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THE LARGE THEROPOD FAUNA OF THE LOURINHÃ FORMATION (PORTUGAL) AND ITS SIMILARITY TO THAT OF THE MORRISON FORMATION, WITH A DESCRIPTION OF A NEW SPECIES OF *ALLOSAURUS*

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Abstract—Late Jurassic theropod dinosaurs have been known in Portugal since 1863 but only now are they being fully understood, with the recognition of genera such as *Allosaurus, Aviatyrannis, Ceratosaurus, Lourinhanosaurus,* and *Torvosaurus* from the Lourinhã and Alcobaça Formations (Kimmeridgian/Tithonian). *Ceratosaurus dentisulcatus* can now be reported from Portugal. It represents the only occurrence of this species outside the Morrison Formation. New cranial elements confirm the presence of *Torvosaurus tanneri*, in Portugal. *Torvosaurus* was the largest Late Jurassic land carnivore. New postcranial and cranial elements allow the erection of a new species from Portugal, *Allosaurus europaeus* n.sp. The theropod assemblage of Portugal is similar to that of the Morrison Formation.

Resumo—São interpretados dinossauros terópodes em Portugal desde 1863, mas só agora começam a ser melhor conhecidos, através do reconhecimento de géneros como *Ceratosaurus, Lourinhanosaurus*, *Torvosaurus, Allosaurus* e *Aviatyrannis* das Formações da Lourinhã e Alcobaça (Kimmeridgiano/Titoniano). É dada a conhecer para Portugal a presença de *Ceratosaurus dentisulcatus*, a única ocorrência conhecida fora da Formação de Morrison. Novos elementos cranianos confirmam a presença de *Torvosaurus tanneri*, o maior carnívoro terrestre do Jurássico superior. Novos elementos cranianos e pós-cranianos permitem caracterizar uma nova espécie, *Allosaurus europaeus* n.sp. A fauna de terópodes de Portugal é muito semelhante à da Formação de Morrison.

INTRODUCTION

The Late Jurassic of Portugal is rich in dinosaurs, including theropods (Antunes and Mateus, 2003). To our knowledge, the first dinosaur remains in Portugal were two theropod teeth collected by Carlos Ribeiro at Porto das Barcas, near Lourinhã, on June 20, 1863 (Lapparent and Zbyszewski, 1957; Antunes and Mateus, 2003). Several theropods have been reported in Portugal since then. However, four taxa, at least, are not valid because they are *nomina dubia (Megalosaurus insignis, M. pombali, M. pannoniensis*) or were identified on insufficient material (*Erectopus superbus*). As far as the Cretaceous is concerned, the only valid theropod species known in Portugal is *Euronychodon portucalensis* (Antunes and Sigogneau-Russell, 1991, 1992, 1995, 1996).

In Portugal, the Kimmeridgian/Tithonian Formations of Lourinhã and Alcobaça are, by far, the two dinosaur-richest Late Jurassic units. The Alcobaça Formation is mainly Kimmeridgian while Lourinhã Formation comprises mostly the Tithonian. To date, the theropod genera/species known in Portugal are *Ceratosaurus* sp., *Torvosaurus* sp., *Lourinhanosaurus antunesi, Allosaurus* sp., cf. *Compsognathus* sp., *Aviatyrannis jurassica,* and cf. *Archaeopteryx* sp. (Antunes and Mateus, 2003; Rauhut 2000; 2003).

The eustreptospondilyd *Lourinhanosaurus antunesi* is one of the most interesting Portuguese theropods. It is known after the sub-adult holotype specimen and the discovery of a nest with more than 100 eggs, some with well preserved embryos (Antunes and Mateus, 2003; Antunes et al., 1998; Mateus, 1998, 2005; Mateus et al., 1997, 1998a, 1998b, 2001; Cunha et al., 2004). Such findings have been useful to understand the ontogenetical evolution of theropods (Ricqlès et al., 2001; Mateus, 2005; Mateus et al., in prep.).

Coelurosaur teeth have been reported by Antunes and Mateus (1993), Mateus (2005), Rauhut and Kriwet (1994), Weigert (1995), Zinke (1998), Rauhut (2000; 2003) but are not dealt with here.

