

# Morphometry, microstructure and wear pattern of neornithischian dinosaur teeth from the Upper Cretaceous Iharkút locality (Hungary)

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## Abstract

Teeth of iguanodontian ornithopods and ceratopsians could be remarkably similar, thus the referral of isolated dental material to particular neornithischian clades can be highly problematic. These groups are represented by the rhabdodontid *Mochlodon vorosi* and the basal coronosaurian *Ajkaceratops kozmai* in the Upper Cretaceous Csehbánya Formation at Iharkút (western Hungary). Whereas teeth of ~~the former taxon~~ *Mochlodon* are common elements at the locality, no dental material belonging to ~~the latter species~~ *Ajkaceratops* was identified until now. Here we used mathematical statistical approaches, as well as tooth wear and dental microstructure analysis in order to decide whether the teeth previously referred to *Mochlodon* can be treated as a homogenous sample, or some remains belong rather to *Ajkaceratops*.

According to our results, there was a striking morphological and structural convergence between the teeth of ~~the latter~~ both taxa. However, the wear study revealed the existence of two different patterns within the sample. One is characterized by straight and parallel microstriations that suggest orthal movements during the jaw closure. This pattern was associated with *Mochlodon*. The other pattern appeared only on a few teeth, and it can be differentiated by its distinctive curved microstriations that indicate ~~circumpalinal chewing~~ a significant palinal component. ~~Since~~ Because curved striations ~~were~~ have never ~~been~~ described in ornithopods, but ~~were~~ are found in several neoceratopsians, this pattern was associated here with *Ajkaceratops*. Here we present the first teeth that can provisionally be referred to the latter genus. We believe that the methodology discussed in this paper will facilitate distinguishing ceratopsian and ornithopod teeth in other localities as well.

**Key words:** Upper Cretaceous; ceratopsian *Ajkaceratops*; rhabdodontid *Mochlodon*; tooth morphology; dental histology; wear pattern

# 1. Introduction

*Ajkaceratops kozmai* from the Upper Cretaceous (Santonian) Csehbánya Formation of Iharkút (Veszprém County, Bakony Mountains, western Hungary) ~~was~~is the first unambiguous ceratopsian from Europe. Its original description (Ósi et al., 2010a) was based on a specimen containing the fused premaxillae with the rostral bone and fragments of the rostral processes of maxillae, as well as four premaxillary bones, however, no dental material was identified from the locality up to now. A possible explanation is that the teeth of *Ajkaceratops* could be ~~very~~highly similar to that of *Mochlodon vorosi*, a rhabdodontid ornithomimid, of which maxillary and dentary teeth are considered fairly common elements at the locality (Ósi et al., 2012a). As pointed out by Godefroit and Lambert (2007) and Ósi et al. (2010a, see the supplementary material of the aforementioned article), remarkable convergences can be observed in neornithischian (sensu Sereno, 2005) dentitions, especially between ceratopsians and iguanodontian ornithomimids, and the referral of isolated teeth to particular neornithischian clades can be highly problematic in some cases.

In the present study, we used mathematical statistical approaches based on morphometric measurements, as well as tooth wear and dental microstructure analysis in order to decide whether the dental material previously referred to *Mochlodon* can be treated as a homogenous sample, or some remains belong rather to the basal coronosaurian ceratopsian *Ajkaceratops* ~~or to an as yet undescribed ceratopsian from the area~~. We believe that the methodology discussed in this paper will facilitate distinguishing ceratopsian and ornithomimid teeth in other localities as well.

## 2. Material and methods

### 2.1. Specimens and their localities

Most of the dental material studied here (63 teeth with and 94 without a primary ridge ~~previously referred to genus *Mochlodon*~~) was collected from the Upper Cretaceous (Santonian) fluvial Csehbánya Formation during the productive and continuous excavations carried out in the last fifteen years at Iharkút in the Bakony Mountains of western Hungary (see Ósi et al., 2012b; Botfalvai et al., 2015, 2016 for geological settings). The site provided an exceptionally rich and diverse assemblage of continental vertebrates, including fish, amphibians, turtles, mosasaurs, lizards, pterosaurs, crocodylians, non-avian dinosaurs and birds (see e.g. Csiki-Sava et al., 2015; Dyke and Ósi, 2010; Makádi, 2006, 2013a,b; Makádi et al., 2012; Ósi, 2005, 2008a,b; Ósi and Buffetaut, 2011; Ósi and Makádi, 2009; Ósi and Prondvai, 2013; Ósi and Weishampel, 2009; Ósi et al., 2005, 2007, 2010a,b, 2011, 2012a,b; Rabi et al., 2011; Szentesi and Venczel, 2010, 2012; Szentesi et al., 2013; Szabó et al., 2016a,b), as well as plants (Knauer and Siegl-Farkas, 1992; Bodor and Baranyi, 2012; Bodor et al., 2012). ~~The specimens used here were previously referred to the genus *Mochlodon*. The specimens and~~ are now stored in the Invertebrate and Vertebrate Paleontological Collection of the Hungarian Natural History Museum (MTM) in Budapest. ~~Because several teeth were listed under the same inventory number, a unique ID was designated here for each studied specimen. In order to support the replicability of the present study, the individual teeth were separated into labelled microcentrifuge tubes within their original cardboard containers and the unique IDs were registered on the inventory tags as well. These IDs are indicated here after the inventory numbers, separated by an octothorpe. The following specimens were used in the present study: Their inventory numbers are the following:~~ V. 2000.1. (#27), V. 2000.32. (#29), V. 2000.33. (#30), V. 2001.64. (#26), V. 2001.161. (#28), V. 2001.181. (#16), V. 2010.113.1. (#40A-S), V. 2010.114.1. (#41A-Z), PAL 2012.17.1. (#36A-E), PAL 2012.18.1. (#35A-E), PAL 2014.113.1. (#31), PAL 2014.118.1. (#34), PAL 2014.119.1. (#33),

PAL 2014.120.1. (#32), VER 2016.104. (#17), VER 2016.964 (#18-25), VER 2016.1600. (#14), VER 2016.1601. (#15A-B), VER 2016.1604. (#1-9), VER 2016.2547. (#10A-B), VER 2016.2548. (#11A-D), VER 2016.2549. (#12), VER 2016.2550. (#13A-C), VER 2016.2551. (#37A-L), VER 2016.2552. (#38), VER 2016.2553. (#39A-Z, #39AA-AL), VER 2016.2554. (#46), VER 2016.2555. (#47), VER 2016.2556. (#48), VER 2016.2557. (#49), VER 2016.2558. (#50), VER 2016.2559. (#51), VER 2016.2846. (#71), VER 2016.2847. (#72), VER 2016.2848. (#73), VER 2016.2849 (#74). ~~Several teeth were listed under the same inventory number in some cases, therefore a unique ID was designated for each studied specimen. These IDs are indicated here after the inventory numbers, separated by a hashtag.~~

Additional material was used here in order to establish a baseline of rhabdodontid microwear features and dental morphology that can be used for comparison with ceratopsians.~~for comparative purposes~~ Specimens previously referred to the genus *Zalmoxes* were found in the Upper Cretaceous (Maastrichtian) molasse-type Sânpetru and Densuș-Ciula Formations near Sânpetru (7 teeth with and 4 without a primary ridge) and Vălioara (14 teeth with and 18 without a primary ridge) in the Hațeg Basin of western Romania ~~in the early 20<sup>th</sup> century~~ (see Grigorescu, 2010; Csiki and Benton, 2010; Csiki et al., 2010; Csiki-Sava et al. 2015, 2016 for broader geological context). These successions provided a ~~very~~ rich vertebrate assemblage, including fish, amphibians, turtles, lizards, snakes, pterosaurs, crocodylians, non-avian dinosaurs, birds and even mammals (see e.g. Codrea et al., 2002; Csiki and Grigorescu, 2000; Csiki-Sava et al., 2015; Folie and Codrea, 2005; Grigorescu et al., 1985; Weishampel et al., 1991, 2010), as well as some plant remains (Van Itterbeek et al., 2005; Csiki et al., 2008; Lindfors et al., 2010). The specimens studied here ~~(previously referred to genus *Zalmoxes*)~~ are housed in the Paleovertebrate Collection of the Geological and Geophysical Institute of Hungary (MFGI) in Budapest. Their inventory numbers and unique IDs are the following: Ob.3072 (#42-45), V.13514 (#56A-Q), V.13531 (#57A-E), V.15490 (#58), V.15491 (#59), V.15492 (#60), V.15509 (#61), V.15512 (#62), V.15520 (#63), V.15521 (#64), V.15522 (#65), V.15523 (#66), V.15528 (#67), V.15530 (#68), V.15531 (#69), V.15577 (#70), V.13.01944.1 (#52), V.13.03071.1 (#53), V.13.03073.4 (#54-55).

Six isolated teeth from Fox Amphoux and four dentary bones with *in situ* teeth from La Boucharde (Aix-en-Provence, France) are now stored in the National Museum of Natural History of France (MNHN) in Paris. A left mandible (Mn 227) with *in situ* teeth from Montplo (Hérault, France) is housed in the Museum of Cruzy (MC). These remains were found in the Campanian-Maastrichtian sediments of southern France, and were previously referred to *Rhabdodon priscus* (see Allain and Suberbiola, 2003 and Csiki-Sava et al., 2015). ~~The aforementioned material was used here for comparative purposes, but t~~he low sample number of the *Rhabdodon* material did not allow us to involve these specimens in the mathematical statistical tests.

## 2.2. Terminology and morphometric measurements

Dental terminology used here (Fig. 1) ~~is~~ was based on the work of Smith and Dodson (2003) and it is similar to that of Weishampel et al. (2003), Godefroit et al. (2009), Chanthasit (2010) or Ósi et al. (2012a) used for rhabdodontids, and to that of Lindgren et al. (2007) or Tanoue et al. (2009) used for ceratopsians.

Distance measurements ( $L$ ,  $L_{pr}$ ,  $H$  on Fig. 1/B and D) were taken by the usage of a digital calliper with a precision of 0.003 millimetres. The lowermost points of the mesial and distal rims around the indentations were used here for defining a baseline for the height measurements. Although this method results in a somewhat lower value than the total crown height of an *in situ* tooth, it can easily be measured in isolated specimens as well.

