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Abstract
Ornithischian dinosaurs are uncommon elements in Late Cretaceous faunal assemblages of many Gondwanan landmasses, particularly Africa. The best-documented post-Cenomanian record of purported ornithischian body fossils from Africa consists of a left humerus, with associated cranial and costal fragments, from the Santonian-Campanian Quseir Formation of Kharga Oasis, Egypt (Fig. 1) (Awad and Ghobrial, 1966). We show that this specimen pertains instead to a dyrosaurid crocodyliform, and restrict known African ornithischian body fossils to pre-Turonian sediments. The apparent absence of this dinosaur clade from the post-Cenomanian Late Cretaceous of Africa is probably a consequence of limited sampling; nevertheless, a comparable ornithischian absence from coeval sediments in Madagascar and possibly Indo-Pakistan constitutes a notable faunal similarity among these landmasses.

Comments
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NOTE

FROM DINOSAURS TO DYROSAURIDS (CROCODYLIFORMES): REMOVAL OF THE POST-CENOMANIAN (LATE CRETACEOUS) RECORD OF ORNITHISCHIA FROM AFRICA

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Ornithischian dinosaurs are uncommon elements in Late Cretaceous faunal assemblages of many Gondwanan landmasses, particularly Africa. The best-documented post-Cenomanian record of purported ornithischian body fossils from Africa consists of a left humerus, with associated cranial and costal fragments, from the Santonian-Campanian Quseir Formation of Kharga Oasis, Egypt (Fig. 1) (Awad and Ghobrial, 1966). We show that this specimen pertains instead to a dyrosaurid crocodyliform, and restrict known African ornithischian body fossils to pre-Turonian sediments. The apparent absence of this dinosaur clade from the post-Cenomanian Late Cretaceous of Africa is probably a consequence of limited sampling; nevertheless, a comparable ornithischian absence from coeval sediments in Madagascar and possibly Indo-Pakistan constitutes a notable faunal similarity among these landmasses.

Institutional Abbreviations—**CGM**, Egyptian Geological Museum, Cairo; **MRAC**, Musée Royal d'Afrique Central, Tervuren, Belgium; **USGS SAP**, United States Geological Survey, Saudi Arabian Collection, Saudi Arabia; **YPM**, Yale Peabody Museum, New Haven.

Anatomical Abbreviations—**dpc**, deltopectoral crest; **hd**, humeral head; **rac**, radial condyle; **ulc**, ulnar condyle.

SYSTEMATIC PALEONTOLOGY

CROCODYLOMORPHA Walker, 1970
CROCODYLIFORMES Hay, 1930
MESOEUCROCODYLIA Whetstone and Whybrow, 1983
DYROSAURIDAE de Stefano, 1903

Referred Specimen—CGM 30975, a complete left humerus (Figs. 2, 3A, Table 1), associated with fragments of the cranium and dorsal ribs (Awad and Ghobrial, 1966).

Locality—Approximately four kilometers east of the road between Gaga and Baris, southern Kharga Oasis, Western Desert of Egypt (paraphrased from Awad and Ghobrial [1966]; approximately 24° 44′ N, 30° 37′ E) (Fig. 1). We recognize the inadequacy of this description; nevertheless, the stratigraphic provenance of CGM 30975 is known with certainty.

Horizon and Age—Quseir Formation (=“variegated shale” of the Nubia Formation [Awad and Ghobrial, 1966; Weishampel, 1990]; =Baris Formation [Hendriks et al., 1987]), Santonian-Campanian (Late Cretaceous) (Churcher, 1995; Mahmoud, 1998).

Description—The humerus is elongate and slender, bowed ventrally, and modestly expanded at its proximal and distal extremes. There is slight torsion between the ends of the element. As seen in ventral view, the proximal margin of the humerus forms an approximate right angle with the lateral surface of the shaft, resulting in a distinctive “squared” appearance (Fig. 2A, 3A). The slightly abraded deltopectoral crest extends more than one-third the length of the humerus, but is low throughout its length. The hemispherical humeral head projects from the dorsal surface of the proximal end of the element (Fig. 2B). The medial margin of the shaft is shallowly concave through its proximal third but essentially straight distally. The distal end of the humerus flares laterally and is nearly as transversely expanded as the proximal portion (Table 1). The cranial and rib fragments associated with the specimen could not be located for study.

