

# The teeth of the unenlagiine theropod *Buitreraptor* from the Cretaceous of Patagonia, Argentina, and the unusual dentition of the Gondwanan dromaeosaurids

FEDERICO A. GIANECHINI, PETER J. MAKOVICKY, and SEBASTIÁN APESTEGUÍA



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The Unenlagiinae is a clade of Gondwanan dromaeosaurid theropods mainly known from incomplete skeletal material. The group includes two recently discovered theropods, *Buitreraptor* and *Austroraptor*, from which cranial remains are available with in situ maxillary and dentary teeth, thus allowing the study of tooth morphology. Among the derived traits that diagnose the dentition of unenlagiines are: (i) high tooth count, (ii) small size of individual teeth when compared with skull height, (iii) absence of denticles and carinae, and (iv) presence of longitudinal grooves on the tooth crown. This suite of dental characteristics, shared between *Buitreraptor* and *Austroraptor*, can be considered as diagnostic of the Unenlagiinae or, at least, a more exclusive clade within the group. The teeth of *Buitreraptor* exhibit a remarkable labiolingual compression, whereas *Austroraptor* possesses more conical teeth, probably respective autapomorphic features. On one hand, these dental morphologies differ from those observed in most Laurasian dromaeosaurids and, for instance, could be considered as further proof of the purported vicariant evolution of the lineage on the southern continents. On the other hand, the morphological similarities (e.g., absence of denticles) between the teeth of unenlagiines and other theropod lineages, including Mesozoic birds and ornithomimosaurs, can be considered as the result of parallel trends related to dental reduction.

Key words: Theropoda, Dromaeosauridae, Unenlagiinae, teeth, Cretaceous, Argentina.

Federico A. Gianechini [smilodon.80@gmail.com] and Sebastián Apestegúa [sebapestegua@gmail.com], CONICET. Fundación de Historia Natural “Félix de Azara” – CEBBAD – Universidad Maimónides. Hidalgo 775, 7° piso (1405BDB), Buenos Aires, Argentina;

Peter J. Makovicky [pmakovicky@fieldmuseum.org], Field Museum of Natural History, 605 South Lake Drive, Chicago, USA.

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## Introduction

Dinosaur teeth of both herbivorous and carnivorous species are useful biogeographical tools. They permit the recognition of lineages in regions or strata that lack other well preserved skeletal records (e.g., Rauhut and Werner 1995; Rauhut 1999; Sankey 2001; De Valais et al. 2003; Amiot et al. 2004; Vullo et al. 2007; Casal et al. 2009; Ezcurra 2009). Furthermore, even among the relatively uniform dentitions of theropod dinosaurs, peculiar morphological features allow the recognition of not only major clades, but also of new species (although sometimes of questionable taxonomic validity), particularly within deinonychosaurs (e.g., *Richardoestesia gilmorei*, Currie et al. 1990).

In recent years, our knowledge on the morphology of deinonychosaurs has increased substantially, not only through the discovery of new Laurasian taxa (e.g., Xu et al. 2002, 2003; Norell et al. 2006; Turner et al. 2007; Turner et al. 2007b), but also after the discovery and recognition of a monophyletic

group of Gondwanan dromaeosaurids, the unenlagiines (Bonaparte 1999; Makovicky et al. 2005; Novas et al. 2009). Furthermore, this new evidence provided new insights into the anatomical and ecological disparity of these theropods. In this regard, unenlagiines display a wide range of sizes, from the small-sized purported unenlagiine *Rahonavis* (Forster et al. 1998) to the 5-meter-long *Austroraptor* (Novas et al. 2009). These taxa also show a remarkable disparity in relative arm lengths, with possibly volant or gliding long-armed forms (*Rahonavis*, *Buitreraptor*) to short-armed gigantic forms (for deinonychosaur standards) such as *Austroraptor*.

Until 2005, the Gondwanan deinonychosaur record consisted of fragmentary taxa based on skeletal remains without preserved dentition, including *Unenlagia comahuensis* (Novas and Puerta 1997), *U. paynemili* (Calvo et al. 2004), and *Neuquenraptor argentinus* (Novas and Pol 2005). The record also includes unassociated isolated teeth (e.g., Rauhut and Werner 1995; Poblete and Calvo 2003; Fantí and Therrien 2007; Casal et al. 2009; Ezcurra 2009). Nevertheless, the re-

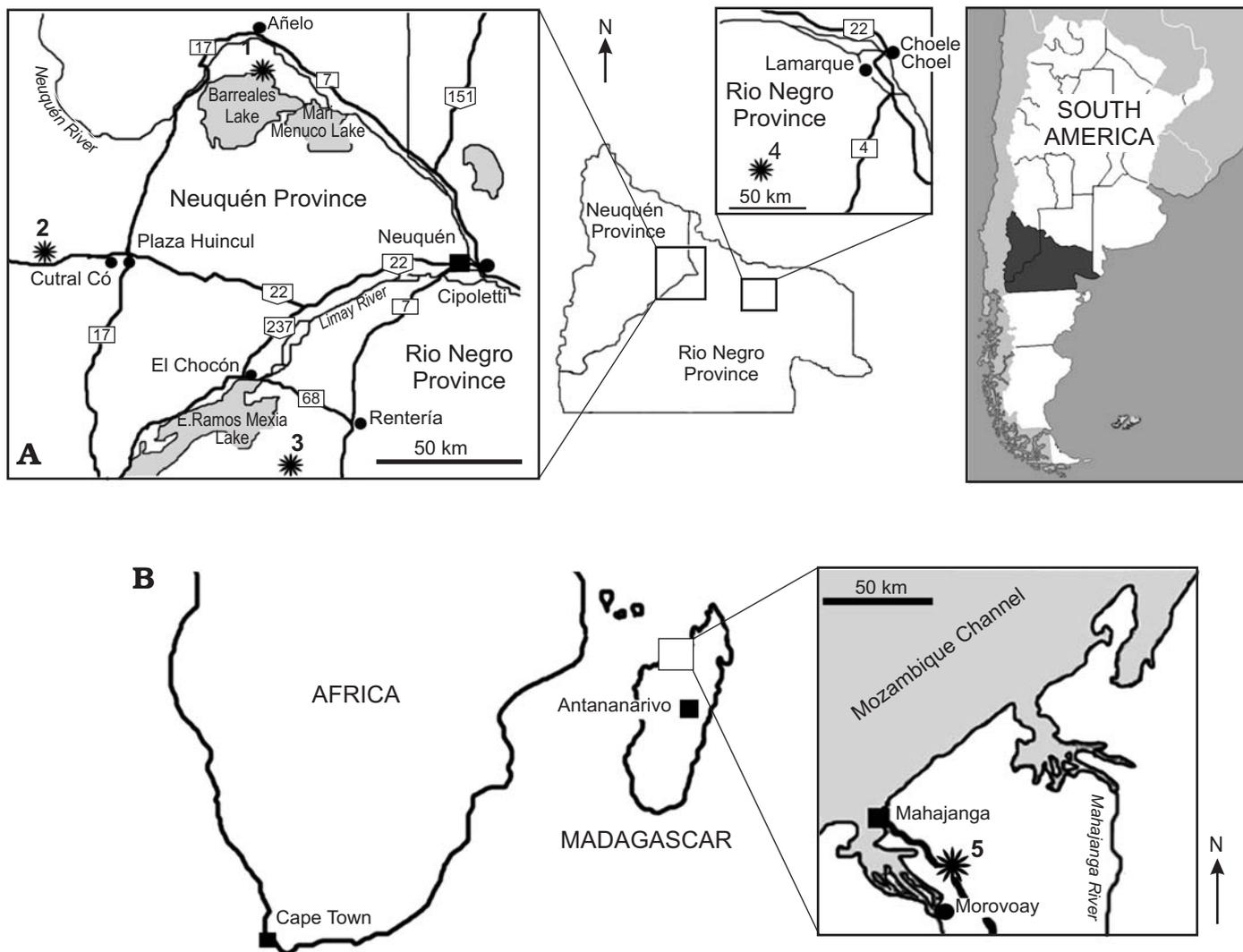


Fig. 1. Geographic provenance of all unenlagiine theropods. The localities which yielded the holotypes of each taxa are indicated by a star and a number. *Buitreraptor* came from “La Buitrera”, a locality situated about 80 km from Cipoletti, close to the south shore of the Ezequiel Ramos-Mexía Lake, north-western Río Negro Province, Argentina. A. South American localities: 1, Futalognko site, Centro Paleontológico Lago Barreales, Portezuelo Formation (Turonian–early Coniacian): *Unenlagia paynemili*; 2, Sierra del Portezuelo, Portezuelo Formation: *Unenlagia comahuensis*; 3, La Buitrera, Candeleros Formation (Cenomanian–Turonian): *Buitreraptor gonzalezorum*; 4, Bajo de Santa Rosa, Allen Formation (Campanian–Maastrichtian): *Austroraptor cabazai*. B. African locality: 5, Mahajanga, Maevarano Formation (Campanian): *Rahonavis ostromi*.

cent discovery of *Buitreraptor* and *Austroraptor* (Makovicky et al. 2005; Novas et al. 2009), both with in situ teeth, permits the comparison of tooth morphology of both taxa. Among them, *Buitreraptor gonzalezorum* is the most complete and better preserved unenlagiine to date. *B. gonzalezorum* was found in beds of the Upper Member of the Candeleros Formation (Cenomanian–Turonian; Corbella et al. 2004) of Río Negro Province, Argentina (Figs. 1, 2). This taxon was briefly described (Makovicky et al. 2005) and a longer description is in preparation. In the meantime, the anatomical information provided by its dentition merits its own description.

**Institutional abbreviations.**—MACN, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina; MPCA, Museo Provincial Carlos Ameghino, Cipoletti, Río Negro, Argentina.

**Other abbreviations.**—CH, crown height; CBL, crown base length; CBW, crown base width; CA, crown angle; CBR, crown base ratio: CBW/CBL; CHR, crown height ratio: CH/CBL; DSDI, denticles size difference index.

