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SHORT COMMUNICATION

THE SYSTEMATIC UTILITY OF THEROPOD ENAMEL WRINKLES

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Isolated theropod dinosaur teeth are common fossils and are frequently used to extend the temporal and geographic ranges of taxa known elsewhere from more complete specimens. Problems with assigning isolated teeth to higher-level taxa have been noted (Currie et al., 1990; Farlow et al., 1991), but recently-developed quantitative methods offer much potential to rectify these difficulties (Smith 2005; Smith et al. 2005). In the absence of quantitative methods, many authors have relied on qualitative characters to both diagnose taxa and assign isolated teeth to higher-level taxa. One frequently-cited qualitative character is wrinkled enamel, which has been regarded as diagnostic of Carcharodontosauridae, a Cretaceous clade that includes some of the largest known theropods (Sereno et al., 1996; Chure et al., 1999; Vickers-Rich et al., 1999). The carcharodontosaurids *Carcharodontosaurus* (Stromer 1931; Sereno et al., 1996:fig 2) and *Giganotosaurus* (Coria and Salgado, 1995) are characterized by lateral teeth with strong, arcuate enamel ridges that often extend across the labial and lingual margins. Similar wrinkles have been documented in isolated teeth worldwide, and are often the basis for assigning specimens to Carcharodontosauridae (Kellner and Campos, 1998, 2000; Chure et al., 1999; Vickers-Rich et al., 1999; Rich et al., 2000; Veralli and Calvo, 2003, 2004; Candeiro et al., 2004; Canudo et al., 2004; Martinelli and Forasiepi, 2004; Rauhut, 2006).

Although wrinkles have been noted in other theropod taxa (e.g., tyrannosaurids: Chure et al., 1999; Vickers-Rich et al., 1999; Smith, 2005), many authors continue to regard these structures as a secure rationale for assigning isolated teeth to Carcharodontosauridae. However, the morphology of wrinkles among carcharodontosaurids is poorly described, and the distribution and morphology of wrinkles in other theropod taxa are not presented in the literature. Our observations of a wide range of theropod teeth reveal that these structures are more widespread than currently thought, and are enormously variable both within and among taxa. These observations call into question the systematic utility of enamel wrinkles, especially the practice of assigning isolated teeth to Carcharodontosauridae based on the mere presence of these structures. Below we briefly review the taxonomic distribution of enamel wrinkles and comment on their variability. We do not intend to provide an exhaustive survey of wrinkle distribution and morphology, only a discussion of the pitfalls of using enamel wrinkles in theropod systematics.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York; **BNHM**, Burpee Museum of Natural History, Rockford, Illinois; **BYU**, Earth Science Museum of Brigham Young University, Provo, Utah; **CMN**, Canadian Museum of Nature, Ottawa, Canada; **FMNH**, Field Museum of Natural History, Chicago, Illinois; **MNN**, Musée National du Niger, Niamey; **MOR**, Museum of the Rockies, Bozeman, Montana; **MUCP**, Museo de la Universidad Nacional del Comahue, El Chocon collection; **NMMNH**, New Mexico Museum of Natural History and Science, Albuquerque; **OUMNH**, Oxford University Museum of Natural History, Oxford, England; **ROM**, Royal Ontario Museum, Toronto, Canada; **SGM**, Ministére de l'Energie et des Mines, Rabat, Morocco; **UCMP**, University of California Museum of Paleontology, Berkeley; **UMNH**, Utah Museum of Natural History, Salt Lake City.

DESCRIPTION

Enamel wrinkles (also described as "crenulations" or "undulations") are corrugated structures on the external surface of the crown, comprised of parallel ridges and grooves of varying strength (Fig. 1). These structures extend perpendicular to the apicobasal axis of the crown, always flank the serrations, and curve basally towards the root as they continue across the labial or lingual surfaces of the crown. In some specimens, wrinkles originating from the mesial and distal crown margins may connect to form a continuous wrinkle (herein termed "band") across the labial or lingual surfaces. The function of these structures is unclear, but they may have served a mechanical role in feeding (Currie and Azuma, 2006), or represent a byproduct of growth. It is possible that some wrinkles are preservational artifacts, but their consistent presence and morphology in specimens of the same taxon (e.g., *Carcharodontosaurus*) from disparate preservational environments is inconsistent with this hypothesis.