Angles ( $ang_{occl}$  on Fig. 1/A and C, as well as  $ang_{mes}$ ,  $ang_{pr}$ ,  $ang_{dist}$  on Fig. 1/BD) were measured with ImageJ software (Rasband, 1997-2015) on images taken from properly oriented teeth. The general outline of a tooth can be considered broadly symmetrical to its labiolingual plane (i.e. to the plane

that splits the tooth into mesial and distal halves). This plane and the primary ridge of the tooth crown were assumed here to be near apicobasal when viewed from labial or lingual direction. In order to approximate a hypothesized life position, the apex of the crown was oriented toward the top of the image if the primary ridge was present (Fig. 1/D) and toward the bottom if the ridge was absent (Fig. 1/B). In mesial and distal views, each tooth was rotated around its apicobasal axis until the occlusal surface had become parallel to the intended plane of the photograph and only its edge was visible (Fig. 1/A and C). The angle formed by the wear facet and the opposite side at the apex (namely  $ang_{occl}$ ) was measured both in mesial and distal views and an average was calculated for each tooth.

Descriptive statistical parameters of the measurements (which are summarized in Table 1) were obtained by the usage of R (R Development Core Team, 2008).

### 2.3. Distribution analysis

Normality of the measured morphometric parameters were checked visually using the histograms and Q-Q plots (see below) of each variable. In a few cases, especially when the sample size is small, it can be hard to assess normality on the basis of visual methods alone, therefore Kolmogorov-Smirnov tests were also performed on each variable by the `ks.test()` function of R software (R Development Core Team, 2008). The true distribution function of a given variable was compared to a cumulative distribution function that had the same mean and standard deviation as the variable in question. Decisions were made at an alpha level of 0.05.

Quantiles are values which divide the ordered data into a given number of equal-sized subsets. For example, the median is the 2-quantile, which divides the ordered data into two halves. The normality of the distributions were checked by regressing the quantiles of the data against the quantiles of a normal distribution with the same mean and standard deviation as the sample. This is a non-parametric approach, which is easy to interpret and usually more powerful than analysing the shape of a histogram itself. In the case of normally distributed data, the points plotted on such Q-Q plot ("Q" stands for quantile) should fall approximately on a straight line ~~(Fig. 2/A)~~. Lack of fit to the regression line suggest deviations from the normality. An arched arrangement of the points, for example, indicates that the sample distribution is more skewed than the normal theoretical distribution ~~(Fig. 2/C and D)~~. An "S"-shaped arrangement of the points indicates that the sample distribution is either bimodal ~~(e.g. in the case of Fig. 2/B)~~ or has heavier tails than the normal theoretical distribution (Helsel and Hirsch, 2002; Thode, 2002).

If normality was rejected here based on the above mentioned methods, the measured morphometric parameters were also tested for log-normality using the following theorem: if our collected data conform to a log-normal distribution than the logarithmic transformation of these data should fit the expectations of a normal distribution by definition (Limpert et al., 2001). Thus we checked the log-transformed measurements for normality with the same methods as above (by visual inspection of the histograms and Q-Q plots, as well as by Kolmogorov-Smirnov tests). If normality of a transformed distribution was confirmed than the original distribution was considered here as log-normal, otherwise log-normality of the original distribution was also rejected.

~~After a simple logarithmic transformation of log-normally distributed data, the resulting values should fit a more or less normal distribution by definition, and so, the same methods can be used on the transformed values in order to prove the log-normality of the initial distribution. In other words, a distribution can be defined as a log-normal one, if the data are normally distributed at the log level (Limpert et al., 2001).~~

There is also a relative, but easy check of the symmetry of a given distribution. In the case of symmetrically distributed data, the mean and median values are relatively close to each other

(considering the full extent of the data). A symmetrical distribution, however, does not necessarily mean normality, but ~~significant~~ a notable asymmetry means ~~significant~~ deviation from ~~the latter~~ it.

Box and whisker plots were used to identify the outliers in the data. Such plots are visualizing the data through their quartiles (i.e. 4-quantiles). The extent of the box is defined by the first and third quartiles, whereas the band inside the box indicates the second quartile (i.e. the median). The whiskers extend to the most extreme data points still within 1.5 times the interquartile range from the box. Any data outside the range defined by the whiskers were plotted as outliers with individual dots (Helsel and Hirsch, 2002; Thode, 2002).

## 2.4. Tooth wear analysis

Mapping of microstriations on the well-preserved wear facets of 37 teeth were applied in order to reconstruct how the lower tooth row moved against the upper, and so to get some insights of the jaw mechanism of the examined taxa. Based on the criteria established by Teaford (1988), only highly regular and roughly parallel striations that concentrated to the occlusal surface and showed no evidence of multiple abrupt shifts were considered here as genuine microwear. There were no signs of obliteration and dulling of the features (such as depicted in King et al., 1999), which would indicate post-mortem alteration of the studied areas.

The facets were photographed under reflected light by a Leica DFC420 digital camera attached to a Leica DMLP light microscope. The individual teeth were oriented labially or lingually (with the occlusal surface facing toward the camera) using the same way that was described in Section 2.2 but each tooth was further rotated around its mesiodistal axis until the wear facet had become perpendicular to the camera angle. Images were obtained with Image-Pro software. Measurements on each image were made with ImageJ software (Rasband, 1997-2015).

Present study used the intersection of the wear facets and the labiolingual plane (~~i.e. the one that splits the teeth into mesial and distal halves~~) as a reference line for measuring the angle of microstriations. ~~The latter~~ This line is called here as the transverse axis of a wear facet (see on Fig. 65). All data taken from the literature were converted here if the original work used a different system. The projection of the transverse axis is identical with the projection of the apicobasal axis of the same tooth in labial and lingual views. However, their projection can be different in mesial and distal views if the occlusal facet is not vertical but slanted toward the labial or lingual direction. Although this trait is not an issue, when measuring features in labial or distal views, but we retained this terminological distinction here in order to avoid confusion.

## 2.5. Dental histology

Five of the above mentioned teeth (MTM V.2010.113.1. #40A, #40F and #40G, MTM PAL 2012.18.1. #35D, MTM VER 2016.2551. #37L) were also selected for sectioning, but prior to the destructive methods, moulds and casts were made for archiving purposes following the method used by e.g. Ósi (2014). Specimens were cleaned with cotton pads soaked with ethyl alcohol. After drying, each tooth was covered with Coltène Affinis Precious Regular Body polyvinyl siloxane impression material extruded onto the surface using a cartridge dispenser. Casts were then made with EPO-TEK 301 two component epoxy resin. This procedure allows the reproduction of morphometric details with a resolution of a fraction of a micron. In addition, the original teeth were sputter coated with approximately 5 nanometres of gold-palladium in order to increase conductivity and eliminate electron charging in the high-vacuum SEM chamber. Micrographs were taken with a Hitachi S-2600N SEM.

The teeth were embedded in two component epoxy resin in order to facilitate sectioning and prevent fracture propagation. Sections were cut according to various pre-~~definite~~-defined planes with a rock slabbing saw with a ~~very~~-thin, industrial diamond-covered blade in order to minimize the loss of material. In accordance with Sander (1999), a section that is parallel with the apicobasal axis of a tooth is called longitudinal. Several different longitudinal sections can be cut out from the same tooth, but the teeth were always sectioned here along their labiolingual plane. A section that is perpendicular to the apicobasal axis is called cross section. Such sections were made here in the mid-crown region. In addition, tangential sections were cut parallel to the tooth surface. The cut surfaces were polished with abrasive powder with a grit size of 1000 in the last step in order to remove the scratches left by the saw blade. Etching was performed with 2N HCL for 3-5 seconds. The etched surfaces were prepared for a SEM study using the same approach described above. The sputter coated surfaces were then polished again in order to remove the conductive film and the effects of etching. ~~The polished surfaces, and then they~~ were glued to glass slides. The majority of the embedded part were cut off by rock slab saw and the remaining sections were thinned further using abrasive powder. Micrographs were taken with the light microscope mentioned above using trans-illumination with and without crossed Nicol prisms. Measurements on the images were made with ImageJ software (Rasband, 1997-2015).

The terminology used here to describe the enamel microstructure is identical to that of Sander (1999) developed for sauropsids based on the system of Koenigswald and Clemens (1992) for mammals. The terminology recognizes five levels of structural complexity, namely the crystallite level, the module level, the enamel type level, the schmelzmuster level, and the dentition level. The ~~latter~~-dentition level was not studied here due to the small sample size and the lack of numerous properly associated teeth especially in the case of *Ajkaceratops*. In accordance with Sander (1999), The-the descriptions presented here used a “bottom up” approach, similarly to Sander (1999), since because features at a given level of hierarchy are the building components of the next higher level. The enamel-dentine junction (EDJ) was used as a reference plane for descriptions, since because this is the plane where amelogenesis initiates.

## 3. Results and discussion

### 3.1. Tooth morphology

#### 3.1.1. Description

One side of the teeth studied here is always more heavily ornamented than the opposite side. Based on the absence or presence of a well-developed primary ridge on the ornamented side, the teeth can be classified into two basic morphogroups (Fig. 32 and Fig. 43, respectively; or see Fig. 1 for schematic representations), which slightly differ in other features as well.

*Morphogroup 1.* Most of the teeth studied here have a subrectangular crown shape in labial and lingual views. The ornamented side possesses 8-13 more-or-less parallel, apicobasally oriented ridges, which are surrounded mesially, basally and distally by a continuous and slightly elevated rim (sometimes called the cingulum). A more prominent central ridge might appear on some teeth (see e.g. Fig. 32/A), but these ridges are not as developed as in the case of teeth that belong to the other morphogroup (see below), and they never completely confluent with the elevated rim, but slightly set back from ~~the latter~~it. In accordance with the terminology used by Weishampel et al. (2003), Godefroit et al. (2009) and Ósi et al. (2012a), ~~S~~such features were not considered here as primary ridges. It is visible on unworn or slightly worn teeth that ridges culminate in denticles along the

margin of the crown. Such denticles can appear on even those parts of the crown margin where no ridge terminates. The other side of the teeth are ornamented by faint subparallel ridges, which usually disappear as wear facets are developing. In the early stages of wear, paired mesial and distal wear facets appear on this side, which usually merge together as the wear proceeds (compare Fig. 32/C, E and M; more details of the facets are discussed in a ~~separate chapter~~Section 3.2.1).

On some teeth that belong to ~~the latter~~this morphogroup, the long and robust root is also preserved. There is no ~~significant-remarkable~~ angulation between the root and the crown, which means that the ornamented side of the crown appears in continuity with the convex surface of the root in mesial and distal views (see e.g. Fig. 32/B). An elliptical scar is sometimes visible on this surface (see e.g. Fig. 32/C), which marks the contact with the crown of the replacement tooth. The opposite surface of the root, connected to the wear-affected part of the crown, is more-or-less straight in mesial and distal views (see e.g. Fig. 32/B). A longitudinal shallow groove is often present on both the mesial and distal sides (see e.g. Fig. 32/M), giving the root an hourglass shape in cross section, which indicates that teeth were closely packed.

