A brief history of quantitative wear analyses
with an appeal for a holistic view
on dental wear processes

Ellen Schulz-Kornas, Thomas M. Kaiser, Ivan Calandra, and Daniela E. Winkler

Introduction

This chapter is a comprehensive overview about the development in the field of quantitative wear analysis during the last 20 years. It focuses on specific interdisciplinary approaches that either introduced new viewpoints or solved technical problems, and in particular guided our projects within the DFG research unit 771 at the University of Hamburg. The scope of our group’s interest facilitates the historical shift from qualitative to quantitative wear analysis. Our research was driven by the urge to gain a deeper understanding of wear, which is much more than just traces, and develop a holistic view of the wear process on diverse materials. We start with a condensed historical review of selected developments, focus on the major debates that have influenced our understanding of tooth wear as a part of oral food processing, and set the context of our work within the larger theoretical framework. We show examples that the field of dental wear analyses is evolving on all scales, and that we are only beginning to comprehend the complex dental wear process as one factor amongst many driving evolution through dental adaptation. In particular, the combined studies based on museum material, in vivo, and in vitro experiments have shed new light on the importance of abrasives in the wear process, but also raised new questions for future research.

From traces to textures

Dental wear has been widely investigated in paleobiology and paleoanthropology to infer diet, habitat and climatic conditions. For decades, the approaches mostly revolved around qualitative description of wear in various research disciplines. In paleontology, dental wear analyses have a long history and the works of Simpson (1926, 1933), in which he relates striations on dental wear facets to chewing direction, might be considered a starting point. Since then, the literature on and interest in wear processes have rapidly expanded. Russian scientists used the term traceology to describe use-wear marks on edges and surfaces of prehistoric stone and bone tools (Semenov 1957, Korobkova 1970). They employed traceology as a term to refer to the study of any trace (whether residues or surface alteration), usually in the context of tool use (Korobkova 1977, 1978, 1979, 1981). Later in archeology it has been used as a synonym for microwear to describe scarring, striations, edge rounding, smoothing, polishing and beveling (Hayden 1979, Keeley 1980, Kamminga 1982, Mecks et al. 1982). However, the fascination of use-wear analysis goes even further back in time, e.g. to the mid-19th century when the Swedish zoologist Sven Nilsson mentioned use-wear on flint-knapped artifacts by early inhabitants in Scandinavia (Nilsson, 1834–1843). Already during these early days of traceology Sergej A. Semenov and Galina L. Korobkova conducted extensive systematic experimental research using stereomicroscopy to describe the “microscopically small” wear traces they found (for a review, see Anderson et al. 2005). During the 1950s and 1960s wear traces in mammalian teeth were the object of considerable interest in the fields of vertebrate paleontology, paleoanthropology and also dentistry. Teeth were considered guiding structures of mastication and their wear reflected particular diets. In particular, Butler and Mills (Butler 1952, Mills 1955, Butler and Mills 1959, Mills 1963, 1966, 1967) as well as Kay and Hiemäe (1974) suggested that striations as evidence of occlusal movement represent areas of contact or close approximations of antagonistic teeth. These studies focused preferentially on the mechanics of chewing per se. Later, Dahlberg and Kinzey (1962) studied human teeth using light microscopy and related the scar patterns on tooth enamel to the properties of the ingesta. Additionally, they differentiated between attritional (tooth-tooth) and abrasive (tooth-diet) contacts. Since then, dental microwear research has been widely conducted in paleobiology and paleoanthropology. For a review of the developments from 1950 to 1998, and with special reference given to application in hominins, see Rose and Ungar (1998). More details and particular aspects of facet striation and terminology are discussed in Schultz et al. (2018, 2020, this volume).

Here, we do not detail every single development made or every animal group microwear has been applied to. Instead, we focus on specific interdisciplinary approaches that either introduced new viewpoints or solved technical problems, and in particular influenced our approach and in turn, the design and execution of our projects within the DFG research unit 771 at the University of Hamburg, metaphorically speaking, “from traces to textures”.