We have identified enamel wrinkles in several theropod taxa, including carcharodontosaurids, an array of basal tetanurans, and tyrannosauroids. These structures do not seem to be present in coelophysoids (e.g., *Dilophosaurus*: UCMP 37302, 37303), ceratosaurs (e.g., *Ceratosaurus*: BYU 12893, UMNH VP 5278; *Majungasaurus*: FMNH PR 2100; *Rugops*: MNN IGU1), or maniraptorans, although Smith (2005) cites the presence of wrinkles in a single specimen of *Dromaeosaurus* (AMNH 5356), though we have not had the opportunity to examine this specimen ourselves.

Among carcharodontosaurids, the presence, distribution, and form of enamel wrinkles are variable among taxa. Wrinkles are known in *Carcharodontosaurus* (*C. saharicus*: Fig. 1A, see also Sereno et al., 1996:fig 2, Benton et al., 2000; *C.* n. sp.: Fig. 1C),

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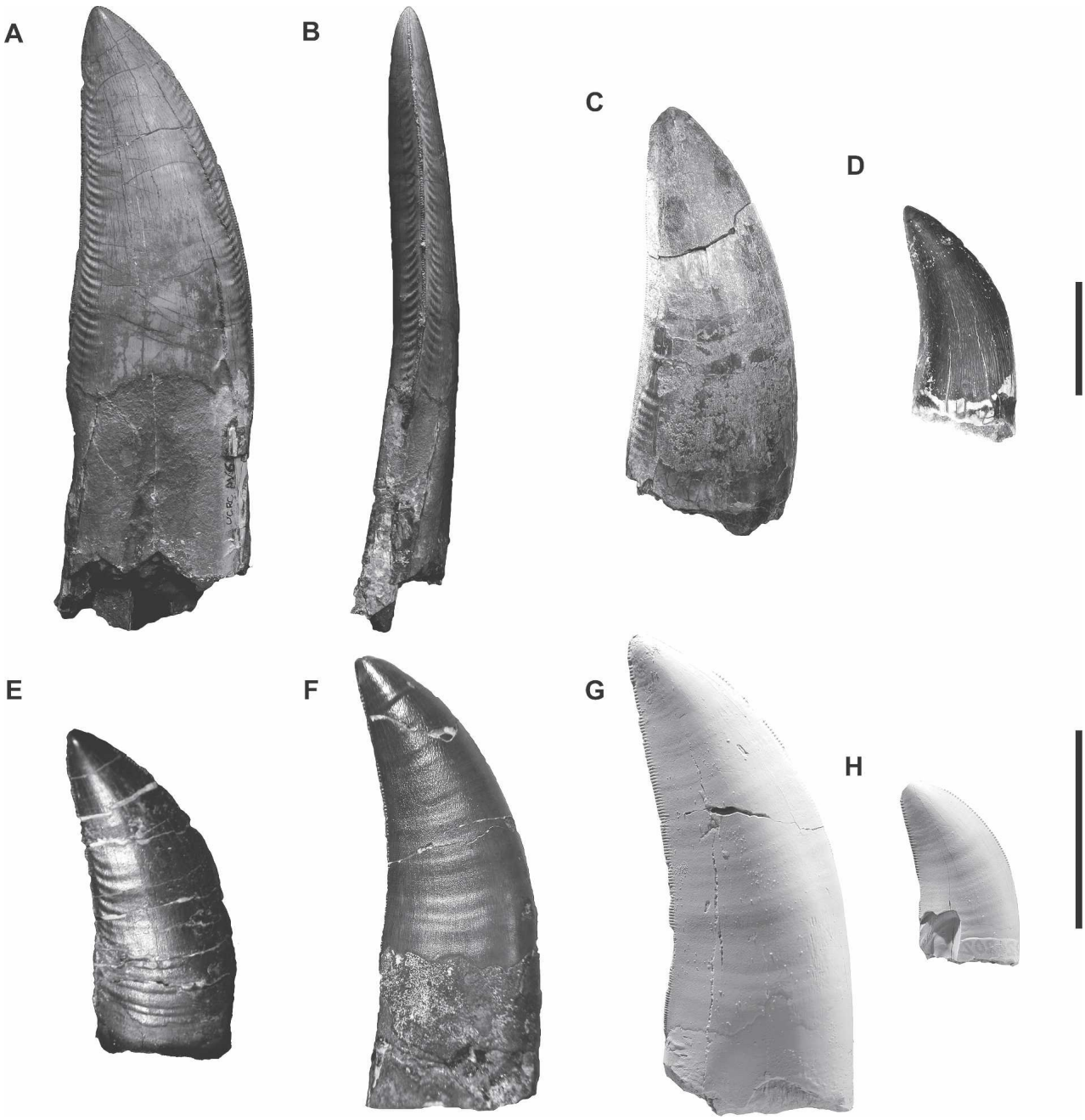

