid dinosaurs, the microwear patterns of small areas are not identical to those of whole teeth.

Key words: Dinosauriformes, *Silesaurus opolensis*, dental microwear, jaw movement, herbivory, Triassic, Poland.

Tai Kubo [t-kubo@dinosaur.pref.fukui.jp], Fukui Prefectural Dinosaur Museum, 51-11 Terao, Muroko, Katsuyama, Fukui 911-8601, Japan;

Mugino O. Kubo [mugino@um.u-tokyo.ac.jp], The University Museum, The University of Tokyo, 7-3-1 Hongo, Bunkyo-ku, Tokyo 113-0033, Japan.

Received 21 March 2013, accepted 29 May 2013, available online 5 June 2013.

Copyright © 2014 T. Kubo and M.O. Kubo. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

## Introduction

*Silesaurus opolensis* Dzik, 2003 belongs to the Silesauridae, the closest sister group to dinosaurs (Nesbitt 2011; see Langer et al. 2010 for other phylogenetic hypotheses). Their palaeoecology is of great interest for considering ancestral character states of dinosaurs. From its gross dental morphology, *Silesaurus* was deduced to be a herbivore (Dzik 2003). However, this raised questions concerning the diet of the common ancestor of dinosaurs, which was previously assumed to be a faunivore (Barrett et al. 2011). If the herbivorous diet of *Silesaurus* is confirmed, understanding the jaw movements of *Silesaurus* is essential in order to explore the modification of mastication toward herbivory within basal Dinosauriformes.

Dental microwear analysis was used to examine microscopic scars on tooth enamel surfaces that were produced in vivo by tooth–tooth or tooth–food contact during feeding. The method has been widely used to reconstruct diets and jaw movements of extinct mammals, particularly primates, but also other mammals such as rodents, ungulates, and carnivores (Rensberger 1978; Van Valkenburgh et al. 1990; Solounias and Hayek 1993; Teaford 2007). Because there are no living analogues, dietary interpretation of herbivorous archosaurs from their dental microwear is challenging and rather than for detailed diet reconstruction, it has been

used to provide evidence of niche partitioning between sympatric species (Fiorillo 1998; Goswami et al. 2005) or as an indicator of similarities and differences in diet between closely related species (Upchurch and Barrett 2000; Fiorillo 2011; Whitlock 2011). However, microwear analysis is a powerful tool for reconstructing the jaw movement of extinct archosaurs because it does not necessarily depend on data from modern analogues (Fiorillo 1998; Rybczynski and Vickaryous 2001; Williams et al. 2009). Dental microwear can reveal jaw movements that are not detectable from tooth gross morphology. For instance, propalinal jaw movement was inferred by qualitative observation of microwear in *Euplocephalus*, which was unexpected from their simple leaf-shaped teeth (Rybczynski and Vickaryous 2001).

A microwear analysis of hadrosaurid dinosaurs showed that the orientation of scratches was indistinguishable between microscopic observation sites in the same teeth, among teeth in the same jaw, and even between individuals (Williams et al. 2009). This is possible for hadrosaurids and other dinosaurs that possess dental batteries because teeth of these dinosaurs form one large wear facet. This may not be the case for more basal dinosauriform herbivores with leaf-shaped teeth that do not share a wear facet with other teeth. Thus, we examined whether or not the microwear features of a small area were identical to those of the whole tooth in *Silesaurus*.

We first aimed to analyze dental microwear of *Silesaurus*

to assess its jaw movement and diet and second to compare the scratch angles on different regions of the same teeth of *Silesaurus* to assess whether or not scratch orientation is indistinguishable as it is in hadrosaurid dinosaurs.

*Institutional abbreviations.*—ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

## Material and methods

Fourteen *Silesaurus* teeth from six jawbones were examined. Specimen numbers of the jawbones are ZPAL Ab III/1930 (right dentary), ZPAL Ab III/939/1 (left dentary), ZPAL Ab III/1216 (left dentary), ZPAL Ab III/361/27 (left dentary), ZPAL Ab III/361/26 (right maxilla), and ZPAL Ab III/1218 (left maxilla). Surfaces of the teeth were cleaned using acetone and cotton swabs under a stereomicroscope. Moulds of these surfaces were made using Affinis Regular Body polyvinylsiloxane (Coltene Whaledent Inc., Altstätten, Switzerland) and directly mounted onto scanning electron microscope (SEM) stubs using conductive paste (Dotite Paint, JEOL DATUM Ltd.), with any wear facet present oriented horizontally. After platinum sputter-coating, the dental impressions were imaged at 300 $\times$  magnification, using a JEOL JSM-5910LV (JEOL Ltd.) scanning electron microscope with an accelerating voltage of 5 kV and a working distance of 48–49 mm.

Maxillary teeth possess a wear facet on the lingual surface and dentary teeth exhibit a wear facet labially. The 14 teeth that possess wear facet(s) were examined. Among these teeth four maxillary and two dentary teeth had a planar facet at the crown apex separate from a lingual or labial wear facet. These facets at apexes are small and roughly perpendicular to the longitudinal axis of teeth without much tilt to the mesial or distal side. Other teeth may have had a wear facet on the crown apex that later merged with a lingual or labial wear facet as it expanded. It is difficult to identify the opposing wear facets on *Silesaurus* teeth because the upper and lower jaws that preserve teeth have not been found in articulation. From our observations and the original description in Dzik (2003), we determined that the facet at the crown apex was the wear facet produced by tooth–food–tooth contact. SEM observation revealed that only one wear facet at the crown apex of the tooth from the left maxilla (ZPAL Ab III/1218; Fig. 1A) preserved clear microwear features (Fig. 1B) that are distinct from postmortem wear illustrated in King et al. (1999). Enamel of *Silesaurus* is thin and microwear features of the wear facet are preserved on dentine. Because depressions with rough texture exist at the border between enamel and dentine and no microwear features continue across the border, we could not confirm whether microwear features are similar on enamel and dentine. Nevertheless these dentine microwear patterns are generally similar to non-facet microwear patterns preserved on enamel that are described below. SEM images were combined to compose an image of the entire wear facet (Fig. 1C) so that the lengths of all microwear