In his pioneering light microscopy work, Philip L. Walker (1976) discussed orientation and density of striations in non-human primates in relation to feeding substrate and...
mechanical properties of ingesta. Later studies unfortunately did not explore this aspect further. Instead, they focused on the technical improvement (higher resolution using scanning electron microscopy, SEM) and on the taxon-specific dietary signatures dependent on the enamel structure (Walker 1977, Rensberger 1978, Walker et al. 1978, Rensberger 1982). Based on their studies on hyraxes, Alan C. Walker et al. (1978) found that seasonal changes in diet are reflected in microwear signatures. Consequently, microwear has been suggested to mainly originate from opal phytoliths intrinsic to ingesta of certain kinds; this interpretation stimulated new research avenues in paleobiology and especially towards dietary reconstruction and ecological niche assignment in extant and extinct mammals.

The limits of microwear were discussed from the early days of microwear research and, more than once, the optimistic but simplistic notion that microwear traces reflected the immediate past diet or type of ingesta was challenged. Peters’ (1982) in vitro experiments rejected the idea that some primate foods such as dicotyledonous seeds do not produce microwear by themselves. Recently, this criticism has been renewed by van Casteren et al. (2020) based on their results of in vitro nanoscale experiments and mechanical models. However, we should not forget that inference based on in vitro experiments is limited to a specific species, the type of abrasive particles used in the experiments (hardness, shape, size), and the force setting and scale; the latter being difficult to control, and generalization should be cautious.

One of the earliest attempts to demonstrate the limitations of microwear were the three-month lab-based feeding experiments with American opossum, Didelphis marsupialis, by Covert and Kay (1981). Their experiments indicated that similar microwear patterns resulted from the three investigated diets (cat food alone and cat food mixed with soybean hulls or insect chitin). However, Gordon and Walker (1983) questioned these results, arguing that they reflected methodological limitations rather than fundamental limits of what microwear can tell us. In turn, Kay and Covert (1983) rebutted the arguments that grit and plant opalines should originate from opal phytoliths intrinsic to ingesta of certain kinds; this interpretation stimulated new research avenues in paleobiology and especially towards dietary reconstruction and ecological niche assignment in extant and extinct mammals.

We use the umbrella term dental microwear texture analysis (DMTA) for all types of 3D dental microwear analysis. Where necessary, we introduce further terms and acronyms to refer to specific methods, e.g., scale-sensitive fractal analysis (SSFA) for the approach according to Ungar et al. (2003) and 3D surface texture analysis (3DST) for the approach according to Schulz et al. (2010). From the beginning, we have chosen a terminology that follows the descriptions in the ISO standards. We decided for the term 3D surface texture analysis (3DST) to emphasize that this method does not just serve to classify particular features such as scratches or pits (like in microwear sensu lato), but to quantify the whole surface, made possible by full automation. During the last decade 3DST was applied to natural (i.e. teeth and bone, see below) as well as additive manufactured materials (for a review see Townsend et al.)
2016). Hence, we simplified the term from 3D areal surface texture standards (Schulz et al. 2010) to 3D dental area surface texture analysis (DASTA, Calandra et al. 2012) and finally to 3D surface texture (3DST, Winkler et al. 2016).

One has to keep in mind that SSFA describes the change of surface features across scales, while 3DST is applied to one specific scale that is set. This results in relative advantages of the 3DST method compared to the SSFA method, i.e. as discussed for application in primates by Calandra et al. (2012). In general, in 3DST the advantages are (1) the huge variety of at least 46 standardized parameters from two international standards (ISO 25178, ISO 12781) and three additional industrial driven analyses (i.e. motif, furrow and texture direction); some even call it the parameter rush (Stout 2000); (2) the parameters quantify in exceptional details the geometry and topography of the whole surface texture; (3) the parameters were developed and linked with a functional interpretation without a certain taxonomic or dietary affiliation of the sampled individual in mind. The disadvantage of 3DST is that choosing and interpreting a parameter requires expert knowledge in tribology on pre-processing and wavelength filtering, which is challenging to achieve, while for SSFA the pre-processing is minor and SSFA parameters are directly related to food properties.