DISCUSSION

Post-Cenomanian African Ornithischian Absence—CGM 30975 was originally recognized as an ornithischian dinosaur humerus (Awad and Ghobrial, 1966:pl. IV; El-Kashab, 1977; Klitzsch et al., 1979; Weishampel, 1990; Gomani, 1999). If accurately identified, the specimen would be of importance, as reliable records of Ornithischia are unknown from post-Cenomanian deposits in Africa. Ichnites from the Turonian of southern Egypt were tentatively referred to a small ornithischian; however, the poor preservation of these specimens renders their identification uncertain (Demathieu and Wycisk, 1990). Mateer et al. (1992), citing Furon (1963), reported the occurrence of the Jurassic dryosaurid ornithopod *Dryosaurus* sp. in Late Cretaceous deposits of Mali. This record was emended to Dryosauridae indet. by Gomani (1999). However, Furon (1963) mentioned only sauropod and theropod dinosaur material from the Cretaceous deposits in question, and the dyrosaurid crocodyliform *Dyrosaurus* from overlying Paleocene sediments. We believe that, given the similarity of their generic names, Mateer et al. (1992) unintentionally transposed Furon's (1963) report of the crocodyliform *Dyrosaurus* for the ornithopod *Dryosaurus*. Assuming that nonavian dinosaurs did not survive into the Paleocene, Mateer et al. (1992) assigned the specimen to the Late Cretaceous. Mateer (pers. comm., 2002) has recently acknowledged this possibility. The record of Ornithischia in the Late Cretaceous of Mali is therefore probably invalid.

Putative ornithopod caudal vertebrae were reported from the purportedly Upper Cretaceous Ameki Formation of Nigeria (Nopcsa, 1925; Molnar, 1980). However, these sediments were subsequently shown to be Eocene in age (see Arua and Rao, 1987), and the specimens in question pertain to a dyrosaurid crocodyliform (Swinton, 1930).

Weishampel (1990), Jacobs et al. (1996), and Gomani (1999) noted indeterminate ornithopod remains from the Turonian-Santonian of Kenya. Weishampel (1990) cited an unpublished manuscript by J. M. Harris and D. A. Russell. However, according to Russell (pers. comm., 2002), the specimens mentioned therein are fragmentary, were observed only in the field and never collected, may be pre-Turonian (?Cenomanian) in age, and cannot be confidently assigned to Ornithischia. Jacobs et al. (1996) and Gomani (1999) cite Wescott et al. (1993), who note only “dinosaur bones” from the deposits in question. Similarly, Arambourg and Wolff (1969), cited by Gomani (1999), mention only possible sauropod bones. In summary, there is no firm evidence of ornithischians in the Late Cretaceous of Kenya.

Comparison with Ornithischia—To elucidate its affinities, we compared the Egyptian humerus with several Cretaceous tetrapod clades, including Ornithischia. CGM 30975 bears little resemblance to the hu-

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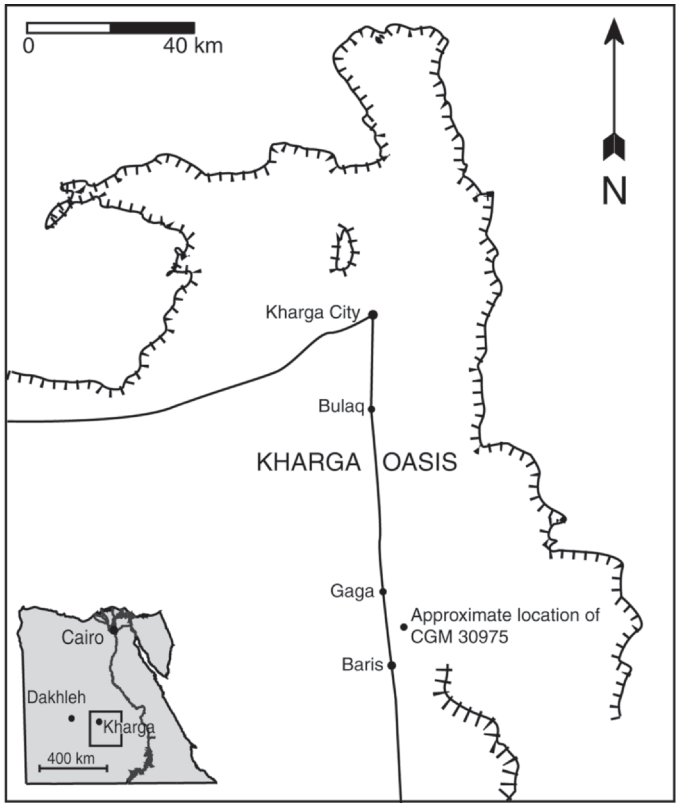

FIGURE 1. Location of discovery of CGM 30975, Kharga Oasis, Western Desert of Egypt.

