Paleontología y dinosaurios desde América Latina

Jorge Calvo, Juan Porfiri, Bernardo González Riga,
Domenica Dos Santos (Editores científicos)

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Este libro compendia interesantes descubrimientos, trabajos científicos y proyectos educativo-turísticos sobre paleontología realizados en América Latina y Europa.

Como obra, fue generado a partir del III Congreso Latinoamericano de Paleontología de Vertebrados, realizado en la provincia de Neuquén (Patagonia, Argentina) durante el año 2008.

Refleja el crecimiento que ha tenido la paleontología en América Latina, donde observamos un incremento de hallazgos excepcionales, un mayor número de paleontólogos jóvenes y el desarrollo de congresos internacionales de gran envergadura y nivel científico. Por ello, el presente libro, no sólo reviste interés científico, sino también educativo para Argentina y el resto del mundo.

Ilustración de tapa: Favio Pastori

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Evolutionary major trends of ornithopod dinosaurs teeth

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Teeth: major trends and structural changes

Among Ornithopoda, teeth underwent considerable transformations, from the "typical" basal ornithischian tooth to the highly modified dentition in Hadrosauria possibly adapted for continuous mastication. All of the major morphological forms bridging these extreme conditions are well-documented in the fossil record. Some of the most important major trends are: (i) relative decrease in tooth size (Sereno 1997, Sereno and Wilson 2005); (ii) increase in number of tooth files; (iii) increase of replacement rate (Horner 1983); (iv) restriction of the enamel to one crown side only (to opposing sides of the crown in maxillary versus dentary teeth) (Sereno 1997); (v) on the enameled side of the crown there is an increasing prominence of a ridge, called primary ridge; (vi) the shape of the crown adjusts for efficient packing, allowing more teeth per unit area (Norman *et al*. 2004); (vii) complete loss of the premaxillary teeth (Norman 2004); (viii) increasing number of denticles (this paper); (ix) occlusal area of the teeth row relative to the mandible dimensions increases (due to the increasing number of functional teeth, e.g. Gates and Sampson 2007); (x) increasing number and distinctiveness of root facets for adjacent teeth (this paper); and (xi) differential construction between maxillary and dentary teeth (e.g. Norman 1980). Not many structural changes have been regarded as so in the literature, however some are noteworthy: increasing tooth longevity or dentine formation rates (Erickson 1996, p.14626), also, the accuracy of occlusion seems to increase, materialized by precise tooth to tooth occlusion, whereas in basal taxa biconcave wear facets were often present (Weishampel 1984).

The biological and functional roles of many structural changes is not yet understood (e.g. increasing number of denticles), and some of them have to be assessed quantitatively in order to draw a better picture (e.g. Hwang 2005), for example, thickness determination of enamel among several taxa and even between labial and lingual sides of the tooth (figure 1).

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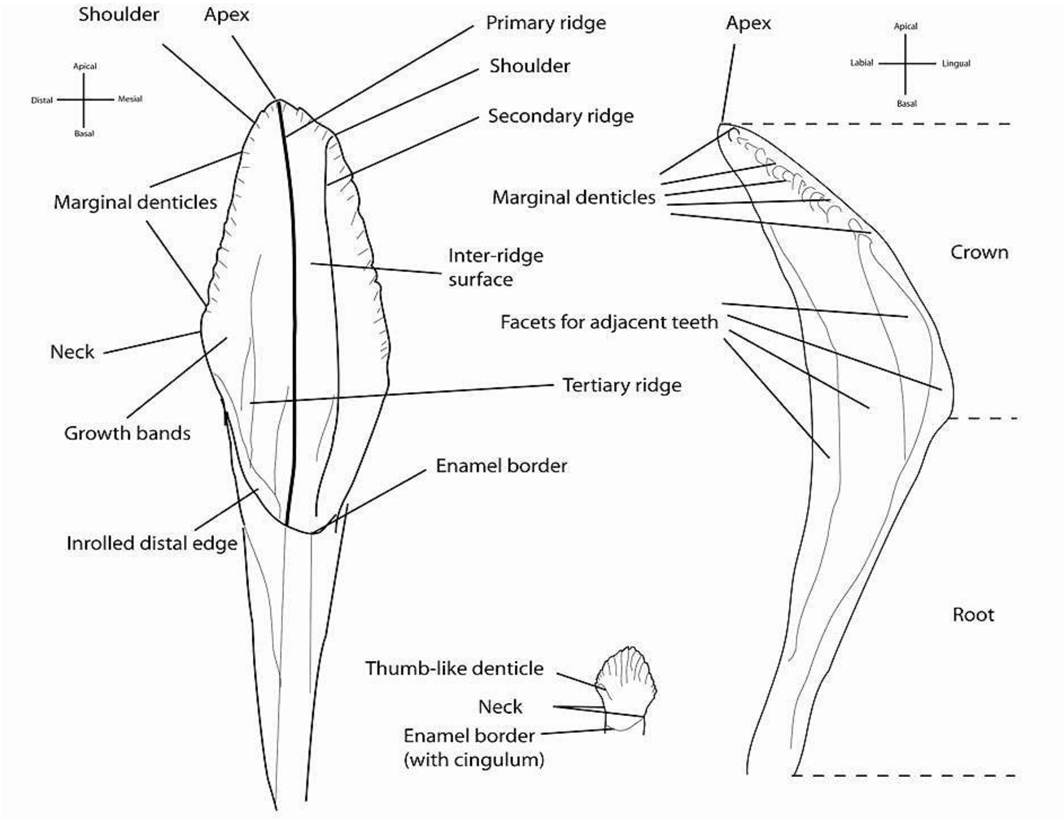