*Morphogroup 2.* The teeth referred to the other morphogroup have a diamond-shaped crown in labial and lingual views. The ornamented side is surrounded mesially, basally and distally with an elevated rim and it bears a well-developed, more or less centrally positioned primary ridge that is confluent with the ~~latter~~rim. The primary ridge and the rim limit two unequal, concave and U-shaped indentations, each of them is ornamented by 5-7 subparallel secondary ridges, which (contrary to the other morphogroup) usually do not reach the basal margin. Marginal denticles are present on these specimens as well. The other side of the unworn teeth is ornamented by faint subparallel ridges (see Fig. 43/B and E), which gradually disappear as the wear proceeds. In the early stages of wear, paired mesial and distal wear facets appear on this side, which tend to merge indistinguishably in heavily worn teeth. The roots are similar but somewhat shorter than in the case of the other morphogroup.

### 3.1.2. Discussion and comparison with other taxa

Considering the observations of Ósi et al. (2012a), the specimens from Iharkút which does not possess a well-developed primary ridge (*i.e. which belong to Morphogroup 1*) are the upper teeth of *Mochlodon vorosi*, and according to Weishampel et al. (2003), Godefroit and Lambert (2007) or Chanthasit (2010) they are ~~very~~-similar to that of *Zalmoxes* and *Rhabdodon*. ~~The latter~~These authors also pointed out that the lower teeth of rhabdodontids possess a primary ridge, thus they are ~~very~~ similar to ~~the other morphogroup described above~~Morphogroup 2. However based on the figures and descriptions presented by many authors (e.g. Maryańska and Osmólska, 1975; Sereno, 1987, 2000; Xijin et al., 1999; Hailu and Dodson, 2004; Lindgren et al., 2007; Tanoue et al., 2009; Sereno et al., 2010; Farke et al., 2014; Varriale, 2011a, 2016), both the dentary and the maxillary teeth of ceratopsians (especially of those which are assumed to be closely related to *Ajkaceratops* by Ósi et al. (2010a)) are ~~very-also~~ similar to ~~the latter morphology~~Morphogroup 2, consequently the taxonomic identification of the isolated teeth with a well-developed primary ridge could be highly problematic.

As noted above, the roots of both morphogroups on one side are usually notched by a well-developed elliptical facet (see e.g. on Fig. 32/C or on Fig. 43/H). Such scars (or resorption circles) are related to the pressure exerted during the replacement process by the crowns of the succeeding tooth generation (see e.g. Sereno, 1987), thus they always appear on the lingual side of both maxillary and dentary teeth. In contrast, the upper teeth are positioned somewhat labially relative to the lower teeth in the case of almost all toothed tetrapods, thus wear facets are usually forming on the labial side of dentary and on the lingual side of maxillary teeth. Based on the observations of Chanthasit (2010) and Ósi et al. (2012a), this condition was certainly true for *Rhabdodon* and

*Mochlodon*, but the same reasoning was used by Ósi et al. (2014) for distinguishing isolated upper and lower teeth of the ankylosaurian *Hungarosaurus* or by Godefroit and Lambert (2007) for ascertaining the position of a ~~teeth-tooth~~ which was referred to *Craspedodon lonzeensis*, a species with a highly controversial phylogenetic position (see the supplementary material of Ósi et al., 2010a for details). Consequently, if an isolated tooth from Iharkút possesses a pressure scar and a wear facet on the same side and a primary ridge on the other side, then it certainly is an upper tooth which could not have belonged to *Mochlodon* but rather can be referred as a ceratopsian. Although this method seems promising, unfortunately, no such teeth were found in the sample studied here. However, the roots were broken off in most specimens.

Ósi et al. (2010a) placed *Ajkaceratops* within Coronosauria closely related to the Asian bagaceratopsids, however, they noted that the exact position of this genus is unclear. According to the phylogenetic analysis of Farke et al. (2014), due to the incomplete nature of the material, *Ajkaceratops* could either be a basal neoceratopsian or a sister taxon to *Bagaceratops*. Nevertheless, the latter hypothesis is more congruent with the geological age of the taxa. According to Sereno (2010), bifurcated roots (closely linked to the evolution of dental batteries) appeared first within the clade Ceratopsoidea, which is a sister group to the clade that contains bagaceratopsids and protoceratopsids. Thus, if the sample studied here contains teeth of *Ajkaceratops*, it seems that this genus with only one root was more basal than ~~the members of Ceratopsoidea~~ ~~the latter clade~~, which is in agreement with both of the aforementioned phylogenetic interpretations.

### 3.1.3. Implications of the distribution analysis

Biological variables (e.g. the size parameters of a tooth) are usually effected by several independent variables, such as age, nutrition, disease exposure as well as the genotype at particular loci. According to Limpert et al. (2001) and Grönholm and Annala (2007), if the effects of these determining variables define the resulting variable in an additive way, than the ~~latter-resulting variable~~ will be approximately normally distributed regardless of the underlying distributions as a ~~result-consequence~~ of the so called central limit theorem. In contrast, multiplicative effects will induce log-normal distributions. In practice, many measurements show skewed distributions, especially, when there is a natural limit for the value (size measurements, for example, cannot be negative), the mean is close to the limit and the standard deviation is relatively large. Such distributions can also closely fit the log-normal distribution.

Therefore, it is not surprising if someone expect normal or log-normal distribution from a biological variable if it comes from a single homogenous sample population. However, if a measurement data is more or less unimodally and normally or log-normally distributed that does not necessarily mean that the measured specimens belong to the same species, but this conclusion is more likely true compared to the opposite situation, which obviously needs some explanation (e.g. sexual dimorphism or mixing of similar but different taxa within the sample).

According to the phylogenetic analysis of Ósi et al. (2012a), *Mochlodon* (including *M. vorosi* from Hungary and *M. suessi* from Austria) is a member of Rhabdodontidae and a sister taxon to *Zalmoxes* (including *Z. robustus* and *Z. shqiperorum* from Romania). Together, these two genera form an eastern European ~~lineageclade~~, which is a sister taxon to the western European *Rhabdodon* ~~lineage clade~~ (including *R. priscus* from northern Spain and southern France).

The mathematical statistical results presented in this article are in agreement with this ~~assumption~~ ~~phylogenetic interpretation~~.

If we combine the measurements ~~data-oftaken on~~ the specimens from the Hațeg Basin and from Iharkút, none of the size variables in the resulting sample are normally distributed (see e.g. the mesiodistal length of the teeth with and without a primary ridge; Fig. 54/A and F, respectively). The

histograms are noticeably asymmetrical and positively skewed. Several specimens (especially the larger ones) were judged as outliers. The points on the Q-Q plots have an arched arrangement. The mean and the median of the combined values are ~~significantly-noticeably~~ different in both cases compared with the full extent of the data. The Kolmogorov-Smirnov tests rejected the null hypotheses that the samples are drawn from a normal distribution at a 0.05 alpha level. The data ~~is~~ ~~are~~ not even normally distributed at the log level. The same reasoning is true for the height of the tooth crown in the case of the teeth with and without a primary ridge (Fig. 54/C and H, respectively).

Considering that the material from Iharkút and the Hațeg Basin represent two different genera (*Mochlodon* and *Zalmoxes*, respectively), it can be stated that the methodology used here was able to show at least the genus level intermixing of two similar morphologies. Using the estimations of Ósi et al. (2012a), the body length of an adult *M. vorosi* was around 1.6-1.8 m, whereas the subadult size of the two *Zalmoxes* species were ca. 2.4-2.5 m. The size differences are also true for the teeth. For example, the mesiodistal length of the teeth without a primary ridge ranges from 3.5 mm up to about 10.3 mm (with a mean of 6.7 mm) in the case of the Iharkút sample, whereas it varies between 10.5 mm and 21.0 mm (with a mean of 14.5 mm) in the case of the material from the Hațeg Basin. Only 4 teeth were suitable for this measurement in the *Rhabdodon* material from France, but these data ranges from 9.9 mm to 22.4 mm which is somewhat similar to that of *Zalmoxes* even if the adult size of ~~the latter species~~ *Rhabdodon priscus* could reach up to 5-6 m, according to Ósi et al. (2012a). Further size comparisons can be made based on the data presented in Table 1.

If the samples are separated geographically (which is equal to taxonomically in this case), the mesiodistal length becomes normally distributed in the case of the Iharkút material (Fig. 54/B and G). The histograms look symmetrical which is confirmed by the fact that the means and the medians now differ only about 0.2 mm, whereas the full extent of the data ~~are-is~~ around 7.0 mm in both cases (Table 1). The outliers disappear except to one. The points on the Q-Q plots fall approximately on a straight line. The Kolmogorov-Smirnov tests accepted the null hypotheses that the samples are drawn from a normal distribution at a 0.05 alpha level. In contrast, the data are more close to but still not have a normal distribution in the case of the specimens from the Hațeg Basin. The more restrained interpretation is that it can be a result of the relatively small sample size, although there is a biological explanation as well.

According to Weishampel et al. (2003) and Godefroit et al. (2009), the material from the Hațeg Basin still represents a mixture of teeth referable to two different species, *Zalmoxes robustus* and *Z. shqiperorum*, therefore it is not surprising that the results suggest that the sample cannot be treated as a homogenous group. Unfortunately, the teeth of ~~the latter two~~ these species are highly similar, and so it is not possible to separate them from each other, not to mention that further categorization would result in small, statistically meaningless groups. However, it seems that even species level intermixing of morphologically similar material can be detected with the methodology described above.

Looking at Figure 54/D and Figure 54/I, it is obvious that the height of the tooth crown did not become normally distributed even after the geography based separation of the samples, however, with a simple logarithmic transformation of the data, this problem can easily be resolved (Fig. 54/E and J). It means that this variable has a log-normal distribution. The sample from the Hațeg Basin slightly deviates from normality even at the log level, but the explanation of this observation is the same as above. The reason that this variable is not originally normally distributed is that the measurements were taken not only in unerupted or unabraded teeth, and wear is a process which takes its effect in one direction, hence greatly distorts the initially symmetrical distribution, but only toward decreasing heights.

In summary, based on the distribution analysis of the size variables, such as the mesiodistal length of the tooth or only the primary ridge (if present) and the height of the tooth crown, it can be

concluded that the Iharkút sample is morphologically homogenous, even if it does not necessarily means that it indeed is indivisible based on other features. In a similar manner, it neither does not means that it only contains teeth referable to *Mochlodon*. If the teeth once belonged to *Ajkaceratops* are truly very-similar to that of *Mochlodon*, and only a few of them are mixed into the material, it is not to be expected that the specimens will stick out from the data as outliers, nor that they will significantly-remarkably distort the otherwise normal distributions.