## Materials and methods

The following description is based on the teeth preserved in the skull of the holotype of *Buitreraptor gonzalezorum* (MPCA 245). Five teeth are preserved in the right maxilla and eight in the lower jaw (Fig. 3, Table 1) all of them in situ. Additionally, five isolated teeth devoid of roots were found associated with that specimen: MPCA 245 (A1–A5). These associated teeth preserve the same morphology of

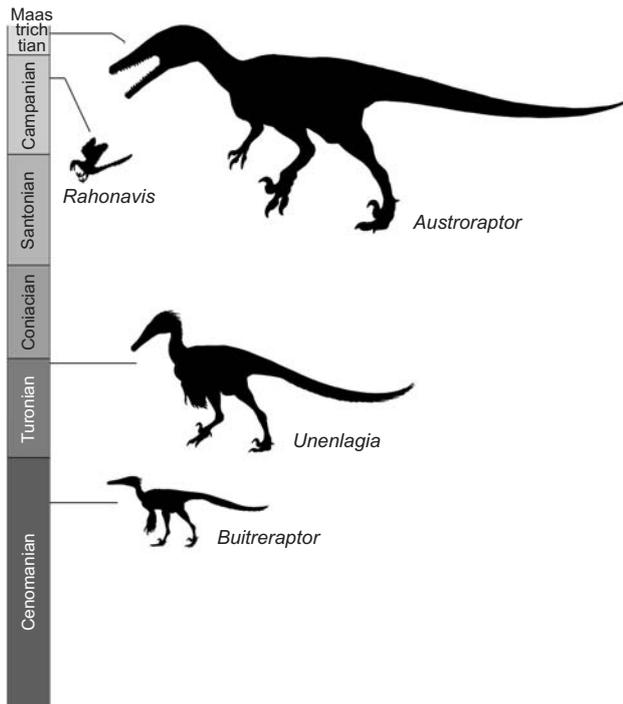


Fig. 2. Stratigraphic provenance of unenlagiine taxa, including *Buitreraptor*. The different taxa silhouettes are in scale each to other.

those in situ and are considered as part of the holotype (Figs. 4, 5). Observations were made with a stereo-microscope and a Philips model XL30 TMP New Look SEM at the MACN. Measurements and ratios proposed by Smith et al. (2005) were taken with a digital caliper.

## Systematic palaeontology

Dinosauria Owen, 1842

Theropoda Marsh, 1881

Maniraptora Gauthier, 1986

Dromaeosauridae Matthew and Brown, 1922

Unenlagiinae Bonaparte, 1999

Genus *Buitreraptor* Makovicky, Apesteguía, and Agnolín, 2005

*Type species:* *Buitreraptor gonzalezorum*, “La Buitrera”, northwestern Río Negro Province, Argentina, Candeleros Formation, Cenomanian–Turonian, Upper Cretaceous.

*Buitreraptor gonzalezorum* Makovicky, Apesteguía, and Agnolín, 2005

Figs. 3–5.

*Holotype:* MPCA 245, consisting of an almost complete adult skeleton, including a partial, articulated skull, with both incomplete maxillae with teeth in situ, left jugal, both postorbitals, both quadrates, right squamosal, both incomplete nasals, both frontals, both parietals, the occipital condyle, and mandibular bones, including both dentaries with in situ teeth, both splenials, left angular, and left surangular. The holotype also includes several isolated teeth. The postcranium includes cervical, dor-

sal, sacral, and caudal vertebrae, cervical and dorsal ribs, chevrons, both scapulocoracoids, furcula, both ilia, right ischium, both humeri, right radius and ulna, metacarpals and manual phalanges, both femora, right tibia and fibula, left incomplete tibia and fibula, metatarsals, several pedal phalanges, and undetermined fragments of bone.

*Type locality:* “La Buitrera”, situated about 80 km southwest from Cipolletti, close to the south shore of the Ezequiel Ramos-Mexía Lake, northwestern Río Negro Province, Argentina.

*Type horizon:* Candeleros Formation, Cenomanian–Turonian, Upper Cretaceous.

*Referred material.*—MPCA 238, consisting of an incomplete sacrum, right ilium and pubis, right hindlimb (femur, tibia, astragalus, metatarsals, and phalanges), all preserved in articulation.

*Description.*—The holotype skull of *Buitreraptor gonzalezorum* bears six alveoli in the preserved part of the right maxilla and five more are located on its posterior section (Fig. 3A, D). The preserved part of the right dentary bears at least twenty alveoli, with three teeth in their sockets in the anterior region, and three more in the mid-region (Fig. 3A–C). The left dentary has traces of around fifteen alveoli and only preserves two teeth in situ at the rostral tip (Fig. 3E–G). The exact number of alveoli is difficult to establish due to breakage, but be-

Table 1. Quantitative characters of the teeth of the unenlagiine theropod *Buitreraptor gonzalezorum* from the Upper Cretaceous of La Buitrera, northwestern Río Negro, Argentina. D, dentary teeth. Numbers do not refer to exact positions in the tooth row, but its position with respect to the other teeth in situ, i.e., Mx right 1 refer to the first tooth preserved in the right maxilla, Mx right 2 refer to the second tooth preserved posterior to the first, and so on. All measurements are in millimeters.

Isolated teeth							
Collection number	CH	CBW	CBL	AL	CA	CBR	CHR
MPCA 245 A1	4.6	0.8	2.4	6.3	40.4	0.33	1.92
MPCA 245 A2	2.5	0.2	0.8	2.2	58.9	0.25	3.13
MPCA 245 A3	2.7		1.2	1.6	48.6		2.25
MPCA 245 A4	3.6	0.1	1.3	3.9	46.2	0.08	2.77
MPCA 245 A5	4.2	0.9	1.8	3.5	53.6	0.50	2.33
In situ teeth							
Position	CH		CBL	AL	CA		CHR
Mx right 1	1.1		0.7	2.2	36.8		1.57
Mx right 2	0.9		0.7	1.7	35.7		1.29
Mx right 3	1.5		0.7	2	49.8		2.14
Mx right 4	1.1		0.7	1.3	50.1		1.57
Mx right 5	0.8		0.6	0.9	28.3		1.33
D right 1			1.1				
D right 2	2.4		1.3	2.5	66.3		1.85
D right 3	3.1		2	3.4	59.9		1.55
D right 4	1.2		0.9	1.4	41.6		1.33
D right 5	0.6		0.4	0.7	49.2		1.50
D right 6	0.9		0.8	1.1	54.6		1.13
D left 1	2.6		1.8	2.7	54.4		1.44
D left 2	3.4		1.9	3.7	62.2		1.79
Average measurements of teeth							
	CH	CBW	CBL	AL	CA	CBR	CHR
	2.19	0.50	1.17	2.42	49.21	0.29	1.82

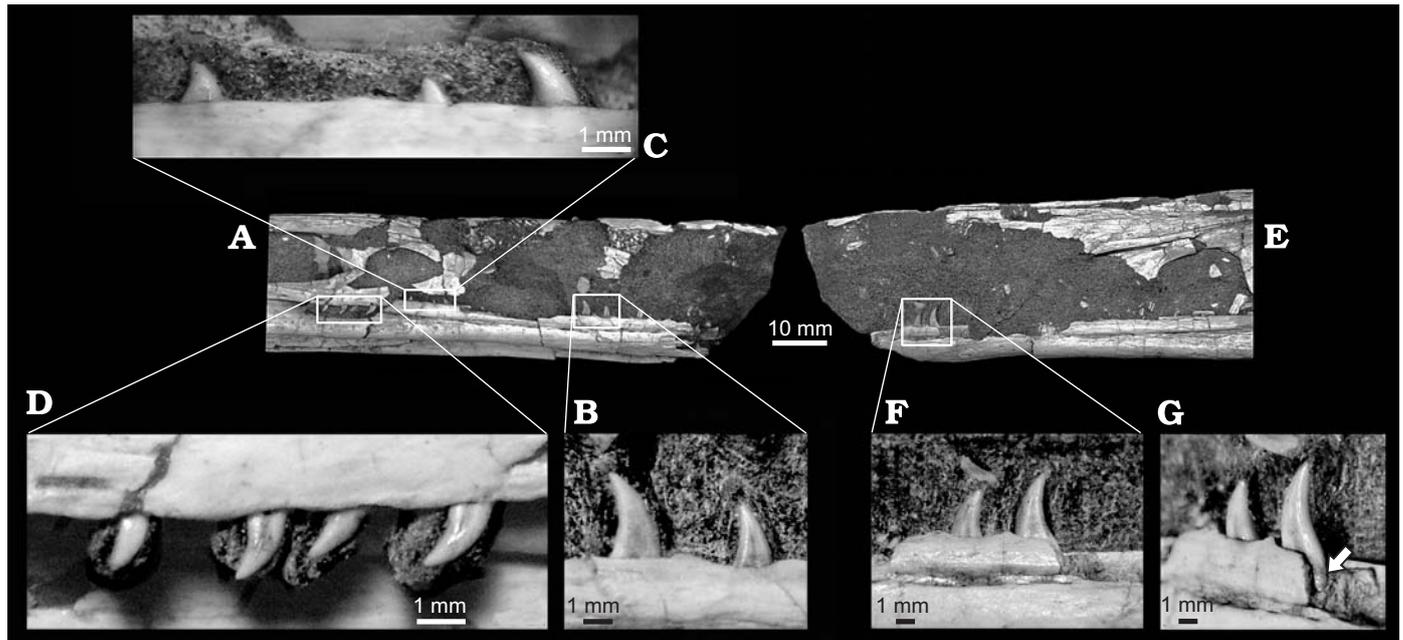


Fig. 3. In situ teeth of the unenlagiine theropod *Buitreraptor gonzalezorum* Makovicky, Apesteguía, and Agnolín, 2005 (MPCA 245) from the Upper Cretaceous of La Buitrera, northwestern Río Negro, Argentina. **A.** Right side of skull, showing the zones of the mandible and maxilla with preserved teeth. **B.** Second and third tooth preserved in the right mandible (the first tooth is very poorly preserved). In the second tooth the central groove is visible on the lateral side of the crown flanked by shallow ridges. **C.** Fourth, fifth and sixth teeth preserved in the right mandible. **D.** First to fourth tooth preserved in the right maxilla. Here the central grooves also are visible on the lateral side of the crowns, like **B.** **E.** Left side of the skull, showing the zone with preserved teeth. **F.** First and second teeth preserved on the left mandible. Also visible are the grooves and the ridges of the lateral sides of the crown. **G.** Posterior view of **F.** The arrow shows the broken zone of the mandible, where is visible the root of the second tooth.

cause of the length of the dentaries, the extension of the dental row and the size of the alveoli it is estimated that about twenty five alveoli were present in the jaw. Although the articulation of the lower jaw precludes the observation of the lingual side of the maxillary teeth, this surface is available in five isolated teeth found associated with the skeleton during preparation.

