Wear pattern, dental function and jaw mechanism in the Late Cretaceous ankylosaur *Hungarosaurus*

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ABSTRACT

Feeding in thyreophoran dinosaurs is poorly understood. Although the group existed for over 130 million years, only the Early Jurassic basal thyreophoran *Scelidosaurus harrisonii* and the Late Cretaceous ankylosaurid *Euoplocephalus tutus* have been studied from this perspective in detail. In contrast to the earlier, conservative hypothesis of a simple "orthal pulping" feeding mode with no or limited tooth–tooth contact, recent studies have demonstrated precise dental occlusion with differing jaw mechanisms in these two species. Here we describe the first detailed study of feeding related characters in a nodosaurid ankylosaur, *Hungarosaurus tormai*, from the Late Cretaceous of Hungary. Dental wear patterns comprising small, apical, low-angled facets on the maxillary and steep, extended, bowl-like facets on the dentary teeth reveal sophisticated tooth–tooth contact in this basal nodosaurid. The presence of two different scratch generations (vertical and low-angled) on the dentary teeth unambiguously demonstrate a multiphasic powerstroke, which is further supported by the morphology of the quadrate-articular and mandibular symphyseal joints, and by the architecture of the reconstructed jaw adductors. Chewing started with an initial slicing phase associated with orthal movement that was followed by a retractive powerstroke with significant occlusal contact. Due to the curved tooth rows, these movements were probably facilitated by some mediolateral translation and/or axial rotation of the mandibles to produce precise shearing along the whole tooth row. These results demonstrate that complex jaw mechanisms and dental occlusion were more widespread among thyreophorans than thought previously and palinal movement was present in at least two ankylosaurian lineages.

INTRODUCTION

Feeding in thyreophoran dinosaurs (i.e. basal thyreophorans, stegosaurs and ankylosaurs) has generally been regarded as uniform, with a relatively simple orthal jaw mechanism and an absence of systematic occlusion, a feeding mode referred to as "orthal pulping" (Owen, 1861; Galton, 1986; Weishampel, 1984; Weishampel and Norman, 1989; King, 1996). Although some earlier studies discussed the feeding and masticatory apparatus of ankylosaurs (e.g. Owen, 1861; Nopcsa, 1928; Russell, 1940; Haas, 1969; see reviews in Barrett, 2001, and Rybczynski and Vickaryous, 2001), the first detailed study on ankylosaur jaw mechanisms and dental function was that of Coombs (1971) who studied among others *Euoplocephalus tutus*, *Panoplosaurus mirus* and *Edmontonia rugosidens*. Scratches on the dental wear facets indicated simple, vertically oriented orthal jaw closure, but suggested that the orientation of the jaw adductors implied the use of anteroposterior mandibular movements during jaw closure (Coombs, 1971). Rybczynski and Vickaryous (2001) reviewed the evidence for jaw function in *Euoplocephalus* and examined the wear patterns of additional specimens (e.g. TMP 96.75.1): this study demonstrated the unambiguous occurrence of sophisticated tooth–tooth contact during a retractive powerstroke (i.e. palinal movement) along with a mediolateral displacement of the dentary tooth row during mandibular closure. A similar mechanism involving orthal adduction and retractive shearing has also been inferred for *Saichania chulsanensis* (Carpenter et al., 2011).

Among other thyreophorans, Barrett (2001) suggested the presence of a precise occlusion in combination with a strictly orthal mandibular closure in the Lower Jurassic basal thyreophoran *Scelidosaurus harrisonii*. Examination of the maxillary and dentary teeth and wear facets revealed an unusual wear pattern in this taxon: all of the scratches are vertically oriented, but whereas the wear facets on the dentary teeth are bowl-like and steeply inclined, those of the opposing maxillary teeth are small and apically restricted. It was suggested that this combination of features indicated a puncture-crushing feeding mechanism that lacked translational mandibular movements (Barrett, 2001).

Regarding nodosaurid ankylosaurs, Lambe (1919:41) described wear facets on the inner side of the in situ maxillary teeth of *Panoplosaurus mirus* and noted that "the upper teeth bit outside the lower ones". Sternberg (1928:plate III) mentioned possible wear on teeth referred to *Edmontonia longiceps* and Coombs (1990) also discussed all of these teeth referred to *Panoplosaurus* and *Edmontonia*, but neither of these authors described the details of the wear facets or their functional implications.

These initial observations clearly indicate that the feeding mechanisms of thyreophoran dinosaurs, including basal forms, was probably more sophisticated than recognized previously and, at least in some derived ankylosaurids, a complex multiphasic chewing action can be reconstructed. Nodosaurid ankylosaur feeding, however, has not been studied in detail.

Hungarosaurus tormai is a medium-sized (total body length 4.5 m) nodosaurid ankylosaur from the Santonian Csehbánya Formation of Iharkút, western Hungary (Ősi, 2005). Based on seven partial skeletons and hundreds of isolated elements (Ősi and Makádi, 2009, Ősi and Prondvai, 2013), this species is one of the best known European ankylosaurs. Cranial remains, including associated mandibles with in situ dentition, provide an excellent opportunity to study the mandibular morphology, jaw joint, attachment areas of cranial msuculature, dentition, and dental wear patterns. The aim of this study is to use this material to reconstruct the feeding mechanism of *Hungarosaurus* by elucidating its patterns of dental occlusion and mandibular movements.

MATERIAL AND METHODS

Material

Cranial material of *Hungarosaurus* is known from two associated skeletons and various isolated elements (Fig. 1). The holotype skeleton includes the following: left and right premaxillae (MTM 2007.26.1-2), vomer (MTM 2007.26.3), right postorbital+jugal (MTM 2007.26.4), fragmentary left prefrontal (MTM 2007.26.5), fragmentary left lacrimal (MTM 2007.26.6), fragmentary left frontal (MTM 2007.26.8), fragmentary pterygoid (2007.26.9), right quadrate (MTM 2007.26.10, Fig. 1A), fragmentary left quadrate (MTM 2007.26.11), condylus occipitalis (MTM 2007.26.12), 22 teeth with roots (MTM 2007.26.13), and a fragmentary right mandible (MTM 2007.26.15, Fig. 1B, D, F–H). The referred, fifth partial skeleton includes the left mandible (MTM 2007.25.1, Fig. 1C) and the right dentary (MTM 2007.25.2, Fig. 1D). Besides the associated skeletal material, only an isolated partial skull (skull roof+basicranial+occipital regions, MTM PAL 2013.23.1, Ősi et al. 2014) and the posterior (post-dentary) part of an isolated mandible (MTM PAL 2013.39.1.) have been included in this study.

Methods

Reconstruction of the jaw adductors in *Hungarosaurus* was based mainly on the positions of their origination and insertion scars as inferred for other ankylosaurs in the work of Haas (1969), Holliday (2009) and (Carpenter et al. 2011).

Dental macro- and microwear patterns were based on the gross morphology of individual wear facets, and documentation of scratches and pits on the wear surfaces. Following Ungar (1996), pits are defined as having length-width ratios < 4:1, whereas in scratches, this ratio is > 4:1. A Nikon Eclipse LV100 light microscope was used to examine the morphology and orientation of the wear facets and macrowear features. Additional details of the macrowear features, including the morphology of the enamel-dentine interface (EDI), and mapping of microwear patterns were documented using a Hitachi S-2360N scanning electron microscope (SEM).

Molds of in situ tooth crowns from *Hungarosaurus* were prepared following the procedure described by Grine (1986). Specimens were cleaned with cotton swabs soaked with ethyl alcohol. Impressions were made using Coltene President Jet Regular (polysiloxane vinyl) impression material, and casts were made with EPO-TEK 301 epoxy resin.

Details of the alveoli, tooth roots and replacement teeth were also studied using computed tomographic (CT) scanning of the two mandibles from the fifth skeleton (2007.25.1, 2007.25.2) at the Institute of Diagnostic Imaging and Radiation Oncology in the University of Kaposvár. For the CT scanning a Siemens Stomatom Definition Flash machine was used. Fossils were scanned using a resolution of 1.0×0.6×0.6 mm in three different directions (sagittal, horizontal and coronal). CT scans were manipulated using RadiAnt DICOM Viewer Software.

Institutional abbreviations

AMNH – American Museum of Natural History, New York, NY, USA; **DMNH**, Denver Museum of Natural History, Denver, CO, USA, **MTM** – Hungarian Natural History Museum, Budapest, Hungary; **NHMUK** – The Natural History Museum, London, UK; PIN, Paleontological Institute of the russian Academy of Sciences, Moscow, Russia; **ROM** – Royal Ontario Museum, Toronto, Canada; **TMP** – Royal Tyrrell Museum of Paleontology, Drumheller, AB, Canada; **ZPAL** – Institute of Palaeobiology of the Polish Academy of Sciences, Warsaw, Poland.