## 3.2. Wear pattern

### 3.2.1. Description

Well-developed, merged wear facets are present on most of the teeth from Iharkút and a few paired facets are visible on those that are slightly worn. Only six unworn teeth (MTM V. 2010.114.1. #41B and #41L, MTM VER 2016.1604. #4, MTM VER 2016.2548. #11A, MTM VER 2016.2554. #46, MTM VER 2016.2555. #47) were found in the sample (two of them are shown on Fig. 43/A-E). The surface of the facets forms an angle (namely  $\text{ang}_{\text{occl}}$ ) of 34-76° (with a mean around 54°) to the opposite side at the apices of the teeth with a primary ridge and 51-90° (with a mean around 70°) in those, which do not possess a primary ridge. In the case of the material from Hațeg Basin,  $\text{ang}_{\text{occl}}$  varied between 56-81° (with a mean around 70°) in the case of the teeth with a primary ridge, and between 68-83° (with a mean around 75°) in those without a primary ridge.

Ósi et al. (2012a) stated that the facets of *Mochlodon vorosi* formed an angle of approximately 65-70° to the horizontal plane in early stages of wear, whereas this angle was around 35-45° in heavily worn teeth. Unfortunately, *in situ* teeth with well-developed wear facets have not yet been found from Iharkút, thus such values were deduced only by relating the facet orientations to the apicobasal axis of the teeth. It cannot be excluded that the inclination of the facets were rather constantly inclined relative to the horizontal plane, which was achieved by the slight inward rotation of the lower and outward rotation of the upper teeth during tooth replacement. Minimal angle variation might have occurred within the same tooth row, similarly-to just like in the case of several other ornithopods discussed in Weishampel (1984).

Numerous parallel microstriations (or scratches) can be observed on the wear facets of the teeth from Iharkút. These striations are always straight and parallel to each other in the case of the teeth without a primary ridge (Fig. 65/G and H). They are apicomesially-basodistally oriented and they form an angle of around 10-15° to the transverse axis of the facets. Their length ranges from 0.5 mm to 5.0 mm, but most of them run across almost the entire width of the occlusal surface. Their width is less than 10 μm and their spacing varies between 20-100 μm. A similar pattern can be observed on almost all of the teeth that possess a primary ridge (Fig. 65/E and F). A few of ~~the latter~~ these teeth (MTM V. 2010.113.1. #40A, #40E, #40F and #40G, MTM VER 2016.2846. #71, MTM VER 2016.2847. #72), however, possess a remarkably different wear pattern (Fig. 65/I-N). Striations have the same dimensions than above, although they are not straight, but rather curved. The curves initiate their course at the apices of the teeth. They start their course in a slightly apicodistal-basomesial direction that forms an angle of around 10-15° to the transverse axis of the teeth. Then they curve through an arch and their terminal direction forms an angle of around 60-70° to the transverse axis of the facets.

The EDJ on the occlusal surface is always flush at the apex-apices of the teeth, and flush on most teeth at the basal end of the wear facets as well. However, in a few cases (especially when curved striations are present on the occlusal surface), the ~~latter tissues~~ enamel and the dentine are in a stepwise relationship or an elevated rim-ledge appears within the worn dentine. It seems that the

otherwise flat wear facets tend to be shallowly concave in the ~~latter cases~~ case of these specimens (Fig. 43/T, V and Z).

### 3.2.2. Discussion and comparison with other taxa

According to Weishampel (1984), the EDJ on the occlusal surface can be formed in two ways depending on the direction of tooth-to-tooth contact. Along the leading edge, enamel protects the adjacent dentine, which results in a flush interface. Along the trailing edge, unprotected dentine wears off in a greater extent than the adjacent enamel, which produce a stepwise relationship of ~~the latter~~ these tissues. The flush EDJ on the apices of the teeth from Iharkút suggests that the power stroke of the chewing cycle was most likely continuous with the closing phase, during which the dentaries and ~~the~~ associated elements moved upward to bring the lower and the upper tooth rows into occlusion. The similar conclusion was drawn by Weishampel (1984) for most of the iguanodontians they studied (including *Mochlodon suessi*). Once the lower and upper teeth came into contact and the food stuck between them, shearing and pulping of the consumed plant material has begun. The enamel on the leading edges (i.e. on the apices of the teeth) protected the dentine behind it from attrition and abrasion. ~~On the basal side of the wear facets an elevated rim was formed in a few cases (see e.g. Fig. 4/Q and R) due to differential wear or because the opposing teeth did not reach that far in every chewing cycles.~~

The closing of the upper and lower tooth rows resulted in a scissors-like action. The opposing teeth came into contact along the wear surfaces during occlusion, whereas the lingual sides of the lower and the labial sides of the upper teeth diverged from the ~~latter~~ planewear surface. The less divergence has led to more acute cutting edges, which were appropriate for precise cutting of soft plant tissues. The less pointed teeth, however, were capable of shearing tougher food items (Lumsden and Osborn, 1977). According to the data presented in ~~the previous chapter~~ Section 3.2.1, facet surfaces form a slightly more acute angle to the opposite side at the apices of the teeth in the Iharkút sample than in the case of the material from Hațeg Basin, which suggest that *Zalmoxes* might have consumed somewhat more fibrous plant material than *Mochlodon*.

Based on the data presented in Weishampel (1984), the wear facets of all iguanodontians were oblique, they formed an angle of 30-60° to the horizontal plane, from which the ~~latter~~ highest values belonged to *Mochlodon suessi*. Only a single facet was present on the teeth in most cases, but two facets are known to have occurred in e.g. *M. suessi*, where each facet was slightly inclined away from its counterpart. Weishampel et al. (2003) studied both *in situ* and isolated teeth of *Zalmoxes robustus*, and they concluded that teeth in early stages of wear usually bore two facets, which indistinguishably merged together as the wear proceeded. The facets formed an angle of approximately 60° to the horizontal plane in upper and 55-75° in lower teeth. Godefroit et al. (2009) described similar wear properties based on both *in situ* and isolated lower teeth of *Zalmoxes shquiperorum*. The angle of wear ranged from 55-75° to the horizontal plane. Based on the measurements of the MC Mn 227 specimen (Fig. 65/D), the facets on the lower teeth of *Rhabdodon priscus* formed an angle around 65° with the horizontal plane (Fig. 65/A). According to Ősi et al. (2012a), the wear facets of *Mochlodon vorosi* were most plausibly similarly inclined to that of the aforementioned taxa.

The fact that the angle of wear is not close to the vertical plane, but the facets are rather inclined outward, cannot be explained by simple orthal movements during the chewing cycle. Weishampel and Jianu (2000) noted that wear facets were oblique in the case of most ornithopods. They considered these animals as transverse grinders, and they explained the angled wear ~~by that the teeth could move transversely as the result of transverse movement of the lower and upper teeth~~ against each other. ~~Such t~~ Transverse movements (i.e. laterotrusion) are achieved by the unilateral

contraction of the masseter-pterygoid muscle sling in the anisognathous jaw adduction system of many mammals (Turnbull, 1970; Herring, 2007). However, such mechanism was not observed among recent reptiles up to now, thus it was highly implausible in the case of the most likely isognathous jaws of ornithopods.

~~According to Weishampel (1983, 1984) or and Norman and Weishampel (1985) proposed a model in which the maxillae and associated teeth were abducted (i.e. they swung laterally) via pleurokinesis as the opposing mandibular dentition came into occlusion with them. As force was applied during the power stroke, muscle contractions prevented any further rotation, which finally has led to transverse grinding. Holliday and Witmer (2008) noted that despite having intracranial synovial joints and essential protractor muscles, ornithopod dinosaurs lacked permissive kinematic linkages necessary to achieve pleurokinesis. Based on a three-dimensional animation model of the craniodental system of the hadrosaurid *Edmontosaurus*, Rybczynski et al. (2008) pointed out that even a small amount of abduction would have generated extensive secondary movements that would have resulted in unrealistic displacements between several cranial elements. Nevertheless, Williams et al. (2009) agreed with the pleurokinetic model according to the results of a quantitative analysis performed on microwear data recovered from *Edmontosaurus* teeth.~~

~~Bell et al. (2009) and Cuthbertson et al. (2012) proposed an alternative mechanism in which the facial skeleton was considered akinetic and the transverse chewing stroke was achieved by the long-axis rotation of the mandible that was accommodated by a slight flexion at the prementary-dentary joint and possibly by some mobility at the symphysis. Cuthbertson et al. (2012) also concluded that the open dish-shaped articular surfaces on the surangulars could have allowed the slight propalinal and/or transverse excursion of the jaw. These assumptions were further strengthened by the observations of Nabavizadeh (2014) on the craniomandibular system of numerous hadrosauroid specimens. According to Varriale (2016) and Nabavizadeh (2016), it now seems that mandibular long-axis rotation, combined with an orthopalinal power stroke and accessory propalinal movements, is a more viable model of the ornithopod jaw mechanism than pleurokinesis. transverse chewing stroke was achieved in ornithopods by slight rotation and translation of the lower and/or the upper tooth-bearing and associated elements via pleurokinesis. The details of this mechanism were discussed in the literature even more recently (see e.g. Bell et al., 2009 or Cuthbertson et al., 2012). Weishampel et al. (2003) pointed out that *Zalmoxes*, one of the closest relatives of *Mochlodon*, also had intracranial mobility, but it was more restricted than that of the more derived taxa, such as hadrosaurids.~~

Weishampel (1984) stated that randomly spaced, parallel microstriations on the wear facets were formed during the power stroke of the chewing cycle as a result of either small inorganic particles that have been drawn across the occlusal surface, or the harder enamel that have been moved across the less resistant dentine. In the case of the upper teeth from Iharkút that lack the primary ridge, thus undoubtedly belonged to *Mochlodon*, only straight and somewhat apicomesially-basodistally oriented microstriations can be observed with a high degree of parallelism (Fig. 65/G and H). It suggests an orthal or slightly orthopalinal movement of the jaw relative to the cranial elements, but it seems that ~~significant-notable~~ fore and aft movements ~~was-were~~ impossible due to anatomical limitations of the jaw joint and/or constraints in the intracranial mobility. Weishampel et al. (2003) studied the wear pattern of *Zalmoxes robustus*, and they mentioned that scratches formed an angle of maximum 10° to the transverse axis of the wear facets. Chanthasit (2010) studied *Rhabdodon* remains from France and she stated that microstriations were more or less parallel to the transverse axis of the wear facets. This observation is also confirmed by the straight and parallel microstriations visible on the MC Mn 227 specimen (Fig. 65/B and C), which ~~are-forming~~ an angle around 15° with the transverse axis of the facets. The aforementioned values are ~~very~~ similar to those, which were measured in the Iharkút sample.