features could be measured correctly. The line that connects the mesial and distal denticulated ridges was defined as the mesiodistal axis. For measurements and calculations, the distal direction was set as 0° and the lingual direction as 90°. A microwear feature with a length-to-width ratio >4.0 was defined as a scratch, whereas a feature with a ratio <4.0 was defined as a pit (Teaford 2007). The percentage of pits in the wear facet was calculated. The angles and lengths of scratches were measured using the image processing software Image J (Rasband 1997–2012). For curved scratches, the two end points were connected to measure angle and length. To test whether microwear features differ between regions within the same wear facet, mean orientation (mean vector), and mean length of scratches were compared between the distolabial region and the rest of the wear facet. Angular dispersion of the scratches was also calculated, which represents the degree of parallelism. If scratches are aligned, then angular dispersion approaches one, and if scratches are oriented more randomly then it approaches zero (Williams et al. 2009).

Because the upper tooth row of *Silesaurus* lies lingual to the lower tooth row during occlusion, the labial surfaces of the lower teeth and the lingual surfaces of the upper teeth show wear facets produced by tooth–food–tooth contact. Unfortunately, microwear features were not preserved on these wear facets. However, numerous scratches were found outside the wear facets on 13 among the 14 teeth examined. We measured scratch angles from the labial surfaces of three teeth from the same left dentary (ZPAL Ab III 361/27; Fig. 2). These teeth were chosen because the impressions of all teeth were taken in one mould, which allowed comparison of scratch angles between different teeth. For angle measurement, the apical direction was set at 90° and the mesial direction at 0°. Because some scratches extended beyond the SEM observation sites, we could not accurately measure scratch length. For these border-crossing scratches, a point where the scratch crosses the border of the SEM site was taken as an end point to measure the scratch angle. When analyzing these non-facet microwear patterns, we could not set the SEM site of interest horizontally to eliminate the effect of curvature. Mean orientation (mean vector) and angular dispersion of scratches were calculated for each tooth and compared.

For statistical comparisons, Watson's test was used for angular data and the Mann-Whitney U-test was used for length data. All statistical tests were conducted using the statistical software R, version.2.2 (R Core Team 2012) with CircStats, the package for R (Lund and Agostinelli 2007). Rose.NET 0.10.0 (Thompson 2012) was used to draw rose diagrams. We followed Smith and Dodson (2003) for dental terminology.

## Results

**Non-facet microwear of teeth of the left lower jaw** (Table 1).—Dental microwear features were not preserved on the wear facets on the labial surfaces of teeth in ZPAL Ab III