The Guimarota mine (Alcobaça Formation, Kimmeridgian) provided many teeth and other fragmentary material identified as Ceratosauria indet., ?Allosauroidea indet., cf. *Compsognathus* sp., *Aviatyrannis jurassica,* Dromaeosaurinae indet., Velociraptorinae indet., (?) Troodontidae indet., and cf. *Archaeopteryx* sp. (Rauhut, 2000; 2003). The same locality provided thousands of Kimmeridgian microfossils, including theropods that were collected in the 1960s, '70s and '80s under the supervision of the Institute for Paleontology of the Freie Universität Berlin (Antunes, 1998; Martin and Krebs, 2000; Krebs, 2000). Despite the valuable quality and quantity of the work, it is unfortunate that conditions have never been created for a Portuguese scientific cooperation in such context.

Abbreviations: BYU, Brigham Young University Earth Sciences Museum, Provo, Utah; HM, Humboldt Museum, Berlin, Germany; ML, Museu da Lourinhã, Lourinhã, Portugal; MHNUL, Museu de História Natural da Universidade de Lisboa, Portugal; MWC, Museum of Western Colorado, Fruita, Colorado; UUVP, University of Utah Vertebrate Paleontology Collection at the Utah Museum of Natural History, Salt Lake City, Utah.

THEROPODS FROM PORTUGAL WITH MORRISON FORMATION AFFINITIES

Among the six theropod genera from the Late Jurassic of Portugal, three (and possibly four) are also known from the Morrison Formation: *Ceratosaurus*, *Torvosaurus*, *Allosaurus*, and possibly *Aviatyrannus*.

SAURISCHIA Seeley, 1888

THEROPODA Marsh, 1881

NEOTHEROPODA Bakker, 1986

CERATOSAURIA Marsh, 1884

CERATOSAUROIDEA Bonaparte, 1991

CERATOSAURIDAE Marsh, 1884

***CERATOSAURUS* Marsh, 1884**

CERATOSAURUS DENTISULCATUS Madsen and Welles, 2000

Distribution and horizon: The genus *Ceratosaurus* has been un-

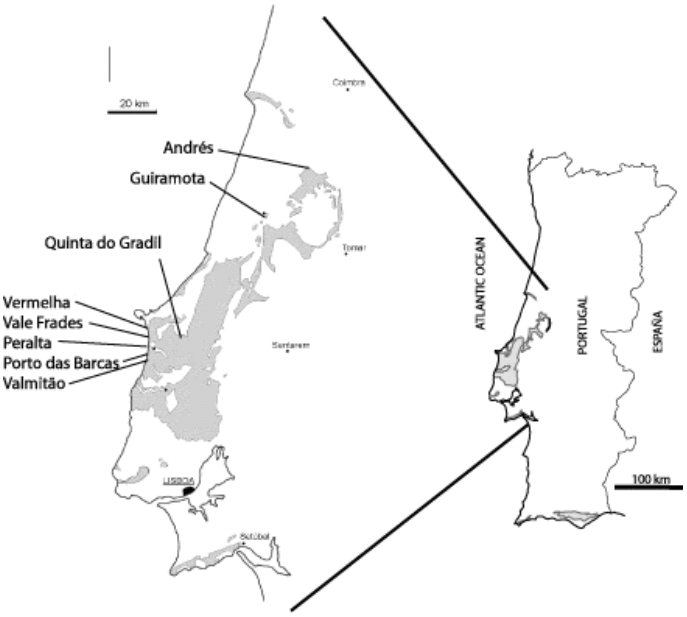

FIGURE 1. Portugal with the Late Jurassic outcrops (shaded) and the localities mentioned in the text.

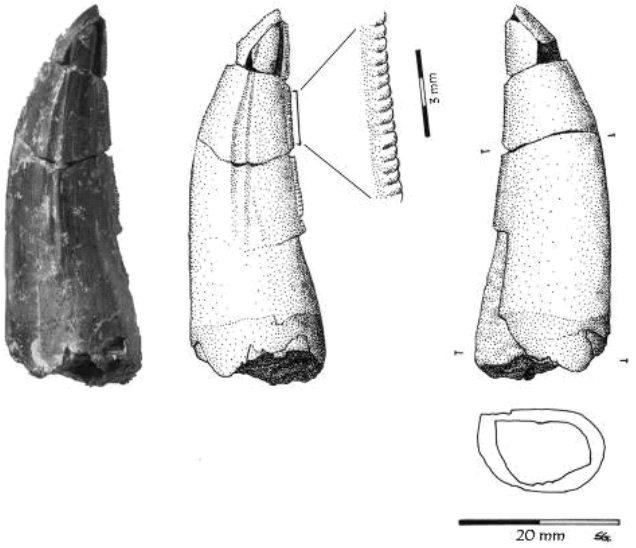

FIGURE 2. *Ceratosaurus* tooth from the Lourinhã formation at Porto das Barcas (Portugal), showing vertical ridges on lingual surface (ML809).

