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The enamel microstructure of *Manidens condorensis*: New hypotheses on the ancestral state and evolution of enamel in Ornithischia

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Published in *Acta Palaeontologica Polonica* 2020 65 (1): 59-70.
https://doi.org/10.4202/app.00658.2019

Supplementary Online Material

Terminology

Orientation of *Manidens* teeth

The evolution of enamel in Ornithischia.

Optimization of enamel in the phylogenetic topology of Ornithischia.

Features varying in enamel of Ornithischia.

Final comments.

Character list and matrix.

References.

Figure 1. Sectioned specimens.

Terminology.

Sander (1999) established solid bases in the terminology and analysis of enamel for non-mammalian amniotes, which is followed in the presented main text. The description of the enamel microstructure was ordered following hierarchical levels of organization (i.e., *crystallite*, *module*, *enamel type*, *schmelzmuster*, and *dentition* levels), giving a broad and detailed perspective of the enamel morphology.

The *crystallite* level describes the orientation of individual crystallite in relation to the enamel-dentine junction (EDJ). Due to its structural simplicity, the configuration of parallel crystallite is considered as the most primitive crystallite state (Sander, 1999). Crystallite may converge or diverge to each other, forming regions were the crystals change their orientation in continuous zones or along discontinuous lines or planes. Crystallite discontinuities (the region were adjacent crystallite change their direction abruptly), and incrementing lines (changes of crystallite morphology related to the discontinuous enamel growth, evident in longitudinal and cross sections) are considered at the crystallite level. A special type of parallel crystallite defined by Sander (1999), crystallite diverging from one point and forming slender groups or bunches with unclear limits, corresponds to incipient divergent columnar units. Nevertheless, this type of parallel crystallite was addressed at the crystallite level in the description, but as a poorly defined divergent columnar enamel in the phylogenetic analysis, representing an early stage of differentiation of divergent columnar enamel.

The *module* level is defined as the repetition of units formed by different arrangements of crystallite, delimited by planes of discontinuity between units or zones were the orientation change between crystallites (Sander, 1999). Parallel crystallite does not form structures at the module level. Dinosaurs only developed different types of columnar units at the module level, being these divergence columnar units and convergence columnar units (Hwang, 2005). The divergence columnar units are the most common module type in Dinosauria, being units higher than wide, formed by divergent crystallite (disorganized or forming a middle divergence line) and limited by planes of convergence between modules. These columnar divergence units take a polygonal form when sectioned transversally (tangential section), with marked or rounded edges in their boundaries. The convergence columnar units show the opposite arrangement of crystallite than the divergence units, being only reported in a ceratopsian tooth (Sander, 1999; Hwang, 2005). Tubules and empty spaces (voids) in enamel are features described in this hierarchy, due that these are present between units evaluated at the module level. Tubules are unmineralized passages that start from the EDJ through the interior of the enamel, in some cases reaching the EES, while the enamel voids are zones of variable size without mineralizing within the enamel.

The *enamel type* level comprises continuous enamel volumes formed by the repetition of the same modules or arrangement of crystallite (for the parallel crystallite enamel). The complete enamel of a certain crown can be integrated by the same or different kinds of enamel types, arranged in layers parallels to the EDJ, or taking another arrangement (Sander, 1999; Hwang, 2005, 2011). Dinosauria differentiated parallel crystallite enamel (e.g. Theropoda), columnar enamel (e.g. Ceratopsia), wavy enamel (e.g. Hadrosauridae), the basal unit layer, and the external ornamentation as different enamel types (Sander 1999; Hwang, 2005). By definition, parallel crystallite enamel is completely integrated by crystallites with parallel to slightly divergent disposition, and divergent crystallite forming incipient columnar units (Hwang, 2005). Divergence columnar enamel is enamel composed by crystallites forming divergence columnar enamel. Wavy enamel shows imbricated crystallites disposed in an angular arrangement relative to the EDJ that varies vertically towards the surface of the enamel in a wave-like arrangement in cross-section. The basal unit layer is a thin layer of polygonal units adjacent to the EDJ, being the first enamel produced during amelogenesis. Similarly, the micro-ornamental features of the EES correspond to the cessation of enamel deposition and the end of amelogenesis, also studied at the enamel type level.

The *schmelzmuster* level brings together the three-dimensional arrangement of all enamel types and major discontinuities characterizing a tooth crown of a certain species, summarizing the enamel description at different levels and being the most useful enamel feature to perform a diagnosis.

Finally, the *dentition* level includes the variation of the *schmelzmuster* in morphologically different teeth along the toothrow. The sectioned isolated crowns of *Manidens condorensis* does not represent the entirely dentition, as there is no evidence of enamel morphology in the still unknown premaxillary dentition and the dentary caniniform only preserved at the holotype specimen MPEF-PV 3211. In addition, the maxillary and dentary dentition of *Manidens* were recently reported as extremely heterodont (Becerra et al., 2018). The descriptions performed in the main text only reach to the *schmelzmuster* level for *Manidens*, although was performed also a comparison between dentitions in the matter of enamel structure, thickening and ordering, due that the morphologic differences between opposing dentitions also involves strong enamel disparities. This comparison between the enamel of maxillary and dentary crowns and integration of enamel variation in the dentition may count as certain characterization in a dentition level of the enamel.

Orientation of *Manidens* teeth.

Mesiodistally and apicobasally, all sections can be orientated following three main features of *Manidens* dentition: (i) the occlusal face of the crowns correspond to the apicobasally higher face (dentary teeth) or the shorter face with an enlarged cingular entoloph (maxillary teeth); (ii) the non-occlusal face corresponds to the shorter one (dentary teeth) or the higher one with a slight change in orientation near the base corresponding to the oblique cingular ectoloph; (iii) and that the lingual crest limiting the mesial cavity goes further mesially if compared to the lingual crest of the same cavity for both maxillary and dentary teeth (Becerra et al., 2014, 2018).