In the past each DMTA had its own software platform: for SSFA the affordable SFrax and Toothfrax software (by Surfract, Worcester, USA) were used, while for 3DST the more expensive platform of MountainsMap (by digitalsurf, Besançon, France) was adapted by the instrument suppliers (e.g. usoft analysis in case of Nanofocus, LeicaMap in case of Leica, SensoMap in case of Sensorfax). All software solutions were very time-consuming in the past and only a few studies used both approaches (Schulz et al. 2010, Calandra et al. 2012, Winkler et al. 2013a). For researchers just embarking on this kind of work, it is important to know that a slightly modified SSFA was incorporated as an additional module to MountainsMap (version 7.4.8676) only recently in 2018, although not all SSFA parameters are available yet (77sf is absent). Nevertheless, it is a huge technical improvement and for the first time one can conduct both SSFA and 3DST in a much more sophisticated way.

Another main advantage of using 3DST (Schulz et al., 2010) is the possibility to measure texture direction. To do so, we developed a measuring protocol that takes the facet orientation into account. We did so to follow the approach of Walker (1976). This allowed us to produce quantitative data in order to finally test for correlation between chewing direction and texture direction. We tested for measuring position (facet, tooth and jaw position) and cross-validated our approach with the SSFA approach of Ungar et al. (2003). In a next step, we transferred the approach to primates including the adaptation and application of new statistical tools for small samples (Calandra et al. 2012), tested for the influence of filtering routines to improve the data processing and selection of the scale to be analyzed (Schulz et al. 2013a), and applied the approach to data from a controlled feeding experiment (Schulz et al. 2013c).

We showed that this approach can provide insights into function, tribology and wear processes, i.e. aspects that are difficult to assess with SSFA. We also found the 3DST approach promising for dietary reconstruction in extant and extinct ungulates (Winkler et al. 2013a, b, Gailer et al. 2016) and rodents (Calandra et al. 2016, Winkler et al. 2016).

---

**Fig. 3.1.** Overview of the most recent tooth wear approaches. Images are sorted according to the following three categories scale (μm to cm), main character dimension (2D, 3D) and applied data (quantitative, qualitative).
During the same period, several colleagues explored the new technological avenues of 3D high-resolution surface measurement (Fig. 3.1), e.g., using the focus variation method (Purnell et al. 2012) or a laser-scanning confocal microscope (Kubo et al. 2017) for data acquisition. This resulted in methodological diversification and an issue of multiple levels of data quality and comparability. The challenge for the future might possibly be related to the analysis of large datasets (i.e., “big data”, for example via data mining and artificial intelligence). We need to find solutions for shared databases (e.g., open data initiative) and to combine datasets generated by various instruments (e.g., Arman et al., 2016).

During many years, we were involved in studies combining microwear (µm scale) and mesowear (mm/cm scale) signatures providing both short- and long-term dietary signals (Merceron et al. 2007, Schulz et al. 2007, Rivals et al. 2009a,b). We were fascinated by the easy applicability and the simple nature of mesowear method (no measurements) but we were also aware of the limitations of this approach (i.e., focus on the ectoloph, need for calibration when comparing higher taxa of herbivores, uncontrolled distortion imposed by the ruler approach). We tried to improve the mesowear method within the DFG research unit 771 by testing for relationships to habitat factors (Schulz & Kaiser 2013), by expanding and modifying the scoring system (Winkler & Kaiser 2011, Taylor et al. 2013, 2014) and by applying the method to field studies (Schulz et al. 2013b, Wronski & Schulz-Kornas 2015). We even adjusted it for the application to lagomorphs and rodents (Ulbricht et al. 2015). However, chewing is a three-dimensional process, and therefore, in addition to the 3D surface texture approach we put some effort into developing two 3D occlusal topometry approaches to investigate the extent to which adaptational value of dental morphology reflects tooth function (e.g., occlusal topography according to Winkler et al. 2013b, Gailer & Kaiser 2014; SAGA-GIS according to Nieberg et al. 2009, Bethune et al. 2019). This was a very active field of research at that time and many other researchers were engaged in the development of novel 3D approaches to quantify the occlusal surface (Evans et al. 2007, Kullmer et al. 2009, Heywood 2010, Bunn et al. 2011, Hernesniemi et al. 2011, Saarinen et al. 2015). For an overview see Figure 3.1 with selected approaches sorted by scale (µm to cm), dimension (2D, 3D) and structure of data (quantitative, qualitative).