FIGURE 1. Theropod dinosaur teeth with enamel wrinkles. **A**, *Carcharodontosaurus saharicus*, SGM Din-1, lingual view; **B**, *C. saharicus*, SGM Din-1, distal view; **C**, *C.* n. sp., MNN IGU6; **D**, new carcharodontosaurid species from Niger, MNN GAD14; **E**, *Allosaurus fragilis*, UMNH VP 9168, labial view; **F**, *Megalosaurus bucklandi*, OUMNH J13505, labial view; **G**, Tyrannosauroidea indet., NMMNH P-27297; **H**, Tyrannosauroidea indet., NMMNH P-26202. Scale bars equal 3 cm. Top scale bar for A–D, bottom scale for E–H.

Giganotosaurus (MUCPv-CH-1), *Mapusaurus* (Coria and Currie, 2006:fig 12), and *Tyrannotitan* (Novas et al., 2005:p. 228), but are absent in the probable carcharodontosaurid *Acrocanthosaurus* (Currie and Carpenter, 2000), the potential basal carcharodontosaurid *Neovenator* (Hutt et al. 1996), and a new basal carcharodontosaurid from the Aptian-Albian of Niger (Fig 1D; Brusatte and Sereno, 2006). Wrinkles are most pronounced and numerous in *Carcharodontosaurus saharicus*, in which they are in prominent high relief, present at both mesial and distal carinae on the labial and lingual surfaces, and extend partially or completely across the crown as low bands (Fig. 1A, B). The intact maxillary tooth row of the neotype skull (SGM-Din 1; the status of the holotype and basis for designating a neotype will be discussed in detail elsewhere) shows that this pattern is maintained in all mesial and mid maxillary crowns. Similar pronounced wrinkles are seen in *Giganotosaurus*, but only in the largest maxillary teeth. The enamel wrinkles in a new species of *Carcharodontosaurus* from Niger (Fig. 1C; Brusatte and Sereno, 2005) are much weaker than in *C. saharicus*, and are limited to the base of the distal carina. The wrinkles of *Mapusaurus* and *Tyrannotitan* show this reduced pattern as well. In general, the wrinkles of carcharodontosaurids are especially high, prominent, and deep near the serrations, but become less distinct as they extend toward the center of the crown.

Enamel wrinkles are also present in several other basal tetanurans, including allosauroids (*Allosaurus*, *Fukuiraptor*), spinosauroids (*Torvosaurus*), and *Megalosaurus*. Wrinkles have been observed in the maxillary (Fig. 1E; UMNH VP 9168) and dentary (UMNH VP 9366) crowns of large *Allosaurus* individuals, but are subtle or absent in crowns from smaller individuals. These wrinkles are highest near the serrations but extend across much of the crown surface as narrow but prominent bands. Wrinkles are stronger labially than lingually, and are especially prominent at the distal carina. Wrinkles in *Fukuiraptor* are described and figured by Azuma and Currie (2000:fig 4) and Currie and Azuma (2006). As in *Carcharodontosaurus* and *Giganotosaurus*, these wrinkles are present at the mesial and distal carinae of the labial and lingual surfaces, and are in highest relief near the serrations. Wrinkles are also present in *Torvosaurus*, as a single erupted dentary tooth (BYU 725 2003) has subtle versions of these structures, which continue as bands across the labial and lingual surfaces. These are difficult to detect, and similar structures may have gone unnoticed in other taxa. Finally, wrinkles that extend across the crown surface are present in a tooth in the type dentary of *Megalosaurus bucklandii* (Fig. 1F; OUMNH J13505). These wrinkles are of variable dorsoventral thickness, are more prominent labially than lingually, and are of subequal thickness and strength along their circumferential length. Compared with carcharodontosaurids, the wrinkles of *Allosaurus* and *Megalosaurus* are lower and shallower near the serrations but higher and more prominent across the crown surface. The wrinkles of *Fukuiraptor* are very similar to those of carcharodontosaurids in overall morphology, but are not as pronounced.