The evolution of enamel in Ornithischia.

The coding in the data matrix of the taxa used in the phylogenetic analysis was realized following different authors. The species with more accurate assignment described by Sander (1999) *Plateosaurus engelhardti*, *Iguanodon* sp. and *Edmontosaurus* sp. The species described by Hwang (2005) *Ankylosaurus magniventris*, *Edmontonia rugosidens*, *Sauropelta edwardsi*, indeterminate Pachycephalosauridae (specimens A, B and C), *Psittacosaurus* sp., *Leptoceratops gracilis*, *Protoceratops* sp., *Triceratops* sp., *Tenontosaurus tilleti*, *Bactrosaurus johnsoni*, *Gilmoreosaurus mongoliensis*, *Kritosaurus navajovius*, *Hypacrosaurus altispinus* y *Corythosaurus casuaris*. Finally, the species *Coelophysis bauri*, *Euoplocephalus* sp., *Stegosaurus* sp., *Centrosaurus apertus*, *Pachyrhinosaurus canadensis*, *Thescelosaurus* sp., *Dryosaurus altus*, *Camptosaurus dispar*, *Prosaurolophus maximus*, y *Saurolophus* sp. were considered following the descriptions of Hwang (2011). The branches summarizing the relation of different lineages in the presented topology are constructed following different authors. The arrangement of species within Hadrosauroidea follows the results of Prieto-Marquez (2010), for species in Iguanodontia outside Hadrosauroidea the topology follows McDonald (2012), and for the ornithopods outside Iguanodontia was followed Becerra et al. (2016, supplementary material). Among tyreophorans, the ordering of species in Ankylosauria was constructed following Hill et al (2003), and Maidment et al. (2008) was followed to locate *Stegosaurus* outside Ankylosauria and within Tyreophora. The position of species in Neoceratopsia was realized following Mallon et al. (2011), Sampson et al. (2010) and Fiorillo and Tikosky (2012), and the position of *Psittacosaurus* outside Neoceratopsia was considered following Makovicky (2010). The position of *Manidens condorensis* outside Genasauria was realized following the results of Pol et al. (2011) and Becerra et al. (2016). The topology of internal nodes in Ornithischia (Pachycephalosauria and Ceratopsia, Ornithopoda and Marginocephalia, Tyreophora and Cerapoda) was ordered following the results of Butler et al. (2008) and Becerra et al. (2016). Finally, the relation of *Coelophysis bauri* and *Plateosaurus engelhardti* to each other and outside Ornithischia was realized following Holtz and Osmolska (2004).

An additional comment should be made about the recently characterized enamel microstructure of the rabdodontid *Matheronodon provincialis* (Godefroit et al., 2017) and the jeholosaurid *Changchunsaurus parvus* (Chen et al., 2018), both recovered within lineages near the base of Ornithopoda (e.g., Weishampel et al., 2003; Butler et al., 2011), but excluded from this study due to their poor documentation. Godefroit et al. (2017) use their observations under plane polarized and cross-polarized light with lambda filter to characterize an enamel layer mainly composed by wavy enamel on *Matheronodon*. The authors infer this kind of enamel microstructure following the appearance of a dark-light banded coloration arranged in an undulated pattern.

Nevertheless, Sander (1999) refers to this banding under polarized light as common for all non-prismatic enamel, which little says about enamel microstructure. The study performed by the authors is promising, as the enamel of basal species of Ornithopoda is needed to address the evolution of enamel in this lineage. Unfortunately, up to date there are no studies addressing the comparison between structures identified under polarized light with those in SEM images that support such structural assignation, at least for wavy enamel. A revision of the description is here advised considering more than just one section (longitudinal and tangential sections are needed), and using SEM imaging on the etched enamel section. On the other hand, the study of Chen et al. (2018) follows the methodology standardized by Sander (1999), but yet the inference of enamel micromorphology and its discussion in the phylogenetic context are here considered as poorly supported. Although they use longitudinal and transversal sections together with SEM images, they describe that for *Changchunsaurus* and …"under cross-polarized light, the enamel forms undulating waves that extend parallel to the enamel-dentine junction (EDJ). This pattern is identical to the appearance of hadrosaurid wavy enamel under cross-polarized light. This type of enamel has only been documented elsewhere in dryosauromorph dinosaurs, as well as the rhabdodontid *Matheronodon provincialis*."… Once again, this corresponds to a feature of non-prismatic enamel that not necessarily relates to wavy enamel. However, the authors also address enamel microstructure using SEM imaging over transversal and longitudinal sections "to confirm the presence of wavy enamel in *Changchunsaurus parvus*". Although the first inference of wavy enamel is based on unreliable evidences, the later approach with SEM images still follows the conclusions under polarized light to address the enamel microstructure, a task that might be forcing the resulting interpretations. If considering the descriptions of the poorly differentiated enamel on teeth of *Manidens*, the studies of Sander (1999) and Hwang (2005, 2010, 2011) on the hadrosaurid wavy enamel, and the SEM images of Chen et al. (2018), it can be said that the enamel of *Changchunsaurus* is possibly more similar to that on *Manidens* than to the wavy enamel of dryomorphs. The diverging enamel crystallites at the EDJ are well identified in *Changcunsaurus*, but a BUL (defined as a thin layer of polygonal units adjacent to the EDJ) cannot be characterized based on the presented views (which seems to be absent for the taxon). The authors do not show a tangential section of the enamel in which the boundaries between enamel units adjacent to the EDJ are exposed, and these boundaries are not seen in any of the available oblique views of the EDJ at the longitudinal or transversal sections. In the matter of the wavy enamel, the performing of a tangential section would have exposed the wavy arrangement of crystallite in different directions (Sander, 1999) and given strong evidences to support the performed description. In addition, the well-developed IL in most of the close-up enamel sections seem more likely to be layers of parallel to slightly divergent crystallite enamel (possibly forming IDCU) instead of being faint and indistinct enamel lines related to the staggered organization of crystallites in wavy enamel (Sander, 1999). Finally, the authors addressed the evolution of wavy enamel and casted some doubts on the relation of this enamel type with the complexification of the feeding apparatus to herbivory inferring that is phylogenetically earlier than any other cranial specialization. Nevertheless, the authors ignore in their phylogenetic scenario the already described enamel microstructure of *Thescelosaurus* (poorly differentiated divergent columnar enamel with BUL) and *Tenontosaurus* (well differentiated divergent columnar enamel with BUL that in the outer half of the enamel divide into slenderer columnar structures with sinuous boundaries) that, in fact, lack of wavy enamel. If the information added by *Thescelosaurus* and *Tenontosaurus* is considered under the phylogenetic scenario of