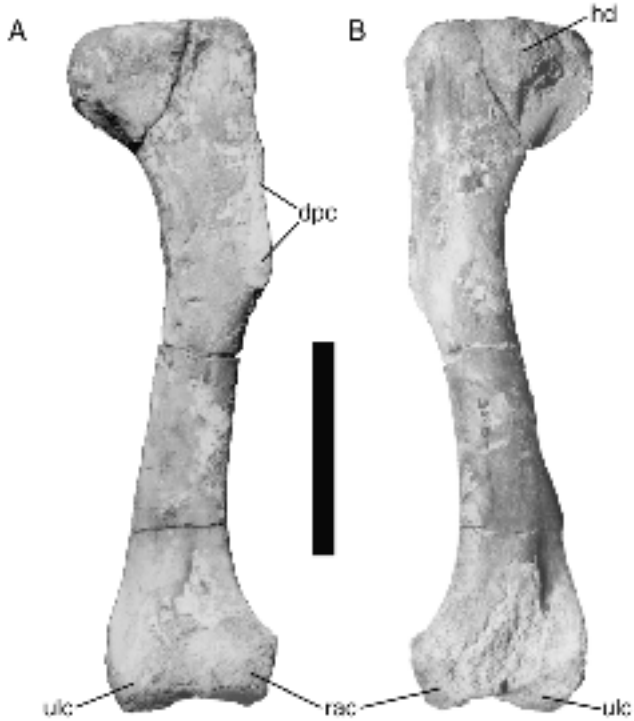

FIGURE 2. Dyrosaurid left humerus, CGM 30975. **A**, ventral (=cranial) view. **B**, dorsal (=caudal) view. Scale equals 100 mm.

meri of Cretaceous thyreophorans and ceratopsians. It does somewhat resemble the humerus of the pachycephalosaur *Goyocephale* (Fig. 3B; Perle et al., 1982), but in that taxon the humerus is more robust, with a strongly expanded and medially deflected proximal portion. Furthermore, as pachycephalosaurs appear restricted to Northern Hemisphere landmasses (Sampson et al., 1998), we regard affinity with that clade as unlikely.

Among ornithischians, CGM 30975 most closely resembles ornithopod humeri. We compared the Quseir specimen to Cretaceous representatives of Ornithopoda from elsewhere in North Africa and the geographically proximal landmasses of Europe, South America, and Antarctica. In the Early Cretaceous North African iguanodontian *Ouranosaurus* (Fig. 3C; Taquet, 1976) and the Late Cretaceous Argentine ornithopods *Anabisetia* (Coria and Calvo, 2002), *Gasparinisaura* (Coria and Salgado, 1996; Salgado et al., 1997), and *Notohypsilophodon* (Fig. 3D; Martínez, 1998), the humerus is superficially similar to CGM 30975. In the ornithopods, however, the proximal margin is sinuous or rounded rather than straight, the maximum concavity of the medial surface occurs near the midpoint of the shaft, and the distal region is medially positioned and notably less expanded than the proximal (Table 1). Moreover, in *Notohypsilophodon,* the deltopectoral crest is virtually absent (Fig. 3D; Martínez, 1998) while in *Ouranosaurus* and *Gasparinisaura* it extends far cranial to the margin of the shaft (Taquet, 1976; Coria and Salgado, 1996). In the humeri of the enigmatic rhabdodontid iguanodontians *Rhabdodon* and *Zalmoxes* from the Late Cretaceous of Europe, the proximal region is medially deflected and the shaft more robust than in CGM 30975 (Pereda-Suberbiola and Sanz, 1999; Weishampel et al., 2003). The humeri of the European hadrosaurs *Telmatosaurus* and *Pararhabdodon* differ strongly from CGM 30975 (Weishampel et al., 1993; Laurent et al., 1997). In the other ornithopods considered, the humerus is either too fragmentary for comparison (Casamiquela, 1964), undescribed (Hooker et al., 1991; Taquet and Russell, 1999) or unknown (Brett-Surman, 1979; Galton and Taquet, 1982; Bonaparte et al., 1984; Cooper, 1985; Powell, 1987; González-Riga and Casadío, 2000).