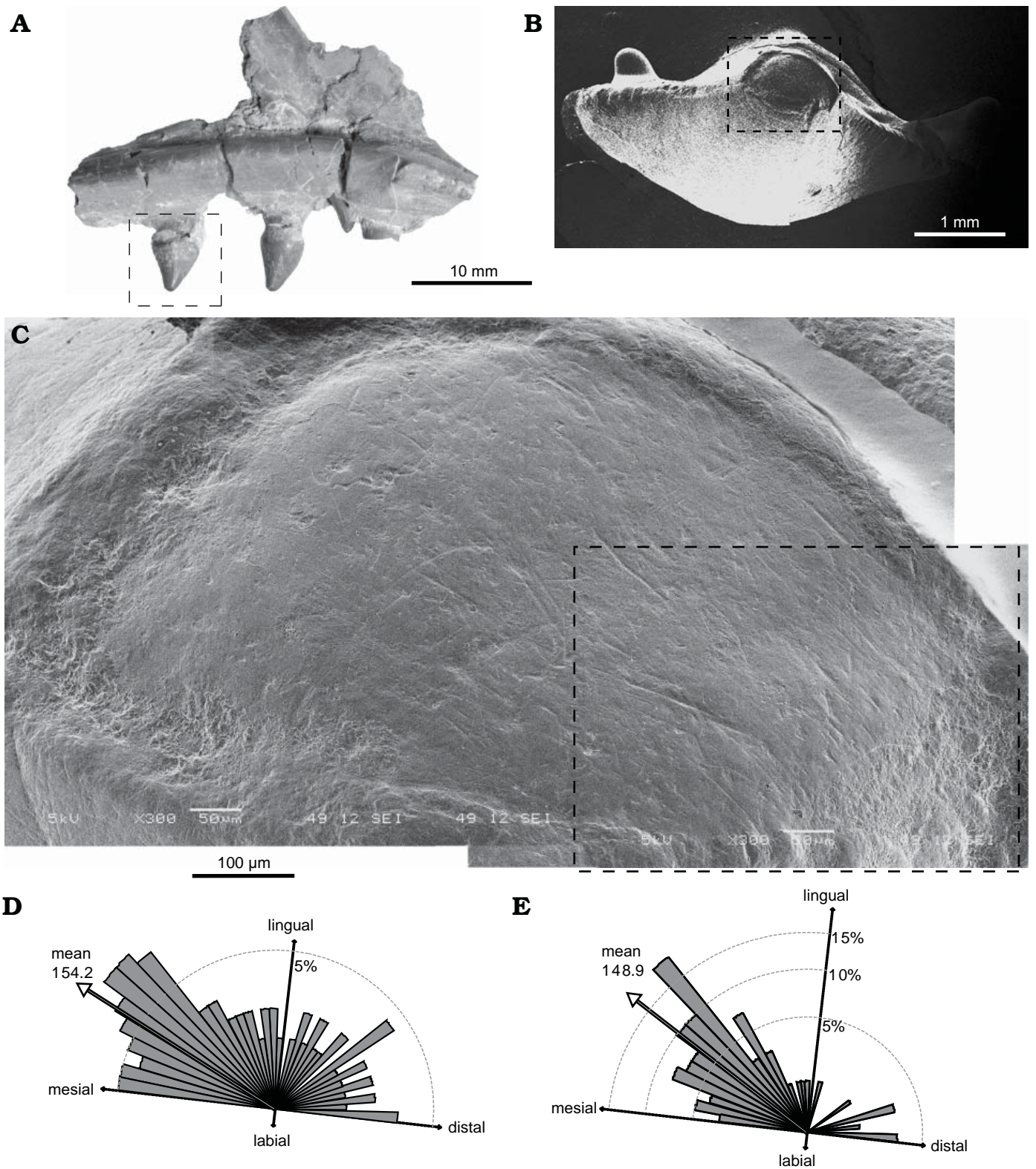


Fig. 1. Microwear on the wear facet of the tooth from the left maxilla (ZPAL Ab III/1218) *Silesaurus opolensis* Dzik, 2003 from the Upper Triassic; Krasiejów, Poland. **A.** Lingual view of left maxilla; the tooth in the dashed-lined box preserves microwear features on its wear facet. **B.** SEM image of the mold of the tooth; the wear facet at the crown apex (dashed-lined rectangle) is magnified. **C.** SEM image of the impression of the entire wear facet. SEM images taken at 300 $\times$  magnification were combined to compose this image. Note that the disto-labial region enclosed by a dashed-lined rectangle is more densely scratched than the rest of the wear facet. **D.** Rose diagram of scratch orientations of the whole wear facet. An open arrow indicates the orientation of the mean vector of the scratches (n = 176). **E.** Rose diagram of scratch orientations of the disto-labial region, the area enclosed by the dashed-lined rectangle in C. An open arrow indicates the orientation of the mean vector of the scratches (n = 73). The diagram shows that scratches are more aligned in this area than in the wear facet as a whole.

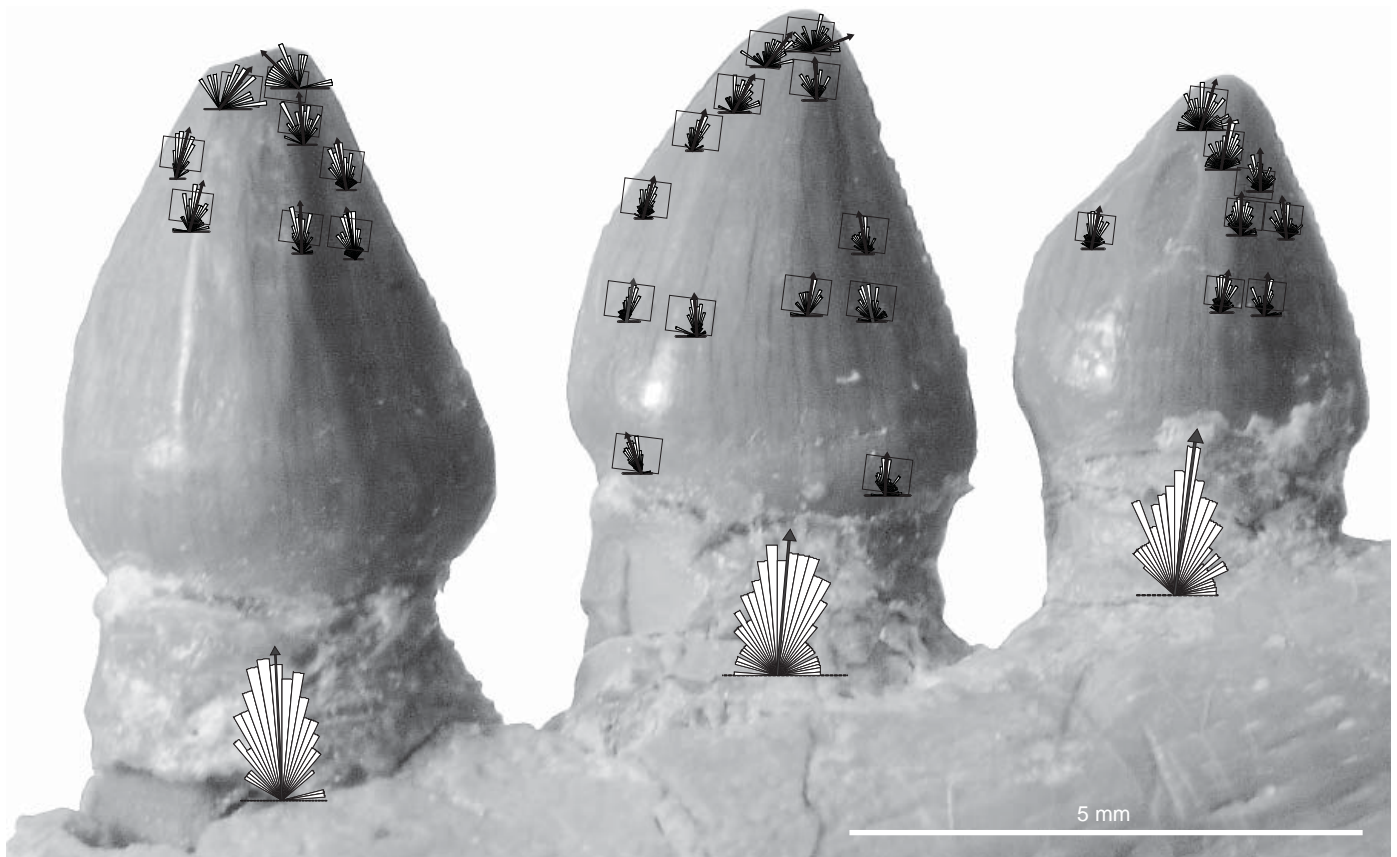


Fig. 2. Non-facet microwear of teeth from the left lower jaw (ZPAL Ab III 361/27) of *Silesaurus opolenensis* Dzik, 2003 from the Upper Triassic; Krasiejów, Poland. Mesial (left), middle and distal (right) teeth have 8, 13, and 8 SEM sites, respectively, shown as open rectangles in the figure, in which scratch angles were measured. The rose diagram located in the middle of each SEM site represents scratch orientations in the site. The black arrow represents a mean vector orientation of each rose diagram. The rose diagram at the base of each tooth represents the scratch orientation of the whole tooth. We could not lay each SEM site horizontal for observation to eliminate effects of mold curvature. Nevertheless, it is clear that scratches are basically oriented in the apico-basal direction for all teeth.