Chen et al. (2018), then the wavy enamel type, formerly unique among reptiles (Sander, 1999), should be depicted as homoplastic within Ornithopoda, appearing at least two times in the evolutionary history of the lineage. Thus, in the matter of the information added by the studies of Godefroit et al. (2917) and Chen et al. (2018) on the enamel of Ornithopoda and its repercussion on the phylogeny of Ornithischia, were not considered. A revision of these descriptions is here advised to avoid misunderstandings on the enamel evolution of Ornithischia. In addition, a more likely enamel type is here mentioned for *Changchunsaurus*, which also fits under the phylogenetic predictions of enamel in the common ancestor of Ornithopoda, the closest node to the location of this species on the phylogeny.

Optimization of enamel in the phylogenetic topology of Ornithischia.

Crystallite level. The parallel crystallite enamel (main text Fig. 5D: character 3) was considered as the most primitive enamel condition *a priori*, due to its structural simplicity (Sander, 1999). The presence of IL (main text Fig. 5G: character 6) is usually linked with parallel crystallite, although also is observed in other enamel types (Sander, 1999; Hwang, 2005, 2011). The strong presence of IL was also considered as the primitive state (Sander, 1999). Although enamel of IDCU is considered as rare parallel crystallite enamel type (Sander, 1999; Hwang, 2005), this enamel was here addressed as a poorly developed stage of DCE (see below, *enamel type level*). The presence of parallel crystallite dominating the enamel type and with IL in *Coelophysis bauri* (most basal Theropoda explored) defines the ancestral state in Theropoda (3:0, 6:0). When considering the species *Plateosaurus* (most basal Sauropodomorpha included), the dominance of parallel crystallite enamel type over IDCU enamel type, allows optimizing the parallel crystallite as the plesiomorphic and most generalized enamel type in Saurischia (3:0). The lesser participation of parallel crystallite enamel as a structural component in *Manidens* (3:1), which is dominated by IDCU (with parallel crystallite enamel appearing in patches), allows optimizing an ancestral state of Ornithischia similar to *Manidens* (3:1). Although the parallel crystallite is a dominant type over the IDCU in *Plateosaurus*, the presence of IL is rather sporadically developed as in *Manidens* (6:1) (Sander, 1999). This character is optimized at the base of Saurischia and Ornithischia as sporadically developed (6:1), with a reversal to the most primitive state in *Coelophysis* (6:0).

In Tyreophora, the enamel micromorphology of *Stegosaurus* represents the state of Stegosauria (Hwang, 2011). The dominant presence of parallel crystallite with IL in enamel of *Stegosaurus* allows optimizing the primitive state for both characters in Stegosauria (3:0, 6:0). In Ankylosauria, only in the enamel of *Euoplocephalus* the IL (only in the BUL and parallel crystallite between the inner DCE and the outer parallel crystallite without IL) and the parallel crystallite enamel are not the dominant type (3:1, 6:1). The rest of the species in Ankylosauria possess a lesser participation of parallel crystallite enamel (3:1) but with an important structural component of enamel with IL (6:0). These character states are also recovered as the ancestral condition of Tyreophora, with only a reversal to dominant parallel crystallite enamel in *Stegosaurus*. The IL in greater proportion than the parallel crystallite corresponds to a feature unique in Ankylosauria, due to IL are also developed over DCE types (Sander, 1999; Hwang, 2005, 2011). Hwang (2005) concludes on the similar teeth and enamel morphology between pachycephalosaurids and ankylosaurs.

The *schmelzmuster* in pachycephalosaurids was described as composed by divergent crystallite bunches with IL over the BUL in premaxillary/anterior dentary teeth (pachycephalosaurid A); and IDCU above the BUL (with faint IL) followed by parallel crystallite alternating firstly without IL and then with IL in maxillary/posterior dentary teeth (pachycephalosaurid B and C). In Pachycephalosauridae, the IL are observed in both parallel crystallite and IDCU, but both parallel crystallite and IL are optimized as not the dominant enamel type (3:1, 6:1). In Ceratopsia, the enamel is entirely dominated by columnar units (3:2). Although the presence of IL in *Centrosaurus* and *Pachyrhinosaurus* over DCE is a strong difference with other ceratopsians, both the absence of parallel crystallite enamel and absence of IL are optimized as the ancestral state of Ceratopsia (3:2, 6:2). The ancestral state of Marginocephalia corresponds to the lesser proportion of parallel crystallite enamel and IL (3:1, 6:1), ancestral states also shared with Genasauria (Tyreophora + Cerapoda) and Cerapoda (Marginocephalia + Ornithopoda, see below).