RESULTS

Skull

Cranial remains of the holotype specimen are disarticulated and in some cases fragmentary, so they do not allow a precise skull reconstruction for *Hungarosaurus*. Nevertheless, the morphology of these elements, together with some isolated specimens (e.g. MTM PAL 2013.23.1, Ősi et al., 2014), suggests that the overall skull proportions and the positions of the different cranial openings and tooth rows were similar to those of other nodosaurid ankylosaurs, especially *Pawpawsaurus* (Lee, 1996), *Sauropelta* (Carpenter and Kirkland, 1998) and *Silvisaurus* (Eaton, 1960; Carpenter and Kirkland, 1998). *Hungarosaurus* probably had a skull that was longer than wide and that was approximately two times wider in the orbital region than at the rostrum. The central portion of the skull roof in MTM PAL 2013.23.1 indicates that the rostrum slopes anteroventrally from the orbital region. This specimen shows that the basisphenoid is unusually ventrally oriented, indicating a deeper post-orbital (i.e. temporal) region relative to that of other ankylosaurs (e.g. *Sauropelta*, Carpenter and Kirkland, 1998:fig. 9; *Pawpawsaurus*, Lee, 1996:fig. 5).

Based on the strongly ventrally curved anterior part of the left dentaries (MTM 2007.25.1, MTM 2007.25.2, Fig. 1C, E), and the presence of wear on the anterior dentary teeth that were presumably caused by occlusion with the premaxillary teeth, it is likely that the anterior part of the rostrum (i.e. premaxilla) curved downwards with an angle of at least 40° relative to the maxilla. The premaxillae have a rounded anterior margin with an inverted U-shaped notch medially, and anteriorly and anterolaterally they bear rugose ornamentation that extends into the rostrolateral edge of the scalloped oral margin. Medioventrally, the premaxilla possesses an anteroposteriorly short, strongly dorsally concave secondary bony palate. Laterally and slightly anterolaterally the premaxilla (MTM 2007.26.1-2) is bordered by a massive, ridge-like tomium that would have supported a rhamphotheca. Between this lateral margin and the premaxillary alveoli a deep groove is present (see Ősi, 2005:fig. 2A). The type premaxilla bears 3–4 alveoli, though the posterior segment of the premaxillary tooth rows are broken, thus the total number of premaxillary alveoli was probably higher. Although the maxillary tooth row is unknown in the associated skeletons of *Hungarosaurus*, the mandibles show a tooth row that is strongly arched both horizontally and vertically (Fig. 1C, E), a feature typically seen in nodosaurid ankylosaurs with premaxillary teeth (Coombs, 1971; Lee, 1996).

The overall shape of the quadrate and the proportions of the pterygoid and quadratojugal processes in the holotype specimen (MTM 2007.26.10, Fig. 1A) are reminiscent of those of *Pawpawsaurus* (Lee, 1996). This implies an anteroventrally oriented quadrate with distal articular condyles that are slightly rotated anteromedially. The distal articular surface is relatively robust, rhombus-shaped, and anteroposteriorly expanded (Fig. 1A): the slightly convex medial condyle is slightly longer anteroposteriorly than the lateral condyle. The medial and lateral condyles are confluent and are not separated by an intercondylar groove, forming a continuous, slightly obliquely oriented, and convex condylar surface.

Intermandibular and quadrate–articular joints

The mandible of *Hungarosaurus* is deep dorsoventrally and slightly arched in lateral view (Fig. 1C-E). Its anterior part (from the 7th alveolus) is strongly curved ventrally with an angle of at least 40° relative to the horizontal plane. As in probably all ankylosaurs (Vickaryous et al., 2004), the symphysis of *Hungarosaurus* was also unfused, and the two mandibles were connected via a short (ca. 2 cm), most probably mobile symphyseal surface (see below). The predentary is not preserved. The symphyseal region is markedly curved medially to form a relatively wide, rounded anteroventral margin for the oral cavity (Fig. 1G). The medial surface of the symphysis is ornamented by 4–5 subhorizontal ridges for attachment of the fibrocartilagous pad in the symphysis. Anterior to the first alveolus, an approximately 2 cm long, crest-like diastema is present. The triangular coronoid process is high, ending approximately 3 cm above the occlusal plane. The dorsal-most part of the coronoid process is almost two times thicker than its more ventral parts. The posterior edge of the coronoid process is steeply inclined, slightly convex and its ventral-most part borders the glenoid laterally. The external mandibular fenestra is closed. The retroarticular (post-glenoid) process is very short (15 mm in MTM 2007.26.15), massive, and triangular in outline. The glenoid is oval in outline, slightly concave and wider transversely than anteroposteriorly long (29 x 26 mm in the holotype [MTM 2007.26.15. Fig. 1D]). There is no transverse ridge or buttress on the posterior side of the glenoid. Based on the right quadrate (MTM 2007.26.10) and the post-dentary part of the right mandible (MTM 2007.26.15) preserved in the holotype skeleton, the glenoid is 5-6 mm longer anteroposteriorly and 4-5 mm wider lateromedially than the quadrate articular surface. The quadrate articular surface in *Hungarosaurus* is relatively longer anteroposteriorly than that of *Euoplocephalus*, and the glenoid is not as expanded anteroposteriorly (1.5–2 times) relative to the quadrate condyles as that demonstrated in *Euoplocephalus* (Rybczynski and Vickaryous, 2001:fig. 14.5).

Reconstruction of the jaw adductors

The lack of a *Hungarosaurus* skull with preserved palatal and temporal regions prevents the recognition of many muscle origination and insertion sites and precise reconstruction of many jaw adductor orientations. Nevertheless, the preserved right quadrate (MTM 2007.26.10) of the holotype and numerous mandibular retains nicely preserved muscle insertion surfaces that help to infer the architecture and the approximate sizes of the jaw adductors (Fig. 2). The anterior surface of the quadrate just above the distal quadrate condyles, is the origin of m. adductor mandibulae posterior (MAMP; Haas, 1969; Carpenter et al., 2011), and is a slightly concave, smooth area on MTM 2007.26.10 which does not bear any crests or protuberances.

The mandibular remains of the holotype material (MTM 2007.26.15) and that of the fifth, referred skeleton (MTM 2007.25.1) show the main features of the lower jaw. The muscle attachment areas, especially in the medial and ventral sides of the mandibular adductor fossa are, however, relatively poorly preserved. An isolated post-dentary part of the mandible (MTM PAL 2013.39.1.), being morphologically almost identical with the former specimens (i.e. in the shape of coronoid process, length of the retroarticular process, glenoid shape and relative size, and external ornamentation), is tentatively referred to *Hungarosaurus* and used here to demonstrate the main adductor insertion regions (Fig. 2B–D). Haas (1969) suggested that a triangular area anterior to the mandibular glenoid in *Euoplocephalus* was the insertion of MAMP, whereas Carpenter et al. (2011) concluded that in *Saichania* it attached to the anterior edge of the articular. Holliday (2009) proposed that MAMP in sauropsids inserted into the medial part of the mandibular fossa. In *Hungarosaurus*, the area anterior to the glenoid is not very well preserved on the type mandible but this region is clearly lateromedially wide and anteroposteriorly extended and could have served as the attachment area of MAMP.

Regarding mm. pterygoideus, their insertion surfaces can be detected on the mandibles, but their origins cannot be examined. All previous authors working on ankylosaur jaw adductors (Haas, 1969; Coombs, 1971; Holliday, 2009; Carpenter et al., 2011) agree that, as in crocodiles (Iordansky 1964), the insertion of m. pterygoideus ventralis (MPTV) is on the lateral and lateroventral surface of the posterior end of the mandible (i.e. lateroventral surfaces of the articular and angular). This part of the mandible in *Hungarosaurus* is lateromedially wide and anteroposteriorly expanded, being generally similar to those of other ankylosaurs suggesting a well-developed MPTV comparable to other forms (Fig. 2B, C). Haas (1969) proposed that the insertion surface of m. pterygoideus dorsalis (MPTD) was on the ventral and lateroventral surfaces of the posterior end of the mandible, in a similar postion to that of MPTV. Conversely, Holliday (2009) reconstructed it on the medial surface of the articular, whereas the anterior edge of the articular was suggested for *Saichania* (Carpenter et al., 2011). In *Hungarosaurus* there is no obvious, unambiguous insertion for MPTD, but the bony surface between the glenoid and the insertion area of MAMP seems resonable.

As noted by others (e.g. Ostrom, 1961; Carpenter et al., 2011), the mm. adductor mandibulae externus (MAME) would have been important adductors in ankylosaurs; the well-developed coronoid eminence and the extended origination surfaces in the dorsal part of the temporal region suggest that these external adductors were relatively more developed in ankylosaurs than in extant crocodilians (Iordansky, 1964; Busbey, 1989). The origins of these muscles cannot be reconstructed in *Hungarosaurus*, but the mandibular remains show attachment surfaces inferred to represent their insertions (Fig. 2B–D). Earlier workers (e.g. Holliday, 2009) suggested that m. adductor mandibulae externus profundus (MAMEP) inserted on the coronoid eminence, and Haas (1969) specified an attachment to its medial side. The coronoid of *Hungarosaurus* is strongly extended dorsally, even more so than in *Panoplosaurus* (Holliday, 2009) or *Euoplocephalus* (AMNH 5405). The pointed, dorsal end of the coronoid process is two times thicker than its ventral part and ornamented by numerous parallel striae indicating extensive attachments for muscles and/or aponeuroses in this area.

