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LATE JURASSIC DINOSAURS FROM THE MORRISON FORMATION (USA), THE LOURINHÃ AND ALCOBAÇA FORMATIONS (PORTUGAL), AND THE TENDAGURU BEDS (TANZANIA): A COMPARISON

OCTÁVIO MATEUS

Museu da Lourinhã, Rua João Luis de Moura, 2530-157 Lourinhã, Portugal. Phone: +351.261 413 995; Fax: +351.261 423 887; Email: omateus@museulourinha.org; and Centro de Estudos Geológicos, FCT, Universidade Nova de Lisboa, Lisbon, Portugal

Abstract—The Lourinhã and Alcobaça formations (in Portugal), Morrison Formation (in North America) and Tendaguru Beds (in Tanzania) are compared. These three Late Jurassic areas, dated as Kimmeridgian to Tithonian are similar paleoenvironmentally and faunally. Four dinosaur genera are shared between Portugal and the Morrison (*Allosaurus, Torvosaurus, Ceratosaurus* and *Apatosaurus*), as well as all non-avian dinosaur families. Episodic dispersal occurred until at least the Late Jurassic. The Portuguese dinosaurs did not developed dwarfism and are as large as Morrison and Tendaguru dinosaurs.

Resumo em português—São comparadas as Formações de Lourinhã e Alcobaça (em Portugal), Formação de Morrison (na América do Norte) e as Tendaguru Beds (na Tanzânia). Estas três áreas do Jurássico Superior (Kimmeridgiano/Titoniano) têm muitas semelhanças relativamente aos paleoambientes. Quatro géneros de dinossauros são comuns a Portugal e Morrison (*Allosaurus, Torvosaurus, Ceratosaurus* e *Apatosaurus*), assim como todas as famílias de dinossauros não-avianos. Episódios migratórios ocorreram pelo menos até ao Jurássico Superior. Os dinossauros de Portugal não desenvolveram nanismo e eram tão grandes como os dinossauros de Morrison e Tendaguru.

INTRODUCTION

The Morrison Formation in North America and the Tendaguru Beds in Tanzania have been widely compared due to their striking similarities regarding the fauna, ecosystem, paleoenvironments, age and sedimentology. However, other noteworthy but often ignored rocks contemporaneous with the Morrison Formation and Tendaguru Beds are the Lourinhã and Alcobaça formations of Portugal. Together they are Kimmeridgian to Tithonian in age and are remarkably similar in fossil content to their overseas counterparts. Sediments in the three areas indicate continental fluvial and lacustrine paleoenvironments, with strata basically comprising sandstone and mudstones. They appear to represent semiarid climates with the greatest abundance and diversity of herbaceous and arborescent plants concentrated near bodies of water. Marine transgressions were frequent in coastal areas, as well as alternating wet-dry conditions (Rees et al., 2004). The three areas existed at similar paleolatitudes (30-35 degrees), but with Tendaguru in the Southern Hemisphere. The Morrison Formation has been the subject of continuous work by numerous researchers, being probably the best known continental Jurassic formation and one of the richest areas for Late Jurassic vertebrates. Such knowledge allows interesting comprehensive paleoecological analysis (Dodson et al., 1980; Coe et al., 1987; Russell, 1989; Foster, 1996, 2000, 2001, 2003; and Turner and Peterson, 2004).

The Lourinhã Formation (Fig. 1) is mainly composed of continental and some shallow marine deposits. Alluvial fan and fluvio-deltaic environments during the Kimmeridgian and Tithonian were punctuated by periodic marine transgressions. Lithologically, the Lourinhã is formed by intercalations of sandstones and mudstones (channel to interdistributary areas, Fig. 2). The Lourinhã Formation is underlain by the Kimmeridgian limestones of Amaral Formation and bounded at the top by a discontinuity with the Cretaceous sandstones (Hill, 1988, 1989; Leinfelder and Wilson, 1989; Sousa, 1998; Alves et al., 2003; Cunha et al. 2004). The Lourinhã Formation as been considered in part equivalent to the Alcobaça Formation by several authors (see, for example, Manuppella, 1996, 1998; Manuppella et al., 1999), but the Alcobaça Formation is in part older and is more marine than the Lourinhã Formation.