In Ornithopoda, the occurrence of parallel crystallite is documented only in basal species outside Dryomorpha (*Thescelosaurus* and *Tenontosaurus*), while is completely absent in derived species. On the other hand, the presence of IL in Ornithopoda shows an alternant appearance in stem species of Hadrosauroidea (*Thescelosaurus*, *Dryosaurus* and *Iguanodon*, but absent in *Tenontosaurus* and *Camptosaurus*). In *Thescelosaurus*, the presence of IL is seen in cross-section but rare in longitudinal section, while the parallel crystallite is restricted to the outer enamel layer. Ornithopoda takes an ancestral state for both characters as present but not the dominant type (3:1, 6:1), while parallel crystallite enamel is depicted as absent in Dryomorpha and more exclusive nodes (3:2). The presence of IL is ambiguous in nodes inside Ornithopoda until Hadrosauroidea (6: [1 2]), and absent in more exclusive nodes. Parallel crystallite in *Tenontosaurus* and *Thescelosaurus* (Sander, 1999) could likely be relictual in Ornithopoda or acquired independently, while the absence of parallel crystallite in Dryomorpha restricts the presence of IL to the BUL (*Dryosaurus*; Hwang,

2011) or as thin lines in coarse wavy enamel (e.g., *Iguanodon*, Sander, 1999). The sporadic development of IL in ornithopods outside Hadrosauroidea can be related to the low organization of columnar enamel (e.g., *Thescelosaurus*; Hwang, 2011).

Module level. The presence of empty spaces or voids (main text Fig. 5K: character 10) in enamel is structurally related to the wavy enamel (although are also described in DCE), since are identified between wavy units in enamel of Dryomorpha and internal nodes (excluding *Saurolophus*). Voids are common in coarse wavy enamel, while the regular arrangement and reduced size of crystallite in fine wavy enamel in Hadrosauroidea reduces the frequency of enamel voids (Hwang, 2005). Enamel voids are recovered as synapomorphic for Dryomorpha and shared with *Psittacosaurus*. In the later, the well-defined boundaries between divergence columnar units (DCU) in the inner half of the enamel highlights the presence of tubules and enamel voids between them (10:1), being more difficult to identify in the well-packed DCU of the outer half of the enamel. In Neoceratopsia, the enamel voids are scarce (10:0), while is completely pierced by enamel tubules going inside and between columnar units, branching in different directions and even parallel to the EDJ (Hwang, 2005). In the rest of Ornithischia and Saurischia, the complete absence or low frequency (in the case of Neoceratopsia) of enamel voids is optimized (10:0).

The tubules (main text Fig. 5I: character 8) are the most common enamel feature in Ornithischia, widely varying depending on the enamel type (from scarce in *Manidens* to extremely abundant in Neoceratopsia), and going from the BUL to the EES. Excepting in Pachycephalosauridae, *Iguanodon, Saurolophus* and *Prosaurolophus*, the presence of tubules in the rest of sampled Ornithischia is confirmed. In Ankylosauria the enamel tubules pierce from the BUL and through the DCE above the BUL but usually do not pass through the outer layer of parallel crystallite to reach the EES, while in *Stegosaurus*, tubules only pierce the BUL (Hwang, 2005, 2011). Tubules that do not completely cross the enamel are optimized as the ancestral state of Ankylosauria, Stegosauria and Tyreophora (8:1). In specimens of Pachycephalosauridae the tubules are absent (8:0), possibly related to the poorly organized IDCU or to the poorly defined BUL. Tubules are present *Psittacosaurus* (and more common than enamel voids) but extremely abundant in Neoceratopsia (Hwang, 2005). In *Thescelosaurus* and *Tenontosaurus* (with columnar enamel but poorly marked and well defined, respectively), the tubules between DCU are common from the EDJ and through the BUL, but the outermost layer of parallel crystallite interrupts their way to the EES. Tubules in rest of Dryomorpha are only present in the BUL, whereas no information of tubules is described in *Prosaurolophus* and *Saurolophus*. In addition, the BUL with tubules between columnar units in hadrosaurids was characterized as structurally similar to the enamel in Neoceratopsia (Hwang, 2005). Tubules seem to be common in the limits of columnar units but not in coarse or fine wavy enamel or parallel or divergent crystallite enamel. Thus, in Ornithopoda and excluding the mentioned species, tubules are developed but not reaching the EES (8:1). *Manidens* is an interesting study case in the matter of tubules, because although enamel is structurally similar to Pachycephalosauridae, tubules are present and sporadically developed at least in the maxillary dentition, closely resembling enamel of Ornithopoda and Tyreophora. The presence of tubules in the maxillary dentition but not in the dentary dentition in *Manidens* leads to consider this character as ambiguous, resulting in the same for Ornithischia (8: [0 1]), being absent in Saurischia and Pachycephalosauridae (8:0), not reaching the EES in Genasauria, Tyreophora, Cerapoda, Marginocephalia and Ornithopoda (8:1), and crossing the entire enamel in Ceratopsia (8:2).

Enamel type level. The BUL (main text Fig. 5F: character 5) is identified in enamel of most amniotes, being present even in the primitive species *Prolocophon* and *Captorhinus* (Sander, 1999). However, the species *Plateosaurus*, *Coelophysis* and *Manidens* lack of the BUL, optimizing the same character state in Saurischia, Sauropodomorpha, Theropoda and Ornithischia (5:0). This character is optimized as present (5:1) in species and internal nodes within Genasauria. This phylogenetic scenario of Ornithischia indicates that the acquisition of a BUL occurred only once at the early stages of enamel evolution of Ornithischia, and then spread out with the origin of most important lineages. The development of a BUL seems to be homoplastic, appearing once at the base of Sauropoda, but several times in Theropoda (Hwang, 2011). Although the presence of a BUL is recovered as synapomorphic of Genasauria, is quite variable in the matter of thickness (Sander, 1999; Hwang, 2005, 2011). A more exhaustive sampling considering basal species of the major lineages in Ornithischia will allow giving strong evidence to the evolution of this character or refute the conclusions here addressed.