The available evidence suggests that the jaw adductors of *Hungarosaurus* were similar to those of other ankylosaurs, with highly developed MAME relative to mm. pterygoideus in contrast to the situation in extant crocodilians. MAME had an anteroventral-posterodorsal line of action (Fig. 2A), whereas the mm. pterygoideus had a significant lateromedial component in their line of action, as seen in most sauropsids (Holliday, 2009).

Dentition and tooth morphology

Tooth rows

As in other ankylosaurs (particularly nodosaurids, Vickaryous et al., 2004), *Hungarosaurus* possessed unusual sinuous premaxillary-maxillary and dentary tooth rows. This is due to the marked curvature of the tooth rows both in the horizontal and vertical planes (Fig. 1C, E) and resulted in very complex jaw mechanisms to permit occlusion, at least in some species (Coombs, 1971; Rybczynski and Vickaryous, 2001, see below). As in *Gargoyleosaurus* (DMNH 27726), *Silvisaurus* (Eaton, 1960), *Pawpawsaurus* (Lee, 1996) and *Sauropelta* (Ostrom 1970), the anterior upper tooth row of *Hungarosaurus* includes the premaxillary dentition. In ventral view, the anterior-most section curves medially to form a slightly bent, medially concave premaxillary tooth row. Besides this curvature, it is likely that the premaxillary tooth row curved ventrally at an angle of approximately 40° relative to the maxillary segment of the upper tooth row as indicated by the orientation of the dentary tooth row and evidence of occlusion between the premaxillary and anterior-most dentary teeth. At the premaxilla–maxilla junction the opposing tooth rows are closest to each other; the shortest distance between these teeth is approximately 5 cm in the holotype of *Hungarosaurus* and ca. 3.5 cm in *Pawpawsaurus*. The orientation of the premaxillary teeth in *Hungarosaurus* is not clear; only a small, unworn tooth is preserved embedded in the medial surface of the holotype right premaxilla. Eaton (1960:fig. 3) illustrated markedly linguoventrally oriented premaxillary teeth in *Silvisaurus*, whereas *Gargoyleosaurus* bears ventrally or slightly labioventrally pointed premaxillary teeth.

The orientations of the maxillary tooth rows in *Hungarosaurus* can be reconstructed only on the basis of the presumably complementary tooth row orientation of the mandibles (MTM 2007.25.1, 2007.25.2, Fig. 1C, E, G). The dentary tooth row suggests that around the premaxilla-maxilla junction the upper tooth row gradually curves laterally forming the posteriorly divergent maxillary tooth row. A similar orientation is present in most ankylosaurs, but in some ankylosaurids (e.g. *Euoplocephalus* AMNH 5405, *Saichania* *chulsanensis* Maryańska, 1977) the anterior portion of the maxillary tooth row is also divergent. The orientation of the maxillary teeth in *Hungarosaurus* is unknown. In other ankylosaurs, including both nodosaurids and ankylosaurids, the anterior maxillary teeth are vertically oriented whereas the posterior half or one-third of the maxillary teeth tend to be oriented markedly labioventrally. It not clear how sinuous the maxillary tooth row of *Hungarosaurus* was, and it is unknown if is was as bowed as in *Pawpawsaurus*, or straight, as in *Silvisaurus* (see Carpenter and Kirkland, 1998). Nevertheless, the most complete mandibular tooth rows preserved in MTM 2007.25.1 and MTM 2007.25.2 indicate that the maxillary teeth opposite to the 14th to 17th dentary teeth are in a slightly more ventral position than the anterior ones.

Tooth morphology

The tooth morphology of *Hungarosaurus* was described earlier (Ősi, 2005; Ősi and Makádi, 2009), so here only a few important characters are mentioned. The dentition of *Hungarosaurus* is homodont, and composed of labiolingually flattended, mesiodistally denticulate teeth. In situ dentitions are known only in the dentary. Dentary teeth are closely packed in an en echelon arrangement (Fig. 3A), so that the mesial margin of each tooth crown lies lingual to the distal margin of the tooth mesial to it. The mesially situated dentary teeth are slightly smaller (mesiodistal width: 7 mm) than the distal ones (8–9 mm). Seven coarse denticles are present on the mesial and distal crown margins. Each tooth crown bears a prominent, slightly crenelated cingulum both labially and lingually (Fig. 3). The exact orientation of the dentary teeth is not completely clear as both mandibles (MTM 2007.25.1 and MTM 2007.25.2) preserving in situ dentary dentitions are slightly compressed lateromedially. However, on the basis of wear facet morphology, it is suggested that the dentary teeth would have had an orientation complementary to that of the upper teeth to enable occlusion (see below). In the case of the mandibular dentition, replacement teeth should be positioned ventrolingual to the functional ones. On the functional teeth, the lingual side of the upper half of the root and the base of the tooth crown (including the lingual side of the cingulum) bear a shallow groove, most probably to accomodate the replacement tooth (Fig. 3E: see below).

The only preserved premaxillary tooth, being two times smaller than the other teeth associated with the holotype, is badly preserved, but no cingulum can be observed, as is also the case in *Gargoyleosaurus* (Kilbourne and Carpenter, 2005).

In situ maxillary teeth are unknown in *Hungarosaurus* but a few specimens, among others associated with the holotype material, can be identified (Fig. 3J–K). Although Coombs (1990:269) noted that in “ankylosaurs there appears to be no way to distinguish upper teeth from lowers”, in *Hungarosaurus* the maxillary teeth can be distinguished from the dentary teeth. All of the teeth referred to *Hungarosaurus* can be characterized by a shallow groove on the upper part of the root and this groove continues and deepens onto the basal part of the crown. Due to this furrow, the cingulum on this side is not straight or slightly concave in occlusal view, as it is on the other side, but is slightly sinusous. A similar groove, though not as well developed as in *Hungarosaurus*, can be also observed, for example, in *Gargoyleosaurus* (DMNH 27726). This groove, related to tooth replacement, always appears on the lingual side of the dentary and maxillary teeth (Fig. 3C, E, G, J). Another feature characterstic of almost all *Hungarosaurus* teeth is the wear facet. In almost all toothed tetrapods the upper teeth are positioned labially relative to the dentary teeth: thus in forms with occlusion, dental wear is present on the lingual side of the upper and the labial side of the dentary teeth. So, if an isolated tooth possesses both the basal groove and the wear facet on the lingual side, then it is certainly an maxillary tooth (Fig. 3C, J); if the wear facet is on the other side then it is from the dentary (Fig. 3E, G). Except for these differences (and the nature of the wear facets, see below), the maxillary teeth are identical in morphology with the dentary ones (Fig. 3I–K).

Tooth replacement

Replacement teeth can be seen in various thyreophorans including, *Scelidosaurus* (NHMUK R1111), *Tarchia gigantea* (PIN N3142-250), *Pinacosaurus grangeri* (ZPAL MgD-II/1), and *Gargoyleosaurus* (DMNH 27726). Independently of their alveolar position, replacement teeth are always medial to the functional tooth, but their degree of eruption varies along the tooth row and between taxa. In case of the left (MTM 2007.25.1) and right (MTM 2007.25.2) dentaries of the fifth partial skeleton of *Hungarosaurus*, most of the medial side is covered with hard sandstone preventing study of the replacement teeth. However, preparation of the medial side of the left dentary between the 6th and 11th alveolus revealed the presence of replacement teeth in the 6th, 8th, 9th, and 11th alveoli. These replacement teeth are identical in morphology with the functional teeth and are of the same size.

We also used CT scanning to investigate the interior structure of the alveoli and that of the tooth row. Unfortunately, the dentaries contain significant amounts of pyrite, especially within the alveoli around the tooth roots, which strongly obscures the distal ends of the functional tooth roots and the replacement teeth. Although replacement teeth can be seen in the anterior region ventromedial to most alveoli, on the CT scans only some questionable data suggest their presence.

Dentary tooth wear

Of the preserved in situ and isolated teeth referred to *Hungarosaurus* almost all exhibit some wear. Isolated teeth, however, cannot be definitively referred to specific tooth positions (though they can be assigned to tooth rows, see above), thus in the description mainly in situ teeth preserved in the mandibles MTM 2007.25.1 and MTM 2007.25.2 (belonging to one of the associated skeletons) are used. These mandibles do not bear all of the teeth in the tooth row, and teeth are exposed in labial view only. Consequently, the wear patterns described herein are all from the labial surface (Fig. 4). The preserved teeth, available from the anterior (1st to 6th), central (7th to 14th) and posterior (15th to 18th) segments of the tooth row, are all characterized by extensive wear facets, i.e., the external enamel layer was usually completely missing in the worn area. We describe the wear patterns on the in situ dentary teeth, but also provide informtion on the gross morphology of tooth wear on several associated maxillary teeth from the holotype skeleton.