Table 1. Number of scratches, mean orientation, and angular dispersion of non-facet microwear patterns from the labial side of three teeth of the same left dentary (ZPAL Ab III 361/27) of *Silesaurus opolenensis*. See Fig. 2 for rose diagrams showing scratch orientation.

	Number of scratches	Mean orientation of scratches (°)	Angular dispersion
Mesial tooth	464	88.4	0.91
Middle tooth	919	94.9	0.88
Distal tooth	566	99.2	0.89

361/27. However, outside these wear facets scratches were observed. For the mesial, middle, and distal teeth, microwear features were observed in 8, 13, and 8 SEM sites, respectively (Fig. 2). The mean orientation of scratches was significantly different between teeth (all Watson's test:  $p < 0.001$ ; Table 1).

**Wear facet microwear of the tooth from the left maxilla** (Table 2).—Microwear features were preserved on the wear facet at the crown apex of the tooth from the left maxilla, ZPAL Ab III/1218 (Fig. 1A, B). Compared with the non-wear facet microwear of ZPAL Ab III 361/27, the microwear features were less aligned (angular dispersion, non-wear facet: 0.88–0.91 and wear facet: 0.65, Tables 1 and 2). Within the

wear facet, the distolabial region that had an area of 0.097 mm<sup>2</sup> (Fig. 1C: the area within the broken-lined rectangle) showed more dense and aligned scratches compared with the rest of wear facet (0.21 mm<sup>2</sup>), as reflected in the greater angular dispersion and feature density of the distolabial region (Table 2). Overall scratch orientation was 154.2° in the distolabial to mesiolingual direction (Fig. 1D). Statistical comparison indicated that scratch orientation differed significantly between the distolabial region and rest of the wear facet (Watson's test:  $p < 0.001$ ; Table 2), with the former being more inclined to the lingual direction (Fig. 1E). Scratch length did not differ significantly between the regions (Mann-Whitney U test:  $p = 0.54$ ; Table 2). Pitting percentage was lower in the distolabial region (Table 2).

## Discussion

**Jaw movement inferred by microwear.**—The orientation of scratches was interpreted as reflecting the direction(s) of jaw movement in previous studies on extinct dinosaur dental microwear (Fiorillo 1998; Barrett 2001; Rybczynski



Table 2. Microwear features of the wear facet of the left maxilla (ZPAL Ab III/1218) of *Silesaurus opolensis* Dzik, 2003 from the Upper Triassic; Krasiejów, Poland. The whole wear facet and two regions within the facet, the distolabial region (the area enclosed by the broken-lined rectangle in Fig. 1C) and the rest of the facet are presented separately. The eight scratches that cross the border of the two regions are excluded from statistical comparisons of the two regions. See Fig. 1 for the SEM image and rose diagrams showing scratch orientation.

	Number of features	Feature density per mm <sup>2</sup>	Pit %	Mean orientation of scratches (°)	Angular dispersion	Mean scratch length (µm)
Whole wear facet	198	637	11	154.2	0.65	29.8
The disto-labial region	77	792	5	148.9	0.74	27.4
Rest of the wear facet	113	529	15	169.1	0.35	29.8

and Vickaryous 2001; Schubert and Ungar 2005; Williams et al. 2009), except Whitlock (2011) who interpreted the low consistency of scratch orientation as being caused by hard or brittle food rather than complex jaw motion. Nevertheless, the assumptions made by Whitlock (2011) cannot explain the systematic scratch orientation of hadrosaurid dinosaurs reported by Williams et al. (2009). In addition, Whitlock (2011) assumed that the non-facet microwear features of sauropods were caused by scraping of nearby vegetation during feeding. Because the labial surfaces of *Silesaurus* lower teeth were overlapped by the teeth of the upper jaw, vegetation could scrape the lower teeth only when it was trapped between upper and lower teeth. Thus, we consider that the observed non-facet microwear of *Silesaurus* was mainly produced by tooth–food–tooth contact during mastication and the orientation of scratches on *Silesaurus* teeth reflects jaw motion rather than food texture.

Non-facet scratches were more aligned in orientation than those on the wear facet. Although the mean orientation of non-facet scratches differed significantly among teeth, it was roughly apicobasal (dorsoventral) on all three teeth analyzed (Fig. 2). This implies apicobasal orthal jaw movement, similar to in the Triassic archosauromorph *Azendohsaurus* (Flynn et al. 2010), for which jaw movement was also inferred from non-facet dental microwear (Goswami et al. 2005).

Most of the fully erupted maxillary and dentary teeth possess a high-angle flat wear facet on the lingual or labial side, respectively, and not on the mesial or distal sides. Thus the upper and lower teeth are probably fairly aligned and not interdigitating (sensu Upchurch and Barrett 2000). Also planar lingual and labial wear facets may support inferred orthal jaw movement. Unfortunately, no microwear features were preserved on the lingual or labial wear facets of *Silesaurus*. Thus, these non-facet microwear and macrowear patterns are currently the only evidence available to reconstruct the jaw movement of *Silesaurus* in the sagittal plane.