In the matter of columnar enamel type (main text Fig. 5E: character 4), the identification of poorly differentiated IDCU with parallel crystallite enamel in *Manidens* is similar to the condition described in *Plateosaurus* (4:1), but more abundant in the first. This state is optimized in Ornithischia and Saurischia. Thus, the enamel entirely formed by parallel crystallite in *Coelophysis* and Theropoda should be considered as a reversion to the absence of columnar enamel for this character (4:0). Is not surprising to identify similar enamel types in *Plateosaurus* and *Manidens* (since they represent the first adaptive stages for their corresponding lineages to herbivory) and more complex than *Coelophysis* (a carnivorous species). Nevertheless, this shared enamel micromorphology between *Manidens* and *Plateosaurus*, its possible relation with an early evolutionary stage of herbivory in their corresponding lineages. Specially referring to the IDCU enamel type and without knowing the enamel micromorphology of other taxa near but outside Dinosauria, this enamel type is optimized as the ancestral state of this clade, but should be taken carefully (as all other not mentioned states for Dinosauria in this study). The hypothetic common ancestry of IDCU since Dinosauria rather than parallel crystallite enamel contrasts with two widely accepted hypothesis: the independent acquisition of the herbivorous diet differentiation in Sauropodomorpha and Ornithischia; and the hypothetic carnivorous-omnivorous diet of basal Dinosauria (e.g., Weishampel and Norman 1989; Barrett, 2000 Barrett et al., 2010). Additionally, the common ancestry of IDCU between *Plateosaurus* and *Manidens* does not fit with the recent hypothesis of Ornithoscelida (Theropoda + Ornithischia), optimizing the same hypothesis even with *Coelophysis* more closely related to ornithischians than to *Plateosaurus* (Baron et al., 2017). The exploration of enamel micromorphology in Dinosauriformes and basal species of major dinosaur lineages are needed to support or reject this hypothesis of common ancestry IDCU enamel between Sauropodomorpha and Ornithischia, as for other states of enamel. In Ankylosauria, the absence of well-defined limits between DCU in most species (excepting *Euoplocephalus*) allows optimizing a poorly defined columnar enamel (4:1), contrary to the well-defined columnar enamel in *Psittacosaurus* and Neoceratopsia (4:2) (Hwang, 2005). In Pachycephalosauridae, the parallel/divergent crystallite forming IDCU but differing in development between premaxillary/anterior dentary teeth and maxillary/posterior dentary teeth resembles the IDCU of *Plateosaurus* and *Manidens* on one side, and to Ankylosauria on the other, optimizing this character as enamel of IDCU (4:1) for Pachycephalosauridae. In Ornithopoda (Hwang, 2005, 2011), the DCE in

Thescelosaurus is poorly differentiated (4:1), the DCU of *Tenontosaurus* are developed normal to the EDJ in the inner half, have sinuous boundaries and ramified into up to four new columns per unit in the outer half (4:2), and enamel lacks columnar divergence units in Dryomorpha (4:0, excepting on their BUL, which by definition is formed by DCU). This scenario leads to optimize IDCU or poorly defined DCU in Marginocephalia, Cerapoda, Genasauria, Ornithischia, Saurischia and Dinosauria.

Wavy enamel was recently described in *Matheronodon provincialis* (Godefroit et al., 2017) and *Changchunsaurus parvus* (Chen et al., 2018), although these were not included in this description for being poorly documented (see above). As in other studies (Hwang, 2011), wavy enamel is recovered as synapomorphic of Dryomorpha (main text Fig. 5H: character 7), but the tri-dimensional setting of DCU in enamels of species outside Dryomorpha seems to preclude the origin of wavy enamel. Both *Thescelosaurus* and *Tenontosaurus* have DCE, but the later also shows sinuous limits between ramified DCU in the outer enamel. The enamel in Ornithopoda seems to have gone through a process structural complexification from IDCU-poorly differentiated DCU optimized in Ornithopoda, to poorly differentiated DCE (*Thescelosaurus*), to wavy enamel (Dryomorpha). These enamel types are linked together with an intermediate state of columnar enamel well developed and externally branched into smaller columnar units with sinuous margins (*Tenontosaurus*). More research focused on sampling basal Ornithopoda will allow detailing on this possibly transitional enamel specialization that modelled columnar enamel into a unique enamel type in amniotes, the wavy enamel.

The micro-ornamentation at the EES (main text Fig. 5: character 9) was interpreted by several authors as a convergence between Neoceratopsia and Hadrosauriformes surely related to the acquisition of a tooth battery (Sander, 1999;

Hwang, 2005, 2011), here depicted as a synapomorphy of these clades (9:1). All other considered species in this phylogenetic topology lack of external enamel micro-ornamentation, optimized also as absent in all internal nodes of Ornithischia and also in Saurischia (although wrinkled external enamel is documented since Sauropodiformes and more exclusive nodes [Becerra et al., 2017]).