*Buitreraptor* teeth are small when compared to skull height, ranging from 0.6 to 4.6 millimeters (mean CH: 2.19 mm; ratio between the height of the crown and the height of the lower jaw: 0.29) (Table 1). They are distally curved and labiolingually compressed (CBR medium: 0.29), with a very acute end (Fig. 4). All teeth, those in situ and those isolated, present the same morphology, differing only in their size. The latter becomes evident in the right dentary, where the anterior teeth are slightly larger than those from the mid-dentary (Fig. 3A–C, Table 1). The preserved teeth are in different stages of eruption, with some completely erupted and others barely so. It is evident that continuous tooth replacement occurred in this species.

All crowns are straight in mesial and distal views, without any lateral deflection (Fig. 4B, D). In side view, the crowns are often moderately recurved distally along their full length. However, in some teeth, especially the largest, the base of the crown is quite straight while the apex shows a strong curvature toward the tip (Fig. 4A, C).

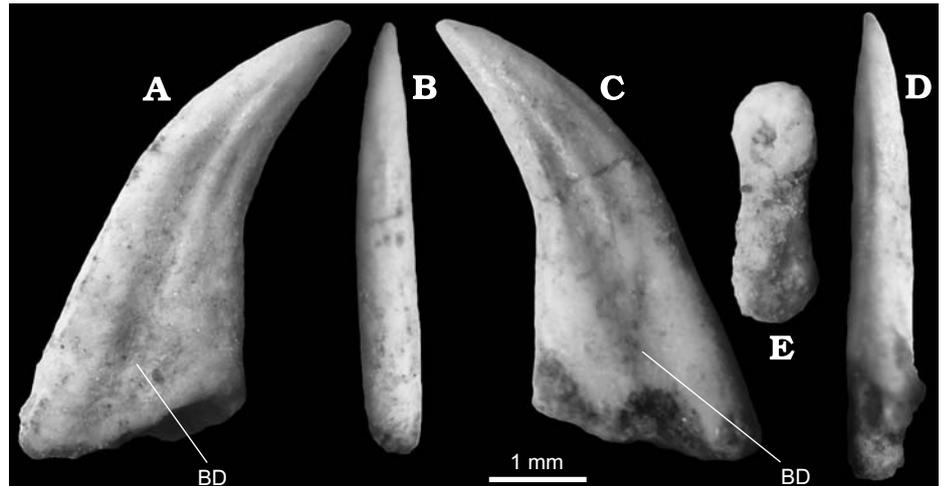
The second preserved tooth of the left dentary (MPCA 245 D8) is situated in an alveolus with a broken posterior rim. This reveals that the distal base of the crown is continuous with the

root, without any constriction (Fig. 3G), and contrasting with troodontids and other groups of non avian coelurosaurs (e.g., ornithomimosaurs, Pérez-Moreno et al. 1994; oviraptorosaurs, Balanoff et al. 2009; therizinosauroids, Kirkland and Wolfe 2001; Clark et al. 1994). The curvature of the distal border of the crown changes at this point and the distal border of the root continues fully straight. Both mesial and distal borders of the crown are slightly rounded and devoid of carina and denticles in all preserved teeth (Figs. 4B, D, 5A).

The labial and lingual sides of the crowns are very similar to each other, and it is difficult to observe any difference in their convexity that could allow us to distinguish between these sides, especially in the isolated teeth. An important feature in all the observed teeth is an elongated longitudinal depression on both labial and lingual surfaces, which confers a figure-eight cross-section to the crown (Figs. 3B–D, F, 4A, C, E). In some teeth, a groove arises from this depression and extends toward the apex without reaching it (Fig. 4A). This median groove is flanked by shallow ridges in some teeth (Fig. 3B, F).

Another distinctive feature is the presence of a system of parallel longitudinal ridges and grooves, at both sides of the central depression (Figs. 3B, F, 4A, C, 5B). In some teeth these grooves and ridges are located closer to the distal border, distally with respect to the central depression (Fig. 5B). These ridges and grooves do not follow a defined pattern and their number is not constant, being sometimes asymmetrical in both sides of the same crown, and differing in their depth. They extend from the base of the crown almost to the apex (Fig. 5B) or

Fig. 4. Isolated tooth associated with the holotype of the unenlagiine theropod *Buitreraptor gonzalezorum* Makovicky, Apesteguí, and Agnolín, 2005 from the Upper Cretaceous of La Buitrera, northwestern Río Negro, Argentina (MPCA 245 A1), in lateral (A, C), mesial (B), distal (D), and basal (E) views. In lateral view, note the basal lateral depression (BD). Visible in the apical half is one central ridge flanked by two grooves. Note the absence of carinae and denticles in both mesial and distal edges. In basal view, note the figure-eight shaped form.



can be also restricted to the apical half of the crown (Fig. 4A, C). In several teeth there are two grooves on each side of the crown, framed by a ridge of the same extension on both sides (Fig. 4A, C). To summarize, the complete topographical system of *B. gonzalezorum* teeth is composed by a median ridge, two framing grooves, a ridge on the mesial side, and one on the distal side. In other cases, three or more grooves and ridges are restricted to only the distal region, close to the edge (Fig. 5B). Some teeth do not have these features, except for the central depression on each side (Fig. 5A). The recognition of a pattern between the number and distribution of grooves and ridges and the position of the teeth in the tooth row is hampered due to a lack of more complete dental series (Fig. 3A, E).

**Stratigraphic and geographic range.**—Candeleros Formation (Cenomanian–Turonian), basal unit of the Neuquén Group, Río Limay Subgroup, Río Negro province, Argentina.

## Discussion

The characterization of the dromaeosaurid dentition has been mainly based on the dental morphology exhibited by the Laurasian taxa, where the record of the group is still better than in southern continents. This greater diversity of Laurasian dromaeosaurids responds to continuous discoveries and research of new taxa in the last eighty years in Laurasian territories. Conversely in Gondwana (mainly in South America), only since the late 1990s have new forms of this group of theropods been discovered.

Teeth in Laurasian dromaeosaurids are generally characterized by the presence of laterally compressed and distally curved crowns, with serrated carinae on both mesial and distal borders. Some dromaeosaurids from Liaoning are the exception because they do not have serrations on the mesial or both mesial and distal borders, like *Sinornithosaurus* and *Microaptor* (Xu et al. 1999, 2000; Xu and Wu 2001; Xu 2002). Conversely, Gondwanan dromaeosaurid remains with teeth in situ (i.e., *Buitreraptor* and *Austroraptor*) demonstrate a substantially different dental morphology than that of Laurasian

forms. In this respect, each dental feature characterizing the Unenlagiinae will be considered separately, adding comparisons with dental morphology of other dromaeosaurids.

**High tooth count.**—Laurasian dromaeosaurid dentaries commonly bear among 11 to 16 teeth (Norell and Makovicky 2004), whereas in *Buitreraptor* the full content can be estimated at approximately 25 teeth (Fig. 3A, E), a condition similar to that of *Austroraptor*, in which at least 25 teeth are present (Novas et al. 2009). Furthermore, *Austroraptor* has a maxillary count of 24 teeth, differing from the low count of 9 to 15 maxillary teeth in other dromaeosaurids (Norell and Makovicky 2004; Novas et al. 2009). However, it must be noted that a very high tooth count is also found in troodontids, ornithomimosaur (*Pelecanimimus*), and alvarezsaurids (*Shuvuuia*) (Pérez-Moreno et al. 1994; Chiappe et al. 1998; Makovicky and Norell 2004). In this way, a high tooth count could be considered as a homoplasy in the Unenlagiinae and the other mentioned taxa (see Supplementary Online Material [SOM] at [http://app.pan.pl/SOM/app56-Gianechini\\_etal\\_SOM.pdf](http://app.pan.pl/SOM/app56-Gianechini_etal_SOM.pdf)).