On the planar wear facet at the crown apex of *Silesaurus* teeth, scratch orientation shows a unimodal distribution, mainly distolabial to mesiolingual in orientation, but also included scratches in almost all orientations (Fig. 1D). This implies simple jaw movement in a single direction without tight occlusal control.

**Possible diet of *Silesaurus*.**—A number of microwear studies have been conducted for extant mammals. To the best of our knowledge, unfortunately, no study has quantitatively

compared microwear features among diverse mammalian groups. This may be due to: (i) methodological differences (e.g., magnification or size of the observation area), and inter-observer differences in counting microwear features that might make it difficult to directly compare metrics; (ii) phylogenetically diverse taxa exhibit considerable variation in tooth morphology, and it might not be possible to compare functionally equivalent tooth wear facets; and (iii) the mastication stroke of mammals is generally divided into two functionally different phases, phase I (upward movement of lower molars from initial contact on antagonists to centric position, involving shearing of foods), and phase II (downward movement of lower molars from the centric position until loss of contact, involving crushing and grinding of food), and microwear features differ between these phases (Kay and Hiiemae 1974).

However, we consider a quantitative summary of the previous studies to be informative for inferring the diets of extinct animals lacking living analogues as well as for future comparative studies. We selected microwear studies that adopted similar observational methodologies and presented comparable measurements, i.e., feature density per mm<sup>2</sup>, pitting percentage, and scratch length (Table 3). In summary, this shows that among extant mammals with low-crowned (bunodont) molars, food hardness is influential for characterizing tooth microwear, and animals that consume hard objects such as seeds, chitinous insects, or the bones of large vertebrate prey have more pits on the crushing facets of their tooth enamel. However, herbivorous ungulates have a sophisticated masticatory system and their high-crowned cheek teeth are specialized for shearing and grinding fibrous plant materials. Their mastication stroke is predominantly composed of phase I movements; thus, the differences in tooth microwear among ungulates appear more straightforward than among other bunodont mammals: the higher abrasiveness of ingested foods, caused by internal (silica phytoliths) or external (adherent soil and grit) particles, in grass-eating species results in a higher density of scratches on grazers' teeth than on browsing species' teeth. The high pit frequency observed in browsers is not caused by crushing of hard objects but by tooth–tooth contact and the resultant enamel microfractures (Ozaki 2006); thus, it may not be directly comparable to other bunodont taxa with high pitting percentage (i.e., faunivorous mammals and frugivorous primates).

Gordon (1982) compared the microwear of chimpanzee

Table 3. Quantitative microwear features from selected microwear studies on extant mammals. We categorize mammals into nine feeding types: grass-eating ungulates (grazers); browse-eating ungulates (browsers); herbivorous ungulates intermediate between the above dichotomy (mixed feeders); leaf-eating mammals other than ungulates (folivores); mammals that eat both leaves and fruits (foli-frugivores); primates consuming fruits and nuts (frugivores); primates that consume bulbs, tubers, or rhizomes (underground storage organ feeders); carnivorous mammals (carnivores); and insectivorous mammals (insect and small vertebrate eaters). Taxonomic groups that are included in each feeding type are shown in parentheses. Insect and small vertebrate eaters include Afrosoricida, Chiroptera, Cingulata, Erinaceomorpha, Primates, and Soricomorpha. The median value and range of feature density, scratch length, and pit percentages are shown for each feeding type. For some species, all three variables were not available. When possible, feature density per mm<sup>2</sup> and pit percentages were calculated from data provided in the original literature. Note that in some cases the magnification of SEM observations is lower than the standard (500×). References: 1, Solounias and Hayek 1993; 2, Solounias and Moelleken 1993; 3, El-Zaatari et al. 2005; 4, Green and Resar 2012; 5, Teaford 1988; 6, Teaford and Walker 1984; 7, Ungar et al. 2006; 8, Rafferty et al. 2002; 9, Teaford and Runestad 1992; 10, Silcox and Teaford 2002; 11, Teaford 1985; 12, Daegling and Grine 1999; 13, Robson and Young 1990; 14, Van Valkenburgh et al. 1990; 15, Strait 1993.

Feeding type	Number of species	Feature density per mm <sup>2</sup>	Scratch length (μm)	Pit %	SEM magnification	References
Grazer (ungulates)	8	1993 (1710–2306)	51 (33–56)	19 (4–38)	500	1, 2
Mixed feeder (ungulates)	4	1882 (1627–2053)	31 (29–33)	39 (27–43)	500	1, 2
Browser (ungulates)	8	1308 (597–1610)	34 (25–49)	49 (22–59)	500	1, 2
Folivore (Primates and Pilosa)	4	1140 (403–3087)	57 (30–74)	10 (3–42)	500	3, 4, 5, 6, 7
Foli-frugivore (Primates and Pilosa)	8	2694 (1797–5414)	31	25 (13–57)	500	3, 4, 5, 6, 8, 9
Frugivore (Primates)	8	2665 (1406–43490)	30 (10–34)	44 (8–65)	500	3, 5, 6, 7, 9, 10, 11
Underground storage organs feeder (Primates)	2	354 (350–3138)	18	40 (24–48)	200 and 500	3, 7, 8, 10
Carnivore (Carnivora and Dasyuromorphia)	10	448 (327–590)	43 (31–104)	37 (32–68)	150 and 250	13, 14
Insect and small vertebrate eater	18	7368 (2065–46472)	10 (9–16)	48 (24–60)	500	4, 9, 10, 15

Table 4. Quantitative microwear features of Mesozoic archosauromorphs obtained from the literature and the present study. Variables except for pit percent were often not recorded in previous studies. Note that differences in masticatory system and tooth morphology may cause different microwear characteristics between mammals and archosauromorphs.

