Kurtén developed a broad perspective to paleontological research on a global scale. This approach became a trademark of the paleontological research in Helsinki, and it was further developed by Kurtén's successor Professor Mikael Fortelius. As a result, the University of Helsinki now hosts a leading paleontological research community with wide-reaching global connections. Kurtén was careful to keep speculations out of his research hypotheses. Nonetheless, in his novels he presented ideas about ancient human behavior, especially interbreeding of modern humans and Neanderthals, which were later confirmed by ancient DNA studies. This autumn, 2024, Kurtén's legacy will be honored with several events, especially a memorial symposium 19th November 2024, at Tieteiden talo, Helsinki. A memorial volume will be published in the journal Annales Zoologici Fennici.

Lähdeluettelo

Hård, G., 1984. Björn Kurtén – ett författarporträtt. Horisont 31 (5), 36–39.

Kurtén, B., 1952. The Chinese *Hipparion* fauna. Commentationes Biologicae, Societas Scientiarum Fennicae 13, 82 s.

Kurtén, B., 1953. On the variation and population dynamics of recent and fossil mammal populations. Acta Zoologica Fennica 76, 1–122.

Kurtén, B., 1968. Pleistocene mammals of Europe. Aldine Publishing Co., Chicago, 326 s.

Kurtén, B., 1971. The age of mammals. Weidenfeld & Nicolson, London, 250 s.

Kurtén, B., 1972. Jääkausi. WSOY, Porvoo, 178 s.

Kurtén, B., 1975. Björnen från Drakhålan. Aldus, Stockholm, 145 s.

Kurtén, B., 1982a. Musta tiikeri. Tammi, Helsinki, 217 s.

Kurtén, B., 1982b. Kuinka mammutti pakastetaan. Tammi, Helsinki, 192 s.

Kurtén, B., 1984. Mammutin suojelija. Tammi, Helsinki, 206 s.

Kurtén, B., 1988. Viattomat tappajat. Tammi, Helsinki, 146 s.

Kurtén, B. & Anderson, E., 1980. Pleistocene mammals of North America. Columbia University Press, New York, 442 s.

NOW Community, 2024. New and Old Worlds Database of Fossil Mammals (NOW). https://nowdatabase.org/now/database/ [18.9.2024]

Schlosser, M., 1903. Die fossilen Säugetiere Chinas nebst einer Odontographie der recenten Antilopen. Abhandlungen der Bayerischen Akademie der Wissenschaften 22, 1–22.

Making a mountain out of a molar

MEBIN GEORGE VARGHESE, SUSANNA SOVA AND OTTO STENBERG

Geologists are familiar with aspect maps or orientation maps used in topographic analysis of terrains. However, in recent decades, orientation maps have also been applied in the study of mammalian tooth morphology. Mammalian tooth crowns exhibit a wide range of complexity, from simple single-cusped forms to intricate structures with multiple cusps, crests, and wrinkles (cover image). Due to their high mineral content, teeth are durable and abundant in the fossil record, making them crucial for studying evolutionary changes over time. Mammalian teeth, especially those of herbivores, provide valuable information not only about the animal and its size but also serve as proxies for reconstructing past environments. Teeth are also widely used in developmental biology and genetics, as they form completely before use, allowing for more accurate studies of the genetic basis of organogenesis than in many other organs.

The advances in imaging, especially micro-CT imaging, have enabled acquisition of three-dimensional (3D) data on teeth. Before the advent of more advanced methods, dental morphology was primarily assessed using linear measurements. These measurements involved quantifying aspects such as tooth crown width and height or distance between cusps, which provided basic but limited insights into the overall structure and function of the teeth. Even when 3D data became available, comparative methods often relied on landmarks, where the dimensions and distances of the same specific features were measured and compared.