Figure 1. General anatomical nomenclature used for ornithopod teeth, based on an diagramatic *Iguanodon* dentary tooth).

The purpose of this paper is to summarize the most important major trends on the teeth across ornithopod evolution as well as clarify the most relevant anatomical terms used in descriptions. The observations presented on this paper derive from examination of 49 different ornithopod taxa. Where possible, the present analysis considers matured unworn teeth in the middle of the tooth-bearing bones.

Apex

The apex of the tooth tended to be acutely pointed in basal taxa, but the redistribution of enamel and the overall reconfiguration of tooth shape led to blunt teeth in iguanodontians including most hadrosaurids (see, for example, *Iguanodon* or *Lambeosaurus*). However, *Hypacrosaurus* for example, had pointed teeth since the closely packed arrangement of the adjacent teeth shaped the diamond design of the crown into an acute apex. Thus, the apex although morphologically similar to those in basal taxa, it is genetically different.

The orientation of the apex in dentary teeth could be mesial or distal in some basal ornithopods (e.g. mesial in *Bugenasaura*, and distal in *Zephyrosaurus*), however it tended to become aligned with the apicobasal axis of the tooth in all more derived taxa.

Marginal denticles

In basal ornithopods the number of denticles is coincident with the number of ridges. This condition changed in more derived taxa when the denticles become unsupported by ridges. This is the reason why both features that form crown ornamentation should be treated separately phylogenetically. In basal ornithopods each denticle was accompanied by an apicobasal groove, and both features were intrinsically related. However, in ankylopollexian ornithopods the ridges start becoming independent from the denticles and increase in number relative to the ridges. In hadrosaurids the denticles are very small (e.g. *Kritosaurus incurvimanus*, see also Pinna 1979) or absent (e.g. *Edmontosaurus regalis,* see Lambe 1920), and fewer in number (maximum 16 denticles) when compared with non-hadrosaurid iguanodontids. In some hadrosaurid taxa, the denticles tend to become more irregular in size along the margin of the crown such as *"Trachodon cantabrigiensis"* (BMNH R4472).

Retention of the plesiomorphic condition, the embryonic *Hypacrosaurus stenbergi* has got well-developed denticles along the margin of the crown (Horner *e* Currie 1994, pg. 315). In adult *Hypacrosaurus altispinus* there is an emargination around the borders of the teeth that are the remnants of the denticles.

The presence of a thumb-like denticle in basal ornithopods is also represented in some specimens of *Camptosaurus* (e.g. YPM 1880). We do not foresee a functional reason for this feature to be reacquired.

It is noteworthy that in the *Iguanodon* genus, in particular in the dentary teeth, there is sub-denticles displayed linguolabially (Norman 1980). A similar sub-denticle condition is also verified in *Drinker nisti*, for example, where a denticle is sub-divided in three cusps (Bakker *et al*. 1990). However, in *Drinker nisti* sub-denticles are oriented mesiodistally. The formation of subdenticles, therefore, appears to surge independently.

Ridges

Norman (2004, p. 424) referred a major trend relative to the distribution of ridges considering them to be divergent or parallel in basal forms, and tending to become simplified in derived taxa. This general trend seems to be confirmed for subsidiary ridges, but persists in the primary ridge. There is indeed an overall tendency for the simplification of ornamentation (ridges and denticles) among Ornithopoda, and only the functionally effective features seem to be retained, namely the primary ridge.