Weishampel (1984) noted that the wear pattern of ornithopod teeth on the left and right side were essentially just the mirror images of each other, whereas scratches followed basically the same direction relative to the body on the lower and upper facets. It is therefore logical to expect that the microstriations on the lower teeth of *M. vorosi* are also straight and only slightly angled to the transverse axis of the wear facets (Fig 65/E and F) as it can be observed on most of the teeth from Iharkút with primary ridges. However, 2-5 mm long, curved scratches are visible on a few specimens (MTM V. 2010.113.1. #40A, #40E, #40F and #40G, MTM VER 2016.2846. #71, MTM VER 2016.2847. #72; Fig. 65/I-N), which suggest ~~significant-not negligible~~ palinal movements during the power stroke. It is highly possible that ~~the latter these~~ teeth belonged to a taxon that had a different jaw mechanism than *Mochlodon*.

According to Weishampel (1984) or Norman and Weishampel (1985), striations indicating fore and aft movements during the power stroke are not present within ornithopods. Williams et al. (2009) and Mallon and Anderson (2014), however, observed more or less mesiodistally oriented scratches (in addition to those which were only slightly angled to the transverse axis of the wear facets) in the case of several hadrosaurids, which they explained as the result of supplementary propalinal movements. Nevertheless, none of the above mentioned papers described curved microstriations in ornithopods, thus it seems that the teeth from Iharkút that possess such features might ~~once have belonged to a completely different group the ones, which once belonged to ceratopsians.~~

Weishampel and Norman (1989) and Weishampel and Jianu (2000) considered nearly all ceratopsians (apart from *Psittacosaurus*) as orthal slicers due to their closely packed teeth with more or less vertical wear facets. The more extensive study of Varriale (2008, 2011a,b, 2015, 2016) involved ~~pachycephalosaurians 16 and several different ceratopsians and 2 pachycephalosaurians, and he~~ revealed four different chewing mechanisms within marginocephalians. On the basis of his observations, orthal chewing was limited to pachycephalosaurians and to the basal ceratopsian *Yinlong*. ~~The wear facets of *Psittacosaurus* formed an angle of 50° to the horizontal plane and the straight microstriations met the transverse axis of the facets at an angle around 60°, which suggest that the dentaries and the associated jaw bones were elevated and retracted posteriorly at the same time. The inclined facets combined with posteriorly diverging tooth rows and an orthopalinal motion fostered continuous occlusion during the power stroke of the chewing cycle within an akinetic skull. This unique style of chewing was termed clinolineal by Sereno et al. (2010). Oblique wear facets with straight striations inclined around 60° to the transverse axis of the wear facets suggested clinolineal chewing for *Chaoyangsaurus* and subsequent ceratopsians. According to Tanoue et al. (2009), the latter genus was somewhat derived than *Yinlong* but more basal than *Psittacosaurus*. Sereno et al. (2010) proved that *Psittacosaurus* also had clinolineal chewing, which was achieved in an akinetic skull by only the combination of palinal and orthal movement of the dentaries and the associated jaw bones. The relatively flat articular surface allowed the jaw to slide fore and aft against the quadrate during the chewing cycle. As the posteriorly divergent lower tooth rows were drawn posterodorsally into occlusion, the lateral tension between the upper tooth rows increased, which was accommodated by oblique shear. According to their measurements, the wear facets formed an angle of 50° to the horizontal plane and the striations met the transverse axis of the wear facets at an angle around 60°.~~

Varriale (2008, 2011a,b, 2016) pointed out that the microstriations on the vertical wear facets of the basal neoceratopsian *Liaoceratops* and *Archaeoceratops* were curved. The curves begun their ~~course at the apices of the teeth in a slightly apicodistal-basomesial orientation and ended in a mesiodistal orientation at the mesial base of the facets of dentary teeth. Maxillary teeth showed a counterpart curvature. The same pattern was observed by him in the case of some leptoceratopsids, bagaceratopsids and protoceratopsids. The curved striations indicate that the power stroke of the~~

chewing cycle was composed of both orthal and palinal motions. The dentaries and the associated jaw bones moved upward and backward simultaneously during the beginning of adduction, just like in clinolineal chewing, but the palinal component progressively outpaced the orthal. This style of chewing was termed circumpalinal by Varriale (2016). ~~stated that curved scratches as an indication of true palinal chewing appeared first in the basal neoceratopsian *Liaoceratops*.~~

~~Based on the work of Varriale (2011a,b, 2016) and Mallon and Anderson (2014), some derived ceratopsids had~~ He also noted that orthopalinal chewing with vertical wear facets and with straight scratches inclined about 15-45° to the transverse axis of the ~~wear facets was a synapomorphic trait of Ceratopsoidea. Mallon and Anderson (2014) described similarly inclined scratches in the case of derived ceratopsids,~~ which can be associated with an orthopalinal power stroke. ~~However, the angle of these striations relative to the apicobasal axis was not as large as those of clinolineal chewers, having more of an apicobasal than mesiodistal component.~~ In addition, they also observed ~~numerous more-mesiodistally oriented straight striations on the teeth,~~ which they explained as a result of occasional popalinal excursion of the fully adducted jaw ~~during the initiation of the gape cycle.~~

~~According to these information, we think that the~~ The few teeth from Iharkút with 2-3 mm long, curved scratches on the wear facet and a well-developed primary ridge on the other side ~~most plausibly belonged to an animal that of the crown once belonged to the basal ceratopsian *Ajkaceratops*. This suggests that the latter taxon had a similar circumpalinal jaw mechanism to which was characteristic for most non-ceratopsid neoceratopsians. According to Varriale (2008, 2011a,b, 2016), circumpalinal chewing~~ This feature in this group occurred already in the case of the most basal ~~members neoceratopsians,~~ but disappeared within Ceratopsoidea ~~(but definitely within Ceratopsidae),~~ after the divergence of the latter clade from the closely related bagaceratopsids and protoceratopsids ~~(Varriale, 2011). This hypothesis would be in agreement~~ In accordance with the phylogenetic interpretations of ~~both~~ Ősi et al. (2010a) and Farke et al. (2014), *Ajkaceratops* could either be a basal neoceratopsian or a sister taxon to *Bagaceratops*, which means that it is reasonable to assume that it also had circumpalinal jaw mechanism. Based on this information and the observed similarities with neoceratopsians in both overall morphology and wear pattern, we provisionally assign the teeth with curved scratches to *Ajkaceratops*. Although there could be other undescribed taxa in the area, *Ajkaceratops* is the only known ceratopsian in the studied region up to now.

According to Varriale (2011a, 2012), a large number of non-ceratopsid neoceratopsians possessed a labial shelf at the basal edge of the occlusal surface on their dentary teeth, whereas basal ceratopsians and derived ceratopsids lacked this feature. The shelves exhibited variable morphology depending on taxonomy, alveolar position and degree of wear. When a shelf was present and prominent, it either had the appearance of a scalene triangle in labial view, or it looked like a single conspicuous sloping ledge depending on how many maxillary teeth were intersecting with a single dentary tooth. When a shelf was incipient, it appeared as a small ridge at the basal edge of the occlusal surface. The transition between the shelf and the occlusal surface was either abrupt, or it was stepwise with many small ledges gradually connecting the shelf and the occlusal surface.

Varriale (2011a, 2012) also noted that the edge of a shelf always had the same orientation as the microstriations on the adjacent part of the occlusal surface. For example, when the scratches were curved, the nearby shelf was not straight but concave, having the same curvature as the wear features. This led to the conclusion that the labial shelf is most likely a product of differential wear between the maxillary teeth and their dentary counterparts and the shape of the shelf reflects the motion of the lower jaw. In the case of palinal or circumpalinal chewing, the relative motion of teeth against each other became mesiodistal before the chewing cycle was completed. As a consequence, the occluding teeth were not able to completely slide past each other. Due to this incomplete shear, shelves emerged near the base of some dentary teeth. In the case of orthal chewing the dentitions

sheared completely past each other, which resulted the development of a single planar occlusal facet on each tooth.

It seems that the wear facets of *Mochlodon vorosi* are more or less straight, which is in agreement with their orthal chewing. ~~whereas they are rather concave in the case of the teeth with curved striations (see Fig. 4/T, V and Z). This condition is most plausibly the result of that the angle of wear remained close to vertical during the tooth migration in ceratopsians, and while the opposing apical parts gradually became thinner with abrasion and attrition, the thickness of the basal parts that were out of reach remained the same. Although Weishampel (1984) stated that the wear facets of *Mochlodon suessi* could also be shallowly concave, he also noted that such features could vary even within the same mandible in the case of a few ornithopod taxa.~~ Based on the descriptions and images presented in Weishampel et al. (2003) and Godefroit et al. (2009), as well as on the specimens studied here, the facets are also more or less straight in the case of *Zalmoxes*. In contrast, the facets are rather concave in the case of the teeth with curved striations (see Fig. 3/T, V and Z), which we assume once belonged to a non-ceratopsid neoceratopsian (most likely *Ajkaceratops*). These concavities can be interpreted as incipient labial shelves similar to those, which were observed in the case of e.g. bagaceratopsids and protoceratopsids by Varriale (2011a). Although decisive curved microstriations were not preserved on the occlusal surface of the MTM PAL 2012.18.1. #35C specimen, an elevated ledge (assumably a labial shelf) was formed along its basodistal edge (Fig. 3/Q and R). The curved edge of this shelf suggest that it was formed as a result of circumpalinal chewing, thus we provisionally assign this specimen also to *Ajkaceratops*.

According to Erickson et al. (2012, 2015), the dentine of many derived ceratopsians and ornithopods were built up from multiple tissue variants (such as mantle dentine, orthodentine, vasodentine) with differing hardness. The more wear-resistant mantle dentine and orhodentine (together with the enamel) usually formed high-relief cutting edges along the apices and sides of the occlusal facets, whereas the softer vasodentine corresponded to a centrally located low-relief basin. If these tissue variants were present in the case of *Ajkaceratops*, they certainly could have contributed to the above described concave or stepped topography of the wear facets. However, we have no reason to assume that the differential wear would have resulted a greater difference in the occlusal relief near the basal area of a wear facet (where the labial shelf is located) than along the leading edges. In fact, it usually resulted in steeper topography around the apices of the teeth (as it can be seen on the images of Erickson et al. 2012, 2015 or Mallon and Anderson, 2014).