ambiguously identified in the Morrison Formation in Colorado and Utah by: *C. nasicornis*, *C. dentisulcatus,* and *C. magnicornis* (Madsen and Welles, 2000). The two last species are from the Brushy Basin Member of Morrison Formation at the Cleveland-Lloyd Quarry (dated as 146.7 to 147.3 M.a. by Bilbey, 1992, i.e., Tithonian) and the Fruita Paleontological Area. *Ceratosaurus nasicornis* is from the Garden Park section (Marsh-Felch Quarry; Tithonian, 150.33 +0.26 M.a.; Kowallis et al., 1998; Gradstein and Ogg, 2004). *Ceratosaurus* specimens have also been found at nine other localities in the Morrison Formation.

The ceratosaur material from the Tendaguru Beds in Tanzania was attributed to *C. roechlingi*, but is regarded as a *Ceratosaurus* sp. by Madsen and Welles (2000) and *nomen dubium* by Tykoski and Rowe (2004). See Mateus (this volume) for the Morrison, Portugal and Tendaguru comparison.

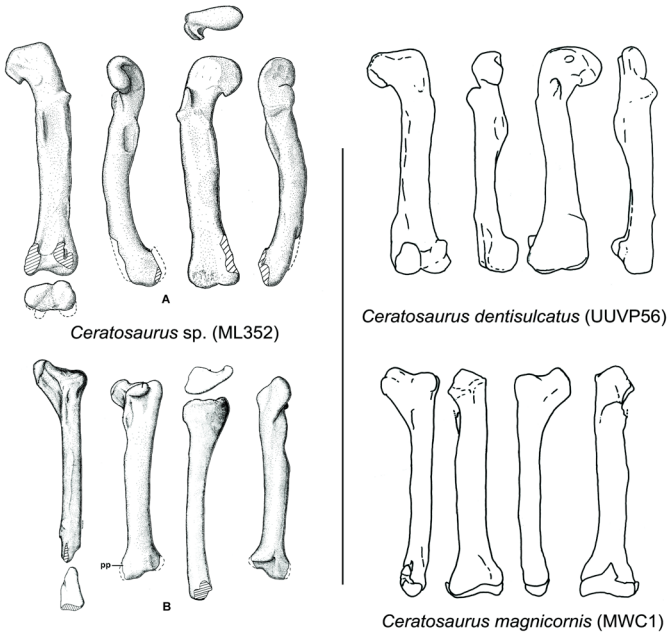

FIGURE 3. Femur (A) and tibia (B) of *Ceratosaurus*. Material from Portugal on the left; that from the Morrison Formation on the right (after Madsen & Welles, 2000).

Description: The material from Portugal was collected in Lourinhã Municipality (right femur and left tibia ML352 from Rodela do Valmitão, figure 2, tooth ML809 from Porto das Barcas, tooth ML737 from Peralta and tooth ML342 from Merendeiro; figure 1). The most identifiable material is from the Praia da Amoreira Member, in the lower part of the Lourinhã Formation (Kimmeridgian).

The right femur ML352 is 64.7 cm long which allows a body weight estimate (based on Anderson et al., 1985) of about 560 kg, which is within the range of most *Ceratosaurus* specimens from the Morrison.

The specimen ML352 is clearly from *Ceratosaurus*. Similarities include: presence of a trochanteric shelf; anterior trochanter not blade-shaped; femoral head projects anteromedially; deep sulcus along lateral side of the crista tibiofibularis; lack of the lateral longitudinal groove at the distal end of tibia; the femoral head is projected anteromedially (Mateus and Antunes, 2000a; Antunes and Mateus, 2003; and compare with Gilmore, 1920, and Madsen and Welles, 2000; figure 3, 4 and 5).