***Schmelzmuster* level.** Enamel thickness (main text Fig. 5B, C: characters 1, 2), and enamel symmetry (main text Fig. 5L: character 11) are evaluated at the *schmelzmuster* level, because although do not make any reference of the enamel type and discontinuities, these features comprise a level above of the enamel type level and below of the tooth level. Minimum and maximum enamel thickness show a similar tendency in Ornithischia (regardless of enamel symmetry). More specialized herbivorous (i.e., Hadrosauridae and Neoceratopsia) show a minimum enamel thickness between 100 and 200 µm (1:1), including also *Iguanodon* and *Tenontosaurus* (as autapomorphies). In Neoceratopsia, the minimum enamel thickness goes higher than 200 µm in *Leptoceratops* (1:2) and lesser than 100 µm in *Protoceratops* (1:0), optimizing this character as ambiguous in internal nodes of Neoceratopsia and the ancestral node of *Protoceratops* with more derived neocetratopsians (1:[0 1]). Derived neoceratopsians present an enamel thickness between 100 and 200 µm (1:1). In the rest of Ornithischia and internal nodes, enamel thickness is optimized as lesser than 100 µm (1:0). If considering maximum enamel thickness, the thickest values of enamel occur independently at least three times in ornithischian evolution (Nodosauridae, Neoceratopsia and Hadrosauridae). As for minimum enamel thickness, enamel in Hadrosauridae is the thickest in Ornithopoda (2:1), optimizing in nodes and species of non-hadrosaurid ornithopods a maximum enamel thickness lesser than 100 µm (2:0) excepting *Tenontosaurus* and *Iguanodon* (2:1). Similarly, the enamel of Nodosauridae corresponds to the thickest in Ankylosauria, with values of thickness between 100 and 200 µm (2:1), while the rest of Ankylosauria possess thinner enamel (2:0). The thickest enamel in Ornithischia is measured in Neoceratopsia, with values exceeding the 200 µm in all species (2:2) excepting *Protoceratops* (2:1), optimizing this character as ambiguous between 100 and 200 µm and exceeding 200 µm in Neoceratopsia and the node of *Protoceratops* with all other neocetratopsians (2: [1 2]). Maximum enamel thickness in all other species of Ornithischia and Dinosauria measures less than 100 µm (2:0), being optimized as such in all internal nodes and in Dinosauria as well.

The asymmetry in enamel distribution is a well-described feature in ornithischian lineages, and in this topology is addressed aiming to compare it with other features of enamel. The asymmetric enamel between crown faces is here optimized as independently occurring in Ornithopoda, Ceratopsia, and *Euoplocephalus*. In *Manidens* and the indeterminate pachycephalosaurid A (Hwang, 2005), the enamel distribution is symmetric or asymmetric between opposing dentitions (*Manidens*) or depending on the region (indeterminate pachycephalosaurid), but their state of enamel distribution is considered as ambiguous. The state of these two species and *Stegosaurus* allows optimizing this ambiguous state for internal nodes comprising Tyreophora, Pachycephalosauridae, Marginocephalia, Cerapoda, Genasauria and Ornithischia (11:[0 1]). Nonetheless and as mentioned in the main text, several lines of research describe and optimize that an additional process of enamel thickening and development of enamel asymmetry occurs within Heterodontosauridae, counting in both cases as the fourth process of this kind in Ornithischia. Summarizing, these authors (Sereno, 2012; Becerra et al., 2014, 2016, 2018) detail that enamel is symmetric in basal species *Fruitadens*, *Echinodon* and *Tianyulong*; an asymmetry in enamel distribution between faces in derived species *Abrictosaurus* and *Lycorhinus*; and the complete absence of enamel in the functional face of the crowns in *Heterodontosaurus*. Similarly, enamel gets thicker in the non-functional face of most derived species of Heteroidontosauridae if compared with the basal species *Fruitadens*, *Echinodon* and *Tianyulong* (Butler et al., 2012; Sereno, 2012; Becerra et al., 2014). If the change of enamel distribution is mapped in the more complete sampling performed by Becerra et al. (2016) in Heterodontosauridae and basal Ornithischia, the optimized states indicates that instead of being ambiguous, the symmetric enamel corresponds to the ancestral state at least for Ornithischia, Genasauria and Tyreophora (nodes affected in the optimization by the ambiguous state of *Manidens*). In Ceratopsia, the asymmetry of enamel is codified for all considered species, and the ancestral state for the lineage is optimized as asymmetric (11:1). A similar inference should be done with Pachycephalosauridae: the ambiguous enamel distribution of a few specimens possibly does not represent the entire variation in enamel distribution for Pachycephalosauridae, which was optimized as symmetric by Becerra et al. (2016). Finally, all species representing Ornithopoda show an asymmetric enamel distribution, and this state is optimized in Ornithopoda and all internal nodes (11:1). A better sampling in basal ornithischian species of most important lineages presented by Becerra et al. (2016) codified the enamel distribution on basal Neornithischians *Agilisaurus*, *Kulindadromeus* and *Hexinlosaurus* as symmetric. Similarly, a symmetric enamel distribution is codified for *Scutellosaurus*, *Scelidosaurus* and *Emausaurus* in basal Tyreophora, *Goyocephale* in Pachycephalosauridae and *Orodromeus* in basal Ornithopoda. Enamel studies in *Changchunsaurus* support its symmetric distribution between labial and lingual faces (Chen et al., 2018), while is present in both faces but asymmetric in *Matheronodon* (Godefroit et al., 2017), which together with the information casted on the data matrix of Becerra et al. (2016) imply a possible symmetric/asymmetric transition of enamel distribution within Iguanodontia. The optimization of enamel distribution in Becerra et al. (2016) strongly supported that asymmetry in enamel is a convergence occurring four times in ornithischian evolution, optimizing enamel distribution as symmetric in Cerapoda, Marginocephalia, Stegosauria, Ankylosauria, Tyreophora, Heterodontosauridae, Genasauria, Ornithischia, Saurischia and Dinosauria (Becerra et al., 2016).

Features varying in enamel of Ornithischia.