The Tendaguru Beds, dated as Kimmeridgian-Tithonian, are dominated by calcareous sandstones and siltstones, with brackish and shallow marine influence demonstrated by the occurrence of marine dinoflagellates, corals, mytiloids and pterioid bivalves, ammonites, gastropods, and sharks (Aberhan et al. 2002; see Table 1).

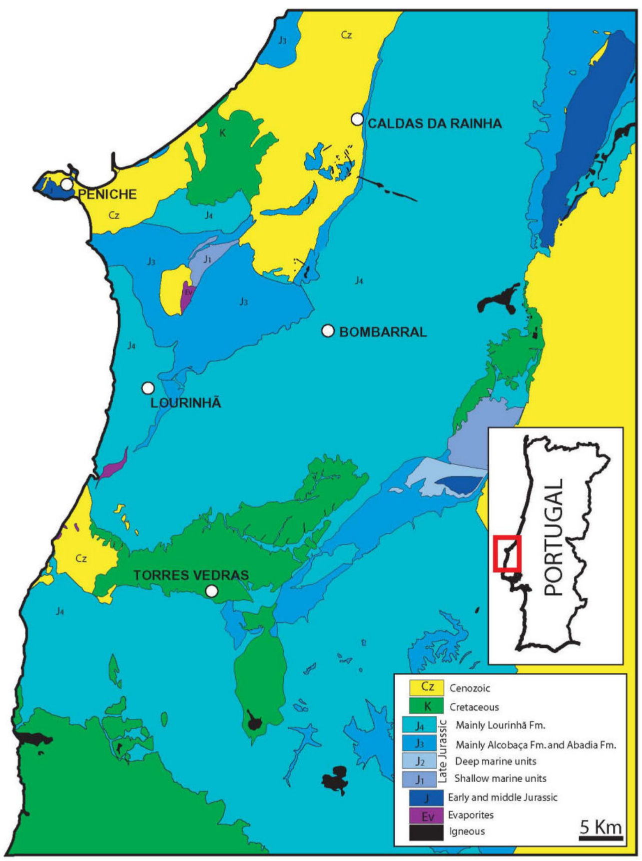

FIGURE 1. Regional geological map of central west Portugal based on Alves et al. (2003).

Institutional abbreviations: ML: Museu da Lourinhã (Portugal); BYU: Brigham Young University (USA).