Taxa	Feature density per mm <sup>2</sup>	Scratch length (μm)	Pit %	SEM magnification	References	Note
<i>Azendohsaurus madagaskarensis</i>	N/A	87	less than 1	300	Goswami et al. 2005	non-facet
Hadrosaurid from North America	N/A	N/A	11 (4–13)	up to 1000	Fiorillo 2011	
<i>Diplodocus</i> sp.	N/A	N/A	0	30 to 2000	Fiorillo 1998	
<i>Camarasaurus</i> sp.	N/A	N/A	26	30 to 2000	Fiorillo 1998	
<i>Edmontosaurus</i> sp.	997	57	0	300	Williams et al. 2009	
<i>Silesaurus opolensis</i>	637	30	11	300	this study	whole wear facet

molars and summarized variations in microwear features from the viewpoint of shear and compression gradients along the molar sequence during the mastication stroke. This idea is also applicable to interspecific variation. If the amount of compression is high and that of shear is low, which would be the case for hard-object eating, then large, deep pits would predominate. If both shear and compression are weak, which would be the case for soft-object (fruits or larvae) eating, short scratches and small shallow pits would predominate. When food shearing is important, as it is for animals that eat fibrous plant leaves or tear the flesh of large prey, long scratches would dominate the wear facet, but the smaller amount of abrasive matter in the latter case would result in lower feature density in the wear facet than in the former.

If we apply these diet-microwear relationships of extant mammals to *Silesaurus*, its low frequency of pits excludes hard objects such as bones, chitinous insects, and seeds from its diet. Thus, *Silesaurus* was probably not faunivorous (carnivores or insect/small vertebrate eaters) or underground

storage organ feeders (Table 3). The scratch length of *Silesaurus* is close to that of extant herbivorous mammals (mixed feeders, browsers, and foli-frugivores; Table 3). All three *Silesaurus* microwear variables shown in Table 4 are within the range of folivorous mammals; thus, their diet may have been similar to that of extant leaf eaters. Note that different body and tooth sizes as well as the SEM magnification may affect these variables.

Barrett (2000) has suggested that animals such as prosauropods and *Silesaurus* that possess teeth with mesio-distally expanded crowns and coarsely serrated mesial and distal edges, often interpreted as herbivores, might have been omnivorous. Can we rule out the possibility of omnivory by microwear analysis of *Silesaurus*? If *Silesaurus* was an omnivore, it must have consumed insects or small vertebrates. Feature density and feature length of *Silesaurus* are sparser and longer than those of insects or small vertebrate eaters (Tables 2, 3), but this may simply reflect body or tooth size as most mammalian insect and small vertebrate eaters compared here

are smaller than *Silesaurus*. Also, mammalian insectivores and small vertebrate eaters show higher pit-to-scratch ratios than *Silesaurus*. Nevertheless, the simple jaw movements and tooth morphologies of dinosauriforms may have caused the low pit-to-scratch ratio compared with those of mammals (Tables 3, 4), although a relatively high pit-to-scratch ratio was observed in some individuals of the sauropod *Camarasaurus* (Fiorillo, 1998). Further microwear studies on extant reptiles with simple tooth morphology are needed to confidently rule out the possibility of omnivory in *Silesaurus*.

Scratches are often inferred to have been caused by either feeding on grasses containing silica phytoliths or by ingesting soil and grit (Williams et al. 2009). Grasses had not evolved in the Late Triassic (Taylor et al. 2009). Therefore, the scratches of *Silesaurus* are perhaps due to adherent soil and grit, although feeding on horsetails, which also contain abundant silica phytoliths, may have produced scratches (Hodson et al. 2005).

#### **Inter- and intra-tooth variability of dental microwear.**—

From comparisons of non-facet microwear among teeth erupting on the same dentary, we found significant differences in scratch orientation among the teeth. This implies that (i) differences in tooth position within the dentition may influence the inter-tooth variability of dental microwear comparable to variation in microwear along the molar sequence (first, second, and third molars of extant chimpanzees; Gordon 1982), and/or (ii) the differences in the time elapsed after tooth eruption. Microwear patterns on the wear facet were preserved in only one tooth of *Silesaurus*, and we could not test differences between teeth.

Unlike the dental microwear observed in hadrosaurids (Williams et al. 2009), the orientation of scratches differed between regions of the same wear facet in *Silesaurus*. In contrast, scratch lengths were not significantly different between regions. Mean orientations were similar between different regions, but scratches were more strongly aligned and distributed more densely in the distolabial region (Fig. 1E); the percentage of pits was also lower in this region (Table 2). These differences imply that more shearing occurred in the distolabial region and that the other region experienced more crushing and grinding, though it is not clear if this feature is shared with other upper teeth of *Silesaurus*. The result indicates that the microwear features of a small area are not representative of whole teeth for *Silesaurus*; this feature is probably common to other basal dinosauriforms that had simple leaf-shaped teeth like *Silesaurus*. Thus, for microwear analyses of basal dinosauriforms, a small single area in a wear facet is not adequate for observing microwear, and multiple observation areas are needed for reliable evaluation.

## Conclusions

Herbivory on soft objects was inferred from comparisons between the dental microwear patterns of *Silesaurus* and those of

extant mammals, although the possibility of omnivory could not be confidently ruled out, and more comparative data on microwear patterns of extant reptiles are needed for reliable diet estimation. The results are consistent with the previous suggestion that *Silesaurus* was herbivorous based on gross tooth morphology (Dzik 2003). The orthal jaw movement of *Silesaurus* was much simpler than that of contemporaneous herbivores such as rhynchosaurs and synapsids (Crompton and Attridge 1986; Goswami et al. 2005). Therefore, silesaurids could exploit floral resources, but not because their masticatory system gave them an advantage. Aetosaur *Stagonolepis olenkae* Sulej, 2010 is more abundant than *Silesaurus* in the Krasiejów biota and the only other large herbivore or omnivore in the biota. *S. olenkae* also does not show adaptation for feeding on hard vegetation (Dzik and Sulej 2007; Sulej 2010). Thus, the masticatory system for hard vegetation may have not been essential in the biota, or adaptive trait(s) other than jaw mechanics may have been advantageous to *Silesaurus*, such as a flexible neck and bipedal stance to forage at various height, faster growth rate, or efficient locomotion (Crompton and Attridge 1986; Fostowicz-Freluk and Sulej 2010; Piechowski and Dzik 2010; Barrett et al. 2011; Kubo and Kubo 2012).