Causes of tooth wear – major debates and the need for a deeper understanding of the etiology of wear

As mentioned above, from the early days of microwear research, an active debate about the causes of tooth wear shook the community: Was it phytoliths, or grit, sand and dust? This debate was re-ignited at least three times during the last 50 years based on various pieces and lines of evidence. At first the focus was on the results of feeding experiments (Covert & Kay 1981, Kay & Covert 1983, Teaford & Walker 1983, Teaford & Oyen 1989a,b, Teaford & Oyen 1989c). The emphasis then shifted to the physical properties of abrasives with particular attention paid to silica phytoliths (Baker et al. 1959, Sanson et al. 2007, Lucas et al. 2013), which seemed to indicate that phytoliths are too soft to scratch enamel, while dental microwear has displayed a positive correlation between the consumption of phytolith-rich graminoids and abundance of scratches (i.e., see Merceron et al. 2007). More recently arguments have emerged based on experimental results from an in-vitro micro-loading and scratching study of phytoliths and metallic spheres on enamel with Xia et al. (2015, 2017, 2018) on the one hand and van Casteren et al. (2018, 2020) on the other.

Recently, we put together a set of hypotheses on the tribology of mammalian herbivore teeth based on the data we had generated during the period of the DFG research unit 771 (Kaiser et al. 2016). From these tribological hypotheses we suggest that there are parallels between artificial recurrent neural networks (e.g., Poznyak et al. 2019) and oral food processing. We started to develop a new theoretical framework and proposed that oral food processing has similarities with a multi-functional network that includes known and unknown variables (factors) which influence each other (Fig. 3.2). In Figure 3.2 variables are represented by dots and influences by lines, and all possible lines without any assessment are given. Based on large controlled experimental datasets it is possible to test and verify all possible connections and influences using mathematical algorithms. These algorithms are based on machine learning methods and can work in forward as well as backward propagation to tune the network with self-correcting methods. Five of these predictive classification methods have yielded promising results for the automatic image recognition of experimental cut- and bite marks (i.e., neural network, support vector machines, k-nearest neighbor, random forest, decision trees; Dominguez-Rodrigo & Baquedano 2018). However, in paleobiology, paleoanthropology, and archeology the large experimental datasets necessary to employ machine learning methods are not available yet. In addition, data exchange between the various DMTA methods based on interferometry, confocal and focus variation is not possible and not advisable (yet) due to technical limits and methodological differences. But it is most probably only a matter of time until large datasets and technical solutions are available.

The structure of artificial networks is referred to as architecture that is by definition organized in layers (i.e., input and output layers). Translated to oral food processing, this means that taxa, vegetation, morphology, abrasives and climate represent input layers (see layer A to D in Fig. 3.2). The resulting tooth wear is considered to be the result of the factors defined for each layer (output layer E in Fig. 3.2). We included all factors we are currently aware of into the
network. Nonetheless the amount of factors is extendable, e.g., in case that new factors will be identified in the future. In many cases of oral food processing, we have only limited knowledge of how strong the variables and their influences are and how to consider their variation; taxa, for example, can adjust their behaviors (e.g., via sensing) and adapt to their environment. The self-correcting adaptive methods of machine learning approaches could be very helpful to run through various sets of influences and factors helping to identify the most promising combinations and seasonal scenarios.