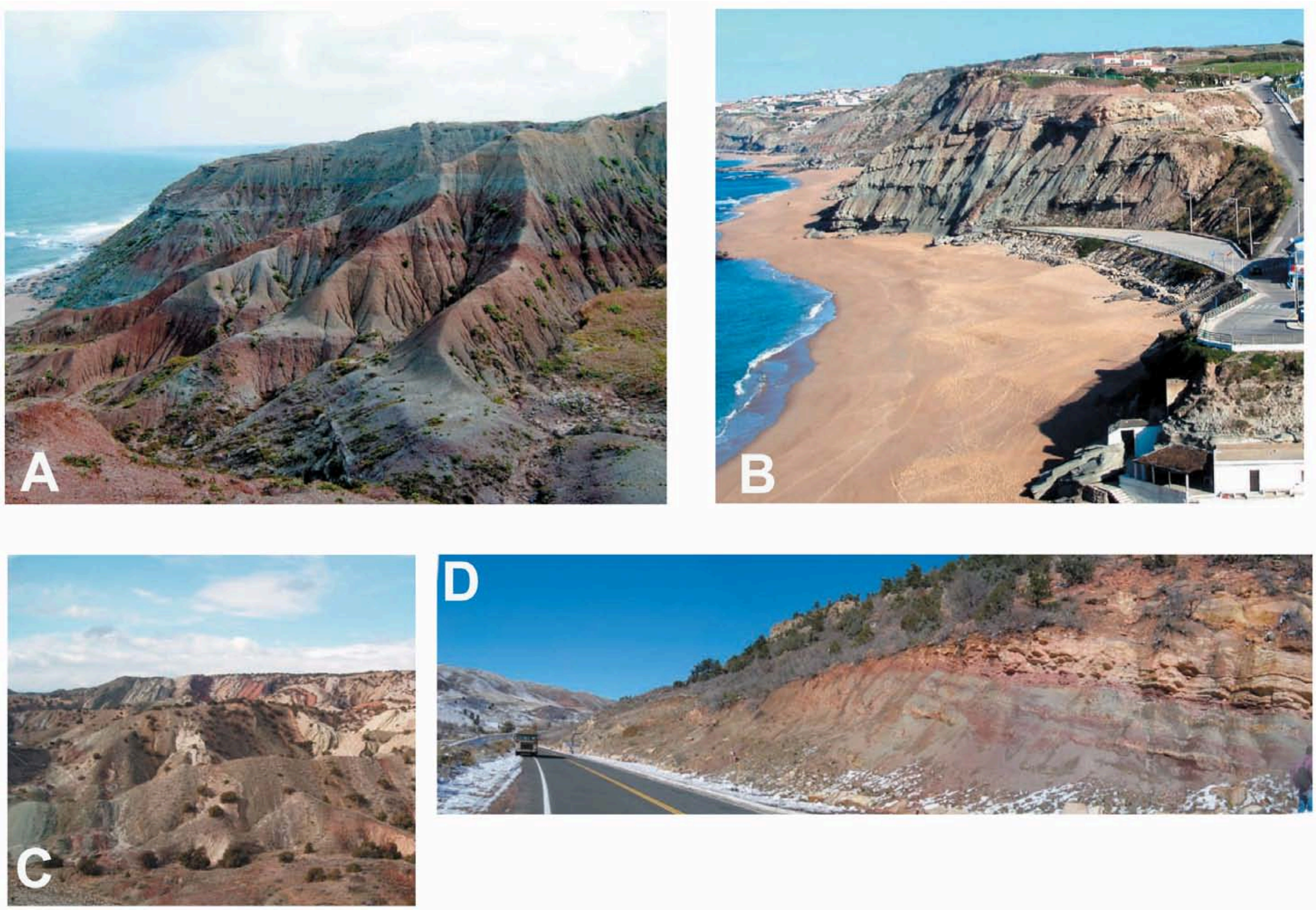

FIGURE 2. Late Jurassic sediments of the Lourinhã Fm. (Portugal) and Morrison Fm.(North America). **A**: Peralta, Lourinhã; **B**: Porto Dinheiro, Lourinhã; **C**- Dinosaur National Monument , Utah; **D**- Morrison stratotype locality, Colorado.

THE LATE JURASSIC OF PORTUGAL, TENDAGURU, AND THE MORRISON COMPARED

Age and Geography

The Lourinhã and Alcobaça formations, the Morrison Formation, and the Tendaguru Beds are approximately contemporaneous, Kimmeridgian to Tithonian in age (Manuppella, 1996; Kowallis et al., 1998; Unwin and Heinrich, 1999). Of these, the Morrison Formation is, without a doubt, the largest (1.5 million km^2, Carpenter, 1997; 1 million km^2 according to Dodson et al., 1980, p. 228) and the most studied area (Fig. 3). Therefore, the Morrison Formation would be expected to present a greater number of dinosaur genera and species than the other regions, and to better represent the Jurassic fauna. The Late Jurassic outcrops of the Lusitanian Basin in Portugal comprise approximately 400 to 550 km^2. However, while the Morrison Formation occupies about 2000 times as much area, it has only 2.3 times more species of dinosaurs than the Portuguese area.

Most of the paleogeographic maps of the Late Jurassic indicate a sea separation between Iberia (Portugal and Spain) and North America prior to the Kimmeridgian-Tithonian (Ziegler, 1988; Rees et al., 2000, 2004; Smith et al., 1994; Golonka, 2005; Mouterde et al., 1979; Ribeiro et al., 1979; Schudack and Schudack, 1989). The paleogeography of the European region (Ziegler, 1988; Schudack and Schudack, 1989) indicates that it was made up of several islands and that Iberia was separated from continental Europe as well as from North America by marine barriers, although the data on which the maps are based do not preclude transient and temporary terrestrial connections. The 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.