## Acknowledgements

TK thanks Rafał Piechowski (University of Warsaw, Poland), and Dorota Konietzko-Meier and Kamil Gadek (both from Opole University, Poland) for their hospitality in Poland. Without the support of all members of the Fukui Prefectural Dinosaur Museum, TK could not have made time to visit Poland. Shin-ichi Sano (Fukui Prefectural Dinosaur Museum, Katsuyama, Japan) explained how to operate the SEM and maintained the machine. Kazuo Terada (Fukui Prefectural Dinosaur Museum) advised about paleobotanical literatures and Triassic flora. Constructive comments from Paul M. Barrett (Natural History Museum, London, UK) and Jerzy Dzik (Instytut Paleobiologii PAN, Warsaw, Poland) and editorial work of Mike J. Benton (University of Bristol, UK) improved the manuscript. The authors thank Enago (www.enago.jp) for the English language review. TK also acknowledges the financial support of the Japan Society for the Promotion of Science (Grant-in-Aid for Encouragement of Scientists No. 23916006).

## References

- Barret, P.M. 2000. Speculation on prosauropod diets. In: H.-D. Sues (ed.), *Evolution of Herbivory in Terrestrial Vertebrates*, 79–122. Cambridge University Press, Cambridge.
- Barrett, P.M. 2001. Tooth wear and possible jaw action of *Scelidosaurus harrisonii* Owen and a review of feeding mechanisms in other thyrophan dinosaurs. In: K. Carpenter (ed.), *The Armored Dinosaurs*, 25–52. Indiana University Press, Bloomington.
- Barrett, P.M., Butler, R.J., and Nesbitt, S.J. 2011. The roles of herbivory and omnivory in early dinosaur evolution. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 101: 383–396.
- Crompton, A.W. and Attridge, J. 1986. Masticatory apparatus of the larger herbivores during Late Triassic and Early Jurassic times. In: K. Padian (ed.), *The Beginning of the Age of the Dinosaurs*, 223–236. Cambridge University Press, Cambridge.