Minor differences from *C. nasicornis* are the more developed fibular crest, and the distal femoral head projects to form a notch that is more developed in ML352. Laterally, the head has a small caudal projection as in *C. nasicornis* and *Coelophysis*. In ML352, there is a small depression between the greater trochanter and the femoral head. In the Portuguese *Ceratosaurus*, the distal end of the femur has a bridge between the two condyles at the posterior (flexor) groove. Such a feature is present but in the Ceratosauria (*Megapnosaurus*, *Carnotaurus*, *Ceratosaurus dentisulcatus*).

The lingual facets of the anterior teeth bear longitudinal grooves, as in Morrison *Ceratosaurus dentisulcatus*. The relative position of the epiphysial expansions in ML352 is different from *C. nasicornis* and *C. magnicornis* in being closer to those of *C. dentisulcatus*, where the distal and proximal expansions turn more from position by the diaphysial axis. The posterior intercondylar bridge of the femur is also present in *C. dentisulcatus*, but is absent in the other species of the genus. Accordingly, we may conclude that the Portuguese species is a *Ceratosaurus* sp. closer to *C. dentisulcatus*, rather than to *C. nasicornis* or *C. magnicornis*.

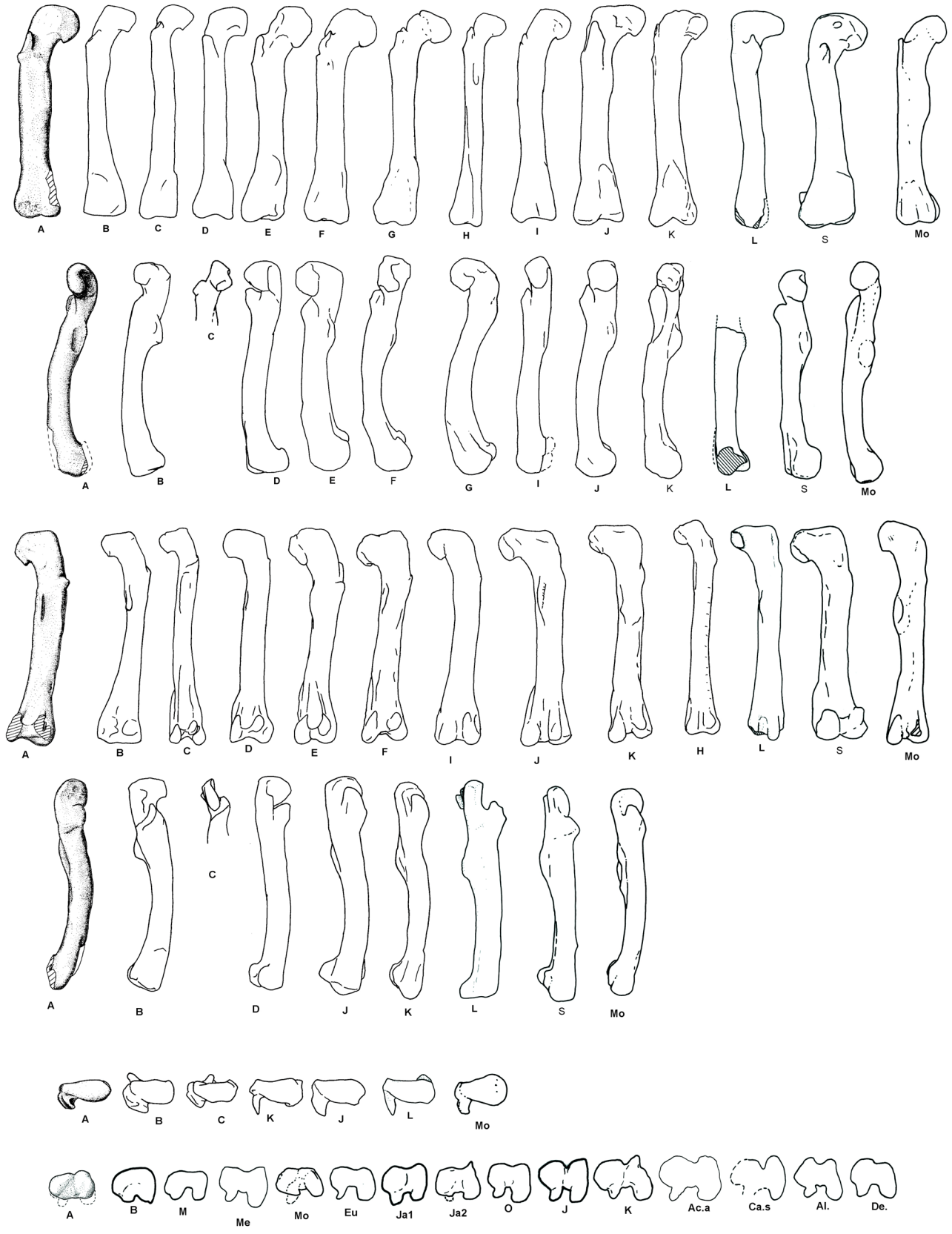

FIGURE 4. Femora of theropods in anterior, medial, posterior, lateral, proximal and distal views. **A.** *Ceratosaurus* sp. ML352; **B.** *Herrerasaurus*; **C.** *Megapnosaurus* (=*Syntarsus*); **D.** *Carnotaurus*; **E.** **Xenotarsosaurus*; **F.** *Ceratosaurus nasicornis*; **G.** *Elaphrosaurus*; **H.** * *Liliesternus* ; **I.** *Megalosaurus* indet.; **J.** *Allosaurus fragilis*; **K.** *Sinraptor*; **L.** *Lourinhanosaurus*; **M.** *Dilophosaurus*; **N.** *Torvosaurus tanneri*; **O.** *Torvosaurus tanneri*; **P.** **Velocisaurus*; **Q.** "*Megalosaurus*"; **R.** * Specimen by Janensch, 1925; **S.** *Ceratosaurus dentisulcatus*; **U.** Specimen by Janensch, 1925; **Mo.** Theropod from Morella, Spain (unpublished); **Ac.a**. *Acrocanthosaurus atokensis*; **Ca.s.** *Carnotaurus sastrei*. Not at the same scale. * image reversed.