The maps presented by Schettino and Scotese (2002) show a full separation of Iberia and North America beginning only in the Lower Hauterivian (131.9 Ma). But the unambiguous marine Kimmeridgian sediments in Portugal refute such a model, in which the continuous linking between these two land masses is overestimated in the Late Jurassic.

The east Africa area, and the Tendaguru Beds, was stable until the Late Jurassic, when the separation of the India and Antarctica blocks from the African mainland marked a significant change. Although in Gondwana, the Tendaguru vertebrate assemblage shows similarities with the Late Jurassic of Europe and North America. On the other hand, the abelisauroids of Tendaguru are of Gondwanan affinity (Rauhut, 2005). While the fine dating of the Tendaguru Beds is still to be achieved, the Middle Dinosaur Member as been dated as Kimmeridgian by Schudack (1999) using charophytes.

Comparison of Ecosystems and Non-dinosaurian Faunas

The resemblance of faunal assemblages is striking among the Morrison, Tendaguru and Portugal. It has been the object of consideration by a number of authors. Comparisons were made between Tendaguru and Morrison by, for example, Schuchert (1918), Galton (1977), Russell et al. (1980), Jacobs (1997), Le Loeuff (1997), Maier (1997; 2003), and between Portugal and Morrison by, for example Lapparent and Zbyszewski (1957), Galton (1980), and Schudack et al. (1998). Schudack et al. (1998) compared the ostracodes and charophytes of the Morrison with Iberia, and suggested a close but complex biogeographic relationship between Europe and North America during the Late Jurassic. They also indicated that the Morrison Formation charophyte flora is more similar to that of central Europe than to Portugal.

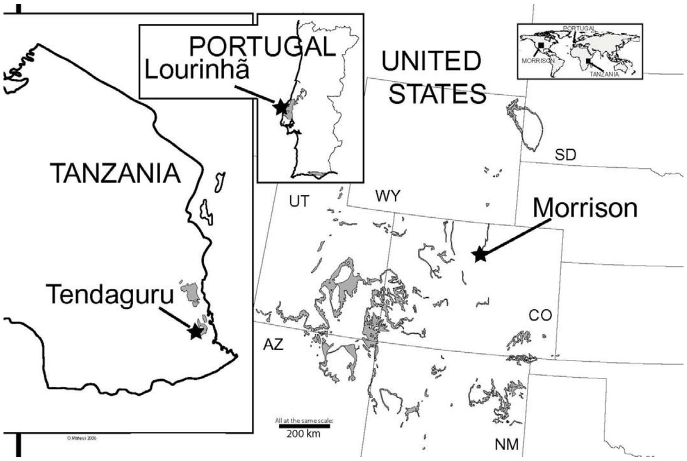

FIGURE 3. The Late Jurassic outcrops (shaded) of Portugal, the Tendaguru Beds, and the Morrison Formation, at the same scale.

Several plants have been reported equally in the Late Jurassic of Portugal and the Morrison: Coniferales (*Pagiophyllum*), Taxodiaceae (*Elatides*), Cheirolepidiaceae (*Cupressinocladus* and *Brachyphyllum*), Bennettitales (*Otozamites*), Pterophytes (*Coniopteris*), Hepatophytes (*Marchantites*) as well as the charophytes *Echinochara* and *Porochara* (Schudack et al 1998; Chure et al, 1998). Regarding the palynomorphs, the known spores in both Portugal and in the Morrison include *Deltoidospora, Obtusisporis, Concavissimisporites, Tribosporites, Ischyosporites, Lycopodiumsporites , Retitriletes, Cicatricosisporites, Aequitriradites, Gleicheniidites* and *Distaltriangulisporites* and the pollen *Corolina* (see Sousa, 1998, for the data of Portugal, and Chure et al., 1998 for the Morrison Formation).The only invertebrates reported in the two areas are the ostracods *Cetacella armata, Cetacella striata, Rhynocipris, Candona, Theriosynoecum wyomingense, Bisulcocypris pahasapensis, Timiriasevia* and *Darwinula* (Martin & Krebs, 2000; Schudack, 1998). Among the vertebrates, squamates (*Paramacellodus* and *Dorsetisaurus*), choristoderes (*Cteniogenys*), crocodiles (*Goniopholis*), dinosaurs (*Ceratosaurus, Torvosaurus, Allosaurus* and *Apatosaurus*) and mammals (*Dryolestes* and *Laolestes*) were identified in Portugal and in the Morrison Formation.