Most dietary reconstructions published so far rely on fossil teeth or bones, which means that reconstructing input layers from measuring the output layer is the actualistic paleontology approach (as proposed by Richter 1928). Hopefully in the future, using the network structure concept of habitat and vegetation can be conducted in a more holistic way by following the evidence of connections between the identified factors within the layers. Feeding observations, in vitro and in vivo experiments have already helped to characterize the factors in more detail and to test the connection between these factors and the interplay between the layers. However, there is currently no consensus in the dental wear community on the importance of specific layers and interaction between the factors, especially when it comes to the contribution of ingested abrasives from different sources. It is well known that factors act on different temporal scales; e.g., microwear, and mesowear do not record the same timeframe in the life history of an individual. In addition, it could be concluded that our knowledge on abrasives, no matter if internal (phytoliths) or external (dust, grit, soil or ashes), as well as the chewing kinematics and the sensing of abrasives is still very limited. This lack of knowledge has led to conflicting results in studies employing different proxies for dietary reconstruction (e.g., tooth wear vs. stable isotopes). This is mostly because determining the local in vivo mechanical properties of biogenic materials, such as opaline phytoliths on the ingesta side of the antagonistic system, and dental hard tissues (enamel and dentin) plus protein pellicle on the tooth side, is a challenging task with many unknowns.

To complicate matters further, material properties of materials that are wet in their native state (phytoliths and teeth) change during chemical or heat-mediated extraction processes necessary for material testing (Cabanes & Shahack-Gross, 2015). To overcome these problems, we established a new extraction protocol for opal phytoliths (Braune et al. 2012) and conducted nano-indentation hardness tests with phytoliths and tooth material under wet and dry conditions (Schulz-Kornas et al. 2017, Kaiser et al., 2018). Our data suggest that phytoliths, as well as enamel and dentin, are less hard when measured dry. Native phytoliths can easily indent native dentin and certainly contribute to the scouring of dentin. In nature the effects of internal abrasives almost always act together with the effect of external abrasives. Like Xia et al. (2018), we raised the question if phytoliths from living cells could act as inefficient wear agents (Schulz-Kornas et al. 2017, Kaiser et al., 2018), while grit had higher potential as an agent of tooth wear. We further proposed the idea that phytoliths impose a higher selective pressure on dentin as abrasives. In turn, this would affect the enamel ridges of herbivorous mammals because the dentin basins otherwise become too deep to maintain the structural integrity of the occlusal surface (Kaiser et al. 2018). Hypotheses relating the evolution of hypsodonty to increased roughage feeding, as frequently assumed (Strömberg 2006, Damuth & Janis 2011), are challenged by our findings. Also, we support the claim that phytoliths from living (wet) biomass may in fact play a subordinate role in tooth enamel wear.

Animals at the end of droughts or prolonged dry seasons are forced to eat dry food. Dry phytoliths being harder, dry food leads to different tooth wear effects and signals (Winkler et al. 2019b). This hypothesis needs to be tested for dead (dry) biomass in field experiments. In addition, the impact of grit and dust (including its morphology and abundance) is still enigmatic (Winkler et al. 2020). Hence, the debate remains open.
The DFG research unit 771 provided a great opportunity to exchange ideas with many researchers from various fields. But it also set the foundation for new developments and achievements made during the years after until today. Some of these will be highlighted in the following paragraphs.

As already pointed out, in vitro material testing as well as feeding experiments opened up new avenues for testing tooth wear-related hypotheses. New experimental designs, however, may involve methodological pitfalls and thus are debated. In vivo studies provide much-needed reference data, e.g., regarding the time involved in overwriting textures and variations in texture patterns (Ramdarshan et al. 2016, Schulz et al. 2013c). In vivo studies indicated that variable water content from consumed plant matter is a source of texture variation (Winkler et al. 2019a). But still, especially in the in vivo experiments, we found evidence for a dietary signal in tooth wear. That led us to expand DMTA to groups that have never been investigated with DMTA, i.e., fossil tritylodontids (Kalthoff et al. 2019) and extant lepidosaurs (Winkler et al. 2019b).

After recent experimental studies successfully measured tooth volume loss (Müller et al. 2014, 2015), as well as mesowear variation (Ackermans et al. 2018), it appears highly promising to combine both, realizing that wear processes act on different scales, which can lead to discrepancies observed in microwear and DMTA. These combined studies have facilitated our understanding and highlight that formation of microwear (texture) does not necessarily lead to substantial tooth volume loss (Martin et al. 2020, Schulz-Kornas et al. 2020). Additionally, field studies combining surface texture, feeding observations and chewing efficiency in chimpanzees pointed out that periodical dust loads (external abrasives) are detectable in the surface texture and lead to less efficient comminution (Schulz-Kornas et al. 2019, Stuhlträger et al. 2019). Further, Schulz-Kornas et al. (2019) showed that seeds in a frugivorous diet like that of chimpanzees could be very variable in size and less important for the chewing efficiency. They also showed that not every seed can be considered a hard particle, particularly if other tools are used to crack them as some animals have the option to process their foods with tools other than their teeth.