Despite ~~of~~ the low sample number and assuming that our above described taxonomic assignments are correct, it is possible to draw some conclusions about the chewing mechanism of *Ajkaceratops*. The flush EDJ on the apices of the teeth suggests that the power stroke was continuous with the closing phase, such as in the case of *Mochlodon*. However, the closing mechanism involved not purely orthal movements, but the power stroke progressed smoothly into a palinal phase ~~also synchronous palinal movements. The latter was.~~ The transition was not swift and abrupt (such as in the case of e.g. *Hungarosaurus*; see Ósi et al., 2014, 2016 for details), but it had spread over the entire power stroke, which was achieved either by adequately timed muscle movements or by a passive mechanism ~~(mentioned in Mallon and Anderson, 2014),~~ namely that the jaw was pushed backward as the prey was traced an arc defined by its contact with the inner surface of the rostral bone during adduction (Varriale, 2011a, 2016; Mallon and Anderson, 2014). This was followed by the opening phase, when the jaw returned to its initial state and the process started all over again.

### 3.3. Enamel microstructure

### 3.3.1. Description

According to Sander (1999), the orientation of individual crystallites in the enamel can only be observed in the SEM but not in the thin sections, however, based on the work of e.g. Hillson (2005), some features on higher hierarchical levels of complexity might be visualized by the appearance of an extinction pattern in polarized light microscopes. Despite that, the enamel bands of the examined Iharkút specimens were homogenous under polarized light (Fig. 76/A, B and D), but the SEM study of the etched sections revealed the major features.

On the crystallite level, it is visible in the longitudinal section of all the studied teeth from Iharkút that not all of the crystallites are parallel to each other and none of them are perpendicular to the former secretory surface and thus to the incremental lines (see below). They are rather arranged in a fishbone-like pattern (Fig. 76/G), with the axes of the pattern being perpendicular to the forming face, ~~while-whereas~~ the side branches being angled to ~~the-latter~~. Adjacent side branch areas are separated by crystallite discontinuities (i.e. abrupt changes in crystallite orientation). Crystallites in the adjacent branches meet at an angle of 80-100°. Within the side branches, the crystallites are sometimes combined into small groups (Fig. 76/H). In contrast to microunits, they are not diverging from, but rather parallel to each other in these 0.1-0.3 µm wide and 1-2 µm long bundles. A gradual transition may occur between isolated and bundled crystallites.

On the module level, columnar divergence units delimited by planes of crystallite convergence can be observed (Fig. 76/G). Ideally, these bounding planar discontinuities are complete, but sometimes they can be underdeveloped. The units are oriented more or less perpendicularly to the former secretory surface. A line of crystallite divergence is located in the centre of each unit. The crystallites (both the isolated ones and the bundles as well) are diverging from this line toward the outer surface of each columnar unit when moving away from the EDJ. The cross sections of the units (visible in tangential and slightly oblique cross sections) are uniformly hexagonal, but somewhat rounded (Fig. 76/J and K). These roundish figures become more elongated as the sectioning plane becomes more parallel to the axis of the columns. It is obvious that sectioning of such adjacent columnar divergence units on planes perpendicular to the tangential one (including the longitudinal) will result in a fishbone-like pattern described above. The diameter of the columns varies between 3.5-6.5 µm.

The columnar units are sometimes cancelled out by marked incremental lines (similar to “cross striations” in mammalian enamel) with a regular spacing of 2-3 µm, especially in areas where they are poorly developed (Fig. 76/I) or where the enamel is thin. The lines are slightly angled to the EDJ (they meet at approximately 2-3°) and each successive growth layer reaches farther down on the tooth in longitudinal section. Increments can completely dominate the thin parallel crystallite enamel (Fig. 76/E). Such lines are representing a circadian rhythmic variation in the rate of enamel matrix production (Line, 2001; Hillson, 2005; Ungar, 2010). Approximately 20 to 25 striae could be counted throughout the full width of the lateral imbricational enamel in a few cases.

On the enamel type and schmelzmuster levels, the enamel cannot be divided into distinct layers. Columnar enamel makes up the total enamel thickness in most of the sections. In addition, parallel crystallite enamel is present in the case of the weakly enamelled side of the teeth (Fig. 76/F). The total enamel thickness varies between 30-80 µm (with an average of 50-60 µm) on the side that possess thicker enamel (Fig. 76/A-C), and between 5-7 µm on the other side (Fig. 76/D-F). Within the same side of the same tooth, the enamel is largely uniform in thickness, except the crown base, where it gradually diminishes, and the very core of the ridges, where it may become minimally thickened (Fig. 76/L).

### 3.3.2. Discussion and comparison with other taxa

Teeth with somewhat different morphological traits and wear features have been involved in the analysis. One of the sectioned teeth (MTM VER 2016.2551. #37L) without a primary ridge had straight scratches on a flat occlusal surface, thus it can be referred as an upper tooth of *Mochlodon*. Another tooth (MTM PAL 2012.18.1. #35D) had a primary ridge and straight scratches on a flat occlusal surface suggesting that it most likely can be referred as a lower tooth of *Mochlodon*. Three examined teeth (MTM V. 2010.113.1. #40A, #40F and #40G) had primary ridges but the occlusal surfaces were shallowly concave and had curved scratches on them, thus ~~they plausibly belonged~~ we provisionally assigned them to *Ajkaceratops* ~~according to the previous chapter~~ (see Section 3.2.2 for details). Despite these facts, no notable structural differences were observed between the teeth that would have supported ~~significant~~ appreciable variability within the dentition or taxonomic differences within the sample. According to Hwang (2005, 2010), the enamel microstructure has only a limited distinctive value among dinosaurs, however it could be informative to compare the above described features with the enamel of other taxa.

Based on the observations of Sander (1999), ~~the hypsilophodontid~~ *Thescelosaurus*, (an ornithomimid more basal than iguanodontians), had parallel crystallite enamel, but no columnar units were described in the case of this group, not like in the material studied here.

Sander (1999) and Hwang (2005) described a unique-looking wavy enamel, which was most plausibly a synapomorphic trait of the clade that consisted *Iguanodon* and hadrosaurids. Stanton Thomas and Carlson (2004) also depicted wavy enamel in the case of the hadrosaurid *Edmontosaurus*. As noted by Hwang (2005), *Tenontosaurus*, an iguanodontian more basal than ~~hadrosaurids, the latter group~~ but more derived than rhabdodontids (Ősi et al., 2012a; Werning, 2012), did not possess wavy enamel, but had a peculiar columnar arrangement with wavy unit boundaries, which can be interpreted as the precursor of the microstructure observed in more derived euornithomimids. The fact that the studied specimens from Iharkút (including the upper tooth without the primary ridge, which undoubtedly belonged to *Mochlodon*) lack the wavy unit boundaries, suggest that this feature appeared later than the emergence of rhabdodontids, and that ~~the latter group~~ rhabdodontids had plesiomorphic enamel microstructure within iguanodontians (sensu Sereno, 2005).

Dauphin et al. (1998) described the enamel microstructure of *Protoceratops*. They concluded that the teeth contained a “non-prismatic” outer layer, ~~which having a~~ thickness ~~was~~ less than 5  $\mu\text{m}$ , and a thick “prismatic” inner layer. The prisms were built up from “divergent acicular crystallites” and no “interprismatic substance” had been observed. The maximal enamel thickness was approximately 60  $\mu\text{m}$ . The cross section of the prisms were rounded and their diameter was usually around 5  $\mu\text{m}$ . They also stated that the prismatic appearance was somewhat irregular, in terms that the prisms were not always visible, their boundaries were sometimes underdeveloped (which was obvious in longitudinal section), and they could sometimes merge into thicker modules with a diameter up to 17  $\mu\text{m}$ . In addition, they noted that it is not clear whether such structures are homologous to the real prisms in the mammalian enamel, or not (see Supplementary Text 1 for further details). Nevertheless, it seems that the enamel microstructure depicted on the SEM micrographs of Dauphin et al. (1998) is ~~very~~ similar to that of the Iharkút sample. The enamel is mainly built up from columnar divergence units with rounded cross sections and the same dimensions in both cases. However, the units do not merge together in the case of the Iharkút specimens.

Hwang (2005) studied a few indeterminate pachycephalosaurid teeth and several different ceratopsians, including *Psittacosaurus*, the neoceratopsian *Leptoceratops* and *Protoceratops* ~~or,~~ as well as the more derived *Triceratops*. In the case of the pachycephalosaurids, she described incipient columnar units emerging from a thin basal unit layer (BUL) and grading into parallel crystallite

enamel toward the outer enamel surface (OES). The teeth of *Psittacosaurus* had enamel on both sides of the crown but the enamel was much thicker on the labial surface of the maxillary and on the lingual surface of dentary teeth. The thickness of the weakly enamelled side was 2-3  $\mu\text{m}$  in average, whereas 60  $\mu\text{m}$  on the other side. Apart from this, the enamel thickness was more or less constant on the same side of each teeth. It only increased a few microns in the very core of the ridges. The enamel contained mainly columnar divergence units with an average diameter of 6.5  $\mu\text{m}$  arisen from a thin basal unit layer (BUL). The units were continuous from the BUL to the outer enamel surface (OES). The cross section of the columnar units were triangular or diamond-shaped. She also found a few enamel tubules, especially in the inner half of the enamel.

Hwang (2005) noted that enamel covered only the labial side of maxillary and the lingual side of dentary teeth in the case of neoceratopsians. She found that the thickness of the enamel varied between 230-420  $\mu\text{m}$  in *Leptoceratops*, 60-120  $\mu\text{m}$  in *Protoceratops*, and 120-325 in *Triceratops*. Their enamel was built up from columnar units arisen from a thin BUL. The average diameter of the units was 10-15  $\mu\text{m}$  and they had a polygonal cross section that ranged from triangles to hexagons. Numerous voids and tubules were present between the modules.

Sander (1999) studied teeth, which belonged to an undetermined ceratopsian with a Campanian age and its teeth organized into dental batteries. He noted that the teeth were enamelled only on one side, and the average enamel thickness was around 150  $\mu\text{m}$ , which is much thicker than that of the Iharkút specimens. Similarly to the As in the case of the Iharkút sample, the thickness was relatively constant over the enamelled part of the teeth. The incremental lines were faint if present at all. He also mentioned a well-developed BUL, which was not observed in the Iharkút specimens. Apart from that, the remaining part consisted only of columnar units, which extended from BUL to OES and had triangular to polygonal cross sections. The diameter of the columns was more or less constant with an average of 15  $\mu\text{m}$ , which is three times greater than that of the Iharkút sample. The crystallites met the unit boundaries at an angle of 30-40° that means 60-80° regarding the crystallites in adjacent units, which is slightly lower than that value in the case of the material studied in the present paper.