Anterior region

In each hemimandible the anterior-most tooth preserved with wear is the 4th tooth, which is in the anteroventrally-curved region of the dentary (Fig. 4A). Although present originally, the teeth are missing from the first three tooth positions in all preserved mandibles. The tooth has a procumbent, mesiodorsal orientation, with its long axis forming an angle of approximately 50° relative to the occlusal plane. The apical two-thirds of the left 4th dentary tooth are missing, so wear can only be seen on its basal region. As typically seen on the other teeth of *Hungarosaurus*, the cingulum is eroded and forms a flush, sloping surface with the labial surface of the crown. In this case, the enamel is usually completely absent and is preserved only on the mesial and distal parts of the crown. A few, short (< 1 mm) mesiobasally–apicodistally oriented scratches (35° relative to the horizontal plane) are present on this surface. The right 4th tooth is more complete (though it was broken from the jaw during preparation, Fig. 4A) and has an extensive abraded surface covering almost 70% of its labial surface (Fig. 5A, B). This area is so worn that the pulp cavity is also exposed (Fig. 5A, B). Although the apex of the crown is not preserved, it is clear that the wear facets, positioned in the middle of the crown, are steeply inclined (ca. 80° relative to the horizontal plane) and extend basally into the cingulum. Because the crown base is labiolingually expanded, the wear facet bends slightly labially. Scratches are dominant, closely packed and usually no longer than 0.5 mm. Besides scratches a few triangular pits (≤ 60 µm × 20 µm) are also present in the apical and mesial regions. Two different scratch generations can be identified: 1) shallow, thin, elongate scratches mainly in the apical half of the crown, with an orientation of 13° and 60° relative to the apicobasal axis of the crown and to the horizontal plane, respectively (Fig. 5B); and 2) mesiobasally-apicodistally oriented scratches (at 40° relative to the horizontal plane) in the central and more basal parts of the wear facet.

The 6th tooth is preserved in both hemimandibles (Fig. 4A, B). Each has an orientation of 65° relative to the occlusal plane. Both lack the apical region. Wear facets cover approximately 50% of the left and 70% of the right tooth. The wear facets of both teeth are quite similar to that of the right 4th tooth, being positioned in the center of the crown, steeply inclined, and extending down within the cingulum. The 6th dentary teeth bear dominantly mesiobasally-apicodistally oriented scratches (at 25–40° relative to the horizontal plane) in the base of the wear facet, which is the curved surface of the abraded cingulum (Fig. 4A). A few scratches are also present that extend subparallel to the apicobasal crown axis. The enamel-dentine interface (EDI) is flush distally and weakly stepped mesially and mesiobasally. Some sub-vertically oriented pits are present on the left 6th tooth.

Central region

The 7th tooth is preserved only in the right dentary, but is in poor condition and no details of the wear pattern can be recognized. The 8th to 10th teeth are present only in the right dentary. Whereas the 8th tooth has an orientation of 77° relative to the occlusal plane, the axis of the 10th tooth is perpendicular to the occlusal plane. All three teeth show a similar wear pattern, in having a centrally positioned wear facet covering approximately 50–60% of the crown, with the denticulate mesial and distal margins preserved unworn. Wear facets extend from the apex to the base of the crown, and the cingulum is almost completely worn. The dominant wear patterns on these teeth are the mesiobasally-apicodistally oriented (approximately 15–30° relative to the horizontal plane) scratches (Fig. 5C, E, F). These scratches are more robust and longer (< 3 mm) at the base of the wear facet (i.e. at the eroded surface of the cingulum) than in the apical region, and some of them (e.g. on the 10th tooth) are not straight, but are slightly curved having a concave side apically (Fig. 4A). The apical regions of these teeth exhibit some differences. Whereas the 8th tooth bears few short scratches parallel to the tooth axis, on the apical two-thirds of the 9th tooth this type of scratch is more frequent. The wear facet on the 9th tooth is so well developed that the pulp cavity is exposed. In case of the 10th tooth small pits (<100 μm × 30 μm) are dominant on the apical two-thirds of the crown. A flush EDI is present on the whole 8th tooth (Fig. 5E), whereas a stepped relationship can be observed on the mesial edge of the 9th tooth. A more gently stepped condition occurs on the distal side of the wear facet of the 9th tooth (Fig. 5C) and on that of the whole 10th tooth (Fig. 4A).

Whereas the 11th tooth is missing from both hemimandibles, the 12th tooth is present on both sides. The wear facet of the right 12th tooth, covers approximately 50% of the crown, is apicobasally elongate and centrally positioned (Fig. 4A, B). The EDI is flush distally but stepped mesially. Scratches of moderate length (< 2 mm) in the apical region are parallel or sub-parallel with the crown axis, but on the basal third of the facet they become curved mesiobasally (as noted for the 10th tooth) and have a mesiobasal-apicodistal orientation (at approximately 25–40° relative to the horizontal plane). The left 12th tooth is more complete: the steeply inclinded, centrally-positioned wear facet covers approximately the 40% of crown surface. Scratches sub-parallel to the crown axis are dominant, but mesiobasally-apicodistally oriented scratches (at approximately 30–45° relative to the occlusal plane) also occur basally.

The 13th tooth is known only from the left hemimandible. The apex is missing and the crown is only slightly worn. The most extensive wear occurs on the cingulum (Fig. 4B). There are two small wear facets separated by a shallow ridge: the mesial facet is the more extensive and bears mainly small (≤ 80 μm × 300 μm), triangular pits. The distal facet is not as deep as the mesial facet, the apical margin of the cingulum is still visible, and mesiobasally-apicodistally oriented scratches occur in this area.

The 14th tooth is preserved in the right dentary only, and is one of the best to illustrate the dental wear typical for *Hungarosaurus* (Figs. 4A, 6). This tooth bears a steeply inclined, relatively smooth and extensive (approximately 70% of the labial surface) wear facet. The cingulum is almost completely abraded and this part of the wear facet bends slightly labially relative to the almost vertical, apical part (Fig. 6B–D). The wear facet is positioned on the mesial half of the crown so that the denticulate mesial margin is also strongly worn. Whereas the EDI is flush distally, the EDI mesially on the denticulate margin shows a slightly stepped relationship (Fig. 5H). As seen on the other teeth, the apical two-thirds of the 14th tooth wear facet is dominated by scratches subparallel to the crown axis (Fig. 5G) and the basal part possesses mainly mesiobasally–apicodistally oriented scratches.

Posterior region

The 15th tooth can be studied only in the left dentary, but is in poor condition. The wear facet extends mostly across the distal part including the cingulum. Only a few, subvertically oriented scratches (at 60–70° relative to the horizontal plane) can be observed on the basal part of the wear facet.

The 16th tooth is preserved in both dentaries, but only the right one is informative (Fig. 4A). This tooth bears two different wear facets: the more extensive one is located centrally on the crown and bears several, relatively long (< 3 mm) subvertically oriented scratches. The cingulum is completely eroded. The EDI is slightly concave and flush. The other facet is on the distal part of the crown and mesiobasally-apicodistally oriented scratches are present. The two facets are separated by a shallow ridge basally, but this interface becomes flush apically. Though the apical third of the crown is broken, the steeply inclined, central wear facet extended from the apex to the base of the crown.

The 17th tooth, preserved on both sides, is generally similar in wear facet morphology to that of the 14th tooth in having elongate, subvertical scratches (at 70–85° relative to the horizontal plane) on the apical two-thirds of the crown. On the left tooth these scratches are 3–4 mm in length. The strongly eroded cingulum on both teeth bears mesiobasally-apicodistally oriented scratches (at 35–45° relative to the horizontal plane). As with the 16th tooth, the 17th tooth also posses a separated, smooth distal wear facet showing only a few, short sub-horizontally oriented scratches (Fig. 4A, B).

The 18th tooth is only partly erupted in the left dentary and covered mainly by the 17th tooth, thus no wear patterns can be observed.

Maxillary tooth wear

Most of the maxillary teeth referred to *Hungarosaurus* are isolated specimens. However, the holotype skeleton includes 22 loose but associated teeth (MTM 2007.26.13) among which at least five maxillary teeth can be identified with confidence on the basis of the aforementioned characters. Macrowear patterns on most of these teeth can be studied, and they differ from those documented from the dentary teeth. Wear facets occur mainly on the apical region of the crown and are usually not as steeply inclined or as extensive basally (Fig.

3C, J, K) as on the dentary teeth. The maxillary tooth wear facets cover up to 20–50% of the lingual crown surface. In many cases, the crown apexes are strongly abraded: in addition, the apexes of the mesial and distal denticles are also worn. In some cases, wear facets extend onto the cingulum and in some cases these form a continuous, steeply inclined facet with that in the apical region. The main difference between the maxillary and dentary tooth wear facets is that the maxillary ones are not bowl-like (i.e. they are not concave, but planar), in most cases they are not as steeply inclined as those of the dentary teeth and the apexes of the mesial and distal denticles are worn.