Enamel wrinkles are common features in tyrannosauroid teeth and have been identified in *Albertosaurus* (ROM 1247), *Daspletosaurus* (CMN 8506), *Tyrannosaurus* (MOR 555, BNHM 2002.004.001), and several unnamed taxa (NMMNH P-27297, P-26202, P-27469; AMNH 6556). Wrinkles are present on the external surfaces of premaxillary, maxillary, and dentary teeth of both large and small individuals (Fig. 1G, H). These structures primarily occur on the labial surface of premaxillary crowns, but are present on both labial and lingual surfaces of maxillary and dentary teeth. Compared to *Carcharodontosaurus* and *Giganotosaurus*, the wrinkles of most tyrannosauroids are lower and less prominent adjacent to the serrations. One exception is the *Tyrannosaurus* specimen MOR 555, which exhibits wrinkles comparable to those of *Carcharodontosaurus saharicus*. However, the continuous enamel bands stretching across the labial and lingual surfaces of many tyrannosauroid teeth are more prominent than those of derived carcharodontosaurids. In tyrannosauroids these bands are often in high relief and vary in dorsoventral depth within the same tooth, whereas in carcharodontosaurids the bands are much weaker than the marginal wrinkles near the serrations and are of a more constant depth, and are sometimes absent altogether.

Wrinkles are also present in some spinosaurids (*Baryonyx*: Charig and Milner, 1997:fig 18), but these parallel the long axis of the crown, do not occur near the serrations, and overall are very different from those of carcharodontosaurids and other theropods described here. These will not be discussed further. However, Rauhut (pers. comm.) has noted the presence of transverse enamel wrinkles near the serrations in several spinosaurid teeth from the Aptian of northern Africa, suggesting that these structures may be present in some members of this clade, although we have not seen these specimens.

Wrinkles have also been described in a number of isolated teeth that are often referred to Carcharodontosauridae. A partial crown of Late Cretaceous age (Campanian-Maastrichtian) from Argentina (Martinelli and Forasiepi, 2004) exhibits high-relief wrinkles near the serrations at both mesial and distal carinae on labial and lingual sides, as in *Carcharodontosaurus* and *Giganotosaurus*. A crown of Early Cretaceous age from Argentina (Vickers-Rich et al., 1999; Rich et al., 2000) preserves wrinkles only at the distal carina of the labial surface, and these are less distinct than the wrinkles of most carcharodontosaurids. A small crown of Late Cretaceous age (Cenomanian-Turonian) from Japan (Chure et al., 1999) exhibits wrinkles at mesial and distal carinae of the labial and lingual surfaces, but these structures are lower, shallower, and less prominent than those of carcharodontosaurids.

DISCUSSION AND CONCLUSIONS

Although enamel wrinkles are often treated as a single, invariant feature and regarded as diagnostic of Carcharodontosauridae, these structures are exceedingly morphologically variable and phylogenetically widespread (Fig. 2). We have documented their presence in a wide array of basal tetanurans, including several (but not all) carcharodontosaurids, *Allosaurus*, *Fukuiraptor*, *Torvosaurus*, *Megalosaurus*, as well as basal coelurosaurs (tyrannosauroids). Although the uncertain phylogeny of basal Tetanurae and Coelurosauria renders character optimization premature, it is possible that wrinkles (or the capability to produce wrinkles) may be a tetanuran synapomorphy lost in derived coelurosaurs and certain other taxa. Wrinkles are most prominent in derived carcharodontosaurids (*Carcharodontosaurus* and *Giganotosaurus*), in which they exhibit high relief near the serrations and often continue across the crown as shallow bands. However, wrinkle distribution and strength are variable within *Carcharodontosaurus*, and wrinkles are absent in some carcharodontosaurids. Wrinkles in other taxa are generally lower near the serrations than those of carcharodontosaurids, but are often higher and deeper across the labial and lingual crown faces. In many taxa, wrinkle strength varies depending on position in the tooth row and size of the individual, and wrinkles are often more pronounced at the distal carina, on the labial crown surface, and in larger individuals.