Differentiated outermost enamel layer. Sander (1999) characterizes the presence of parallel crystallite forming the outermost layer of enamel in some durophagous reptilian lineages as an adaptation that increases resistance. The enamel in Ornithischia, an herbivorous lineage, is susceptible to wear, and is highly likely that some of the species included within developed a distinctive outermost enamel layer to increase resistance to breakage and wear. In Ankylosauria, the presence of parallel crystallite enamel in the outermost third not only lacks of enamel discontinuities, but also prevents tubules to reach the EES. In Pachycephalosauria (pachycephalosaurids B and C; Hwang, 2005), the presence of a double layer of parallel crystallite with and without IL (respectively) in the outer third of the enamel volume seems similar to the condition of Ankylosauria, here also taken as at least a poorly developed adaptation to reduce wear. In Neoceratopsia, exists an enamel change in the outer microns, passing from columnar enamel (with abundant tubules) to enamel of amorphous crystallite, which fills the inside of the bumps that characterize the micro-ornamentation of the external enamel surface (Hwang, 2005, 2011). This distinctive outermost layer of amorphous enamel is uniformly distributed in the Centrosaurinae *Centrosaurus* and *Pachyrhinosaurus*, and varies its thickness in the rest of Neoceratopsia (Hwang, 2011). The amorphous enamel crystallite lacks of weakness planes to each other in a regular fashion, here considered as possibly increasing enamel resistance. Regardless, the external layer of amorphous enamel is always identified in species with external globular micro-ornamentation in Neoceratopsia. Is equally likely that both features were independent or intimately related. *Psittacosaurus* lacks of both the outer layer of amorphous enamel and external micro-ornamentation (Hwang, 2005). Nevertheless, a closer look of enamel in *Psittacosaurus* indicates that the inner half of the enamel volume shows well-defined boundaries between columnar units and more frequent tubules and voids than the outer half, where the boundaries between columnar units are hardly recognized (Hwang, 2005). Although *Psittacosaurus* lacks of a hardened outer enamel layer, the outer half of the enamel volume shows to be more compact, a feature that possibly reduce the formation of planes of weakness. *Thescelosaurus* and *Tenontosaurus* in Ornithopoda show an outer layer of parallel crystallite above the poorly differentiated (*Thescelosaurus*) or well-defined (*Tenontosaurus*) columnar enamel. The wavy enamel in Dryomorpha, which possess randomly arranged enamel crystallite and implies the absence of discontinuities, prevents the formation of planes of weakness in the direction of abrasive forces in all the enamel volume. *Dryosaurus* and *Camptosaurus* in Dryomorpha lack of differentiation of the outermost enamel layer, presenting entirely coarse wavy enamel. In *Iguanodon*, the enamel is composed by coarse wavy crystallite, but the outermost microns of enamel are differentiated into a different kind of wavy enamel, and lacks of external micro-ornamentation (Sander 1999). Contrasting with the condition of Neoceratopsians and Hadrosauroidea, the distinctive outer layer of wavy enamel is not related to the presence of external micro-ornamentation. The species in Hadrosauroidea included in this comparison show a thin layer of outer fine wavy enamel, which lacks of unmineralized spaces, and micro-ornamentation of bumps at the external enamel surface. The fine wavy enamel is more resistant to wear than the enamel below given the nature and orientation of fine crystallite, enhanced by the absence of unmineralized spaces. The enamel of the species *Manidens* lacks of a distinctive outer layer (as in *Coelophysis*, *Plateosaurus*, *Stegosaurus*, and the premaxillary/anterior dentary dentition of the indeterminate pachycephalosaurid). Although an optimization of this feature is needed but not addressed in this study, the presence of a distinctive outermost layer of resistant enamel is possibly homoplastic in Ornithischia, as occurs with the enamel thickening and the enamel asymmetry. On the other hand, the origin of this distinctive outer enamel layer could be related to two different evolutionary paths. The presence of parallel crystallite as a distinctive outer enamel layer could be related to a remnant of the primitive state retained as the outermost enamel given the documented change of this enamel type (in Pachycephalosauria, Ankylosauria, and basal Ornithopoda), or could correspond to the differentiation of a new enamel type that increased the resistance (as in Neoceratopsia and Hadrosauroidea).

Enamel volume arranged in layers of different enamel types. The development of three or more enamel types is documented in different species of Ornithischia, and possibly indicates an evolutionary tendency of enamel complexification occurring in different lineages. The enamel entirely formed by parallel crystallite forms a unique layer in *Coelophysis* (Hwang, 2011). Similarly, a layer comprising mostly a unique enamel type is described in *Plateosaurus* (parallel crystallite with patches of IDCU) and *Manidens* (IDCU enamel with patches of parallel crystallite and scarce multi-layered enamel) is described. In more derived lineages of Ornithischia, the presence of multi-layered enamel in Ankylosauria is similar to some patches in Pachycephalosauridae (specimens B and C; Hwang, 2011). The condition of a unique enamel type is described in the premaxillary/anterior dentary dentition of the indeterminate pachycephalosaurid (specimen A; Hwang, 2011) and in *Stegosaurus* (excluding the BUL), although the former shows with patches of different enamel type. The enamel of species in Hadrosauriformes and Neoceratopsia can be identified as two layers of enamel above the BUL (a tri-layered enamel, thus). Interestingly these taxa show enamel thickening, external micro-ornamentation, enamel asymmetry, and a differentiated outer enamel layer, together with the development of dental batteries. When considering basal species of Ornithopoda, a progressive change of enamel can be described as a process of complexification that lead to the enamel of Hadrosauriformes. *Thescelosaurus* and *Tenontosaurus* show a similar multi-layered arrangement (a BUL, columnar enamel and a distinct parallel crystallite layer), but *Tenontosaurus* possess more differentiated columnar enamel with wavy boundaries between units ramifying into small units in the outer half of enamel and below the thin parallel crystallite outer layer. This enamel correspond to the most complex columnar enamel described in an ornithopod (Hwang, 2005) and could contain in its morphology a primitive state of development of the wavy enamel. A two-layered enamel of a rudimentary wavy enamel above a BUL described in *Dryosaurus*, in which crystallites are staggered in different angles but do not cluster in bunches separated by large unmineralized spaces (as in hadrosaurids), being in some views as columnar units with ruffled edges. The coarse wavy enamel of *Camptosaurus* above the BUL and making the entire two-layered enamel resembles that of hadrosaurids, while a tri-layered enamel volume formed by the BUL wavy enamel and a different outermost wavy enamel kind in *Iguanodon* but yet lacking of micro-ornamentation is the closest to hadrosauroids. A similar differentiation of enamel is observed between *Psittacosaurus* and Neoceratopsia, the enamel in *Psittacosaurus* is interpreted as a precursor of enamel described in more advanced ceratopsians (Hwang, 2005). Enamel complexification is intimately related with tooth morphology and the specialization to an herbivorous diet, leading to increase the resistance of the tooth (e.g., complex crystallite organization, external thin layer of resistant enamel), maintain a sharp cutting edge (e.g., enamel asymmetry) and lengthen the useful life of the tooth (increased enamel thickness).