Dyrosaurid Affinities—Interestingly, Langston (1995) noted resemblances between the humeri of ornithopod dinosaurs and those of dyrosaurid crocodyliforms. Indeed, CGM 30975 is strikingly similar to the humerus of the dyrosaurid *Hyposaurus natator* (YPM 985; Troxell, 1925) from the Maastrichtian of New Jersey (Fig. 3E), particularly in regard to the "squared" proximal region, the length and morphology of the deltopectoral crest, and the lateral deflection of the distal portion. Slight differences occur in the degree of expansion of the proximal and distal ends and the curvature of the shaft. However, because these features appear to become more pronounced with increasing size in dyrosaurids (Langston, 1995), and the humerus of YPM 985 is only 55% the length of CGM 30975, we attribute these differences to the dimensions of the individuals involved. CGM 30975 also clearly resembles the humeri of the dyrosaurids *Congosaurus bequaerti* (MRAC 1813; Dollo, 1914; Swinton, 1950:pl. VI) from the Paleocene of Cabinda, Angola and *Rhabdognathus* sp. from the Paleocene of Saudi Arabia (USGS-SAP 33-CR-3 and 3-CR-1; Langston, 1995:fig. 24). The relative widths of the proximal and distal ends are similar in CGM 30975 and *C. bequaerti* (Table 1).

The provenance of CGM 30975 offers further evidence in support of a dyrosaurid identification. Dyrosaurids are known from Late Cretaceous-Eocene coastal and estuarine deposits throughout North Africa and the Middle East (see Buffetaut, 1981). Skull fragments probably pertaining to the dyrosaurid *Dyrosaurus* are known from the Quseir Formation of southern Kharga Oasis (Churcher and Russell, 1992; Churcher, 1995). More material tentatively referred to *Dyrosaurus* has been recovered from the coeval Mut Formation of nearby Dakhleh Oasis (Churcher, 1995) and Late Cretaceous sediments elsewhere in Egypt (Gemmellaro, 1921).

Based on the sum of this evidence, we refer CGM 30975 to Dyrosauridae. Due to the limited amount of information available on diagnostic characters of the dyrosaurid appendicular skeleton, we are unable to determine the generic affinities of the Quseir specimen with certainty. Given the probable occurrence of *Dyrosaurus* in the same deposits, it is possible that CGM 30975 pertains to that taxon. Remarkably, along with the occurrences from Mali and Nigeria mentioned above, the Egyptian humerus represents a third putative post-Cenomanian North African ornithischian record that has proven dyrosaurid in origin.

Significance—The referral of CGM 30975 to Dyrosauridae invalidates the occurrence of Ornithischia in the post-Cenomanian Late Cretaceous of continental Africa. Because the African terrestrial vertebrate record for this interval is extremely poorly known, its lack of ornithischian

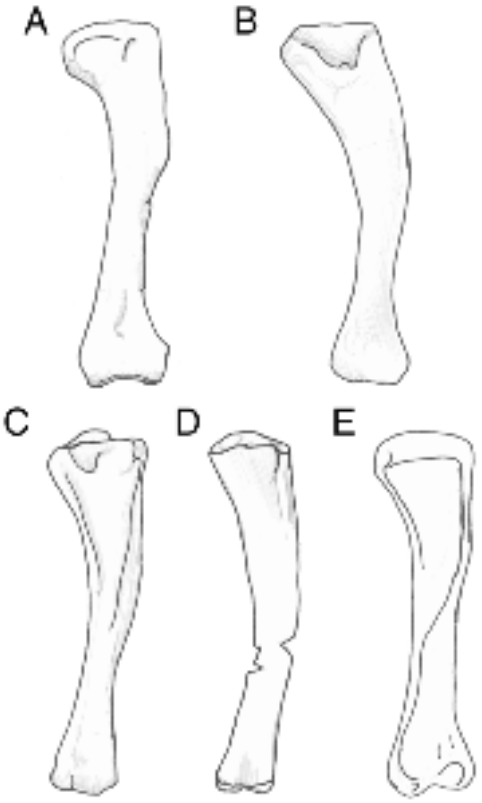

FIGURE 3. Dyrosaurid and ornithischian humeri, not to scale. **A**, CGM 30975 (Dyrosauridae). **B**, *Goyocephale lattimorei* (Pachycephalosauria; after Perle et al., 1982). **C**, *Ouranosaurus nigeriensis* (Ornithopoda; after Taquet, 1976). **D**, *Notohypsilophodon comodorensis* (Ornithopoda; after Martínez, 1998). **E**, *Hyposaurus natator*, YPM 985 (Dyrosauridae; after Troxell, 1925). A, C–E in ventral (=cranial) view; B in dorsal (=caudal) view.

dinosaurs is probably a consequence of incomplete sampling. Intriguingly, however, ornithischians are also not yet known from increasingly well-studied latest Cretaceous deposits in adjacent Madagascar (e.g., Krause et al., 1999; Buckley et al., 2000).