Interpretation of microwear features (e.g. scratch orientation, EDI) on the maxillary teeth is more problematic than in case of the dentary teeth, because the former were not preserved in situ. Nevertheless, it can be concluded that both vertical and low-angled scratches are present, and that the scratches are usually not as long (< 0.5 mm) as those on the dentary teeth. Most scratches are oriented roughly parallel to the crown long axis. Low-angled, slightly curved scratches appear on the worn cingulum.

Some teeth bear wear facets on both crown surfaces. This phenomenon is, however, most probably due to abnormal (more lingual or labial) orientations of these teeth relative to the others in the strongly curved tooth row, and was perhaps also related to the specialized movements of the mandibles (see below).

Similar differences between the maxillary and dentary dental wear facets were also described in the basal thyreophoran *Scelidosaurus* (Barrett, 2001), which possesses extensive steeply inclined, bowl-like facets on the dentary teeth and smaller, low-angled wear facets on the maxillary teeth.

Extensive wear is present on the dentary teeth of *Gargoyleosaurus* (DMNH 27726) and on some teeth of *Euoplocephalus* (Rybczynski and Vickaryous, 2001; A.Ő., personal observation). In these taxa, however, the wear pattern is not as uniform along the whole tooth row as those of *Hungarosaurus* or *Scelidosaurus*. Stegosaurs (e.g. *Stegosaurus* sp. DMNH 2818) possess only weakly developed wear mainly on the apical region and this wear is not developed systematically along the tooth row (Gilmore, 1914; Barrett, 2001). Among ankylosaurids (e.g. *Tarchia gigantea* [PIN N3142-250], *Pinacosaurus grangeri* [ZPAL MgD-II/1]), apical wear facets with mesiodistal denticle wear is the dominant wear pattern, although on some teeth, such as those referred to *Ankylosaurus magniventris* (Coombs, 1990), steep wear facets have been also documented. Among nodosaurid ankylosaurs, only a few taxa possess relatively complete in situ dentitions and extensive tooth wear; in these cases teeth are badly eroded apically and on the mesiodistal denticles. Extensive, steep facets, however, occur only on a few teeth in the tooth row (e.g. *Edmontonia longiceps* [ROM 1215], Coombs, 1990:fig. 20.4E).

The process of tooth-tooth contact

The worn teeth of *Hungarosaurus*, with steeply inclined, bowl-like wear facets on almost all of the dentary teeth, indicate unambiguously that the upper and lower teeth of this taxon occluded, enabling shearing between them. This raises two questions: 1) how exactly did the opposing teeth occlude with each other to provide the above-mentioned wear facets?; and 2) why does the wear differ between the upper and lower teeth?

As pointed out earlier, the morphology of the maxillary and dentary teeth was almost identical, so if the upper and lower teeth were vertically oriented then their occlusion should produce wear facets of approximately similar inclination, shape and extent. The observation that the dentary wear facets are usually steeper, more extensive and frequently bowl-like, whereas the maxillary wear facets are lower angled, smaller and planar, with mesial and distal denticles frequently worn indicates different orientations of the upper and lower teeth relative to the vertical plane. The only way to produce steep, bowl-like facets on the lower teeth was for the apex of the upper tooth crowns only to occlude with the labial surfaces of the lower teeth to form a slightly concave lower facet (Fig. 7A, B). This mechanism is consistent with upper wear facets that are confined to the apical region (including the apexes of the denticles), low-angled and planar or slightly convex surfaces. A similar type of occlusion, namely a "puncturing and crushing mechanism, with the dentary teeth acting as a row of mortars and the maxillary teeth representing a series of pestles" was also suggested for *Scelidosaurus* (Barrett, 2001:35). The main difference between *Hungarosaurus* and *Scelidosaurus* is, however, the lack of low-angled, oblique scratches on the wear facets in the latter taxon, which suggests a more complex jaw mechanism in *Hungarosaurus*.

Jaw mechanism in *Hungarosaurus*

Available information on dental wear implies a complex jaw mechanism in *Hungarosaurus* that has not been reported in any other nodosaurid ankylosaur. The complexity of the mandibular movements is best reflected by the different wear facets of the upper and lower teeth (Fig. 3) and by the two distinct scratch generations (Fig. 6) present on the dentary teeth, both of which were produced on a tooth row curving in both the vertical and horizontal planes (Fig. 4, 8). The following jaw movements may explain this unusual combination of dental features:

1) The main component of jaw action was orthal, as supported by the orientation of the first scratch generation, in which the scratches are approximately parallel to the long axis of the tooth crown, even on anteriorly positioned and slightly procumbent teeth. This movement enabled a shearing contact with the opposing teeth. These first generation longitudinal scratches are much shorter (length > 2 mm) on the anterior, obliquely oriented teeth than those (2 mm < length < 6 mm) on the posterior teeth suggesting that this shearing movement was more pronounced posteriorly. Although dental wear is present on the teeth of both

dentaries of the fifth skeleton (MTM 2007.25.1 and MTM 2007.25.2), wear facets are apparently better developed on the right teeth (Fig. 4). This might be explained by a unilateral rather than bilateral jaw closure in which side-to-side switching of the active and balancing sides occurred. Although unilateral biting would be unusual for a sauropsid, a well-developed unilateral occusion has been reconstructed in several heterodont crocodyliforms (Pol, 2003; Marino and Carvalho, 2009; Ősi, 2013).

2) As mentioned earlier, the dentary teeth might have had slightly oblique orientations (in mesial or distal views) relative to the maxillary teeth, to produce the bowl-shaped lower wear facets and low-angled apical facets on the upper teeth (Fig. 7A, B). Along with this quite unusual type of tooth-tooth contact, the marked horizontal curvature of the tooth row and the slightly irregular orientation of the teeth (i.e. in occlusal view, the teeth are in slightly oblique positions relative to each other, as is the case in the dentary teeth of MTM 2007.25.1 and MTM 2007.25.2) most probably required some limited lateromedial displacement and/or rotation of the mandibles along their long axes during tooth-tooth contact to enable the mandibular teeth to rotate against the apexes of the maxillary teeth (Fig. 8). Both of these accessory movements would have required some mobility of the dentary-dentary and predentary-dentary joints (unfortunately, the predentary is not preserved). The symphysis of *Hungarosaurus* is small and unfused, which would have allowed at least some of this flexibility. The symphyseal surface bears 4–5 horizontal ridges that, though most probably covered by a fibrocartilagous pad, stabilized the dentaries against dorsoventral shearing, but did not preclude mediolateral displacement or rotation, a feature also suggested for *Euoplocephalus* (Rybczynski and Vickaryous, 2001). The glenoid fossa, being 4–5 mm wider than the quadrate condyles, would have allowed mediolateral pivoting of the mandibles (Fig. 7C, 8).

3) The low-angled, mesiobasally-apicodistally oriented scratches on the basal parts of the dentary tooth wear facets indicate unambiguously the occurrence of a backward and slightly upward (palinal) shifting of the mandibles, i.e. a retractive powerstroke. Besides scratch orientation, the morphology of the EDI (step relationship is mainly mesially, mesiobasally) also supports palinal movement (Fig. 7D–G). The length of these low-angled scratches is frequently > 3–4 mm suggesting relatively long lasting tooth-tooth contact during the retractive powerstroke. Some of the obliquely oriented scratches on the basal parts of the wear facets are not straight but curve mesiobasally, as a continuation of the elongate vertically oriented scratches. These features might demonstrate that during some chewing cycles the orthal shearing was accompanied by palinal movements of the mandibles (Fig. 7B). The glenoid fossa is approximately 5 mm longer anteroposteriorly than the quadrate condyles and has no buttress posteriorly, and thus it might have permitted some anteroposterior translation. The low-angled scratches are present both on the anterior and posterior teeth. Due to the presence of a horizontally curved tooth row, occlusion via palinal movements cannot occur simultaneously in the anterior and posterior regions as the tooth rows diverge and would therefore move apart at different points of the chewing cycle. For example, during chewing, posterior movement of mandible that would result in occlusion for the anterior part of the lower tooth row would simultaneously result in the posterior lower teeth moving out of occlusion with the uppers. To avoid this problem, mediolateral translation or some degree of mandibular long-axis rotation might have occured during the power stroke in concert with palinal motion (Fig. 8). A similar accessory movement during the retractive powerstroke was also posited for *Euoplocephalus* (Rybczynski and Vickaryous, 2001).

On the basis of the foregoing description and discussion we propose a three-phase chewing cycle for *Hungarosaurus*:

1) The first phase is the preparatory stroke which begins with the opening of the mouth (Fig. 7D) by contraction of m. depressor mandibulae. The first contraction of the adductor muscles (MAME and MPT) results in contact between the food and the edentulous anterior parts of the upper (cutting edges of the premaxilla) and lower (anterior dentary plus predentary) jaws to grasp and hold the food item. Occlusion was most probably minimal, but the premaxillary and anterior-most dentary teeth probably participated in this phase. The direction of mandibular movement during the preparatory stroke was primarily orthal.