Final comments.

Enamel differentiation adapted to tooth function and jaw improvement in Ornithischia may work in two ways depending on the clade. On the one hand, the complexification of enamel by the ordering of successive layers of primitive states of enamel with unclear or poorly developed module level (i.e. parallel/divergent crystallite without forming divergent units or forming incipient units, with or without IL) optimized as present in the ancestral node Ornithischia, a process occurring in Pachycephalosauria and Ankylosauria. On the other hand, enamel complexification can also occur as the innovative arrangement of crystallite starting from pre-existent and primitive enamel types. The results of Hwang (2005, 2011) and this study indicate that wavy enamel possibly originate from columnar enamel in which the units show sinuous boundaries (*Tenontosaurus tilleti*), an enamel type that possibly developed from incipient divergent units present in *Thescelosaurus* and optimized in basal Ornithopoda, a similar process that leaded to columnar enamel from IDCU in Ceratopsia. A combination of both processes in Ankylosauridae possibly shaped the enamel type of *Euoplocephalus* (Hwang, 2011), were IDCU enamel derived in DCU forming a more complex and resistant structure but yet combined with the successive occurrence of both parallel and divergent enamel without forming DCU. This preliminary hypothesis, however, should be revised in a phylogenetic analysis using a more complete enamel database.

Character list and matrix.

1- Minimum enamel thickness: 0, thin, less than 100 microns; 1, medium, between 100 and 200 microns; 2, more than 200 microns.

2- Maximum enamel thickness: 0, thin, less than 100 microns; 1, medium, between 100 and 200 microns; 2, more than 200 microns.

3- Parallel crystallite (and/or slightly divergent crystallite but without forming incipient columnar units): 0, present, and dominates the enamel crystallite type; 1, present, but is not a dominant type; 2, absent.

4- Columnar enamel (excluding BUL): 0, absent; 1, incipient columnar units formed by diverging crystallites (diverging bunches) with poorly defined limits, or columnar units present but poorly defined, with unclear limits or poorly organized; 2, present, columnar units with well-defined limits.

5- Basal unit layer: 0, absent; 1, present.

6- Lines of incremental growth or incrementing lines: 0, present, widely distributed along most of the crown enamel; 1, present, sporadically developed; 2, absent.

7- Wavy enamel: 0, absent; 1, present.

8- Tubules: 0, absent; 1, present and/or sporadically developed, but each tubule do not go through the complete enamel layer; 2, present and widely developed, each tubule goes through the complete enamel layer.

9- Surface: 0, smooth; 1, micro-ornamentations present (comprising smooth globules, pustules, mamelons and/or striations not confluent with marginal denticles; prominent bumps; complex wrinkling combining micro-ornamentation with macroscopic enamel structures not related with marginal denticles and without affecting the dentine below)

10- Voids or unmineralized areas: 0, absent; 1, present.

11- Enamel in labial and lingual faces of the crown: 0, symmetric; 1, asymmetric or absent in one of the faces

Coelophisis_bauri	00000000000
Plateosaurus_engelhardti	00010100000
Manidens_condorensis	0011010[01]00[01]
*Stegosaurus*_sp.	0001100100[01]
*Euplocephalus*_sp.	00121101001
Ankylosaurus_magniventris	00111001000
Edmontonia_rugosidens	01111001000
Sauropelta_edwardsi	01111001000
*Thescelosaurus*_sp.	00111101001
Dryosaurus_altus	00201111011
Camptosaurus_dispar	00201211011
*Iguanodon*_sp.	11201110011
Tenontosaurus_tilleti	11121201001
*Anatosaurus*_sp.	11201211111
Prosaurolophus_maximus	12201210111
*Saurolophus*_sp.	11201210101
Bactrosaurus_johnsoni	00201211111
Gilmoresaurus_mongoliensis	00201211111
Kritosaurus_navajovius	11201211111
Hypacrosaurus_altispinus	11201211111
Corythosaurus_casuaris	11201211111
*Psittacosaurus*_sp.	00221202011
Leptoceratops_gracilis	22221202101
*Protoceratops*_sp.	01221202101
*Triceratops*_sp.	12221202101
Centrosaurus_apertus	12221102101
Pachyrhinosaurus_canadensis	12221002101
Pachycephalosauridae_indetA	0011110000[01]
Pachycephalosauridae_indetB	00111100000
Pachycephalosauridae_indetC	00111100000

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Figure 1. Sectioned specimens. A, MPEF-PV 10862a, longitudinal section of dentary tooth; B, MPEF-PV 3821, cross-section of maxillary tooth; C, MPEF-PV 10865, tangential section of dentary tooth; D, MPEF-PV 10864, tangential section of maxillary tooth ; E, MPEF-PV 10862b, longitudinal section of dentary tooth, opposite side than A, comprising two different specimens; F, MPEF-PV 10823, longitudinal section of maxillary tooth; G, MPEF-PV 10863, cross-section of dentary tooth.