- Daegling, D.J. and Grine, F.E. 1999. Occlusal microwear in *Papio ursinus*: The effects of terrestrial foraging on dental enamel. *Primates* 40: 559–572.
- Dzik, J. 2003. A beaked herbivorous archosaur with dinosaur affinities from the early Late Triassic of Poland. *Journal of Vertebrate Paleontology* 23: 556–574.
- Dzik, J. and Sulej, T. 2007. A review of the early Late Triassic Krasiejów biota from Silesia, Poland. *Palaeontologica Polonica* 64: 3–27.
- El-Zaatari, S., Grine, F.E., Teaford, M.F., and Smith, H.F. 2005. Molar microwear and dietary reconstructions of fossil Cercopithecoidea from the Plio-Pleistocene deposits of South Africa. *Journal of Human Evolution* 49: 180–205.
- Fiorillo, A.R. 1998. Dental microwear patterns of the sauropod dinosaurs *Camarasaurus* and *Diplodocus*: evidence for resource partitioning in the Late Jurassic of North America. *Historical Biology* 13: 1–16.
- Fiorillo, A.R. 2011. Microwear patterns on the teeth of northern high latitude hadrosaurs with comments on microwear patterns in hadrosaurs as a function of latitude and seasonal ecological constraints. *Palaeontologia Electronica* 14: 20A.
- Flynn, J.J., Nesbitt, S.J., Parrish, J.M., Ranivoharimanana, L., and Wyss, A.R. 2010. A new species of *Azendohsaurus* (Diapsida: Archosauromorpha) from the Triassic Isalo group of Southwestern Madagascar: cranium and mandible. *Palaeontology* 53: 669–688.
- Fostowicz-Frelik, L. and Sulej, T. 2010. Bone histology of *Silesaurus opolensis* from the Late Triassic of Poland. *Lethaia* 43: 137–148.
- Gordon, K.D. 1982. A study of microwear on chimpanzee molars: implications for dental microwear analysis. *American Journal of Physical Anthropology* 59: 195–216.
- Goswami, A., Flynn, J.J., Ranivoharimanana, L., and Wyss, A.R. 2005. Dental microwear in Triassic amniotes: implications for paleoecology and masticatory mechanics. *Journal of Vertebrate Paleontology* 25: 320–329.
- Green, J.L. and Resar, N.A. 2012. The link between dental microwear and feeding ecology in tree sloths and armadillos (Mammalia: Xenarthra). *Biological Journal of the Linnean Society* 107: 277–294.
- Hodson, M.J., White, P.J., Mead, A., and Broadley, M.R. 2005. Phylogenetic variation in the silicon composition of plants. *Annals of Botany* 96: 1027–1046.
- Kay, R.F. and Hiiemae, K.M. 1974. Jaw movement and tooth use in recent and fossil primates. *American Journal of Physical Anthropology* 40: 227–256.
- King, T., Andrews, P., and Boz, B. 1999. Effect of taphonomic processes on dental microwear. *American Journal of Physical Anthropology* 108: 359–373.
- Kubo, T. and Kubo, M.O. 2012. Associated evolution of bipedality and cursoriality among Triassic archosaurs: a phylogenetically controlled evaluation. *Paleobiology* 38: 474–485.
- Langer, M.C., Ezcurra, M.D., Bittencourt, J.S., and Novas, F.E. 2010. The origin and early evolution of dinosaurs. *Biological Reviews* 85: 55–110.
- Lund, U. and Agostinelli, C. 2007. Circstats: Circular statistics R package version 0.2-4. Available from: <http://cran.r-project.org/web/packages/CircStats/index.html>.
- Nesbitt, S.J. 2011. The early evolution of archosaurs: relationships and the origin of major clade. *Bulletin of the American Museum of Natural History* 352: 1–292.
- Ozaki, M. 2006. Correlations between ecology and microwear features in the sika deer (*Cervus nippon*). *Anthropological Science* 114: 244–244.
- Piechowski, R. and Dzik, J. 2010. The axial skeleton of *Silesaurus opolensis*. *Journal of Vertebrate Paleontology* 30: 1127–1141.
- R Core Team. 2012. R: A Language and Environment for Statistical Computing. Available from <http://www.R-project.org>.
- Rafferty, K.L., Teaford, M.F., and Jungers, W.L. 2002. Molar microwear of subfossil lemurs: improving the resolution of dietary inferences. *Journal of Human Evolution* 43: 645–657.
- Rasband, W.S. 1997–2012. Image J. Available from: U.S. National Institutes of Health, Bethesda, Maryland, USA, <http://imagej.nih.gov/ij/>.
- Rensberger, J.M. 1978. Scanning electron microscopy of wear and occlusal events in some small herbivores. In: P.M. Butler and K.A. Joysey (eds.), *Development, Function and Evolution of Teeth*, 415–438. Academic Press, New York.
- Robson, S.K. and Young, W.G. 1990. A comparison of tooth microwear between an extinct marsupial predator, the Tasmanian tiger *Thylacinus cynocephalus* (Thylacidae) and an extant scavenger, the Tasmanian devil *Sarcophilus harrisii* (Dasyuridae: Marsupialia). *Australian Journal of Zoology* 37: 575–589.
- Rybczynski, R. and Vickaryous, M.K. 2001. Evidence of complex jaw movement in the Late Cretaceous ankylosaurid *Euoplocephalus tutus* (Dinosauria: Thyreophora). In: K. Carpenter (ed.), *The Armored Dinosaurs*, 299–317. Indiana University Press, Bloomington.
- Schubert, B.W. and Ungar, P.S. 2005. Wear facets and enamel spalling in tyrannosaurid dinosaurs. *Acta Palaeontologica Polonica* 50: 93–99.
- Silcox, M.T. and Teaford, M.F. 2002. The diet of worms: an analysis of mole dental microwear. *Journal of Mammalogy* 83: 804–814.
- Smith, J.B. and Dodson, P. 2003. A proposal for a standard terminology of anatomical notation and orientation in fossil vertebrate dentitions. *Journal of Vertebrate Paleontology* 23: 1–12.
- Solounias, N. and Hayek, L.-A.C. 1993. New methods of tooth microwear analysis and application to dietary determination of two extinct antelopes. *Journal of Zoology* 1993: 421–445.
- Solounias, N. and Moelleken, S.M.C. 1993. Tooth microwear analyses and premaxillary shape of an archaic antelope. *Lethaia* 26: 261–268.
- Strait, S.G. 1993. Molar microwear in extant small-bodied faunivorous mammals: An analysis of feature density and pit frequency. *American Journal of Physical Anthropology* 92: 63–79.
- Sulej, T. 2010. The skull of an early Late Triassic aetosaur and the evolution of the stagonolepidid archosaurian reptile. *Zoological Journal of Linnean Society* 158: 860–881.
- Taylor, T.N., Taylor, E.L., and Krings, M. 2009. *Paleobotany: the Biology and Evolution of Fossil Plants*. Second edition. 1230 pp. Academic Press, Elsevier, Burlington.
- Teaford, M.F. 1985. Molar microwear and diet in the genus *Cebus*. *American Journal of Physical Anthropology* 66: 363–370.
- Teaford, M.F. 1988. Scanning electron microscope diagnosis of wear patterns versus artifacts on fossil teeth. *Scanning Microscopy* 2: 1167–1175.
- Teaford, M.F. 2007. Dental microwear and paleoanthropology: cautions and possibilities. In: S.E. Bailey and J.-J. Hublin (eds.), *Dental Perspectives on Human Evolution*, 345–368. Springer, Dordrecht.
- Teaford, M.F. and Runestad, J.A. 1992. Dental microwear and diet in Venezuelan Primates. *American Journal of Physical Anthropology* 88: 347–364.
- Teaford, M.F. and Walker, A. 1984. Quantitative differences in dental microwear between Primate species with different diets and comments on the presumed diet of *Sivapithecus*. *American Journal of Physical Anthropology* 64: 191–200.
- Thompson, T.A. 2012. Rose.Net. Available from: <http://mypage.iu.edu/~t-thomps/>.
- Ungar, P.S., Grine, F.E., Teaford, M.F., and El Zaatari, S. 2006. Dental microwear and diets of African early *Homo*. *Journal of Human Evolution* 50 (1): 78–95.
- Upchurch, P. and Barrett, P.M. 2000. The evolution of sauropod feeding mechanisms. In: H.-D. Sues (ed.), *Evolution of Herbivory in Terrestrial Vertebrates*, 79–122. Cambridge University Press, Cambridge.
- Van Valkenburgh, B., Teaford, M.F., and Walker, A. 1990. Molar microwear and diet in large carnivores: inferences concerning diet in the sabretooth cat, *Smilodon fatalis*. *Journal of Zoology* 222: 319–340.
- Whitlock, J.A. 2011. Inferences of diplodocoid (Sauropoda: Dinosauria) feeding behavior from snout shape and microwear analyses. *Plos One* 6: e18304.
- Williams, V.S., Barrett, P.M., and Purnell, M.A. 2009. Quantitative analysis of dental microwear in hadrosaurid dinosaurs, and the implications for hypotheses of jaw mechanics and feeding. *Proceedings of the National Academy of Sciences* 106: 11194–11199.