While the presence of enamel wrinkles is not confined to Carcharodontosauridae, aspects of the form, strength, and distribution of enamel wrinkles may be diagnostic of particular theropod clades. Wrinkles of derived carcharodontosaurids (*Carcharodontosaurus*, *Giganotosaurus*) are more distinctive than those of all

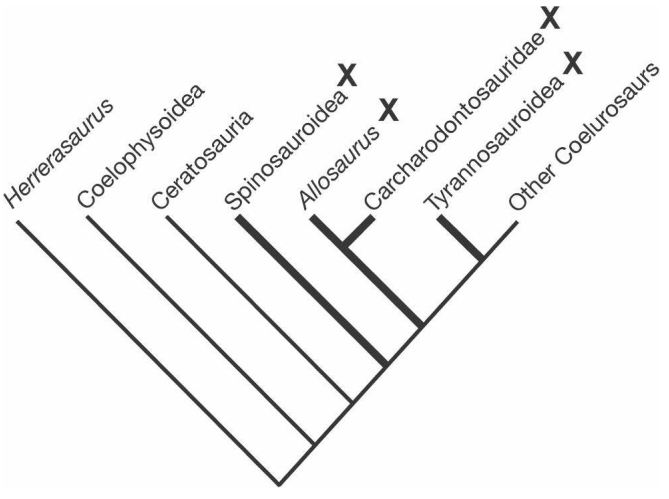

FIGURE 2. A simplified cladogram of theropod dinosaurs showing the phylogenetic distribution of enamel wrinkles (denoted by an X). Wrinkles are known in Spinosauroidea (*Torvosaurus*, *Megalosaurus*), Allosauroidea (*Allosaurus*, *Fukuiraptor*, Carcharodontosauridae), and basal Coelurosauria (Tyrannosauroidea). When optimized onto this simplified tree, enamel wrinkles are a synapomorphy of Tetanurae and lost in derived coelurosaurs.

other theropods, especially near the serrations where they exhibit high relief. The distribution of wrinkles may be diagnostic for *C. saharicus*, in which they are pronounced on both mesial and distal margins of mesial and mid maxillary crowns, not just the broadest crowns as in *Giganotosaurus*. However, it is unclear whether any wrinkle characters clearly diagnose Carcharodontosauridae, as the wrinkles of *Mapusaurus* and *Tyrannotitan* are much weaker than those of derived carcharodontosaurids, and generally similar to the wrinkles of *Allosaurus*, *Fukuiraptor*, and *Megalosaurus*.

Thus, the long-standing use of enamel wrinkles as a "key character" of carcharodontosaurids can no longer be supported, and the common practice of assigning isolated teeth to Carcharodontosauridae based on the simple presence of wrinkles must be abandoned (Kellner and Campos, 1998, 2000; Chure et al., 1999; Vickers-Rich et al., 1999; Rich et al., 2000; Veralli and Calvo, 2003, 2004; Candeiro et al., 2004; Canudo et al., 2004; Martinelli and Forasiepi, 2004; Rauhut, 2006). Additionally, the absence of enamel wrinkles is insufficient grounds to exclude assignment to Carcharodontosauridae as is sometimes practiced (Goodwin et al., 1999; Infante et al., 2005; Canudo et al., 2006), as several carcharodontosaurids do not exhibit wrinkles. Thus, we suggest that all authors using the presence and morphology of wrinkles to assign isolated teeth to theropod clades, especially Carcharodontosauridae, carefully compare their specimens with a wide array of basal tetanurans, including tyrannosauroids. Although qualitative characters such as enamel wrinkles can be useful for theropod systematics, the use of quantitative metrics (Smith, 2005; Smith et al., 2005) is recommended to more rigorously assign isolated teeth to higher-level clades.