Evans (1996) and Evans and Chure (1998) confirm the common presence of the Squamata genera *Dorsetisaurus* and choristodere *Cteniogenys* in the Morrison Formation and at Guimarota, Portugal. Guimarota is assigned a Late Oxfordian to Kimmeridgian age, being the most probably Early Kimmeridgian (Schudack, 1993).

Compared to the Morrison, the Lourinhã and Alcobaça Formations in Portugal exhibit a more brackish-marine environment, which is demonstrated by the occasional occurrence of faunal assemblage with echinoderms, mytiloids, trigonioids, littorinimorphs, gastropods, sharks, plesiochelyid turtles, and teleosaurid crocodyliform. The existence of a sea shore contributes to a higher diversity of habitats and to the relatively high diversity of the fauna. Tendaguru also has some marine influence. The paleoenvironments include: 1) lagoon-like, shallow marine environment, 2) extended tidal flats and low-relief coastal plains, and 3) vegetated hinterland, in a subtropical to tropical paleoclimates with seasonal rainfall alternating with a pronounced dry season (Aberhan et al., 2002).

Dinosaur Assemblages

Portugal has a high diversity of dinosaurs (Fig. 4). Despite new discoveries that may change their status, some of the dinosaur species are, for the time being, known only as endemics for Portugal. In the current state of knowledge, of the 19 known genera from Portugal, 38% are only known in the Late Jurassic of Portugal. Four (21%) also occur in the Late Jurassic of North America (*Ceratosaurus dentisulcatus, Torvosaurus tanneri, Allosaurus* and *Apatosaurus*; see Mateus et al., 2006, this volume), three (17%) in the Late Jurassic of Europe (*Compsognathus, Archaeopteryx*, and *Dacentrurus*), and one (5%) in Africa (if *Allosaurus* is confirmed in the Tendaguru Beds).

The endemics are at the specific and generic levels. Apparently, isolation did not last long enough prior to extinction or extirpation to result in the evolution of different families. All families of non-avian dinosaurs known from Portugal are present in the Morrison Formation, but only 20% of the genera, and two of the species. The Late Jurassic of Portugal and the Morrison Formation of North America share the genera: *Allosaurus, Ceratosaurus, Torvosaurus* and *Apatosaurus*. Pérez-Moreno et al. (1999) and Antunes and Mateus (2005) report the presence of *Allosaurus* in the "Lourinhã Formation", and it is now regarded as *Allosaurus europeaus* (Mateus et al., 2006, this volume). Although distinct, other relatively close generic pairs are: *Lourinhanosaurus* and *Allosaurus* (or, possibly *Marshosaurus*), *Lusotitan* and *Brachiosaurus*, *Lourinhasaurus* and *Camarasaurus*, *Dinheirosaurus* and *Diplodocus*, and *Draconyx* and *Camptosaurus*. Tendaguru also shares with the Morrison Formation four (possibly six) dinosaur genera: *Allosaurus*, *Ceratosaurus*, *Brachiosaurus*, *Dryosaurus*, *Elaphrosaurus*(?), and *Barosaurus*(?).