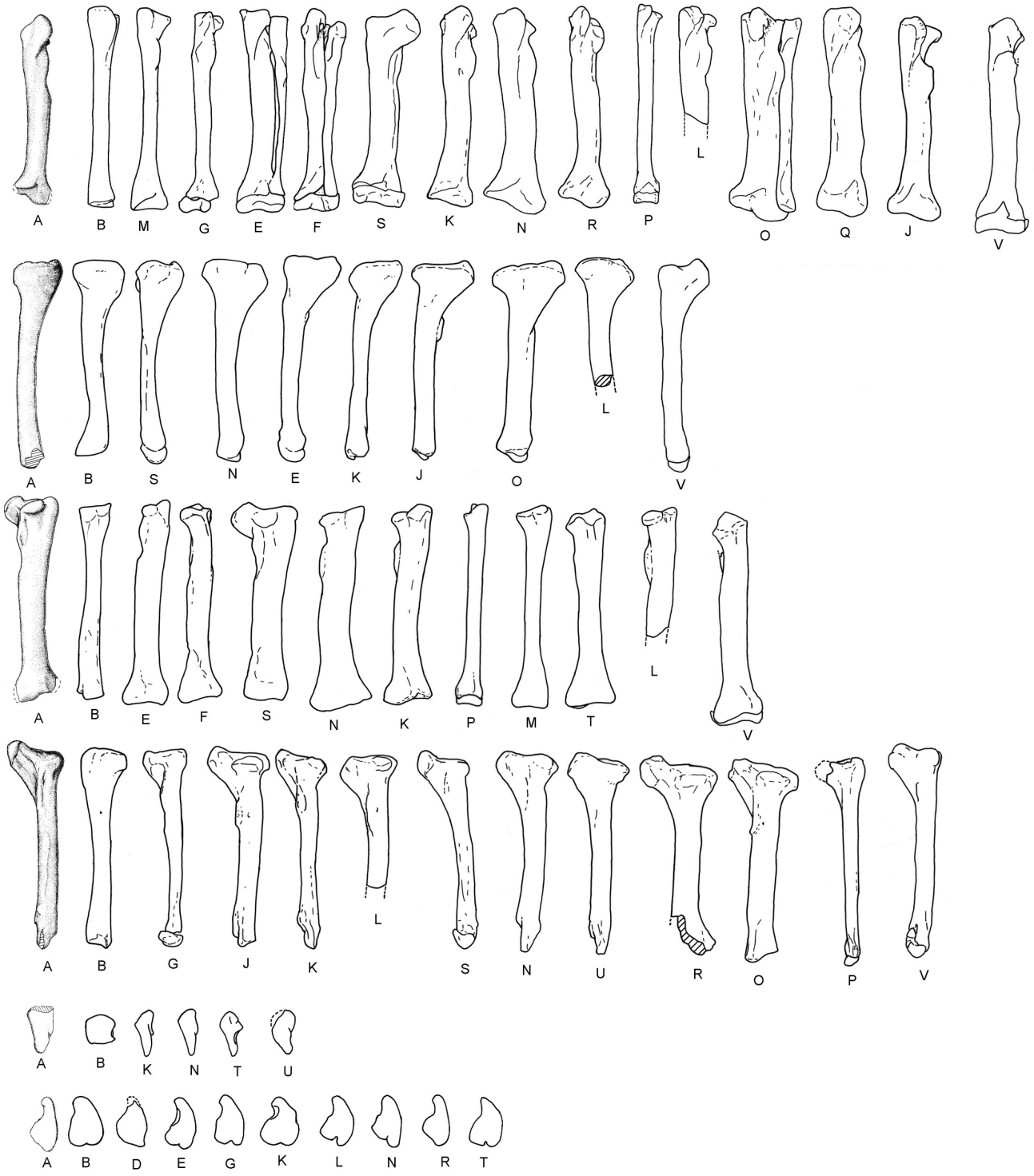

FIGURE 5. Tibiae of theropods. See abbreviations in the previous figure.

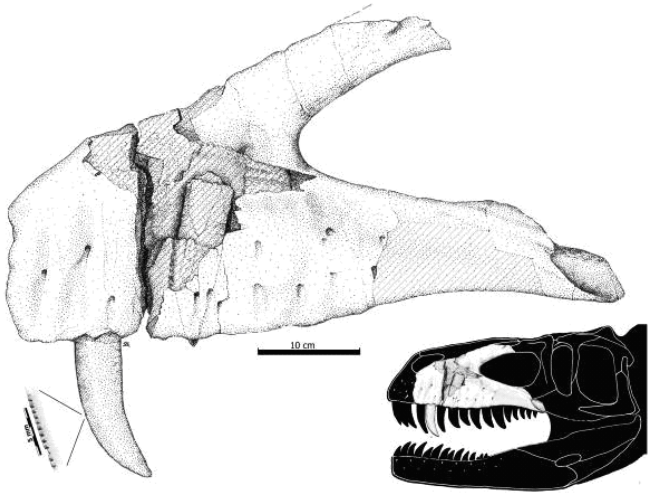

FIGURE 6. *Torvosaurus tanneri* left maxilla (ML1100) in lateral view from Praia da Vermelha, base of the Lourinhã Formation, Portugal.

TETANURAE Gauthier, 1986

TORVOSAURIDAE Jensen, 1985

***TORVOSAURUS TANNERI* Galton and Jensen, 1979**

Distribution and horizon: *Torvosaurus tanneri* is known from the Morrison Formation of Colorado (Dry Mesa Quarry, Britt 1991; lower Upper Brushy Basin Member; also Garden Park and Lily Park), Utah (Cleveland-Lloyd Quarry, Dinosaur National Monument, and the Peterson Quarry), and Wyoming (Como Bluff) (Middle to Late Tithonian; Siegwarth et al., unpublished). The presence of this genus in Portugal is the only one report outside North America. *Torvosaurus* was reported previously by Mateus and Antunes (2000) based on a large tibia from Casal do Bicho (ML430) and now by cranial material from Praia da Vermelha (Fig. 1, Lourinhã Formation, Porto Novo Member, Kimmeridgian).

Description: A left maxilla (ML1100; figure 6) was collected by one of us (A.W.) at Praia da Vermelha on July 27, 2003. More recently, part of a proximal caudal vertebra and part of an unidentified limb bone from the same individual were also recovered.