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LITERATURE CITED

Azuma, Y., and P. J. Currie. 2000. A new carnosaur (Dinosauria: Theropoda) from the Lower Cretaceous of Japan. Canadian Journal of Earth Sciences 37:1735–1753.

Benton, M. J., S. Bouaziz, E. Buffetaut, D. Martill, M. Ouaja, M. Soussi, and C. Trueman. 2000. Dinosaurs and other fossil vertebrates from fluvial deposits in the Lower Cretaceous of southern Tunisia. Palaeogeography, Palaeoclimatology, Palaeoecology 157:227–246.

Brusatte, S., and P. Sereno. 2005. A new species of *Carcharodontosaurus* (Dinosauria: Theropoda) from the Cenomanian of Niger and its implications for allosauroid phylogeny. Journal of Vertebrate Paleontology 25(3):40A.

Brusatte, S., and P. Sereno. 2006. Basal abelisaurid and carcharodontosaurid theropods from the Elrhaz Formation (Aptian-Albian) of Niger. Journal of Vertebrate Paleontology 26(3):46A.

Candeiro, C. R. A., C. T. Abranches, E. A. Abrantes, L. S. Avilla, V. C. Martins, A. L. Moreira, S. R. Torres, and L. P. Bergqvist. 2004. Dinosaurs remains from western São Paulo state, Brazil (Bauru Basin, Adamantina Formation, Upper Cretaceous). Journal of South American Earth Sciences 18: 1–10.

Canudo, J. I., J. I. Ruiz-Omeñaca, M. Aurell, J. L. Barco, and G. Cuenca-Bescos. 2006. A megatheropod tooth from the Late Tithonian-Middle Berriasian (Jurassic-Cretaceous transition) of Galve (Aragon, NE Spain). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 239:77–99.

Canudo, J. I., L. Salgado, J. L. Barco, R. Bolatti, and J. I. Ruiz-Omeñaca. 2004. Dientes de dinosaurios terópodo y saurópodo de la Formación Cerro Lisandro (Cenomaniense superior-Turoniense inferior, Cretácico superior) en Río Negro (Argentina). Geo-Temas 6:31–34.

Charig, A. J., and A. C. Milner. 1997. *Baryonyx walkeri*, a fish-eating dinosaur from the Wealden of Surrey. Bulletin of the Natural History Museum London (Geology) 53:11–70.

Chure, D. J., M. Manabe, M. Tanimoto, and Y. Tomida. 1999. An unusual theropod tooth from the Mifune Group (Late Cenomanian to Early Turonian), Kumamoto, Japan; pp. 291– 296 in Y. Tomida, T. H. Rich, and P. Vickers-Rich (eds.), Proceedings of the Second Gondwanan Dinosaur Symposium. National Science Museum Monographs, Tokyo 15.

Coria, R. A., and P. J. Currie 2006. A new carcharodontosaurid (Dinosauria, Theropoda) from the Upper Cretaceous of Argentina. Geodiversitas 28:71–118.

Coria, R. A., and L. Salgado. 1995. A new giant carnivorous dinosaur from the Cretaceous of Patagonia. Nature 377:224–226.

Currie, P. J., and Y. Azuma. 2006. New specimens, including a growth series, of *Fukuiraptor* (Dinosauria, Theropoda) from the Lower Cretaceous Kitadani Quarry of Japan. Journal of the Paleontological Society of Korea 22:173–193.

Currie, P. J., and K. Carpenter. 2000. A new specimen of *Acrocanthosaurus atokensis* (Theropoda, Dinosauria) from the Lower Cretaceous Antlers Formation (Lower Cretaceous, Aptian) of Oklahoma, USA. Geodiversitas 22:207–246.

Currie, P. J., J. K. Rigby, Jr., and R. E. Sloan. 1990. Theropod teeth from the Judith River Formation of southern Alberta, Canada; pp. 107–125 in K. Carpenter and P. J. Currie (eds.), Dinosaur Systematics: Perspectives and Approaches. Cambridge University Press, New York.

Farlow, J. O., D. L. Brinkman, W. L. Abler, and P. J. Currie. 1991. Size, shape, and serration density of theropod dinosaur lateral teeth. Modern Geology 16:161–198.