In the late 1990s, three young researchers at Stony Brook University – Denné Reed, Peter Ungar and Jukka Jernvall – got excited about using the Geographic Information Systems (GIS) software, typically used for analysing landscape topography, for dental research. They found that by treating cusps as mountains and basins as valleys, GIS could be used to measure the topography of teeth (Fig. 1a) (Reed 1997; Hunter & Jernvall 1998; Zuccotti et al. 1998; Jernvall & Selänne 1999; Ungar & Williamson 2000). This innovative approach eliminated the need for landmarks, even allowing for the analysis of worn tooth surfaces as well as developing teeth (Ungar & M'Kirera 2003; Christensen et al. 2023). This new technique became known as topographic analyses of teeth.

At the time, several competing GIS software were available, and Jukka Jernvall chose to continue using MFworks, developed by Robert Tomlinson, due to its detailed documentation of all the procedures. After establishing his own laboratory at the University of Helsinki, Jernvall worked with two post-doctoral researchers – Alistair Evans from the University of Melbourne and Greg Wilson from Berkeley – who focused on the quantification of the dental complexity.

Orientation Patch Count (OPC) first published by Evans et al. (2007), advanced dental topographic analysis through a GIS-based approach using raster-based digital elevation models (DEMs) of teeth (Fig. 1c). OPC refers to the number of distinct regions on a surface where neighbouring pixels share the same directional orientation. OPC is achieved by mapping the orientation of each pixel of a tooth surface, dividing it into eight principal directions, and counting the number of patches of contiguous pixels with the same orientation.

As a measure of the number of orientation patches on a tooth, OPC reflects the number of 'tools' on the tooth for processing food. With OPC analysis, the Evans et al. (2007) discovered that in two distinct mammalian orders, carnivorans and rodents, OPC values correlate with diet and exhibit similar ranges across both orders. Carnivores, with sharp, blade-like teeth suited for shearing skin and flesh, tend to have low OPC values, while herbivores, with broader molars and more complex surfaces for grinding plant material, have high OPC values. Hence, OPC is independent of both size and phylogeny, meaning taxa with similar OPC values are likely to consume diets with comparable mechanical properties.

Wilson et al. (2012) implemented OPC to infer the diets of a group of extinct mammals, Multituberculata. Multituberculata (Allotheria, Mammalia) was one of the most successful orders of mammals, persisting from the Middle Jurassic, surviving the Cretaceous–Palaeogene mass extinction, and eventually going extinct in the late Eocene. Palaeontologists have long agreed that the success of multituberculate mammals was partly due to their highly derived dentition. However, there had