When compared with the other areas, the Late Jurassic of Portugal presents fewer sauropods (21% of the dinosaurs) and relatively more ornithischians (32%) and theropods (47%). According to Carpenter (1998) and Carpenter et al. (1998), there are 21 sauropod species, 12 theropod species, and 13 ornithischian species in the Morrison Formation. In the Late Jurassic of Portugal, there are four genera of sauropods, nine genera of theropods, and six genera of ornithischians known (Table 2), while in the Tendaguru Beds there are five theropods, seven sauropods, and two ornithischians. If the true diversity in each of the three areas is approximately equal, we can expect to discover more sauropod species in Portugal and more ornithischians in Tendaguru in the coming years. In this interpretation of the dinosaur faunal assemblage of Portugal, it has been assumed that: (1) the numerical ratio between Theropoda, Sauropoda and Ornithischia in the oryctocenosis (fossil assemblage) is similar to the Jurassic biocenosis; and that (2) the Late Jurassic of North America and Portugal had, during the Kimmeridgian-Tithonian, the same numerical ratios of species of each of the major taxonomic groups.

Lillegraven et al. (1979), in speaking of Late Jurassic and earliest Cretaceous resemblances between England and North America, note that the distance between the regions is great enough to be consistent with a low level endemism, even if a continuous land connection was present between the two. Thus, isolation by distance was probably also a factor in Portugal favoring the formation of endemics, particularly in those groups with relatively fast evolutionary rates, as was apparently the case in some dinosaurs. Assuming that the source area was consistently North America with dispersal into Europe, specifically Portugal, regardless of the consistency of land bridges, the differentiation of dinosaurs in situ took place at the generic and specific levels.

COMPARISON WITH OTHER LATE JURASSIC LOCALITIES

During the Late Jurassic, Asia had developed a unique dinosaur fauna due to its isolation from North America and Europe, and there are no similarities between the Late Jurassic genera of Asia and the other two regions. The richest areas of the Upper Shaximiao Formation, Suining Formation, and Shishugou Formation in Mongolia and China provided *Mamenchisaurus, Yanchuanosaurus, Sinraptor, Omeisaurus, Tuojiangosaurus*, and other Asian genera.

The Late Jurassic of South America is poorly represented with respect to dinosaur somatofossils (i.e., fossilised body remain, unlike ichnofossils), with not a single Late Jurassic genus known from the whole continent (Weishampel et al., 2004). The role of South America in the distribution of Late Jurassic dinosaurs is unknown or probably underestimated due to a record bias.

In Africa, outside Tanzania, the most interesting might be the Kadzi Formation in Zimbabwe that provided *Brachiosaurus, Barosaurus,*