2) The second phase is the first part of the powerstroke in which the food is sheared between the leaf-shaped teeth. Although tooth-food-tooth contact is dominant in this phase, tooth-tooth occlusion becames more extensive. Jaw closure was mainly orthal, producing large, steeply inclined wear facets on the dentary teeth and elongate scratches oriented roughly parallel to the long axis of the crown (Fig. 7E, F). Lateromedial translation or axial rotation of the mandibles, powered by the pterygoid muscles, might also have occured during tooth-tooth contact enabling rotational movement of the mandibular teeth against the apexes of the maxillary teeth.

3) The third phase probably involved the addition of a palinal (posterior) movement to the powerstroke, as shown by the presence of curved, low-angled scratches (Fig. 7G, D) both on the maxillary and dentary teeth. Additional shearing of food items occured during this part of the powerstroke, which was accomplished largely by the anteroventrally-posterodorsally oriented bundles of MAME. Nevertheless, the presence of well developed, low-angled, straight scratches on some dentary teeth suggests that orthal movements lacking a significant palinal component occasionally occured during this part of the powerstroke.

CONCLUSIONS

The foregoing analysis suggests that the nodosaurid *Hungarosaurus* possessed an unusual jaw apparatus capable of extensive food processing. Reconstruction of the jaw adductors indicates that MAME was well developed and responsible for palinal shifting of the mandibles during the powerstroke. The general occurrence of extensive, steeply inclined wear facets on the dentary teeth unambiguously demonstrates the presence of precise tooth-tooth contact, whereas consideration of the curved tooth rows, the differential wear on the maxillary and dentary teeth, and microwear patterns including both vertical and low-angled scratches reveal a multiphasic, complex jaw mechanism incorporating different mandibular movements. Besides an orthal component that resulted in vertical shearing between the upper and lower teeth, a palinal component contributed significantly to the powerstroke. Mediolateral pivoting and/or axial rotation of the mandibles might have accommodated these movements, potentially ensuring effective chewing both in the anterior and posterior segments of the tooth row.

The complex jaw mechanism of *Hungarosaurus* is the first documented among nodosaurid ankylosaurs. Besides *Hungarosaurus*, effective chewing with orthal jaw closure has been reported for the Early Jurassic basal thyreophoran *Scelidosaurus* (puncture-crushing mechanism, Barrett, 2001) and, with the addition of more complex palinal and rotational movements, the Late Cretaceous ankylosaurid *Euoplocephalus* (Coombs, 1971; Rybczynski and Vickaryous, 2001). This suggests that the 130 million year evolutionary history of feeding in thyreophoran dinosaurs, one of the most important groups of Mesozoic vertebrate herbivores, was more complex than thought previously. Although oral processing of food was not as extensive or sophisticated as in ornithopod or ceratopsian dinosaurs (Weishampel, 1984; Williams et al., 2009; Varriale, 2011; Erickson et al., 2012), it clearly occured not only in basal thyreophorans, but also in ankylosaurids and nodosaurids. This demonstrates that alongside other herbivorous dinosaurs, ankylosaurs should also be considered as capable of extensive oral-processing.

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FIGURE CAPTIONS

Figure 1. Cranial remains of *Hungarosaurus* used in this study. A, right quadrate (holotype, MTM 2007.26.10) in ventral view. B, right post-dentary part of the mandible (holotype, MTM 2007.26.15) in lateral view. C, left mandible of the fifth partial skeleton (MTM 2007.25.1) in lateral view. D, right post-dentary part of the mandible (holotype, MTM 2007.26.15) in dorsal view. E, right dentary of the fifth partial skeleton (MTM 2007.25.2) in lateral view. F, anterior part of the dentary (holotype, MTM 2007.26.15) in lateral view. G, anterior part of the dentary (holotype, MTM 2007.26.15) in dorsal view. H, anterior part of the dentary (holotype, MTM 2007.26.15) in medial view. Abbreviations: **alv**, alveoli; **cpr**, coronoid process; **di**, diastema; **gl**, glenoid; **nf**, nutritive foramen; **qc**, qudrate condyle; **rpr**, retroarticular process; **sy**, symphysis; **4th**, **6th**, **17th** tooth positions.

Figure 2. Jaw adductors reconstructed in *Hungarosaurus* based on Haas (1969) and Holliday (2009). A, the orientation of the most important jaw adductors in lateral view. Note the anteroventral–posterodorsal orientation of the external adductors. B–D, the insertion surfaces of the different jaw adductors demonstrated on the specimen MTM PAL 2013.39.1 in medial (B), lateral (C) and dorsal (D) views. Abbreviations: **MAMEM**, m. adductor mandibulae externus medialis; **MAMEP**, m. adductor mandibulae externus profundus; **MAMES**, m. adductor mandibulae externus superficialis; **MAMP**, Musculus adductor mandibulae posterior; **MDM**, m. depressor mandibulae; **MPTD**, m. pterygoideus dorsalis; **MPTV**, m. pterygoideus ventralis.

Figure 3. Teeth of *Hungarosaurus*. A, part of the lower tooth row in the right dentary of the fifth partial skeleton (MTM 2007.25.2) in lateral view. B–C, isolated maxillary tooth in labial (B) and lingual (C) views. D–E, isolated dentary tooth in labial (D) and lingual (E) views. F–

H, associated dentary tooth in labial (F), lingual (G), and ?mesial (H) views. I–K, associated maxillary tooth in labial (F), lingual (G), and ?mesial (H) views. Abbreviations: **bwf**, bowl-like wear facet; **ci**, cingulum; **edi**, enamel–dentine interface; **gr**, groove; **wf**, wear facet.

Figure 4. Dental wear map of the teeth preserved in the left (MTM 2007.25.1) and right (MTM 2007.25.2) dentaries of *Hungarosaurus*. Green line: flush enamel-dentine interface, red line: step enamel-dentine interface.

Figure 5. Wear pattern of the right dentary teeth (MTM 2007.25.2) of *Hungarosaurus*. A–B, labial surface of the 4th tooth; C, labial surface of the 9th tooth; D, labial surface of the concave, basal part of the weat facet on the 14th tooth. E–F, labial surface of the 8th tooth. G–H, labial surface of the 14th tooth. Abbreviations: **csc**, curved scratches; **de**, dentine; **edi**, enamel-dentine interface; **en**, enamel; **fedi**, flush enamel-dentine interface; **pc**, pulp cavity; **pi**, pit; **sc**, scratch; **sedi**, step enamel–dentine interface; **wci**, wear on the cingulum.

Figure 6. Wear pattern of the right 14th dentary tooth (MTM 2007.25.2) of *Hungarosaurus*. A, position of the tooth in the jaw. B, light microscope photograph from the basal part of the wear facet. C, the extensive, slightly concave wear facet of the 14th tooth (covered with ammonium chloride). D, technical drawing of the wear facet of the 14th tooth.

Figure 7. Chewing cycle of *Hungarosaurus*. A–B, the interaction of the upper and lower teeth in distal (A) and labial (B) views, when the mandible shifts upward and backward. The solid lines indicate the respective positions of the upper and lower teeth. Dashed lines show the positions of the lower teeth at the end of the powerstroke. Wear facets on the lower teeth are in grey and light grey on the upper teeth. Red crosses connected with red solid lines represent

the shifting route of one of the lower teeth during the palinal powerstroke. C, the anteroposterior movement of the mandible relative to the quadrate condyles (red). D, chewing cycle starts with the opening of the mandibles. E, in the beginning of the closing phase, the mandible shifts forward. F, when the mandible is in a closed position, the upper and lower teeth come into contact. G, the mandible is pulled upward and backward bringing the lingual surface of the upper and labial surface of the lower molariform teeth into a shearing contact.

Figure 8. Possible solutions for dental occlusion in *Hungarosaurus* demonstrated by the curved right upper and lower tooth rows in occlusal view. During the chewing cycle both a lateromedial displacement and a posterior shifting occured. A, the lateromedial displacement might have happened by lateromedial translation when the mandible simply shifted laterally to bring the teeth into contact or the mandibles might not translated but rotated (B) around the pivot point (jaw joint). C, the most realistic version is a combination of both translation and rotation. Posterior movement of the mandible is always the last phase. Red box indicates the areas where occlusion appears.