The maxillary body is robust. The maxilla is almost complete, lacking about 8 cm of the ventroposterior rim. Eight tooth alveolae are present and the presence of two more can be estimated. Interdental plates are fused.

The Portuguese specimens can be ascribed to the genus *Torvosaurus* because the last tooth position is anterior to the orbit, the antorbital foramen is absent, there is no pneumatisation of the maxillary ascending process, the maxillary ascending process is positioned posteriorly, and the tibia is stout.

There are some differences between ML1100 (Portugal) and BYU725 (Colorado), the most striking being the maxillary tooth count. The Portuguese specimen had 10 teeth while BYU725 had 11 to 13 maxillary teeth. The alveoli are larger in the Portuguese specimen. Despite the differences, the Portuguese specimen can be ascribed to *Torvosaurus tanneri.*

The maxilla from Praia da Vermelha is 63 cm long, hence the skull length can be estimated as about 158 cm (*T. tanneri* BYU 725 has a 118 cm skull for a 47 cm long maxilla, Britt, 1991). This points to the largest known Jurassic theropod, followed by some specimens of *Allosaurus* (*Saurophaganax*) *maximus* and *Edmarka rex.* The skull size is similar to some of the largest *Tyrannosaurus rex*. The erupted tooth crown is 127 mm long.

A distal end of a large femur (ML 632, from Quinta do Gradil) tentatively attributed to *Torvosaurus* indicates an individual more than 11 meters long whose weight may be estimated at 1930 kg (Anderson et al., 1985), similar to the mass estimates for the Morrison *Torvosaurus*.

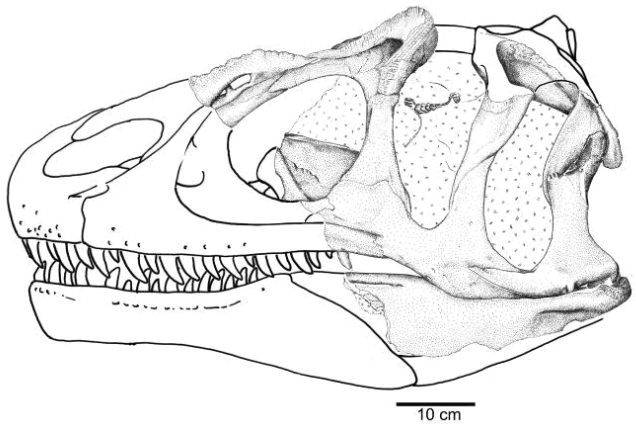

FIGURE 7. Skull of *Allosaurus europaeus* n. sp. (ML415) in left lateral view, from Vale Frades, Porto Novo Member of the Lourinhã Formation, Portugal. The illustration is based on the two sides of the skull.

TETANURAE Gauthier, 1986

AVETHEROPODA Paul, 1988

ALLOSAUROIDEA Currie and Zhao, 1993

ALLOSAURIDAE Marsh, 1878

***ALLOSAURUS* Marsh, 1877**

***ALLOSAURUS EUROPAEUS* n. sp.**

Synonym: *Allosaurus fragilis* in Peréz-Moreno et al., 1999; *Allosaurus* sp. in Antunes and Mateus, 2003.

Etymology: *europaeus* due to its geographic location.

Holotype: ML415, part of the skull (jugal, lacrimal, postorbital, frontal, palatine, quadratojugal, nasal, parietal, prefrontal, squamosal, articular, sclerotic bones, surangular, angular, pterygoid, basisphenoid, paraoccipital process and the most posterior tooth) and the 4th to the 6th cervical vertebrae and ribs (figure 7).

Horizon: Porto Novo Member of Lourinhã Formation; Kimmeridgian, Late Jurassic.

Type Locality: Praia de Vale Frades, 5 km North of Lourinhã, central west Portugal (Fig. 1).

Diagnosis: Like other species of *Allosaurus* except for: jugal participation in the antorbital fenestra; maxilla forked posteriorly; truncated ventroposterior process of the maxilla; nasal with two pneumatic foramina (the anterior foramen twice the size of the posterior); posteroventral projection of the jugal more than twice the posterodorsal projection; large anterior surangular foramen; no lacrimal-maxillary contact; squamosal contacts the quadratojugal by a sigmoidal suture; squamosal projects ventrally into laterotemporal fenestra; lacrimal horn narrow in lateral view; large ventral projection of postorbital; rugose dorsal rim of the nasal; the occipital condyles above the squamosal-quadratojugal contact; the anterior tip of quadratojugal is anterior to the laterotemporal fenestra; the lateral lamina of lacrimal is subtle; palatine contacts the pterygoid dorsoposteriorly; and ventral tip of the postorbital reaches the lower rim of the orbit.