**Small tooth size.**—This character is evaluated as the ratio between the largest tooth of the maxilla (or the dentary if it is the case) with respect to the height of the maxilla at level of the anterior rim of the antorbital fenestra (see SOM). *Buitreraptor* shows a ratio of 0.18 (Fig. 3A, E, Table 1), being comparatively small in relation with Laurasian dromaeosaurids. The latter commonly show larger teeth, in which the ratio is over 0.25, reaching in some cases values close to 0.40 (e.g., Colbert and Russel 1969; Ostrom 1969; Sues 1977; Currie 1995; Xu and Wu 2001; Currie and Varricchio 2004). According to the phylogenetic analysis the smaller teeth of the Unenlagiinae are interpreted as a reversal from the large teeth observed in Laurasian dromaeosaurids. Further, in *Buitreraptor* the teeth are even smaller and thus this character is considered as autapomorphic (see SOM). Taking into account a wider phylogenetic point of view, this ratio can reach comparatively low values in other Maniraptoriformes. In troodontids, for example, these values can be lower than 0.20 (e.g., *Sinornithoides*: 0.15; Russel and Dong 1993; Currie

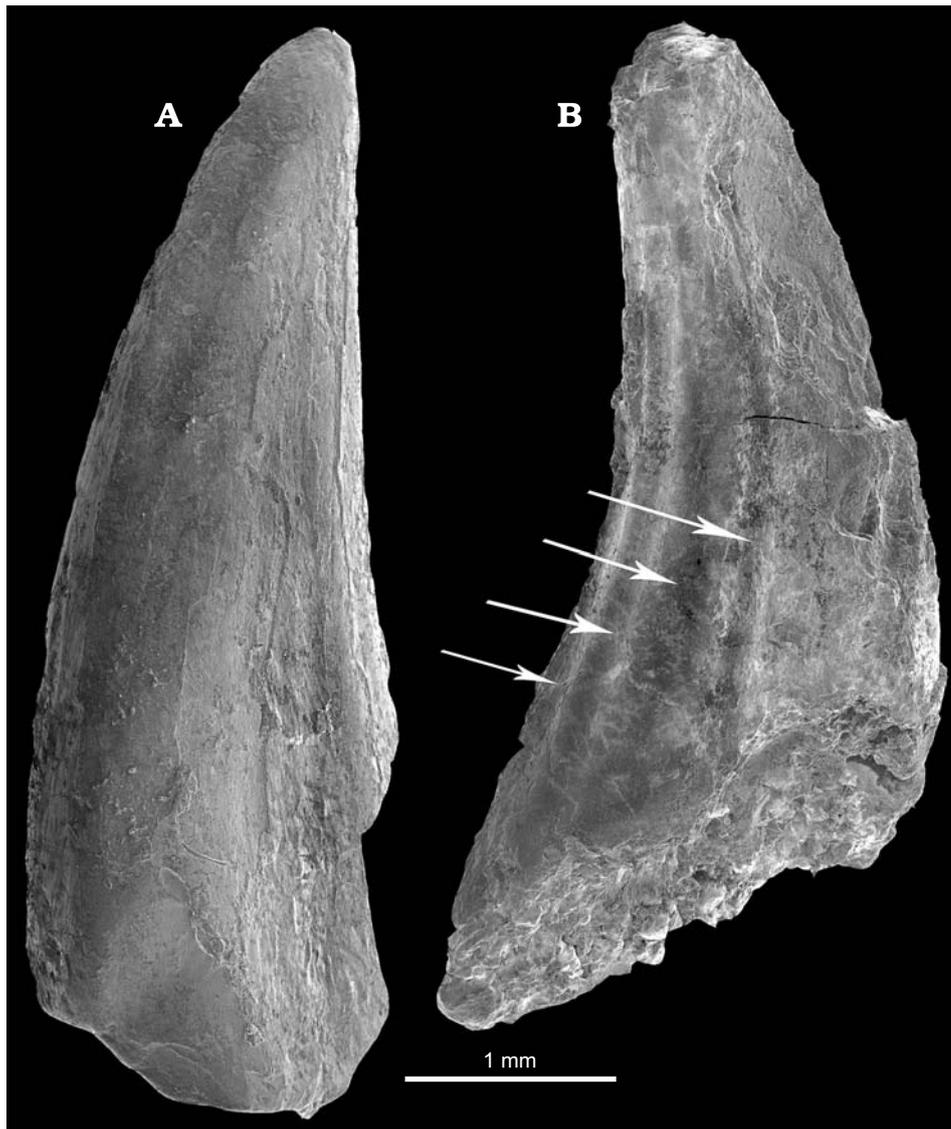


Fig. 5. SEM micrographs of isolated teeth associated with the holotype of the unenlagiine theropod *Buitreraptor gonzalezorum* Makovicky, Apesteguía, and Agnólin, 2005 from the Upper Cretaceous of La Buitrera, northwestern Río Negro, Argentina. **A.** Mesio-lateral view of one isolated tooth (MPCA 245 A2). Note the total absence of carinae and denticles on the mesial edge, and the central depression of the lateral side. **B.** Lateral side of one isolated tooth (MPCA 245 A5). Note the grooves and the ridges located near of the distal edge of the crown, to the left of the image (grooves are marked with arrows).

and Dong 2001; *Sinovenator*: 0.18; Xu 2002; Xu et al. 2002) or even lower than 0.10 (e.g., *Mei*, Xu and Norell 2004). In avialans, the value also can be lower than 0.20 and 0.10 (in *Archaeopteryx* and *Jeholornis* respectively; Elzanowski and Wellnhofer 1996; Zhou and Zhang 2002), similar to that of therizinosauroids such as *Erlikosaurus* (Clark et al. 1994) and *Incisivosaurus* (Balanoff et al. 2009), with ratios lower than 0.20 and 0.10 respectively. Some alvarezsaurids (i.e., *Shuvuuia*, Chiappe et al. 1998) and ornithomimosaurids (i.e., *Pelecanimimus*, Pérez-Moreno et al. 1994) show ratios lower than 0.10. Therefore, a low crown high appears to have a widespread distribution and, in this way, could be considered as a homoplastic condition.

**Absence of serrated carinae.**—In northern dromaeosaurids, tooth denticles are present in both carinae (despite being com-

monly absent in the proximal part of the mesial border). However, the two known unenlagiines with in situ teeth share a complete absence of denticles in both borders of the crown. This feature varies within the Dromaeosauridae; the primitive condition, present in *Dromaeosaurus* (Colbert and Russell 1969; Currie et al. 1990), shows mesial and distal denticles similar in shape and size, whereas in most velociraptorine dromaeosaurids the mesial carina has smaller denticles, quite different in morphology from those of the distal carina (e.g., *Deinonychus*, *Velociraptor*, *Saurornitholestes*; Ostrom 1969; Sues 1977; Currie et al. 1990). Nevertheless, *Saurornitholestes* shows a wide range of variation in the presence or absence of mesial denticles, even within the same specimen (Currie et al. 1990). The complete absence of denticles is not exclusive of the Unenlagiinae, since it is also present in other dromaeo-

saurids, such as *Microraptor zhaoianus*, *Tsaagan*, *Bambiraptor*, and *Shanag* (Xu et al. 2000; Hwang et al. 2002; Burnham 2004; Hwang 2005; Norell et al. 2006; Turner et al. 2007a). In this regard, the premaxillary and anterior dentary teeth of *Microraptor* lack denticles, whereas *Shanag* and *Tsaagan* lack mesial denticles. In *Sinornithosaurus millenii*, the premaxillary, first maxillary, and anterior dentary teeth do not have denticles, whereas posterior teeth have denticles restricted to the distal carina. Conversely, the mesial carina shows a wider variation (Xu and Wu 2001). Recently, Knoll and Ruiz-Omeñaca (2009) described isolated teeth from the Early Cretaceous of Morocco, assigning them to the Maniraptor, Dromaeosauridae indet. or even Velociraptorinae indet. Most of these teeth have no mesial denticles and some also lack distal ones. However, on one hand such taxonomic identification is doubtful, as expressed by the authors given the isolated condition of the material. On the other hand, the record of teeth from Europe with purported dromaeosaurid affinities (e.g., Antunes and Sigogneau 1992; Ruiz-Omeñaca et al. 1996; Zinke 1998; Rauhut 2002; Sweetman 2004; Lubbe et al. 2009) generally includes teeth with serrated mesial and distal borders, or at least with a serrated distal border.

Some troodontids also bear teeth devoid of mesial and distal denticles, like *Byronosaurus* (Norell et al. 2000; Makovicky et al. 2003) and *Urbacodon* (Averianov and Sues 2007). The same feature can be observed in compsognathids (e.g., *Compsognathus*, Ostrom 1978), alvarezsaurids (e.g., *Mononykus olecranus*, Perle et al. 1993a, b, 1994; *Shuvuuia deserti*, Chiappe et al. 1998), ornithomimosaurids (e.g., *Pelecanimimus polyodon*, Pérez-Moreno et al. 1994; Makovicky et al. 2003, 2004; Padian 2004; *Shenzhousaurus orientalis*, Ji et al. 2003), and the incertae sedis *Paronychodon* (Currie et al. 1990; Sankey et al. 2002).

Among tetanuran theropods the presence of mesial and distal serrated carinae is plesiomorphic (see supplementary information). For their part, the Maniraptoriformes and Unenlagiinae show the absence of denticles in maxillary and dentary teeth and therefore this is a synapomorphic feature of both groups (see supplementary information). However, the Deinonychosauria (except the Unenlagiinae) have acquired mesial denticles in some teeth, thus reversing to the ancestral condition of non-Maniraptoriformes. Novas et al. (2009; SOM) regarded the absence of mesial serrations in some teeth as synapomorphic of the Deinonychosauria, and consider the total absence of denticles as synapomorphic of the Unenlagiinae, a position that we follow.

**Grooves on the surface of the crown.**—A distinctive feature of the Unenlagiinae is the presence of longitudinal grooves in the tooth crown. These grooves are present in the teeth of *Buitreraptor* and *Austroraptor*, and have a vague resemblance to the grooves present in basal tetanurans, such as the Spinosauridae and also ceratosaurs such as *Ceratopsaurus* (Madsen and Welles 2000). Among Late Cretaceous southern theropods, a single grooved crown was found in the La Bajada sector of the El Anfiteatro locality (Canudo et al.