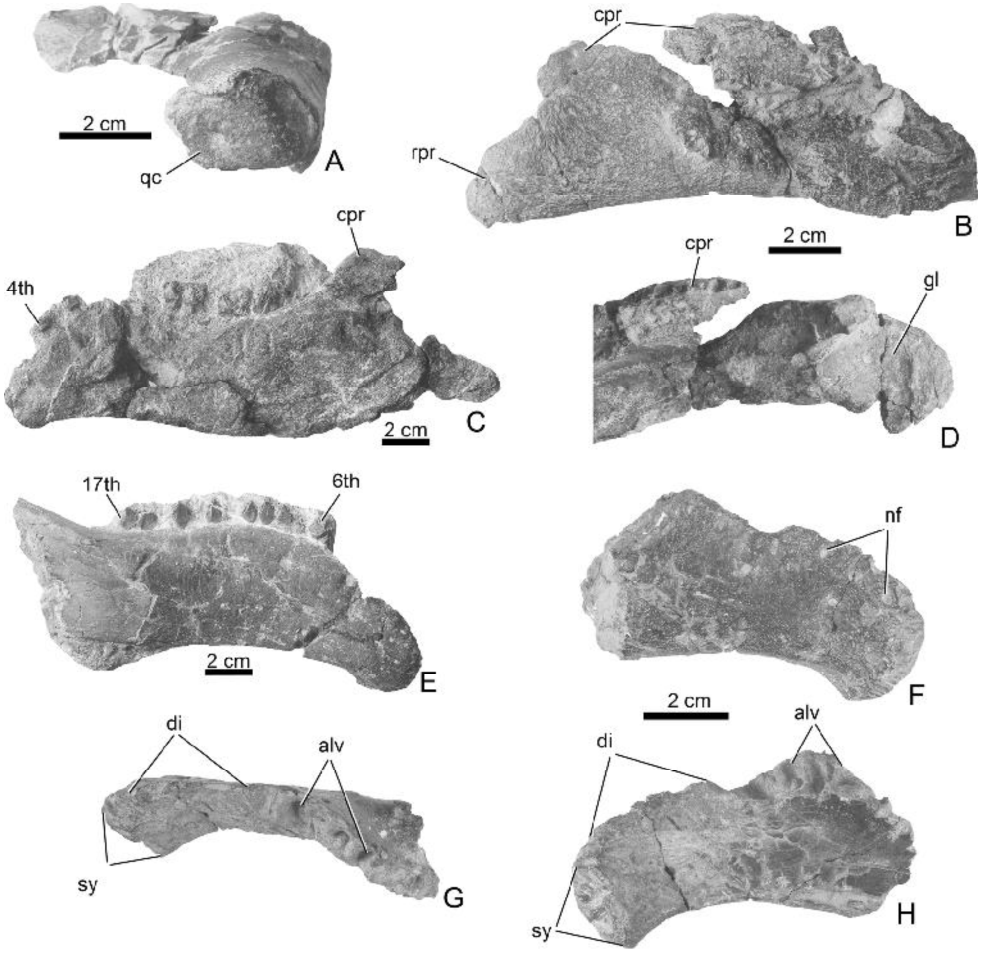

Figure 1.
167x164mm (300 x 300 DPI)

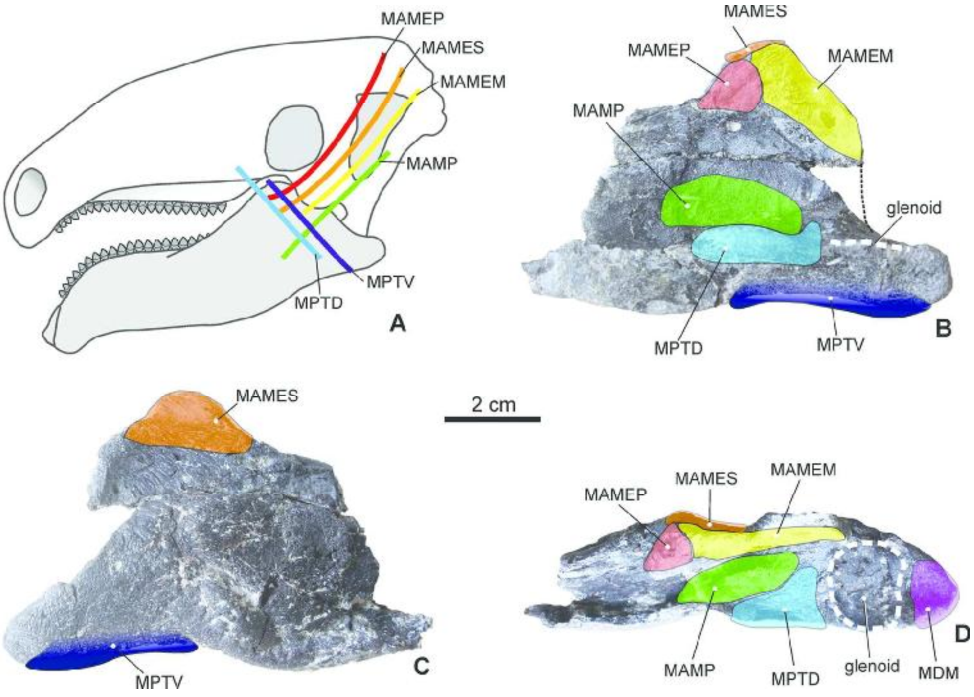

Figure 2.
119x83mm (300 x 300 DPI)

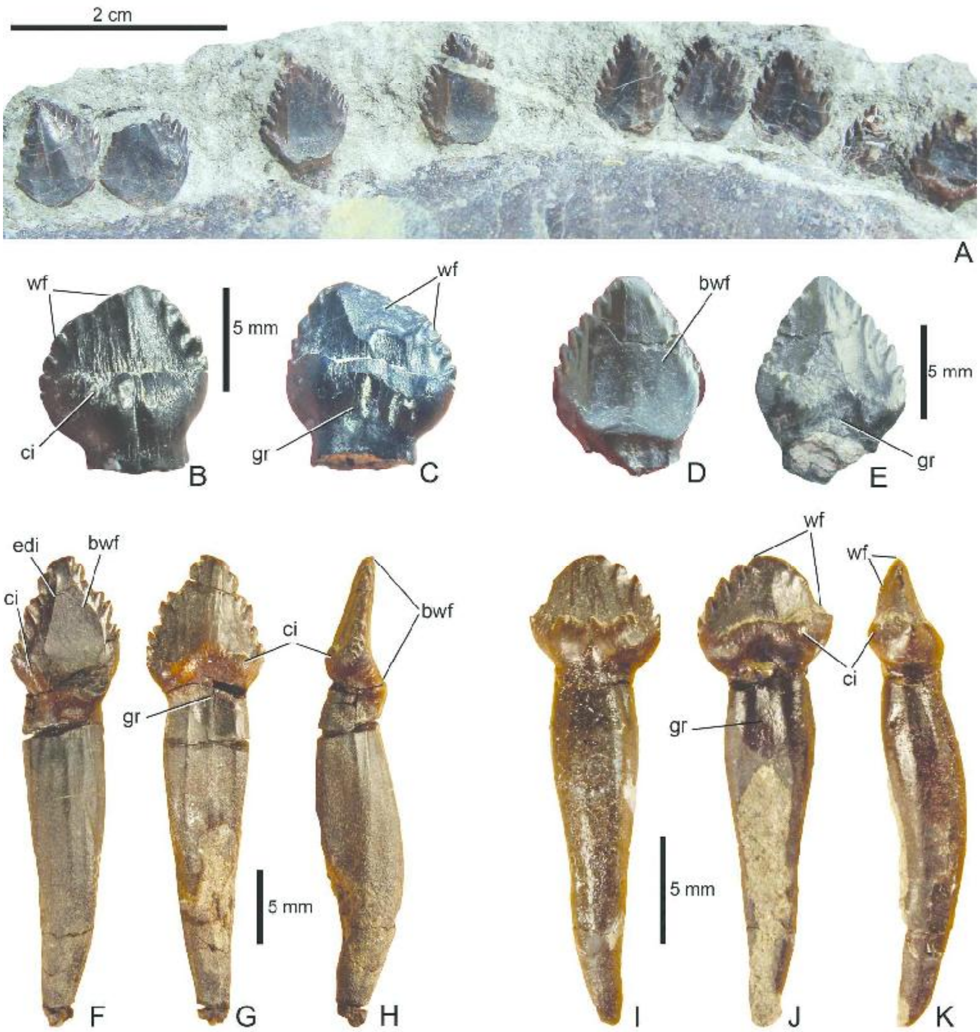

Figure 3.
184x201mm (300 x 300 DPI)