The hope is that our research will open up new research avenues to finally obtain a better understanding of the biomechanics and scaling of the complex and multi-factor interactions taking place during comminution. However, it remains a challenge for future research to characterize the repetitive kinematics of the chewing process, and at the same time the ingesta particles comminuted as well as the resulting complex changes of the occlusal surface. We are just at the beginning of understanding that tooth wear is a multi-scale and multi-factorial process that results in a cumulative wear signature (see Fig. 3.3). The methods we developed for dental microwear texture analysis have also impacted other disciplines. Archeologists have been interested in wear patterns on the surface of archeological artifacts made from e.g. bones or stones (lithics). Traceology has a long history within archeology (see above “From traces to textures”), and while there were early attempts at automatic quantification (Dumont 1982, Beyries et al. 1988), has still not fully recognized the potential of surface texture analysis (3DST) and scale-sensitive fractal analysis (SSFA). Traceology could therefore learn a lot from dental microwear texture analysis (DMTA) (Calandra et al. 2019a), and we have already contributed to this exchange and collaboration between these fields (Pedergnana et al. 2019).

Fig. 3.3. Simplified model of occluding primate molars. The model illustrates that ingesta comminution and the resulting tooth wear are a multi-scale and multi-factorial process resulting in a cumulative wear signature.

New developments, future perspectives and broader implications

The DFG research unit 771 provided a great opportunity to exchange ideas with many researchers from various fields. But it also set the foundation for new developments and achievements made during the years after until today. Some of these will be highlighted in the following paragraphs.

As already pointed out, in vitro material testing as well as feeding experiments opened up new avenues for testing tooth wear-related hypotheses. New experimental designs, however, may involve methodological pitfalls and thus are debated. In vivo studies provide much-needed reference data, e.g., regarding the time involved in overwriting textures and variations in texture patterns (Ramdarshan et al. 2016, Schulz et al. 2013c). In vivo studies indicated that variable water content from consumed plant matter is a source of texture variation (Winkler et al. 2019a). But still, especially in the in vivo experiments, we found evidence for a dietary signal in tooth wear. That led us to expand DMTA to groups that have never been investigated with DMTA, i.e., fossil tritylodontids (Kalthoff et al. 2019) and extant lepidosaurs (Winkler et al. 2019b).

After recent experimental studies successfully measured tooth volume loss (Müller et al. 2014, 2015), as well as mesowear variation (Ackermans et al. 2018), it appears highly promising to combine both, realizing that wear processes act on different scales, which can lead to discrepancies observed in microwear and DMTA. These combined studies have facilitated our understanding and highlight that formation of microwear (texture) does not necessarily lead to substantial tooth volume loss (Martin et al. 2020, Schulz-Kornas et al. 2020). Additionally, field studies combining surface texture, feeding observations and chewing efficiency in chimpanzees pointed out that periodical dust loads (external abrasives) are detectable in the surface texture and lead to less efficient comminution (Schulz-Kornas et al. 2019, Stuhlträger et al. 2019). Further, Schulz-Kornas et al. (2019) showed that seeds in a frugivorous diet like that of chimpanzees could be very variable in size and less important for the chewing efficiency. They also showed that not every seed can be considered a hard particle, particularly if other tools are used to crack them as some animals have the option to process their foods with tools other than their teeth.