Similarly, Indo-Pakistan, which remained connected to Madagascar until the early Coniacian (approximately 88.0 Ma, Storey et al., 1995) has not produced definitive Late Cretaceous ornithischian material to date. Mohabey (1989) described a dinosaurian element that he identified as a braincase from Upper Cretaceous sediments in the western Indian state of Gujarat. He referred this specimen to Ornithischia, but regarded this referral as doubtful. Another specimen from Gujarat, a hollow fragment that Dwivedi and Ghevariya (1984) interpreted as a ceratopsid horncore, may instead pertain to a theropod limb element or a dorsal rib of a theropod or titanosauriform sauropod. Moreover, reports of a fragmentary ornithopod skeleton from the Late Cretaceous of southern India (Narayan Rao and Sesachar, 1927; Molnar, 1980) have never been confirmed.

TABLE 1. Humeral dimensions (mm) in the dyrosaurid crocodyliforms CGM 30975 and *Congosaurus bequaerti* and the iguanodontian ornithopod *Ouranosaurus nigeriensis*. Data for *C. bequaerti* and *O. nigeriensis* from Swinton (1950) and Taquet (1976), respectively.

	CGM 30975	*Congosaurus bequaerti*	*Ouranosaurus nigeriensis*
Proximodistal length	315	295	555
Maximum proximal width	86	85	145
Maximum distal width	79	81	102
Proximal/distal width	1.09	1.05	1.42

Claims of thyreophoran (stegosaurian or ankylosaurian) remains from the Indian Late Cretaceous are relatively common, but all remain unsubstantiated. The putative stegosaur *Brachypodosaurus* was described from an isolated limb element identified as a humerus from the Maastrichtian Lameta Formation of Madhya Pradesh (Chakravarti, 1934). Nevertheless, Galton (1981) could not confirm the identity of the holotype element, and consequently, the affinities of the taxon. *Dravidosaurus*, another purported stegosaur from Coniacian deposits in Tamilnadu (Yadagiri and Ayyasami, 1979), was recently suggested to pertain to Plesiosauria (Chatterjee and Rudra, 1996). Wilson et al. (2003) cast further doubt on the stegosaurian affinities of *Brachypodosaurus* and *Dravidosaurus*, noting that these taxa do not exhibit synapomorphies of that clade. Matley (1923) and Huene and Matley (1933) described a supposed ankylosaur, *Lametasaurus*, from the Lameta Formation, but this taxon was subsequently shown to be based upon a chimera of theropod, sauropod, and possibly crocodyliform material (Chakravarti, 1935; Galton, 1981; Molnar and Frey, 1987; Chatterjee and Rudra, 1996; Wilson et al., 2003). Coombs (1978), Yadagiri and Ayyasami (1979), and Chatterjee and Rudra (1996) mentioned additional reputed thyreophoran material from the Upper Cretaceous of India, but these remains have never been described. Finally, despite a recent increase in research there, ornithischians remain unrecorded from Late Cretaceous deposits in Pakistan (Wilson et al., 2001).

The current lack of unquestionable ornithischian dinosaur material from the post-Cenomanian Late Cretaceous of Africa, Madagascar, and Indo-Pakistan contrasts contemporaneous dinosaurian faunas of most other Gondwanan continents, from which ornithopods and ankylosaurs are known (e.g., Bonaparte et al., 1984; Gasparini et al., 1987, 1996; Wiffen and Molnar, 1989; Hooker et al., 1991; Molnar and Wiffen, 1994; Coria and Salgado, 1996, 2001; Salgado and Coria, 1996; Case et al., 2000; González Riga and Casadio, 2000). Even if genuine, however, this ornithischian absence is not necessarily reflective of a common origin for the Late Cretaceous terrestrial vertebrate assemblages of Africa, Madagascar, and Indo-Pakistan. Nevertheless, it is notable in light of recent hypotheses of Late Cretaceous tetrapod dispersal and resultant faunal affinity between South America, Antarctica, Madagascar, and Indo-Pakistan, and endemism in African assemblages during this interval (e.g., Sampson et al., 1998; Krause et al., 1999; Buckley et al., 2000). An improved understanding of the reality and significance of the apparent Late Cretaceous ornithischian absence from Africa, Madagascar, and Indo-Pakistan is contingent upon continued research in these areas.

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