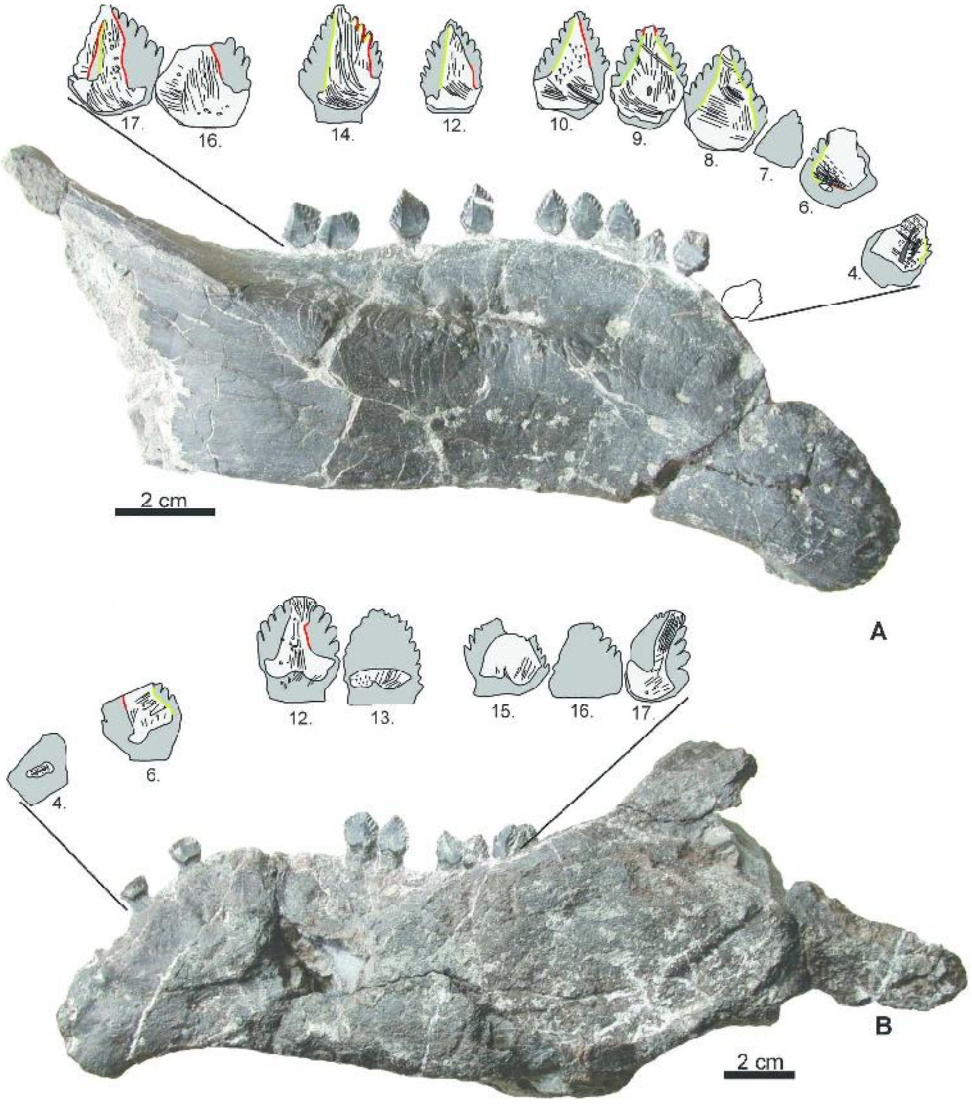

Figure 4.
191x216mm (300 x 300 DPI)

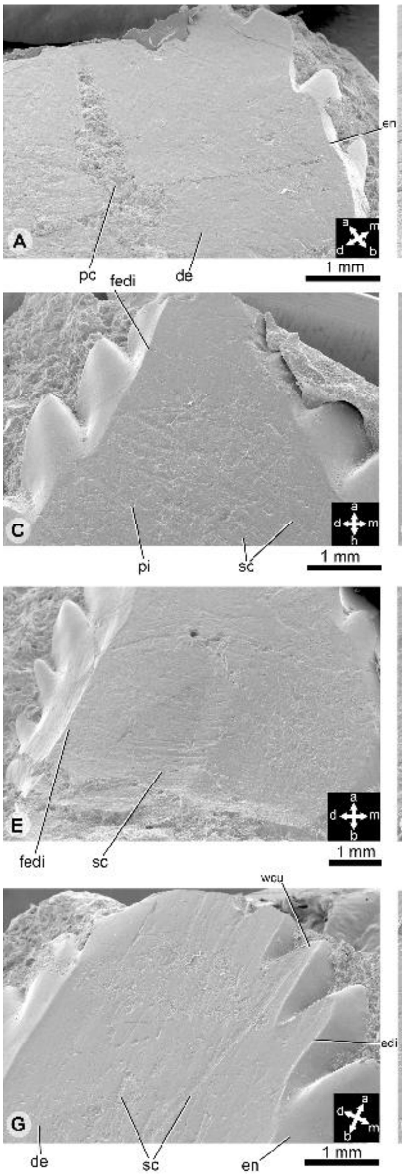

Figure 5.
258x391mm (300 x 300 DPI)

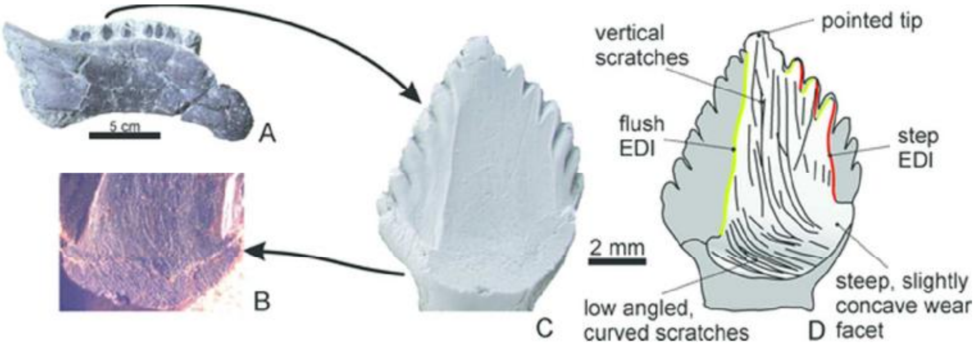

Figure 6.
54x18mm (300 x 300 DPI)

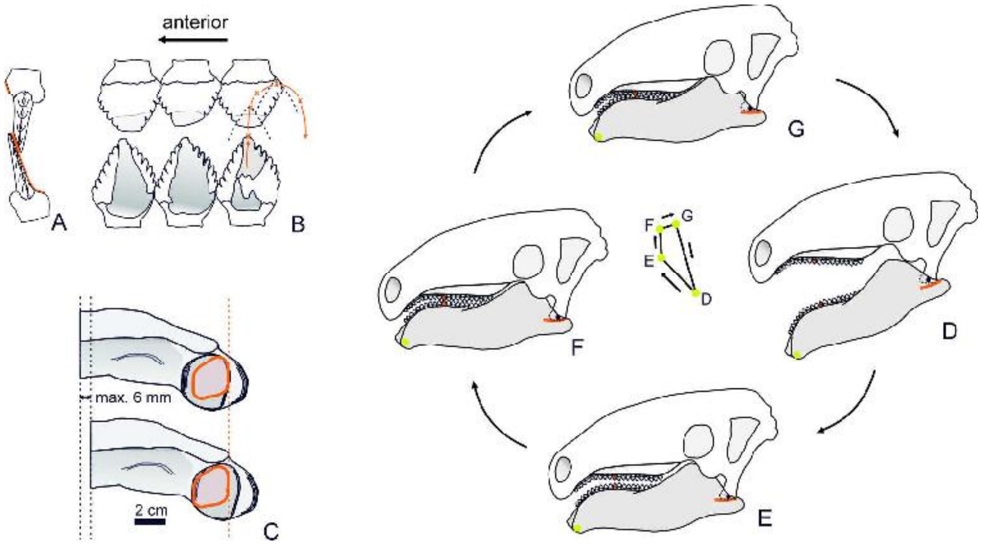

Figure 7.
98x54mm (600 x 600 DPI)

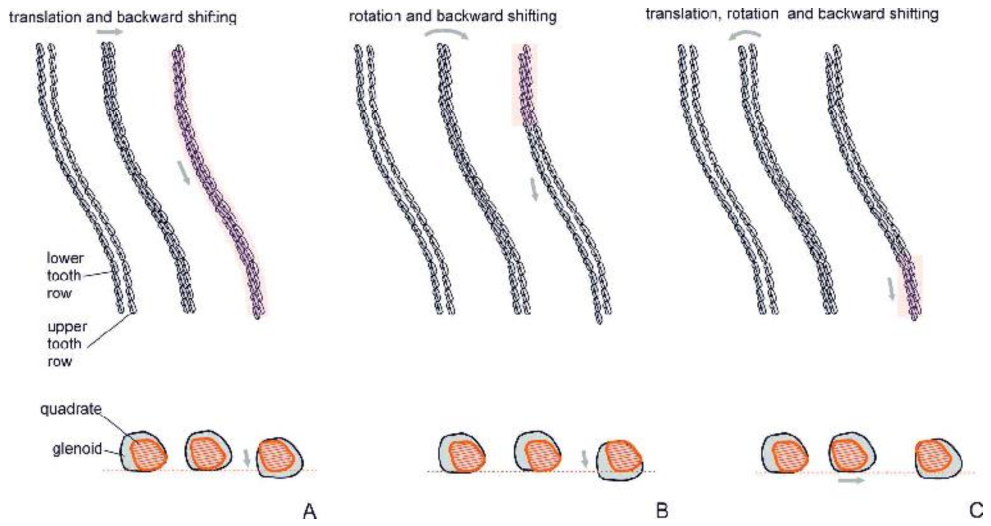

Figure 8.
103x54mm (600 x 600 DPI)