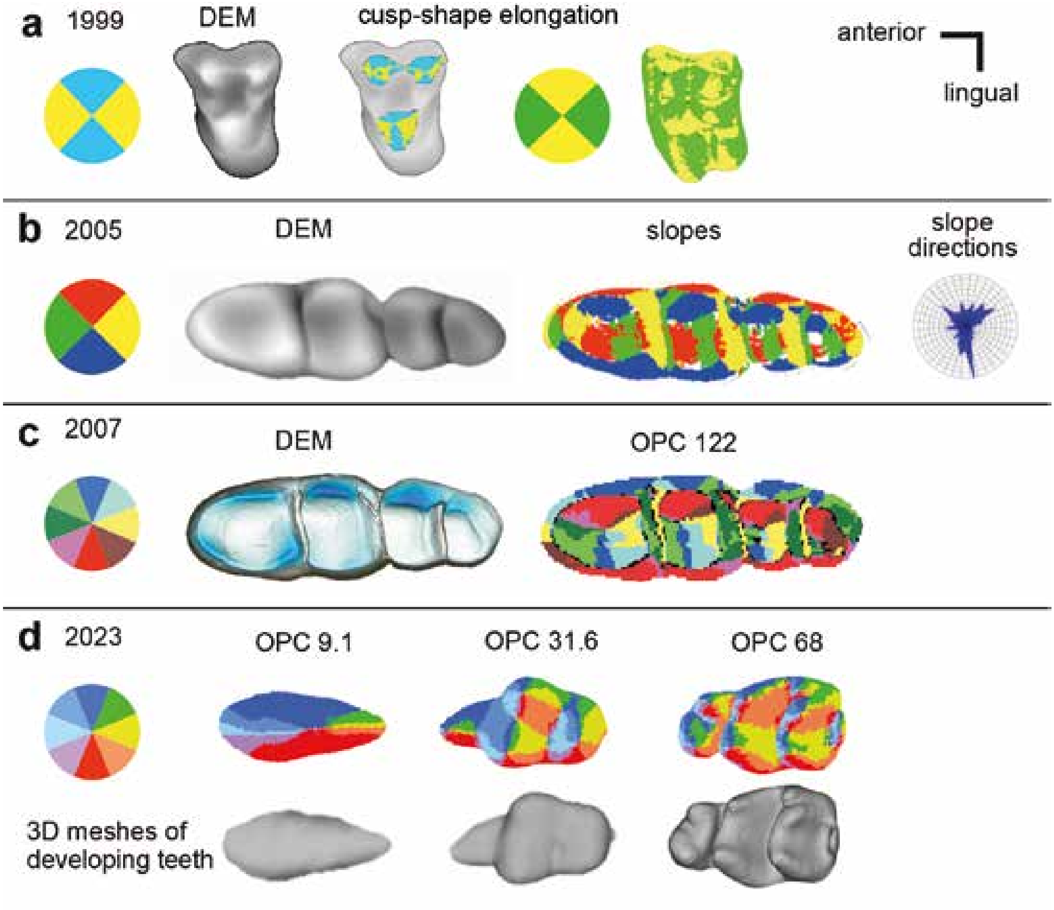

Figure 1. Key developments in OPC methodology for analyzing mammalian teeth: In 1999, two colors were used either to the cusps or the whole crown to measure cusp-shape elongation (a). A more systematic approach to quantify tooth complexity began in 2005, using four cardinal directions. The ratio of the orientation patches was visualized with a rose diagram (b). In 2007, the OPC method was published, categorizing cusp slopes into eight cardinal directions, which is the predominant classification used internationally (c). Currently, OPC is carried out on polygon meshes and the mean value of repeated measurements for eight rotations is used to reduce the effect of any variations arising from the orientation of teeth (d). Teeth are not to scale.

Kuva 1. Askelia OPC:n kehitysvaiheista hammastutkimuksessa. Vuonna 1999 hampaan pinnanmuotojen rasteripohjaisiin GIS-analyyseihin käytettiin kahta väriä kuvaamaan nystermien pitkittäisyyttä ja poikittaisuutta (a). Vuonna 2005 aloitettiin systemaattisempi hampaan pinnanmuotojen analysointi, jolloin käytettiin neljää eri kaadesuuntaa kuvaavaa väriä ja laikkujen määräsuhteita havainnollistettiin ruusudiagrammin avulla (b). Vuonna 2007 julkaistussa OPC-menetelmässä eroteltiin kahdeksan suuntalaikkua, ja niiden määriä vertailtiin lihansyöjien ja kasvinsyöjien välillä (c). Nykyään OPC perustuu polygonisiin malleihin, joissa näytteitä käännetään kahdeksaan eri kulmaan, ja lopullinen OPC-arvo on näiden tulosten keskiarvo (d). Hampaat eivät ole mittakaavassa.

been no consensus on their diets because their teeth and chewing mechanisms were distinct from those of all extant mammals. The OPC analysis showed that the dental complexity of multituberculates began to increase before the end of the Cretaceous, suggesting a shift towards more omnivorous and herbivorous diets–possibly in response to the diversification of angiosperms (Wilson et al. 2012). Similarly, OPC has been used to predict diet within several other mammalian orders (e.g. Santana et al. 2011; Godfrey et al. 2012; Ledogar et al. 2013; Rannikko et al. 2020)