Sander (1999) also described numerous enamel tubules, most of which was-were more or less perpendicular to the EDJ and extended through almost the entire enamel thickness along the unit boundaries. He also found columnar convergence units and even a convergence unit enamel in one case. He assumed that the latter convergence units are most likely related to the frequent presence of tubules, since-because crystallites commonly converge onto the tubules, independently of enamel type. However, Hwang (2005) had not encountered convergence units, despite that she also found densely packed tubules in the enamel of all neoceratopsians. She suggested that the enamel of *Psittacosaurus*, since it have only a few tubules, can be interpreted as a precursor of more advanced ceratopsians, because it only has a few tubules.

Judging from the longitudinal sections studied here, only a few tubules may present at the unit boundaries in the case of the Iharkút specimens, but according to Sander (1999), it might be difficult to differentiate tubules from etching artefacts, and sometimes they are filled up with diagenetic material. No tubule cross sections were observed here on the tangential or slightly oblique planes.

Both Sander (1999) and Hwang (2005) observed that the enamel surface of the most derived ceratopsids was covered with small distinctive globules and somewhat larger bumps which resulted in the irregular bulging of the OES in the sections. They also mentioned a similar feature in the case of hadrosaurids. It seems that this globular surface morphology represents a homoplastic trait for hadrosaurids and the latter group most derived ceratopsids, which is somehow related to the emergence of dental batteries. Similar morphology was not observed on the surface of the teeth from Iharkút, however, most of the specimens are slightly abraded, or dissolved with somewhat rounded edges. The latter This appearance, as it occurs more often in heavily worn teeth, might be

the result of ~~that accidental swallowing of the tooth-teeth was incidentally swallowed~~ with the food during the replacement process, which ~~and~~ then passed through the digestive tract of the animal.

Assuming that the teeth from Iharkút with primary ridges and curved scratches on their shallowly concave occlusal surfaces belonged to *Ajkaceratops*, it seems that ~~the latter this~~ genus was rather similar to *Psittacosaurus* than to neoceratopsians. If *Ajkaceratops* was indeed closely related to bagaceratopsids as suggested by Ósi et al (2010a), it retained some plesiomorphic features, such as the rarity of enamel tubules or the thin enamel layer on the lingual side of upper and on the labial side of lower teeth, which are both peculiar characteristics for a neoceratopsian. The fact that the present study failed to observe a BUL in the enamel of the Iharkút specimens is a striking feature, however, it might be explained by a presently unknown preservation issue.

The observation that the enamel of the aforementioned teeth are identical to that, which once presumably belonged to *Mochlodon* needs some explanation. It can be stated that the microstructure described here can be considered plesiomorphic within both examined groups. It would be parsimonious to assume that columnar enamel represents the ancestral state of at least the clade which unites ceratopsians and rhabdodontids. In that case, the parallel crystallite enamel of the basal ornithomimid *Thescelosaurus* would be a derived feature of that group. Although Sander (1999) considered the parallel crystallite arrangement to be ancestral for sauropsids due to its simplicity, he also noted that columnar enamel is the most common within this group. For example, according to Sander (1999) and Hwang (2005, 2010), ankylosaurians only differ from the ~~latter-purely columnar~~ arrangement by a thin parallel crystallite layer near the OES. Buffetaut et al. (1988, 1986), Line (2001), Stokosa (2005) and Hwang (2005, 2010) depicted columnar divergence units sometimes grading into incremental line dominated parallel crystallite enamel toward the OES in the case of several theropods. Based on the SEM micrographs presented in Sansom (1996), the emergence of columnar units might even be traced back as far as conodonts. Even if the ~~latter-columnar~~ features of conodonts are not necessarily homologous with that of the sauropsids, it seems that columnar arrangement in the tooth enamel is indeed a rather simple and evolutionary ancient micromorphology. In addition, remarkably convergent features, being most likely related to similarities on a cellular-level, such as the globular surface of enamel in both hadrosaurids and derived ceratopsians, were not unprecedented between ornithomimids and ceratopsians.

### 3.4. Dentine microstructure

#### 3.4.1. Description

The dentine of the Iharkút specimens is dominated by parallel tubules (see e.g. Fig. 87/D) following a more or less straight course or a gentle “S” curve through the entire thickness of the tissue from the EDJ to the pulp cavity. The diameter of these dentinal tubules is averaging around 1-2 µm and their spacing varies between 3-7 µm (Fig. 87/C). They often have tiny branching lateral offshoots along their length with a diameter of 0.3-0.7 µm. Each dentinal tubule once enveloped an elongated process of an odontoblast, the cell that secreted the dentine matrix, and which body was attached to the wall of the pulp cavity. ~~Since-Because~~ most of the dentinal tubules studied here contained air, they were filled up in a few cases with the epoxy resin used for embedding the specimens during sample preparation. The etching process then dissolved the material around the tubules, thus ~~revealed-revealing the~~ casts of them through the inversion of the surface (Fig. 87/A and B).

The other prominent feature of the dentine is a lamination that results in a line system approximately perpendicular to the course of the tubules (Fig. 87/E-G). The lines meet the EDJ at approximately 2-3° and have a spacing of 20-30 µm in longitudinal section. The spacing seems larger

when the sectioning plane is not perpendicular to the plane of the lamination. These bands (also called “von Ebner lines”) correspond to the smallest visible incremental lamination in dentine and are most probably the results of a daily growth rhythm (Erickson, 1996a; Hillson, 2005; Ungar, 2010), similarly ~~ly~~ to the cross striations in enamel.

### 3.4.2. Discussion and comparison with other taxa

Erickson (1996b) and Hill et al. (2005) made estimations on tooth formation and tooth replacement rates based on the counts of the above mentioned daily increments found in the dentine of different dinosaur taxa (including theropods, ankylosaurians, hadrosaurids and ceratopsians). They observed a mean incremental width ranging between 10 and 20  $\mu\text{m}$  with an average around 14-16  $\mu\text{m}$ . According to Erickson (1996b), the mean tooth formation rates varied between 132-933 days in the case of the different taxa (it was 381 days in average in the case of *Triceratops*), whereas Hill et al. (2005) described a tooth of a nodosaurid ankylosaur which took an estimated 75 days to form.

The formation of the MTM VER 2016.2551. #37L specimen from Iharkút (referred here as an upper tooth of *Mochlodon*) took at least 65 days based on the incremental line count in the mid-crown region (Fig. 87/G), however, it was not possible to analyse the entire longitudinal section, which would lead most plausibly to higher estimates. The total incremental line count for the MTM PAL 2012.18.1. #35D specimen (referred here as a lower tooth of *Mochlodon*) was 82, and 18 additional lines were reconstructed based on the average line spacing for the part with no visible traces of incremental features. The formation of the MTM V. 2010.113.1. #40G specimen (that ~~possibly belonged~~was provisionally assigned here to *Ajkaceratops*) took minimum 47 days.

Erickson (1996b) concluded that there is a limitation to the amount of dentine formed on a daily basis in teeth of amniotes. The width of the increments normally does not exceed 30  $\mu\text{m}/\text{day}$ . As a consequence, tooth formation (as well as tooth replacement) slowed down as larger tooth sizes were attained and dentine formation rates plateaued. It seems that the teeth from Iharkút had a short formation period (100 days or less), which is in agreement with their small size. However, based on the mean width of the increments that is almost twice as large as in the case of the taxa analysed by Erickson (1996b) and Hill et al. (2005), and that is close to the aforementioned plateau of 30  $\mu\text{m}$ , the dentinogenesis was somewhat rapid in the case of the Iharkút teeth.

The lack of numerous properly associated teeth belonging to the functional and the replacement tooth generations within the same dentary or maxillary bones did not allow us to make tooth replacement rate estimations here. Nevertheless, the observation that the tooth formation was relatively quick, suggest that the studied specimens from Iharkút might have had high tooth replacement rates most plausibly related to an abrasive diet; the same problem, which resulted in the emergence of dental batteries with hundreds of small teeth organized into multiple rows in the case of derived ceratopsians and hadrosaurids (Ostrom, 1966; Line, 2001; Dodson et al., 2004; Stanton Thomas and Carlson, 2004; Hwang, 2005; Bell et al., 2009; Erickson et al., 2012, 2015; Nabavizadeh, 2016).

## 4. Conclusions

It seems that the statistical methodology used here is powerful enough to efficiently separate different but resembling morphogroups (such as *Mochlodon* and *Zalmoxes*) if the sample number of each group is relatively large, thus it can be applied in the future to similar problems in the case of other localities or taxa. However, it could not adequately answer if *Ajkaceratops* teeth are missing

from the sample or those are morphologically almost identical to the teeth of *Mochlodon* and just a few of them are present.

The wear study revealed the existence of two different patterns within the sample. One can be characterized by straight, parallel microstriations, which are somewhat apicomesially-basodistally oriented on the upper teeth and basomesially-apicodistally oriented on the lower teeth, suggesting orthal or ~~very~~ slightly orthopalinal movement of the lower tooth row during the power stroke of the chewing cycle. ~~Since-Because~~ all of the upper teeth (without a primary ridge) that undoubtedly belonged to *Mochlodon* possessed this pattern, this chewing mechanism was associated here with the latter genus.

The other pattern observed here can be differentiated by its distinctive curved microstriations, which indicate a ~~significant-not negligible~~ palinal component that ~~progressively outpaced was highly synchronous with~~ the orthal closing of the jaw. It appeared only on a few teeth with usually shallowly concave wear facets and a primary ridge on the other side. ~~Since-Because~~ curved striations ~~were have~~ never ~~been~~ described in the case of ornithopods so far, but were found in the case of several neoceratopsians ([Varriale, 2008, 2011a,b, 2016](#)), ~~the-latterthis~~ pattern was ~~provisionally~~ associated here with *Ajkaceratops*, ~~a-the only~~ ceratopsian known from the locality. The ~~circum~~palinal movement was achieved either by adequately timed muscle contractions or by a passive mechanism, in which the jaw was pushed backward as the predentary traced an arc defined by its contact with the inner surface of the rostral bone during adduction ([Varriale, 2011a, 2016; Mallon and Anderson, 2014](#)).