2004; Salgado et al. 2009). This tooth crown, Endemas-Pv 6, was interpreted by the authors as belonging to a spinosaurid after its ornamentation, composed of longitudinal crests and large denticles inclined toward the apex. However, the presence of two defined crests with three main grooves in the lingual side of the crown, a series of second order grooves, and distal inclination of the crown are features shown by no-saurid teeth, as observed in the dentary of *Masiakasaurus knopffleri* (Sampson et al. 2001: fig. 2b–d). An additional isolated tooth from the same El Anfiteatro area at Parrita site, regarded as Endemas-Pv 15 (Salgado et al. 2009), was assigned to Maniraptoriformes indet. cf. Unenlagiinae. It effectively shows the diagnostic absence of denticles, a strongly distally curved crown, and a figure-eight shaped basal cross section. Furthermore, it is interesting to note that the authors pointed out the enamel folds slightly parallel and mesiodistal in orientation, a trait that they interpreted as related to ontogenetic variation. We consider that these folds are very similar to the ridges and grooves that we describe here for *Buitreraptor*. Nevertheless, this tooth, having a crown height of 19 mm, is much larger than those of *Buitreraptor*, with a largest tooth crown height of 4.6 mm. It is conceivable that this tooth does not necessarily belong to *Buitreraptor* but to a larger unenlagiine, perhaps related to *Austroraptor*. In summary, we agree with Salgado et al. (2009) in the assignment, although tentative, of Endemas-Pv 15 to the Unenlagiinae. Other isolated ornamented teeth potentially assigned to the Dromaeosauridae with grooves and ridges on both sides were reported from Morocco (SA mcm 158; Knoll and Ruiz-Omeñaca 2009: fig. 4b), Spain (Ruiz-Omeñaca et al. 1996; Rauhut 2002), France (Vullo et al. 2007), Hungary (Ösi et al. 2010), and Canada (Sankey et al. 2002). However, they differ from the teeth of *Buitreraptor* in bearing denticled carinae. Furthermore, they also lack the degree of labiolingual compression present in the South American taxon.

A grooved dental crown is, conversely, mostly absent among Laurasian dromaeosaurid taxa, except for some isolated teeth assigned with doubts to *Dromaeosaurus* (Sankey et al. 2002). Additionally, in the teeth of *Sinornithosaurus* single grooves are present over the lingual side, posterior to the mesial carina, both in the premaxillary and anterior dentary teeth (Xu and Wu 2001; Xu 2002). However, the grooves present in these teeth are unlike those of *Buitreraptor*, both in morphology, density and location. In *Buitreraptor*, two or more grooves are present on both sides of the crown.

As previously mentioned, the incertae sedis *Paronychodon* also shows dental grooves and longitudinal ridges on one or both sides of the crown (Currie et al. 1990; Sankey et al. 2002). However, its morphology departs from that of *Buitreraptor* in that these features are more abundant and narrow. Furthermore, contrasting with *Buitreraptor*, the grooves are not parallel to each other (Currie et al. 1990; Sankey et al. 2002). Additionally, the tooth crown of *Paronychodon* has an oval base with more convex lateral sides (Currie et al. 1990; Sankey et al. 2002), a trait substantially different from the characteristic figure-eight shaped base of the teeth of *Buitreraptor*.

Some non-unenlagiine taxa show a fluted crown (e.g., *Mononykus*); however, the phylogenetic analysis (SOM) demonstrates that this character is, at this level, synapomorphic of the Unenlagiinae.

**Dental features characterizing *Buitreraptor*.**—Differences also arise within unenlagiines. *Buitreraptor* differs from *Austroraptor* in having a remarkable lateral compression of the crown (Fig. 4B, D, E, Table 1). This lateral compression is, actually, a feature also seen in other Gondwanan theropods, like the Carcharodontosauridae and Abelisauridae (e.g., Veralli and Calvo 2004; Smith et al. 2005; Candeiro et al. 2006; Coria and Currie 2006; Smith and Dalla Vecchia 2006; Smith 2007), where the CBR ratio is around 0.4 to 0.5 (see Smith et al. 2005: appendix A). Within the Dromaeosauridae, the ratio is commonly about 0.5, with some exceptions of 0.4 or 0.3 in *Bambiraptor* and *Velociraptor* (see Smith et al. 2005: appendix A). However, no other dromaeosaurid with preserved teeth in situ other than *Buitreraptor* exhibits a CBR ratio of 0.29 (Table 1).

Another relevant feature is the figure-eight shaped tooth base of *Buitreraptor* (Fig. 4E). This trait is related to the presence of longitudinal depressions in the central zone of the crown, on both sides and close to the base. In most dromaeosaurids, the basal section is oval to flattened, either symmetrical or asymmetrical with one side more convex than the other, as in the premaxillary teeth of some taxa (Colbert and Russell 1969; Ostrom 1969; Sues 1977; Currie et al. 1990; Sankey et al. 2002).

However, a figure-eight shaped crown cross-section has been also recorded in *Saurornitholestes* (Currie et al. 1990; Sankey et al. 2002), *Tsaagan* (Norell et al. 2006), and *Pyroraptor* (Allain and Taquet 2000; SA personal observation). In the latter form, some teeth show a mid-depression in the lateral sides of the crown that is longitudinally extended and framed by strong ridges. However, *Buitreraptor* differs from *Pyroraptor* in having a more compressed tooth crown and in the presence of shallow ridges framing the observed depression (Fig. 3B, F). Additionally, it also differs from *Saurornitholestes* in having a narrower central region (see Fig. 4E). *Austroraptor*, for its part, differs in having a conical tooth crown, a rounded base section, and a moderate lateral compression.

Therefore, although *Buitreraptor* and *Austroraptor* share dental features that could be synapomorphic for the Unenlagiinae, they also differ in several traits, such as the conical tooth and rounded basal section of the crowns of *Austroraptor*, and a remarkable lateral compression and a figure-eight shaped base in the teeth of *Buitreraptor*. From a phylogenetic point of view, a figure-eight shaped crown section is autapomorphic of *Buitreraptor*, also considering that in the remaining dromaeosaurids (except the examples already considered) the crown section is generally oval.

**Gondwanan record of dromaeosaurid teeth and paleobiogeographical considerations.**—The presence of dromaeosaurids in Gondwana is documented based on a few but eloquent skeletal remains, but also after numerous isolated teeth

assigned to this group of theropods. Most of the purported Gondwanan dromaeosaurid isolated teeth come from Brazil (e.g., Elias et al. 2004, 2005, 2006, 2007), Argentina (e.g., Poblete and Calvo 2003; Canale et al. 2005; Casal et al. 2009; Salgado et al. 2009), Colombia (e.g., Ezcurra 2009), Africa and Madagascar (e.g., Rauhut and Werner 1995; Rauhut 1999; Amiot et al. 2004; Fanti and Therrien 2007; Knoll and Ruiz-Omeñaca 2009). Many of these assignments to the Dromaeosauridae are based on the strong distal curvature of the crown and on the absence or strong reduction of mesial denticles or even the total absence of serrations. The difference in size between mesial and distal denticles, measured as the ratio between the number of denticles over a certain distance of the anterior and posterior carinae (denticles size difference index: DSDI), has been considered as a very good parameter to distinguish dromaeosaurid teeth (Rauhut and Werner 1995). DSDI has a characteristic value especially in velociraptorine dromaeosaurids, and has been taken as diagnostic for them (Rauhut and Werner 1995). Regarding the absence of serrations, it must be noted, however, that diverse groups of the Maniraptoriformes like troodontids, alvarezsaurids and ornithomimosaurs, show examples of teeth without serrations, and mesial denticles are absent for example in compsognathids (Ostrom 1978; Currie and Chen 2001; Hwang et al. 2004). On the other hand, the teeth of the carcharodontosaurian *Orkoraptor burkei* from the Campanian–Maastrichtian of Patagonia (Novas et al. 2008) are strongly curved distally and devoid of mesial denticles. Therefore, only the absence of denticles in recurved teeth cannot be taken as a definitive character to allow the assignment of isolated teeth to the Dromaeosauridae, being an ambiguous character present in other tetanurans (Ezcurra 2009). Taking into account the record of theropod teeth and the large number of homoplastic appearances in the features associated with these elements, the taxonomic assignment of isolated teeth must be made cautiously (Canale et al. 2007).

Purported dromaeosaurid teeth from Argentina include specimens from the Portezuelo Formation (Turonian–Coniacian) in Neuquén Province (Poblete and Calvo 2003), from the Huincul Formation (Turonian) in Neuquén Province (Canale et al. 2005), from the Bajo Barreal Formation (Cenomanian–Turonian) in Chubut Province (Casal et al. 2009), and from the Plottier Formation (Coniacian–Santonian), at the Anfiteatro Area in Río Negro Province (Salgado et al. 2009). Those of Portezuelo, Huincul and Bajo Barreal Formations are characterized by the absence of mesial denticles, among other features. However, as previously said, a non-serrated mesial border is a widespread character among tetanurans and it is not enough to be considered a diagnostic character of dromaeosaurid teeth. Nevertheless, it is interesting that the teeth of these localities have features that differ from those observed in the unenlagiine teeth. This could mean that: (i) these teeth belong to other groups of theropods for which there already exist records in South America (e.g., neovenatorids or alvarezsaurids), (ii) the teeth belong to other groups of theropods or other lineages of dromaeosaurids for which skeletal remains have not yet been found,

or (iii) teeth belong to other unenlagiines, which would mean that the dental morphology of this group is much more variable than that proposed here. An interesting case already commented on above is the proposed unenlagiine tooth from the Anfiteatro Area (Salgado et al. 2009).

For its part, those teeth from Brazil for which a certain affinity with dromaeosaurids has been proposed (e.g., Elias et al. 2004, 2005, 2006, 2007) are generally small, labiolingually compressed, and with denticles on both the mesial and distal carinae, only on the distal carina or completely lacking denticles. Again, these characters are observed in many other maniraptoran taxa and their presence do not provide enough evidence to unambiguously refer them to dromaeosaurids.

A recently described isolated tooth from Maastrichtian beds of Colombia (Ezcurra 2009) has features resembling those of unenlagiines, mainly a strong distal curvature, a labiolingual compression of the crown, and the complete absence of denticles. However, this tooth differs from those of *Buitreraptor* and *Austroraptor* in lacking lateral grooves on the crown, and neither possessing the marked labiolingual compression and the figure-eight basal cross section observed in the teeth of *Buitreraptor* or the conical shape seen in *Austroraptor*. Therefore, although this shed tooth has features reminiscent of unenlagiines, we agree with Ezcurra (2009) in this assignment is so far only tentative.