Initially, 2.5D surface scans of tooth rows were obtained using a laser scanner and converted into DEMs using commercial GIS software. These DEMs were standardized to a fixed number of rows. An orientation raster, created from each dental DEM using a custom GIS routine (SurferManipulator), served as a map of surface orientation across the tooth, from which OPC was calculated. This GIS-based approach has since been widely adopted for dental morphology studies (e.g., Chester et al. 2010; Bunn et al. 2011; Godfrey et al. 2012). Whereas OPC was originally based on rasterized teeth with a globally decided pixel size, most 3D data today is represented as triangulated meshes. In the last decade, fully 3D approaches have joined GIS-based OPC. Early methods for measuring OPC on polygonal mesh surfaces used custom software (Salazar-Ciudad & Marin-Riera 2013), while more comprehensive tools for 3D dental topographic analysis have since been developed (Pampush et al. 2016; Winchester 2016). These advances, along with improved surface scanning technology, have streamlined the process from scanning to shape analysis. MorphoTester, an open-source Python application, calculates dental topographic metrics like OPC from 3D meshes and provides OPC maps for visualization. As the first tool to apply OPC to polygonal surfaces, it was compared to the original GIS pipeline and found to be equally effective for analysing dental complexity (Winchester 2016). Pampush et al. (2016) also developed a tool, molaR, for 3D dental topographic analyses in R, which, like MorphoTester, calculates different dental topographic metrics. Rishi Das Roy implemented a GUI extension shinyMolar for MolaR (Das Roy 2023, Christensen et al. 2023, Stenberg et al. 2024). ShinyMolar uses colour-blind friendly colours and enables the visualisation of the morphology without shading.

OPC continues to be widely used to infer the diets of mainly mammalian taxa, but also reptiles, and even orthopterans, with higher OPC values generally indicating tooth surfaces adapted for processing tougher or more fibrous foods (Melstrom & Wistort 2021, Stockey et al. 2022; Shipps et al. 2023). For example, Chester et al. (2010) used OPC to suggest that certain creodonts were omnivorous. Evans & Janis (2014) found that the successive increase in the dental complexity of the horse lineage since Eocene is due to the addition of finer-scale morphological features rather than the development of new cusps. Additionally, OPC has served as a metric for assessing phenotypic changes over evolutionary time (Wilson et al. 2012; Evans & Janis 2014), as well as over developmental timescales (Fig. 1d) (Harjunmaa et al. 2012, 2014; Salazar-Ciudad & Marin-Riera 2013; Christensen et al. 2023). Besides OPC, other topographic measures are increasingly being used to explore morphological data (Berthaume et al. 2020). With the advent of high-resolution 3D scanning becoming possible with cell phones, the adoption of topographic analyses can only accelerate further.

Acknowledgements

We thank Jukka Jernvall and Rishi Das Roy from the University of Helsinki for further information and comments.

MSC MEBIN GEORGE VARGHESE
(mebin.georgevarghese@helsinki.fi)
Institute of Biotechnology,
University of Helsinki

MSC SUSANNA SOVA
(susanna.sova@helsinki.fi)
Institute of Biotechnology, University of Helsinki
Department of Geosciences and Geography,
University of Helsinki

MSC OTTO STENBERG
(otto.stenberg@helsinki.fi)
Institute of Biotechnology,
University of Helsinki

Mebin George Varghese, Otto Stenberg and Susanna Sova are doctoral researchers at the University of Helsinki.

Tiivistelmä

Purennan kukkulat

Paikkatietojärjestelmät (GIS) ovat useimmille tuttuja maastonmuotojen analysoinnista, mutta ne soveltuvat mainiosti myös hampaiden tutkimiseen. Nisäkkäiden hampaat voivat olla yksi- tai moninystermäisiä, nystermät joko teräviä tai tylppiä ja purupinta voi olla joko sileä tai uurteinen. Aiemmin hammasmuotojen tutkimus perustui ns. maamerkkien (*landmarks*) etäisyyksien mittaamiseen, mikä vaikeutti esim. kuluneiden hampaiden ja varsinkin kehittyvien hampaiden tutkimusta, joissa muodot ovat vasta syntymässä.

Kuvantamisteknologian kehittyminen viime vuosikymmenten aikana on mahdollistanut työntömitan ja mikroskooppimittausten korvaamisen tietokoneavusteisilla analyyseillä. Helsingin yliopiston tutkijat ovat olleet eturintamassa kehittämässä näitä työkaluja, joista GIS-pohjainen OPC (*orientation patch count*, suuntalaikkujen määrä) on yksi maailmanlaajuisesti käytetyimmistä menetelmistä.