According to the results of the histological study, no notable structural differences were observed within the sample, despite the fact that it contained teeth, which can be referred to both *Mochlodon* and *Ajkaceratops* based on their wear ~~patternfeatures~~. Both taxa possessed columnar divergence unit enamel with the same dimensions. This similarity, on the one hand, can be explained by that columnar enamel was widespread among sauropsids ([Sander, 1999](#)). On the other hand, derived ceratopsians possessed numerous enamel tubules and the enamel was limited to only one side of the teeth, whereas iguanodontians more derived than rhabdodontids had wavy unit boundaries ([Sander, 1999; Hwang, 2005](#)), thus the enamel described here can be considered plesiomorphic within both groups, and it might even be interpreted as the ancestral state within at least the clade that unified *Mochlodon* and *Ajkaceratops*. Based on the width and number of the incremental lines in the dentine, the formation of the teeth from Iharkút took only a short period (less than 100 days) and the dentinogenesis was rapid compared to other dinosaurian taxa ([discussed in Erickson, 1996b and Hill et al. 2005](#)), which might be related to a high tooth replacement rate.

According to the results presented in this article, there was a striking morphological and structural convergence between the teeth of *Mochlodon* and *Ajkaceratops*. The specimens that possessed curved microstriations are the first teeth that ~~most-likely~~ can be referred to ~~the-latter genus~~ *Ajkaceratops* (or to an as yet undescribed ceratopsian from the area). In addition, it seems that the analysis of wear pattern could be an efficient method for separating the morphologically similar and sometimes otherwise indistinguishable teeth of especially iguanodontian ornithopods and ceratopsians, which can be ~~very~~ important on those localities ~~wh~~ere only isolated teeth are available and in some Upper Cretaceous European sites where ceratopsians are expected but have not yet been found. Undisputable confirmation of some of the above mentioned assumptions would only be possible in the future through the discovery of cranial elements that contain properly associated teeth belonging to one or more tooth generations.

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## Figure legends

**Fig. 1.** Schematic representations of an upper (A-B) and a lower (C-D) neornithischian (*Mochlodon vorosi*) tooth of *Mochlodon vorosi* from Iharkút that possesses a primary ridge with the dental terminology and the measurements discussed in the text. **A:** mesial-distal view, **B:** lingual-labial view, **C:** mesial view, **D:** lingual view. Abbreviations: **L:** mesiodistal length of the tooth, **L<sub>pr</sub>:** mesiodistal length of the primary ridge, **H:** height of the tooth crown, **ang<sub>occl</sub>:** the angle formed by the wear facet and the opposite side at the apex of the tooth, **ang<sub>dist</sub>:** the angle between the line defined by the distal end and the lowermost point of the elevated rim around the distal indentation, and the line defined by the lowermost point of the distal rim and the tip of the primary ridge, **ang<sub>pr</sub>:** the angle between the line defined by the lowermost point of the distal rim and the tip of the primary ridge, and the line defined by the tip of the primary ridge and the lowermost point of the mesial rim, **ang<sub>mes</sub>:** the angle between the line defined by the tip of the primary ridge and the lowermost point of the mesial rim, and the line defined by the lowermost point and the mesial end of the mesial rim.

**Fig. 2.** Illustrative histograms, boxplots and Q-Q plots for the distribution analysis discussed in the text. **A:** normally distributed data, **B:** bimodally distributed data, **C:** distribution with a positive skewness, **D:** distribution with a negative skewness. Red curves on the histograms represent a theoretical normal distribution with the same mean and standard deviation as the given sample.

**Fig. 32.** Teeth without a well-developed primary ridge: upper teeth of *Mochlodon* from Iharkút (A-N) and upper teeth of *Zalmoxes* from Vălioara (O-T). MTM VER 2016.1604. #9 in labial (A), mesial (B) and lingual (C) views. MTM PAL 2012.17.1. #36A in labial (D) and lingual (E) views. MTM V. 2010.114.1. #41F in labial (F) and lingual (G) views. MTM VER 2016.1601. #15A in labial (H), ~~distal~~mesial (I) and lingual (J) views. MTM PAL 2012.17.1. #36E in labial (K), distal (L), lingual (M) and mesial (N) views. MFGI V.13.03073.4 #55 in labial (O), mesial (P), lingual (Q) and distal (R) views. MFGI Ob.3072 #45 in labial (S) and mesial (T) views. Scale bars represent 10 mm. Abbreviations: **d:** denticles, **er:** elevated rim, **gr:** shallow groove, **ps:** pressure scar or resorption circle, **r:** apicobasally oriented ridges, **wf:** wear facet.

**Fig. 43.** Teeth with a well-developed primary ridge: lower teeth of *Mochlodon* from Iharkút (A-E, H-RN), a lower tooth of a *Zalmoxes* from Vălioara (F-G), and teeth from Iharkút (SO-Z) that ~~possibly belonged~~ were provisionally referred here to *Ajkaceratops* based on their wear properties (further discussion in the text). MTM VER 2016.2555. #47 in lingual (A) and labial (B) views. MTM VER 2016.2554. #46 in lingual (C), distal (D) and labial (E) views. MFGI Ob.3042 #42 in lingual (F) and mesial (G) views. MTM VER 2016.2559. #51 in lingual (H), mesial (I) and labial (J) views. MTM VER 2016.2667. #49 in lingual (K) and distal (L) views. MTM PAL 2012.18.1. #35A in lingual (M) and distal (N) views. MTM PAL 2012.18.1. #35C in lingual (O), mesial (P), labial (Q) and distal (R) views. MTM V. 2010.113.1. #40A in lingual (S) and mesial (T) views. MTM V. 2010.113.1. #40E in lingual (U) and mesial (V) views. MTM V. 2010.113.1. #40F in lingual (W) and mesial (X) views. MTM V. 2010.113.1. #40G in lingual (Y) and distal (Z) views. Scale bars represent 10 mm. Concavities of the wear facets (assumably labial shelves) are indicated by arrows. Abbreviations: **d:** denticles, **er:** elevated rim, **fr:** faint ridges, **gr:** shallow groove, **ps:** pressure scar or resorption circle, **pr:** primary ridge, **sr:** secondary ridges, **wf:** wear facet.

**Fig. 54.** Histograms, boxplots and Q-Q plots of the mesiodistal length of the tooth (A<sub>-</sub>B, F<sub>-</sub>G) and the tooth crown height (C-E, H-J) in the case of the teeth with (A-E) and without a primary ridge (F-J). Red and green curves on the histograms represent ~~a~~ theoretical normal distributions with the same mean and standard deviation as ~~the a~~ given sample.

**Fig. 65.** Left dentary of a *Rhabdodon priscus* from Montplo (MC Mn 227) in labial view (**D**) with the enlargement of the tooth in the 3<sup>rd</sup> position in mesial (**A**) and lingual (**B**) views, as well as the schematic representation of the wear facet (**C**). Lower tooth of a *Mochlodon* from lharkút (MTM PAL 2012.18.1. #35A) in labial view (**E**) and the schematic representation of the wear facet (**F**). The wear facet (**G**) of an upper tooth of a *Mochlodon* from lharkút (MTM VER 2016.1604. #7) and its schematic representation (**H**). Wear facets of teeth from lharkút that possess curved microstriations and their schematic representations (**I-J**: MTM VER 2016.2847 #72, **K-L**: MTM VER 2016.2846. #71, **M-N**: MTM V. 2010.143.1. #40E). Scale bars represent 10 mm apart from **D**, on which it represents 10 cm. Abbreviations: **scr**: scratches, **tra**: transverse axis of the wear facet, **wf**: wear facet.

**Fig. 76.** Enamel microstructure of the teeth from lharkút. **A-B**: Longitudinal section of the strongly enamelled side of a *Mochlodon* upper tooth (MTM VER 2016.2551. #37L). **B**: Longitudinal section of the strongly enamelled side of a tooth (MTM V. 2010.113.1. #40A) that ~~possibly belonged~~ was provisionally referred here to *Ajkaceratops*. **C**: Columnar enamel is visible on the slightly oblique longitudinal section of the latter tooth. **D-E**: Longitudinal sections of the weakly enamelled side of a *Mochlodon* upper tooth (MTM PAL 2012.18.1. #35D). The enamel is homogenous when viewed under polarized light, but the SEM revealed that it is dominated by incremental lines. **F**: Longitudinal section of the weakly enamelled side of a *Mochlodon* upper tooth (MTM VER 2016.2551. #37L). The enamel is built up from parallel crystallites. **G**: Columnar divergence units on the longitudinal sectional plane of a tooth (MTM V. 2010.113.1. #40A) that was referred here possibly belonged to *Ajkaceratops*. Planes of crystallite convergence are marked by dashed lines. **H**: Close-up of the latter. The crystallite bundles are indicated by arrows. **I**: Columnar units are cancelled out by incremental lines on the longitudinal sectional plane of a tooth (MTM V. 2010.113.1. #40F) that was referred here possibly belonged to *Ajkaceratops*. **J-K**: Slightly oblique cross sections of the columnar units in the enamel of a tooth that was referred here to *Ajkaceratops* (MTM V. 2010.113.1. #40A) and in a *Mochlodon* upper tooth (MTM VER 2016.2551. #37L), respectively. **L**: Cross section of a secondary ridge in the case of the latter tooth. Scale bars represent 50 µm on **A-D**, 20 µm on **E-G** and **I-K**, 5 µm on **H**, whereas 500 µm on **L**. Abbreviations: **cd**: columnar divergence units **d**: dentine, **dt**: dentinal tubules, **e**: enamel, **il**: incremental lines.

**Fig. 87.** Dentine microstructure of the teeth from lharkút. **A**: Epoxy infillings of dentinal tubules revealed by the inversion of the surface due to differential etching on the longitudinal sectional surface of a *Mochlodon* upper tooth (MTM VER 2016.2551. #37L). **B**: The same phenomenon on the longitudinal sectional surface of a tooth that was provisionally referred here possibly belonged to *Ajkaceratops* (MTM V. 2010.113.1. #40F). **C**: The cross section of the dentinal tubules in the case of the latter tooth. **D-E**: Longitudinal and cross section of a *Mochlodon* upper tooth (MTM PAL 2012.18.1. #35D). **F-G**: The incremental lines in the dentine are clearly visible on the longitudinal and cross sectional surface of a *Mochlodon* upper tooth (MTM VER 2016.2551. #37L). Scale bars represent 50 µm on **A-C**, 100 µm on **D-E** and 500 µm on **F-G**. Abbreviations: **d**: dentine, **dt**: dentinal tubules, **e**: enamel, **il**: incremental lines, **pc**: pulp cavity.

**Fig. 8.** Summary phylogeny of main ornithomorphs (**B**) and ceratopsians (**C**) mentioned in this article, and their position within Genasauria (**A**). The basic features of enamel microstructure and tooth wear pattern are shown (if available) in a generalized manner above each taxa. The colours of the branches represent different enamel types on **B** and different jaw mechanisms on **C**. Uncertainties related to the evolution of these features are indicated by question marks. See further discussion in the text.