Goodwin, M. B., W. A. Clemens, J. H. Hutchinson, G. B. Wood, M. S. Zavada, A. Kemp, C. J. Duffin, and C. R. Schaff. 1999. Mesozoic continental vertebrates with associated palynostratigraphic dates from the northwestern Ethiopian Plateau. Journal of Vertebrate Paleontology 19:728–741.

Hutt, S., D. M. Martill, and M. J. Barker. 1996. The first European allosaurid (Lower Cretaceous, Wealden Group, England). Neues Jahrbuch für Geologie une Paläontologie, Monatshefte 1996: 635–644.

Infante, P., J. I. Canudo, and J. I. Ruiz-Omeñaca. 2005. Primera evidencia de dinosaurios terópodos en la Formación Mirambel (Barremiense inferior, Cretácico Inferior) en Castellote, Teruel. Geogaceta 38:31–34.

Kellner, A. W. A., and D. A. Campos. 1998. Review of Cretaceous theropods and sauropods from Brazil. Journal of Vertebrate Paleontology 18(3):55A.

Kellner, A. W. A., and D. A. Campos. 2000. Brief review of dinosaur studies and perspectives in Brazil. Anais da Academia Brasileira de Ciências 72:509–538.

Martinelli, A. G., and A. M. Forasiepi. 2004. Late Cretaceous vertebrates from Bajo de Santa Rosa (Allen Formation), Rio Negro province, Argentina, with the description of a new sauropod dinosaur (Titanosauridae). Revista del Museo Argentino de Ciencias Naturales 6:257–305.

Novas, F. E., S. de Valais, P. Vickers-Rich, and T. Rich. 2005. A large Cretaceous theropod from Patagonia, Argentina, and the evolution of carcharodontosaurids. Naturwissenschaften 92:226–230.

Rauhut, O. 2006. Theropod dinosaurs from the Late Jurassic of Tanzania and the origin of Cretaceous Gondwanan theropod faunas. Journal of Vertebrate Paleontology 26(3):113A.

Rich, T. H., P. Vickers-Rich, F. E. Novas, R. Cuneo, P. Puerta, and R. Vacca. 2000. Theropods from the "middle" Cretaceous Chubut Group of the San Jorge Sedimentary Basin, Central Patagonia. A preliminary note. Gaia 15:111–115.

Sereno, P. C., D. B. Dutheil, M. Iarochene, H. C. E. Larsson, G. H. Lyon, P. M. Magwene, C. A. Sidor, D. J. Varricchio, and J. A. Wilson. 1996. Predatory dinosaurs from the Sahara and Late Cretaceous faunal differentiation. Science 272:986–991.

Smith, J. B. 2005. Heterodonty in *Tyrannosaurus rex*: implications for the taxonomic and systematic utility of theropod dentitions. Journal of Vertebrate Paleontology 25:865–887.

Smith, J. B., D. R. Vann, and P. Dodson. 2005. Dental morphology and variation in theropod dinosaurs: implications for the taxonomic identification of isolated teeth. The Anatomical Record 285A: 699–736.

Stromer, E. 1931. Ergebnisse der Forschungsrisen Prof. E. Stromers in

den Wüsten Ägyptens. II. Wirbeltierreste der Baharje-Stufe (unterstes Cenoman). 10. Ein Skelett-Rest von Carcharodontosaurus no. gen. Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Abteilung, Neue Folge 9: 1–23.

Veralli, C. D. J., and J. O. Calvo. 2003. New findings of carcharodontosaurid teeth (Upper Turonian) on Futalognko Quarry, North Barreales Lake, Neuquen, Argentina. Ameghiniana 40(4):74R.

Veralli, C. D. J., and J. O. Calvo. 2004. Dientes de terópodo carcharodontosaurido del Twoniano superior-Coniaciano inferior del Neuquen Patagonia, Argentina. Ameghiniana 41:587–590.

Vickers-Rich, P., T. H. Rich, D. R. Lanus, L. S. V. Rich, and R. Vacca. 1999. "Big tooth" from the Early Cretaceous of Chubut Province, Patagonia: a possible carcharodontosaurid; pp. 85–88 in Y. Tomida, T. H. Rich, and P. Vickers-Rich (eds.), Proceedings of the Second Gondwanan Dinosaur Symposium. National Science Museum Monographs, Tokyo 15.

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