OPC:ssä hampaan muoto jaetaan kahdeksaan eriväriseen suuntalohkoon, jotka määräytyvät pinnan kaltevuuden mukaan. Näin ollen yksi kartiomainen nystermä jakautuu kahdeksaan yhtenäiseen suuntalohkoon, saaden OPC-arvon 8. Nystermien määrä ja pinnan epätasaisuus nostavat OPC-arvoa. OPC-analyysien avulla on pystytty osoittamaan, että riippumatta taksonomisesta taustasta, kasvinsyöjien hampaat ovat monimutkaisempia kuin lihansyöjien hampaat. OPC:tä on sittemmin sovellettu monien sekä sukupuuttoon kuolleiden että elävien nisäkäslajien hampaiden vertailuun. Sitä on myös käytetty matelijoiden hampaiden ja sirkkojen leukojen monimutkaisuuden tarkasteluun ruokavalion mittarina.

Alkuperäinen OPC perustui rasterikarttoihin, mutta nykyinen OPC on toteutettu vektorimuodossa. Vektorimuotoinen polygoniverkko voi perustua tomografiakuviin tai pintaskanneihin, joista jälkimmäisiä pystyy luomaan myös monilla nykypuhelimilla.

Bibliography

Berthaume, M. A., Lazzari, V. & Guy, F., 2020. The landscape of tooth shape: Over 20 years of dental topography in primates. Evolutionary Anthropology: Issues, News, and Reviews 29, 245–262. https://doi.org/10.1002/evan.21856

Bunn, J. M., Boyer, D. M., Lipman, Y., St. Clair, E. M., Jernvall, J. & Daubechies, I., 2011. Comparing Dirichlet normal surface energy of tooth crowns, a new technique of molar shape quantification for dietary inference, with previous methods in isolation and in combination. American Journal of Physical Anthropology 145, 247–261. https://doi.org/10.1002/ajpa.21489

Chester, S. G., Bloch, J. I., Secord, R. & Boyer, D. M., 2010. A new small-bodied species of Palaeonictis (Creodonta, Oxyaenidae) from the Paleocene-Eocene Thermal Maximum. Journal of Mammalian Evolution 17, 227–243. http://doi.org/10.1007/s10914-010-9141-y

Christensen, M. M., Hallikas, O., Das Roy, R., Väänänen, V., Stenberg, O. E., et al., 2023. The developmental basis for scaling of mammalian tooth size. Proceedings of the National Academy of Sciences 120, e2300374120. https://doi.org/10.1073/pnas.2300374120