Among the teeth from the Early Cretaceous of Morocco assigned to Maniraptora indet. and Velociraptorinae indet. by Knoll and Ruiz-Omeñaca (2009), there are some similarities with unenlagiine teeth in the absence of denticles (those included in Maniraptora indet.) and the presence of grooves and ridges in the tooth crown (that included in Velociraptorinae indet.). However, the morphology of these teeth and other African and Malagasy teeth assigned to the Dromaeosauridae (Rauhut and Werner 1995; Rauhut 1999; Amiot et al. 2004; Fanti and Therrien 2007) has more affinities to that of Laurasian dromaeosaurid teeth, whereas a great morphological discrepancy is observed between African and Malagasy teeth and those of the unenlagiines. In this respect, Knoll and Ruiz-Omeñaca (2009) have invoked a land corridor between Laurasia and Gondwana permitting a faunal interchange during the Late Jurassic–Early Cretaceous, to explain similarities with Laurasian forms. Moreover, a connection between Europe and Africa for these times already has been proposed by previous authors (e.g., Galton and Taquet 1982; Milner and Norman 1984). According to this hypothesis the dromaeosaurid tooth record can be explained as a migratory model previous to the fragmentation of Gondwana (Rauhut and Werner 1995; Knoll and Ruiz-Omeñaca 2009). Thus, dromaeosaurids would have migrated from Europe to Africa during Late Jurassic–Early Cretaceous, and then would have spread to Madagascar and South America. Nevertheless, dromaeosaurids and other non-avian maniraptorans (such as alvarezsaurids), would have reached a global distribution before the break-up of Pangea (Makovicky et al. 2005; Novas and Pol 2005). Subsequently, the separation of Laurasia and Gondwana produced vicariant lineages in both continents (Novas and Pol 2005). This idea

represents a most parsimonious interpretation of the distribution of dromaeosaurids, than an origin on Laurasian territories in the Middle to Late Jurassic and a later spread to Gondwana. Thus, the isolation would have generated in Laurasia the diversification of velociraptorines, dromaeosaurines and microraptorines, and in Gondwana the diversification of unenlagiines (Makovicky et al. 2005; Novas and Pol 2005; Fanti and Therrien 2007; Vullo et al. 2007; Gianechini et al. 2009; Novas et al. 2009).

**Presence of avian dental features and evolutionary implications.**—It is interesting, from an evolutionary point of view, that some traits present in the unenlagiine teeth share several features with Mesozoic birds. Mesozoic bird teeth are numerous, small in size, mostly conical, slightly recurved distally, with a faint constriction between the crown and the root, and devoid of denticles (Martin and Stewart 1977; Martin et al. 1980; Elzanowski and Wellnhofer 1996; Martin and Zhou 1997; Zhang and Zhou 2000; Zhang et al. 2001; Chiappe and Walker 2002; Sereno et al. 2002; Zhou and Hou 2002). Some of these features, such as the absence of denticles and the constriction between the crown and the root are also shared by ornithomimosaurids, alvarezsaurids, therizinosaurids, and troodontids and are synplesiomorphic characters of the Maniraptoriformes and Maniraptora, respectively (see SOM). Also, several of these bird dental features are shared with unenlagiines, such as the absence of denticles, small size, and conical shape (the latter only with *Austroraptor*). However, the constriction between crown and root is absent in all known unenlagiines, and the grooves and ridges are unknown in birds. Except for *Microraptor* (Xu et al. 2000; Hwang et al. 2002), no dromaeosaurid bears a constriction between crown and root. The dental features shared by unenlagiines and birds, and also by some Laurasian dromaeosaurids and troodontids, probably respond to a same general trend that included dental reduction and simplification.

The presence in birds of several deinonychosaurian dental features has been highlighted by several authors (e.g., Martin et al. 1980; Feduccia 2002). Nevertheless, the repetitive appearance in troodontids, unenlagiines and birds of the homogenization, minimization, and simplification of dentition (now exemplified by extant birds), is remarkable. Moreover, other groups of the Maniraptoriformes, such as ornithomimosaurids, alvarezsaurids, and oviraptorosaurs also show a trend towards the minimization and simplification of the teeth, arriving in some cases at the total disappearance of the dentition. Since numerous taxa within the Maniraptoriformes present a reduction of the dentition (see SOM), this general trend explains the condition of unenlagiines and also that of the Avialae.

## Conclusions

The morphological study of the unenlagiine dentition shows that several of its traits can be found in other dromaeosaurids,

as well as in some troodontids, in non-deinonychosaurian theropods, and even in birds. However, the studied combination of features characterizes the Unenlagiinae very well. The lack of serrations and the presence of grooves and ridges on the crown, together with the high tooth count and the small size of the crowns, can be considered as synapomorphic features of the Unenlagiinae. Further, the presence of grooves and ridges should be included as a new character.

The presence of teeth in position in dromaeosaurid skeletons is a key finding because it permits association of the array of isolated teeth to a particular taxon. Furthermore, the peculiar morphological features of the teeth presented here, added to the derived traits recognized in the cranial and postcranial skeletons of *Buitreraptor* and *Austroraptor* (Makovicky et al. 2005; Novas et al. 2009), provide further character support for the monophyly of the Unenlagiinae as an endemic Gondwanan clade of dromaeosaurids. Among these features the presence of grooves and ridges on the crown can be considered as a new important character of this group.

Conversely, the presence of similarities between some dental features of unenlagiines and some Laurasian dromaeosaurids allows recognition of some plesiomorphic traits, such as the presence of a median groove in the lateral sides of the crowns of *Pyroraptor* (SA personal observation), *Tsaagan*, and *Buitreraptor* that creates a figure-eight shaped cross-section.

Under a paleobiological point of view, it is interesting to note that grooved teeth are common in purported piscivorous tetrapods, both aquatic (e.g., mosasaurs, plesiosaurs) as terrestrial (e.g., spinosaurs, noosaurids) and flying forms (e.g., pterosaurs). Both *Buitreraptor* and *Austroraptor*, despite terrestrial forms, inhabited the proximity of fluvial deposits as evidenced by the abundant fish remains that were also found (Apesteguía et al. 2007). A fishing behavior should be in the scope of a paleobiological study of these forms.

The finding of southern dromaeosaurids with evidence of teeth in position allows discussion of peculiar morphological features that can be added to their already recognized anatomical peculiarities. This ensemble of data, especially in the skeletons of *Buitreraptor* and *Austroraptor* (Makovicky et al. 2005; Novas et al. 2009), provides extra support to recognize the Unenlagiinae as a vicariant Gondwanan dromaeosaurid clade.

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## References

- Allain, R. and Taquet, P. 2000. A new genus of dromaeosaurid (Dinosauria, Theropoda) from the Upper Cretaceous of France. *Journal of Vertebrate Paleontology* 20: 404–407.
- Amiot, R., Buffetaut, E., Tong, H., Boudad, L., and Kabiri, L. 2004. Isolated theropod teeth from the Cenomanian of Morocco and their palaeobiogeographical significance. *Revue de Paléobiologie, Volumen Spécial* 9: 143–149.
- Antunes, M.T. and Sigogneau, D. 1992. La faune de petits dinosaures du Crétacé Terminal Portugais. *Comunicações dos Serviços Geológicos de Portugal* 78: 49–62.
- Apesteguía, S., Agnolín, F.L., and Claeson, K. 2007. Review of Cretaceous dipnoans from Argentina (Sarcopterygii: Dipnoi) with descriptions of new species. *Revista del Museo Argentino de Ciencias Naturales, New Series* 9: 27–40.
- Averianov, A.O. and Sues, H.-D. 2007. A new troodontid (Dinosauria: Theropoda) from the Cenomanian of Uzbekistan, with a review of troodontid records from the territories of the former Soviet Union. *Journal of Vertebrate Paleontology* 27: 87–98.
- Balanoff, A.M., Xu, X., Kobayashi, Y., Matsufune, Y., and Norell, M.A. 2009. Cranial osteology of the theropod dinosaur *Incisivosaurus gauthieri* (Theropoda: Oviraptorosauria). *American Museum Novitates* 3651: 1–35.
- Bonaparte, J.F. 1999. Tetrapod faunas from South America and India; a palaeobiogeographic interpretation. In: *Gondwana Assembly; New Issues and Perspectives. Proceedings of the Indian National Science Academy, Part A: Physical Sciences* 65: 427–437.
- Burnham, D.A. 2004. New information on *Bambiraptor feinbergi* (Theropoda: Dromaeosauridae) from the Late Cretaceous of Montana. In: P.J. Currie, E.B. Koppelhus, M.A. Shugar, and J.L. Wright (eds.), *Feathered Dinosaurs*, 67–111. Indiana University Press, Bloomington.
- Calvo, J.O., Pofiri, J.D., and Kellner, A.W.A. 2004. On a new maniraptoran dinosaur (Theropoda) from the Upper Cretaceous of Neuquén, Patagonia, Argentina. *Arquivos do Museu Nacional do Rio de Janeiro* 62: 549–566.
- Canale, J.I., Novas, F.E., and Simón, M.E. 2005. Dientes de terópodos de la Formación Huincul (Turoniano inferior), provincia de Neuquén, Argentina. *Ameghiniana* 42 (Suplemento 4): 63R.
- Canale, J.I., Agnolín, F.L., Ezcurra, M.D., and Novas, F.E. 2007. Notas sobre el registro de dientes aislados de dinosaurios terópodos cretácicos de América del Sur. *Ameghiniana* 44 (Suplemento 4): 8R.
- Candeiro, C.R.A., Martinelli, A.G., Avilla, L.S. and Rich, T.H. 2006. Tetra-