The hope is that our research will open up new research avenues to finally obtain a better understanding of the biomechanics and scaling of the complex and multi-factor interactions taking place during comminution. However, it remains a challenge for future research to characterize the repetitive kinematics of the chewing process, and at the same time the ingesta particles comminuted as well as the resulting complex changes of the occlusal surface. We are just at the beginning of understanding that tooth wear is a multi-scale and multi-factorial process that results in a cumulative wear signature (see Fig. 3.3). The methods we developed for dental microwear texture analysis have also impacted other disciplines. Archeologists have been interested in wear patterns on the surface of archeological artifacts made from e.g. bones or stones (lithics). Traceology has a long history within archeology (see above “From traces to textures”), and while there were early attempts at automatic quantification (Dumont 1982, Beyries et al. 1988), has still not fully recognized the potential of surface texture analysis (3DST) and scale-sensitive fractal analysis (SSFA). Traceology could therefore learn a lot from dental microwear texture analysis (DMTA) (Calandra et al. 2019a), and we have already contributed to this exchange and collaboration between these fields (Pedergnana et al. 2019).
2020). Another promising way of experimental testing is the combination of mathematical modelling with actualistic experiments as conducted in archeology by Martisius et al. (2018, 2020). Here, we transferred 3DST on bone surfaces and employed multilevel multi-variante Bayesian models to explain surface texture variation under experimental conditions and showed that duration of use strongly affected the transformation (overwriting) of the surface texture. In general, 3DST is applicable to bone surfaces as well (Turcotte et al. 2019) to quantify the morphology of extrinsic fiber insertions sites of the biceps brachii of mice in relation to activity level.

The wider application of 3DST in various research fields shows us that there is a need for standardization, repeatability and reproducibility to guarantee high data quality and foster future exchange of data. This is apparent in traceological understanding of the complex wear process is only beginning to grow. The combined effort of studies based on museum material, in vivo, and in vitro experiments has shed light on the importance of abrasives in the wear process, but also raised new questions. With interdisciplinary collaborations involving animal nutritionists, veterinarians, dentists, and computer scientists, many more publications on dental wear and dietary adaptations are to be written.

Conclusion

Our projects within the DFG research unit 771 originally had a strong methodological focus. Since 2008, we developed a new method of dental microwear texture analysis and applied it to a variety of vertebrate groups. Nevertheless, this method was just a tool to answer an array of scientific questions, ranging from wear mechanics and etiology at the microscopic and short-time scales to dental evolution at the macroscopic and evolutionary scales. The field of dental wear analyses is evolving on all scales and our understanding is still in DMTA. Indeed, we showed that changing the numerical aperture of the objective used, one of the most basic properties of an objective, significantly modified the way surfaces are acquired with a laser-scanning confocal microscope (Calandra et al. 2019b). This study is therefore advocating for more transparency on the reporting of methods and results. We also developed a cheap and quick method to relocate the same area of a sample again and again (Calandra et al. 2019c) which is necessary when comparing the same spot before and after an experiment as well as for reproducibility. Although difficult to apply to live animals, this relocation method could prove very useful to acquire the same area with different instruments (in order to better compare the data), or in experiments with artificial chewing machines (Gügel et al. 2001, Hua et al. 2015, Karme et al. 2016).

Acknowledgments

We highly acknowledge the vivid discussions we had with all colleagues of the DFG research unit 771, especially during the yearly meetings in Visselhövede and Mayschoß. In particular, we thank Wighart von Koenigswald (University of Bonn) for initiating the DFG meetings in Visselhövede and Mayschoß. In particular, we thank Marcus Clauss (University of Zurich) who set the highest standards in conducting feeding experiments and encouraged us to question and test many of the ‘given facts’ in the field and especially our own convictions.

Further, we would like to thank our laboratory team for their continuous support (in alphabetical order): Janina Bethge, Elehna Bethune, Caroline Braune, Alexander Daasch, Fenia De Bruin, Sven Fraas, Juan Pablo Gailer, Volker Halley, Lisa Krause, Susanne Krohn, Christina Landwehr, Julia Lingner, Nelson Maccarenhas, Mona Pinnow, Vanessa Piotrowski, Susanne Schwitzer, Mirella Skiba, Lucy A. Taylor, Nicole Töpfer, Jessica Westphalen, and Anna Zickert. We highly appreciate the constructive comments and helpful suggestions made by the two reviewers Florent Rivals and Gordon Sanson.

References

* indicates publications that originated from the DFG Research Unit 771.