Das Roy, R., 2023. ShinyMolar. https://github.com/dasroy/shinyMolar [12.09.2024]
Evans, A. R. & Janis, C. M., 2014. The evolution of high dental complexity in the horse lineage. Annales Zoologici Fennici 51, 73–79. https://doi.org/10.5735/086.051.0209
Evans, A. R., Wilson, G. P., Fortelius, M. & Jernvall, J., 2007. High-level similarity of dentitions in carnivorans and rodents. Nature 445, 78–81. https://doi.org/10.1038/nature05433
Godfrey, L. R., Winchester, J. M., King, S. J., Boyer, D. M. & Jernvall, J., 2012. Dental topography indicates ecological contraction of lemur communities. American Journal of Physical Anthropology 148, 215–227. http://doi.org/10.1002/ajpa.21615
Harjunmaa, E., Kallonen, A., Voutilainen, M., Hämäläinen, K., Mikkola, M. L. & Jernvall, J., 2012. On the difficulty of increasing dental complexity. Nature 483, 324–327. https://doi.org/10.1038/nature10876
Harjunmaa, E., Seidel, K., Häkkinen, T., Renvoisé, E., Corfe, I. J., et al., 2014. Replaying evolutionary transitions from the dental fossil record. Nature 512, 44–48. https://doi.org/10.1038/nature13613
Hunter, J. P. & Jernvall, J., 1998. Decomposing early morphological diversity in ungulates: analysis of early Paleocene arctocyonid teeth. Journal of Vertebrate Paleontology 18, 52A.
Jernvall, J. & Selänne, L., 1999. Laser confocal microscopy and geographic information systems in the study of dental morphology. Palaeontologia Electronica 2, 18. https://doi.org/10.26879/99003
Ledogar, J. A., Winchester, J. M., St. Clair, E. M. & Boyer, D. M., 2013. Diet and dental topography in pitheciine seed predators. American Journal of Physical Anthropology 150, 107–121. https://doi.org/10.1002/ajpa.22181
Melstrom, K. M. & Wistort, Z. P., 2021. The application of dental complexity metrics on extant saurians. Herpetologica 77, 279–288. https://doi.org/10.1655/Herpetologica-D-21-00002.1
Pampush, J. D., Winchester, J. M., Morse, P. E., Vining, A. Q., Boyer, D. M. & Kay, R. F., 2016. Introducing molaR: a new R package for quantitative topographic analysis of teeth (and other topographic surfaces). Journal of Mammalian Evolution 23, 397–412. https://doi.org/10.1007/s10914-016-9326-0
Rannikko, J., Adhikari, H., Karme, A., Žliobaitė, I. & Fortelius, M., 2020. The case of the grass-eating suids in the Plio-Pleistocene Turkana Basin: 3D dental topography in relation to diet in extant and fossil pigs. Journal of Morphology 281, 348–364. https://doi.org/10.1002/jmor.21103
Reed, D. N. O., 1997. Contour mapping as a new method for interpreting diet from tooth morphology. American Journal of Physical Anthropology 31, 517–535.
Salazar-Ciudad, I. & Marín-Riera, M., 2013. Adaptive dynamics under development-based genotype–phenotype maps. Nature 497, 361–364. https://doi.org/10.1038/nature12142
Santana, S. E., Strait, S. & Dumont, E. R., 2011. The better to eat you with: functional correlates of tooth structure in bats. Functional Ecology 25, 839–847. https://doi.org/10.1111/j.1365-2435.2011.01832.x
Shipps, B. K., Peecook, B. R.& Angielczyk, K. D., 2023. The topography of diet: Orientation patch count predicts diet in turtles. The Anatomical Record 306, 1214–1227. https://doi.org/10.1002/ar.25125
Stenberg, O. E., Moustakas-Verho, J. E. & Jernvall, J., 2024. Rewinding the developmental tape shows how bears break a developmental rule. BioRxiv, 2024-02. https://doi.org/10.1101/2024.02.29.582676
Stockey, C., Adams, N. F., Harvey, T. H., Donoghue, P. C. & Purnell, M. A., 2022. Dietary inference from dental topographic analysis of feeding tools in diverse animals. Methods in Ecology and Evolution 13, 1464–1474. https://doi.org/10.1111/2041-210X.13832
Ungar, P. S. & M'Kirera, F., 2003. A solution to the worn tooth conundrum in primate functional anatomy. Proceedings of the National Academy of Sciences 100, 3874–3877. https://doi.org/10.1073/pnas.0637016100
Ungar, P. S. & Williamson, M., 2000. Exploring the effects of tooth wear on functional morphology: a preliminary study using dental topographic analysis. Palaeontologia Electronica 3, 1–18.
Wilson, G. P., Evans, A. R., Corfe, I. J., Smits, P. D., Fortelius, M. & Jernvall, J., 2012. Adaptive radiation of multituberculate mammals before the extinction of dinosaurs. Nature 483, 457–460. https://doi.org/10.1038/nature10880
Winchester, J. M., 2016. MorphoTester: an open source application for morphological topographic analysis. PloS one 11, e0147649. https://doi.org/10.1371/journal.pone.0147649
Zuccotti, L. F., Williamson, M. D., Limp, W. F. & Ungar, P. S., 1998. Modeling primate occlusal topography using geographic information systems technology. American Journal of Physical Anthropology: The Official Publication of the American Association of Physical Anthropologists 107, 137–142. https://doi.org/10.1002/(SICI)1096-8644(199809)107:1%3C137::AID-AJPA11%3E3.0.CO;2-1