- pods from the Upper Cretaceous (Turonian–Maastrichtian) Bauru Group of Brazil: a reappraisal. *Cretaceous Research* 27: 923–946.
- Canudo, J.I., Salgado, L., Barco, J.L., Bolatti, R., and Ruiz-Omeñaca, J.I. 2004. Dientes de dinosaurios terópodos y saurópodos de la Formación Cerro Lisandro (Cenomaniense superior–Turonense inferior, Cretácico superior) en Río Negro (Argentina). *Geotemas* 6: 31–34.
- Casal, G., Candeiro, C.R.A., Martínez, R., Ivany, E., and Ibirucu, L. 2009. Dientes de Theropoda (Dinosauria: Saurischia) de la Formación Bajo Barreal, Cretácico Superior, Provincia del Chubut, Argentina. *Geobios* 42: 553–560.
- Chiappe, L.M. and Walker, C.A. 2002. Skeletal morphology and systematics of the Cretaceous Euenantiornithes (Ornithothoraces: Enantiornithes). In: L.M. Chiappe and L.M. Witmer (eds.), *Mesozoic Birds, Above the Heads of Dinosaurs*, 240–267. University of California Press, Berkeley.
- Chiappe, L.M., Norell, M.A., and Clark, J.M. 1998. The skull of a relative of the stem-bird group *Mononykus*. *Nature* 392: 275–278.
- Clark, J.M., Perle, A., and Norell, M.A. 1994. The skull of *Erlicosaurus andrewsi*, a Late Cretaceous “segnosaur” (Theropoda: Therizinosauridae) from Mongolia. *American Museum Novitates* 3115: 1–39.
- Colbert, E.H. and Russel, D.A. 1969. The small cretaceous dinosaur *Dromaesaurus*. *American Museum Novitates* 2380: 1–49.
- Corbella, H., Novas, F.E., Apesteguía, S., and Leanza, H.A. 2004. First fission-track for the dinosaur-bearing Neuquén Group (Upper Cretaceous), Neuquén Basin, Argentina. *Revista del Museo Argentino de Ciencias Naturales NS* 6: 227–232.
- Coria, R.A. and Currie, P.J. 2006. A new carcharodontosaurid (Dinosauria, Theropoda) from the Upper Cretaceous of Argentina. *Geodiversitas* 28: 71–118.
- Currie, P.J. 1995. New information of the anatomy and relationships of *Dromaesaurus albertensis* (Dinosauria: Theropoda). *Journal of Vertebrate Paleontology* 15: 576–591.
- Currie, P.J. and Chen, P.J. 2001. Anatomy of *Sinosauropteryx prima* from Liaoning, northeastern China. *Canadian Journal of Earth Sciences* 38: 1705–1727.
- Currie, P.J. and Dong, Z.-M. 2001. New information on Cretaceous troodontids (Dinosauria, Theropoda) from the People’s Republic of China. *Canadian Journal of Earth Sciences* 38: 1753–1766.
- Currie, P.J. and Varricchio, D.J. 2004. A new dromaesaurid from the Horseshoe Canyon Formation (Upper Cretaceous) of Alberta, Canada. In: P.J. Currie, E.B. Koppelhus, and M.A. Shugar (eds.), *Feathered Dragons: Studies from the Transition from Dinosaurs to Birds*, 113–132. Indiana University Press, Bloomington.
- Currie, P.J., Rigby, J.K. Jr, and Sloan, R.E. 1990. Theropod teeth from the Judith River Formation of southern Alberta, Canada. In: K. Carpenter and P. Currie (eds.), *Dinosaur Systematics: Perspectives and Approaches*, 107–125. Cambridge University Press, Cambridge.
- De Valais, S., Apesteguía, S., and Udrizar Sauthier, D. 2003. Nuevas evidencias de dinosaurios de la Formación Puerto Yeruá (Cretácico), Provincia de Entre Ríos, Argentina. *Ameghiniana* 40: 631–635.
- Elias, F.A., Bertini, R.J., and Medeiros, M.A. 2004. Nota preliminar sobre novos morfótipos de dentes tetrapodios, coletados na Laje do Coringa, Formação Alcântara, Eo-Cenomaniano do norte do Estado do Maranhão. *IV Simposio Brasileiro de Paleontologia de Vertebrados*, Boletim de Resumos: 21–22.
- Elias, F.A., Bertini, R.J., and Medeiros, M.A. 2005. Review of the occurrences concerning isolated amniotes teeth, in the Cretaceous deposits from the Maranhão State. *II Congresso Latino-Americano de Paleontologia de Vertebrados*, Boletim de Resumos: 99–100.
- Elias, F.A., Bertini, R.J., and Medeiros, M.A. 2006. A diversidade de amniotes do afloramento “Laje do Coringa”, Formação Alcântara, Eo-Cenomaniano do Estado do Maranhão. Inferências com base em registro dentário. In: *Boletim do 7º Simpósio do Cretáceo do Brasil/ 1º Simposio do Terciário do Brasil*, 46. Serra Negra.
- Elias, F.A., Bertini, R.J., and Medeiros, M.A.A. 2007. Velociraptorinae (Maniraptoriformes) teeth from the Coringa Flagstoen outcrop, Middle Cretaceous of the Sao Luis-Grajuau Basin, Maranhao State, Northern-Northeastern Brazil. In: I. de S. Carvalho, R. de C.T. Cassab, C. Schwanke, M. de A. Carvalho, A.C.S. Fernandes, M.A. da C. Rodrigues, M.S.S. de Carvalho, M. Arai, and M.E.Q. Oliveira (eds.), *Paleontologia: Cenários de Vida*, 307–317. Editora Interciência, Rio de Janeiro.
- Elzanowski, A. and Wellnhofer, P. 1996. Cranial morphology of *Archaeopteryx*: evidence from the seventh skeleton. *Journal of Vertebrate Paleontology* 16: 81–94.
- Ezcurra, M.D. 2009. Theropod remains from the uppermost Cretaceous of Colombia and their implications for the palaeozoogeography of western Gondwana. *Cretaceous Research* 30: 1339–1344.
- Fanti, F. and Therrien, F. 2007. Theropod tooth assemblages from the Late Cretaceous Maevarano Formation and the possible presence of dromaesaurids in Madagascar. *Acta Palaeontologica Polonica* 52: 155–166.
- Feduccia, A. 2002. Birds are dinosaurs: simple answer to a complex question. *The Auk* 119: 1187–1201.
- Forster, C.A., Sampson, S.D., Chiappe, L.M., and Krause, D.W. 1998. The theropod ancestry of birds: new evidence from the Late Cretaceous of Madagascar. *Science* 279: 1915–1919.
- Galton, P.M. and Taquet, P. 1982. *Valdosaurus*, a hypsilophodontid dinosaur from the Lower Cretaceous of Europe and Africa. *Geobios* 15: 147–159.
- Gianechini, F.A., Apesteguía, S., and Makovicky, P.J. 2009. The unusual dentition of *Buitreraptor gonzalezorum* (Theropoda: Dromaesauridae), from Patagonia, Argentina: new insights on the unenlagine teeth. *Ameghiniana* 46 (Suplemento 4): 29R.
- Hwang, S.H. 2005. Phylogenetic patterns of enamel microstructure in dinosaur teeth. *Journal of Morphology* 266: 208–240.
- Hwang, S.H., Norell, M.A., Qiang, J., and Keqin, G. 2002. New specimens of *Microaptor zhaoianus* (Theropoda: Dromaesauridae) from Northeastern China. *American Museum Novitates* 3381: 1–44.
- Hwang, S.H., Norell, M.A., Qiang, J., and Keqin, G. 2004. A large compsognathid from the Early Cretaceous Yixian Formation of China. *Journal of Systematic Paleontology* 2: 13–30.
- Ji, Q., Norell, M.A., Makovicky, P.J., Gao, K.-Q., Ji, S., and Yuan, C. 2003. An early ostrich dinosaur and implications for ornithomimosaur phylogeny. *American Museum Novitates* 3420: 1–19.
- Kirkland, J.I. and Wolfe, D.G. 2001. First definitive therizinosaurid (Dinosauria; Theropoda) from North America. *Journal of Vertebrate Paleontology* 21: 410–414.
- Knoll, F. and Ruiz-Omeñaca, J.I. 2009. Theropod teeth from the basalmost Cretaceous of Anoual (Morocco) and their palaeobiogeographical significance. *Geological Magazine* 146: 602–616.
- Lubbe, T. van der, Richter, U., and Knötschke, N. 2009. Velociraptorine dromaesaurid teeth from the Kimmeridgian (Late Jurassic) of Germany. *Acta Palaeontologica Polonica* 54: 401–408.
- Madsen, J.H. and Welles, S.P. 2000. *Ceratosaurus* (Dinosauria, Theropoda) a revised osteology. *Utah Geological Survey Miscellaneous Publication* 00-2: 1–80.
- Makovicky, P.J. and Norell, M.A. 2004. Troodontidae. In: D.B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, 184–195. University of California Press, Berkeley.
- Makovicky, P.J., Norell, M.A., Clark, J.M., and Rowe, T. 2003. Osteology and relationships of *Byronosaurus jaffei* (Theropoda: Troodontidae). *American Museum Novitates* 3402: 1–32.
- Makovicky, P.J., Kobayashi, Y., and Currie, P.J. 2004. Ornithomimosauria. In: D.B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, 137–150. University of California Press, Berkeley.
- Makovicky, P.J., Apesteguía, S., and Agnólin, F.L. 2005. The earliest dromaesaurid theropod from South America. *Nature* 437: 1007–1011.
- Martin, L.D. and Stewart, J.D. 1977. Teeth in *Ichthyornis* (class: Aves). *Science* 195: 1331–1332.
- Martin, L.D. and Zhou, Z.-H. 1997. *Archaeopteryx*-like skull in Enantiornithine bird. *Nature* 389: 556.
- Martin, L.D., Stewart, J.D., and Whetstone, K.N. 1980. The origins of birds: structure of the tarsus and teeth. *The Auk* 97: 86–93.
- Milner, A.R. and Norman, D.B. 1984. The biogeography of advanced ornithomimid dinosaurs (Archosauria: Ornithischia)—a cladistic-vicariance model. In: W.-W. Reif and E. Westphal (eds.), *Third Symposium of Mesozoic Terrestrial Ecosystems, Short Papers*, 145–150. Attempto-Verlag, Tübingen.
- Norell, M.A. and Makovicky, P.J. 2004. Dromaesauridae. In: D.B. Weis-

- hampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, 196–209. University of California Press, Berkeley.
- Norell, M.A., Makovicky, P.J., and Clark, J.M. 2000. A new troodontid theropod from Ukhaa Tolgod, Mongolia. *Journal of Vertebrate Paleontology* 20: 7–11.
- Norell, M.A., Clark, J.M., Turner, A.H., Makovicky, P.J., Barsbold, R., and Rowe, T. 2006. A New Dromaeosaurid Theropod from Ukhaa Tolgod (Ömnögovi, Mongolia). *American Museum Novitates* 3545: 1–51.
- Novas, F.E. and Puerta, P.F. 1997. New evidence concerning avian origins from the Late Cretaceous of Patagonia. *Nature* 387: 390–392.
- Novas, F.E. and Pol, D. 2005. New evidence on deinonychosaurian dinosaurs from the Late Cretaceous of Patagonia. *Nature* 433: 858–861.
- Novas, F.E., Ezcurra, M.D., and Lecuona, A. 2008. *Orkoraptor burkei* nov. gen. et nov. sp., a large basal coelurosaurian theropod from the Maestrichtian Pari Aike Formation, Southern Patagonia, Argentina. *Cretaceous Research* 29: 468–480.
- Novas, F.E., Pol, D., Canale, J.I., Porfiri, J.D., and Calvo, J.O. 2009. A bizarre Cretaceous theropod dinosaur from Patagonia and the evolution of Gondwanan dromaeosaurids. *Proceedings of the Royal Society B* 276: 1101–1107.
- Ösi, A., Apesteguí, S., and Kowalewski, M. 2010. Non-avian theropod dinosaurs from the early Late Cretaceous of central Europe. *Cretaceous Research* 31: 304–320.
- Ostrom, J.H. 1969. Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. *Bulletin of the Peabody Museum of Natural History* 30: 1–165.
- Ostrom, J.H. 1978. The osteology of *Compsognathus longipes* Wagner. *Zitteliana* 4: 73–118.
- Padian, K. 2004. Basal Avialae. In: D.B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, 210–231. University of California Press, Berkeley.
- Pérez-Moreno, B.P., Sanz, J.L., Buscalioni, A.D., Moratalla, J.J., Ortega, F., and Rasskin-Gutman, D. 1994. A unique multitoothed ornithomimosaur from the Lower Cretaceous of Spain. *Nature* 370: 363–367.
- Perle, A., Chiappe, L.M., Barsbold, R., Clark, J.M., and Norell, M.A. 1994. Skeletal morphology of *Mononykus olecranus* (Theropoda: Avialae) from the Late Cretaceous of Mongolia. *American Museum Novitates* 3105: 1–29.
- Perle, A., Norell, M.A., Chiappe, L.M., Clark, J. 1993a. Flightless bird from the Cretaceous of Mongolia. *Nature* 362: 623–626.
- Perle, A., Norell, M.A., Chiappe, L.M., and Clark, J. 1993b. Correction to flightless bird from the Cretaceous of Mongolia. *Nature* 362: 623–628.
- Poblete, F. and Calvo, J.O. 2003. Upper Turonian dromaeosaurid teeth from Futalognko quarry, Barreales Lake, Neuquén, Patagonia, Argentina. *XIX Jornadas Argentinas de Paleontología de Vertebrados*, Resúmenes: 24.
- Rauhut, O.W.M. 1999. A dinosaur fauna from the Late Cretaceous (Cenomanian) of northern Sudan. *Palaeontologia Africana* 35: 61–84.
- Rauhut, O.W.M. 2002. Dinosaur teeth from the Barremian of Ñiña, Province of Cuenca, Spain. *Cretaceous Research* 23: 255–263.
- Rauhut, O.W.M. and Werner, C. 1995. First record of the family Dromaeosauridae (Dinosauria: Theropoda) in the Cretaceous of Gondwana (Wadi Milk Formation, northern Sudan). *Paläontologische Zeitschrift* 69: 475–489.
- Ruiz-Omeñaca, J.I., Canudo, J.I., and Cuenca-Bescós, G. 1996. Dientes de dinosaurios (Ornithischia y Saurischia) del Barremiense superior (Cretácico inferior) de Vallipón (Castellote, Teruel). *Mas de las Matas* 15: 29–103.
- Russel, D.A. and Dong, Z.-M. 1993. A nearly complete skeleton of a new troodontid from the Early Cretaceous of the Ordos Basin, Inner Mongolia, People's Republic of China. *Canadian Journal of Earth Sciences* 30: 2163–2173.
- Salgado, L., Canudo, J.I., Garrido, A.C., Ruiz-Omeñaca, J.I., García, R.A., de la Fuente, M.S., Barco, J.L., and Bollati, R. 2009. Upper Cretaceous vertebrates from El Anfiteatro area, Río Negro, Patagonia, Argentina. *Cretaceous Research* 30: 767–784.
- Sampson, S.D., Carrano, M.T., and Forster, C.A. 2001. A bizarre predatory dinosaur from the Late Cretaceous of Madagascar. *Nature* 409: 504–506.
- Sankey, J.T. 2001. Late Campanian southern dinosaurs, Aguja Formation, Big Bend, Texas. *Journal of Paleontology* 75: 208–215.
- Sankey, J.T., Brinkman, D.B., Guenther, M., and Currie, P.J. 2002. Small theropod and bird teeth from the Late Cretaceous (Late Campanian) Judith River Group, Alberta. *Journal of Paleontology* 76: 751–763.
- Sereno, P.C., Rao, C., and Li, J. 2002. *Sinornis santensis* (Aves: Enantiornithes) from the Early Cretaceous of Northeastern China. In: L.M. Chiappe and L.M. Witmer (eds.), *Mesozoic Birds, Above the Heads of Dinosaurs*, 184–208. University of California Press, Berkeley.
- Smith, J.B. 2007. Dental morphology and variation in *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology* 27 (Supplement 8): 103–126.
- Smith, J.B. and Dalla Vecchia, F.M. 2006. An abelisaurid (Dinosauria: Theropoda) tooth from the Lower Cretaceous Chicla Formation of Libya. *Journal of African Earth Sciences* 46: 240–244.
- Smith, J.B., Vann, D.R., and Dodson, P. 2005. Dental morphology and variation in theropod dinosaurs: implications for the taxonomic identification of isolated teeth. *The Anatomical Record, Part A* 285A: 699–736.
- Sues, H.-S. 1977. The skull of *Velociraptor mongoliensis*, a small Cretaceous theropod dinosaur from Mongolia. *Paläontologische Zeitschrift* 51: 173–184.
- Sweetman, S.C. 2004. The first record of velociraptorine dinosaurs (Saurischia, Theropoda) from the Wealden (Early Cretaceous, Barremian) of southern England. *Cretaceous Research* 25: 353–364.
- Turner, A.H., Hwang, S.H., and Norell, M.A. 2007a. A small derived theropod from Öösh, Early Cretaceous, Baykhangor Mongolia. *American Museum Novitates* 3557: 1–27.
- Turner, A.H., Pol, D., Clark, J.A., Erickson, G.M., and Norell, M.A. 2007b. A basal dromaeosaurid and size evolution preceding avian flight. *Science* 317: 1378–1381.
- Veralli, C. and Calvo, J.O. 2004. Dientes de terópodos carcarodontosáuridos del Turoniano superior-Coniaciano inferior del Neuquén, Patagonia, Argentina. *Ameghiniana* 41: 587–590.
- Vullo, R., Neraudeau, D., and Lenglet, T. 2007. Dinosaur teeth from the Cenomanian of Charentes, Western France: evidence for a mixed Laurasian–Gondwanian assemblage. *Journal of Vertebrate Paleontology* 27: 931–943.
- Xu, X. 2002. *Deinonychosaurian Fossils from the Jehol Group of Western Liaoning and the Coelurosaurian Evolution*. 325 pp. Unpublished Ph.D. thesis, The Chinese Academy of Sciences, Beijing.
- Xu, X. and Norell, M.A. 2004. A new troodontid dinosaur from China with avian-like sleeping posture. *Nature* 431: 838–841.
- Xu, X. and Wu, X.-C. 2001. Cranial morphology of *Sinornithosaurus millenii* Xu, Wang, and Wu 1999 (Dinosauria: Theropoda: Dromaeosauridae) from the Yixian Formation of Liaoning, China. *Canadian Journal of Earth Sciences* 38: 1739–1752.
- Xu, X., Wang, X.-L., and Wu, X.-C. 1999. A dromaeosaurid dinosaur with a filamentous integument from the Yixian Formation of China. *Nature* 401: 262–266.
- Xu, X., Zhou, Z.-H., and Wang, X. 2000. The smallest known non-avian theropod dinosaur. *Nature* 408: 705–708.
- Xu, X., Norell, M.A., Wang, X.-L., Makovicky, P.J., and Wu, X.-C. 2002. A basal troodontid from the Early Cretaceous of China. *Nature* 415: 78–784.
- Xu, X., Zhou, Z.-H., Wang, X., Kuang, X., Zhang, F., and Du, X. 2003. Four-winged dinosaurs from China. *Nature* 421: 335–340.
- Zhang, F. and Zhou, Z. 2000. A primitive enantiornithine bird and the origin of feathers. *Science* 290: 1955–1959.
- Zhang, F., Zhou, Z., Hou, L., and Gu, G. 2001. Early diversification of birds: evidence from a new opposite bird. *Chinese Science Bulletin* 46: 945–949.
- Zhou, Z. and Hou, L. 2002. The discovery and study of mesozoic birds in China. In: D.B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, 160–183. University of California Press, Berkeley.
- Zhou, Z. and Zhang, F. 2002. A long-tailed, seed-eating bird from the Early Cretaceous of China. *Nature* 418: 405–409.
- Zinke, J. 1998. Small theropod teeth from the Upper Jurassic coal mine of Guimarães (Portugal). *Paläontologische Zeitschrift* 72: 179–189.