Allosaurus Marsh 1877 is one of the dinosaurs best known to science, due to the large number of collected specimens, particularly at the Cleveland-Lloyd Quarry in the Morrison Formation. More than one hundred specimens are known and *Allosaurus* was the subject of large monographs by Gilmore (1920) and Madsen (1976). Several species were created since the erection of the genus in 1877. However, according to Holtz et al. (2004), only *A. fragilis* is considered valid while *A. tendagurensis*, based on a single tibia (HM67), may not even be an *Allosaurus*. A new but still undescribed *Allosaurus* species was the subject of work by Dan Chure (Chure, 2000; Holtz et al., 2004). Rauhut (2003) recognizes the following species: *A. fragilis* Marsh 1877*, A.* (*Saurophaganax*) *maximus* (Chure,

1995*),* and *Allosaurus* n. sp. (to be described by D. Chure).

Allosaurus has been reported in the Late Jurassic of USA (Wyoming, Utah, Colorado, New Mexico, South Dakota, Oklahoma, Montana), Portugal, and Tanzania. In Portugal, it was reported by Perez-Moreno et al. (1999) as *A. fragilis* and by Antunes and Mateus (2003) as *Allosaurus* sp. The specimen MHNUL/AND.001 (Peréz-Moreno et al., 1999) from the Late Jurassic of Andrés (near Pombal, Portugal) comprises the right quadrate, some vertebrae, chevrons, dorsal ribs, gastralia, part of pelvis, and hindlimbs. Although diagnostic features of *A. europaeus* cannot be observed in the Andrés specimen, it is provisionally considered as an *A. europaeus* due to its geographical context.

The generic diagnosis of *Allosaurus* was given by Madsen (1976). Chure (cited in Holtz et al., 2004: 103) revisited the Allosauridae and gave the following generic diagnosis: dorsal wall of maxillary antrum fenestrate; large, mediolaterally compressed, dorsally projecting lacrimal horn; spindle-shaped foramen on the lateral surface of the sacral centrum four; and obturator process with elongate lamina that extends past pubic peduncle. Rauhut (2003, p. 23) gives the following generic diagnosis: "distinct 'step' in the ventral margin of the jugal, leading to a significant ventral displacement of the posterior part in relation to the anterior part; neomorph element present in the lower jaw (antircular of Madsen, 1976); well-developed notch in the anteroventral margin of prearticular". The diagnosis provided by Chure (2000, p. 168) for *A. fragilis* is two large pneumatic recesses at the base of the lacrimal cornual process; ventral margin of jugal sharply deflected ventrally at midlength (ventral margin not straight); and metacarpal I shorter.

The Portuguese specimen is clearly an *Allosaurus* due to its general skull design and the autapomorphic large, mediolaterally compressed, dorsally projecting lacrimal horn. But it differs from *A. fragilis* by several differences included in the diagnosis at the beginning of this section. A detailed anatomical description is in progress.

PALEOGEOGRAPHIC IMPLICATIONS

Three theropod genera are shared between Portugal and the Morrison Formation of the USA (*Allosaurus, Torvosaurus, Ceratosaurus*), as well as all other non-avian dinosaur families. During the Late Jurassic, the existence of typical Late Jurassic American theropod genera such as *Ceratosaurus, Torvosaurus*, *Allosaurus* and *Aviatyrannis* (= *Stokesosaurus*) shows that there were Late Jurassic land connections with the Iberian block, although some Iberian isolation, prior to the Kimmeridgian, allowed theropod speciation that originated some new endemic species.

Paleogeography changed. During the Late Jurassic, transgression events led to some isolation of continental areas. This may have contributed to speciation, i.e. in regions as the Iberian block. Some endemic species may have appeared. Later dispersal would certainly profit from subsequent regression events.

These recent finds show that the dinosaur communities from the USA and Portugal contain the most similar Late Jurassic theropod faunas yet to be found on different continents.

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