In some taxa (e.g. *Drinker nisti*) the apical denticle (as well as its accompanying ridge) is more distinctively prominent than the rest; in contrast *Orodromeus makelai* does not bear an accompanying apicobasal ridge. However, it is impossible to distinguish denticles and ridges in some taxa such as *Parksosaurus warreni* and *Anabisetia saldivai* (pers. obser.). Most subsidiary ridges tend to disappear in more derived taxa, although a few remain in both mesial and distal side of the tooth. This means that not all denticles are supported by ridges (e.g. *Tenontosaurus tilleti*, *Dryosaurus altus,* pers. obs.). In some teeth, the primary ridge may not be particularly prominent relative to others. In more derived forms (e.g. *Probactrosaurus gobiensis*, *Penelepognathus weishampeli, Fukuisaurus tetoriensis, Camptosaurus* genus and some specimens of *Iguanodon*) it may occur that two ridges get equally protuberant or only the distal ridge slightly more protuberant (forming a secondary ridge). The primary ridge is distally offset, thus it seems that as secondary ridges fade, the more prominent ridge moves towards the median part of the tooth (see, for example, *Altirhinus kurzanovi* for primitive example; *Telmatosaurus transsylvanicus* for derived condition). The trend is towards an enhancing distinct primary ridge and progressive smoothing of subsidiary ridges (e.g *Probactrosaurus*, *Altirhinus kurzanovi*, *Telmatosaurus transsylvanicus*). In hadrosauroids, despite some teeth still bearing at least two prominent and well-developed ridges (see Company *et al*., 1998, and *Aralosaurus tuberiferus*), most taxa bear one single primary ridge. Retention of the plesiomorphic condition can be seen in the embryonic *Hypacrosaurus stenbergi* that has a faint secondary ridge that is not preserved in the adult specimens (Horner *e* Currie 1994, pg. 315). Finally, amongst lambeosaurines in general, the primary ridge tends to become sinuous (Godefroit *et al*. 2003).

Enamel border

The enamel border is typically dominated by a cingulum (that has been regarded as a possible dental synapomorphy for Ornithischia, Parker *et al*. 2005) in basal Ornithopoda. However, this basal expansion of the enamel border is not present in all Dryomorpha. The transition from the carina of the crown to the cementum of the root is smooth (in basal Dryomorpha) and then abrupt (as in most hadrosaurids).

Neck

Across ornithopod teeth evolution, as the enamel concentrates more on the lingual side of the tooth and cementum on the labial side, the neck tends to disappear or acquires a new form. The neck, considered as a constriction between root and crown, does not exist for Dryomorpha and taxa therein, since cementum on the labial side of the tooth eliminates this feature.

Shoulder

This anatomical entity is only present on taxa bearing a prominent secondary ridge (e.g. *Altirhinus kurzanovi*), i.e. non-hadrosaurid dryomorphans. This happened due to anatomical constraints derived from pressure of adjacent teeth during their ontogenetic process. In order to arrange a large number of teeth in such a confined space, the secondary ridge - as well as the primary ridge - work as structural elements preserving the shape of the tooth. As secondary ridges tend to become less important in hadrosaurids, then the shoulder disappears as well.

Inter-ridge surface

In basal Ornithopoda teeth (e.g. *Orodromeus makelai*, sensu Butler *et al*. 2007) the inter-ridge surface is convex and unornamented. In basal Euornithopoda ridges start to increasingly dominate the inter-ridge surface. Nonetheless, in taxa such as *Thescelosaurus neglectus*, *Anabisetia saldivai* and Rhabdodontidae the inter-ridge surface is extremely reduced, being no more than the grooves that separate the ridges. In Dryomorpha the preponderance of the ridges in the crown is reduced and in subsequently being in more derived taxa only represented by the primary ridge. In Hadrosauria the prominence of the primary ridge produces two concavities in the inter-ridge surface.

Wear facets

In basal Ornithopoda the tooth to tooth occlusion is imperfect, generating in most preserved dentition biconcave wear facets. As the jaw mechanics becomes more precise (Weishampel 1984), the teeth bear a single oblique wear facet.

Another aspect that has not sufficiently been recorded in the literature is the angle between the wear facet and the apicobasal axis of the tooth. Some data was collected by Weishampel (1984), but a more extensive dataset would allow a better understand of ornithopod mastication process and evolution.

Roots

One of the most conspicuous major trends in the roots of Ornithopoda is the development of attachment facets for contiguous teeth. The apicobasal ridges formed are more marked and more numerous as the number of contiguous teeth increases. In basal ornithopods the root is typically sub-cylindrical and in hadrosaurids typically faceted.

Final Remarks

Ornithopod teeth evolution is an admirable example of how anatomical constraints define morphology. As the number of teeth increases during ornithopod evolution, the confined teeth have to be accommodated in a proportionally smaller space. A response to this condition is the overall simplification of ornamentation as the general construction of the tooth, conspicuous in hadrosaurids. It is reasonable to conclude that in general the morphology of ornithopod teeth was not determined by evolutionary novelties but more influenced by the increasing number of teeth per tooth-bearing bone.

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