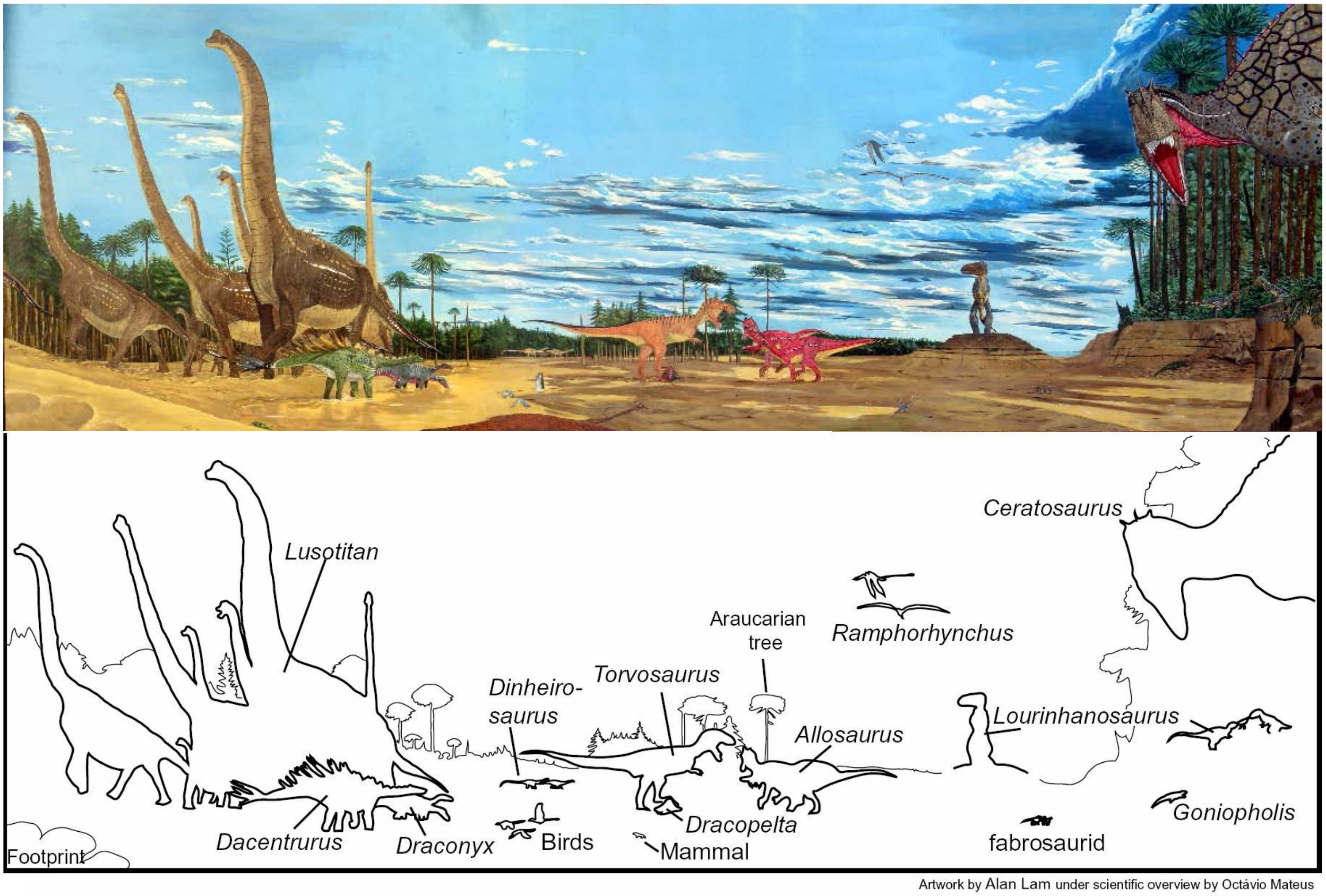

Fig. 4 Artistic reconstruction of Lourinhã fauna during the Late Jurassic (artwork by Allan Lam).

Dicraeosaurus, Janenchia and ?*Camarasaurus* (Raath and McIntosh, 1987; Weishampel et al., 2004). However, the Kadzi Formation is poorly dated and the specimens are quite incomplete. Madagascar does not have Late Jurassic dinosaurs, and the only Late Jurassic localities of Morocco and Niger are mainly track sites. In Ethiopia a cf. *Acrocanthosaurus* has been reported (Goodwin et al., 1999).

The European localities of England, France, Germany and Spain show faunal similitaries with the Portugal-Morrison-Tendaguru set by the presence of the shared genera *Dacentrurus, Archaeopteryx, Dryosaurus, ?Elaphrosaurus* and *Camptosaurus.*

Biochronology

In general, the classification of genera and species of Late Jurassic dinosaurs in Portugal is consistent with their chronological distribution worldwide. The dinosaurs *Ceratosaurus*, *Torvosaurus*, *Allosaurus*, cf. *Archaeopteryx*, *Compsognathus*, and *Dacentrurus* are represented in the Kimmeridgian and Tithonian of other regions, while *Dinheirosaurus*, *Lusotitan*, *Phyllodon*, *Trimucrodon* and *Draconyx* are represented by similar if distinct genera of similar age in other regions. The systematics of *Lourinhanosaurus* still are not clear, being bounced between Eustreptospondylidae (=Megalosauridae) and Allosauroidea (but not Allosauridae) in different phylogenetic analyses (Mateus, 1998; Mateus, 2005; Mateus et al., 2001; Allain, 2002, Holtz et al., 2004). If it is a member of Eustreptospondylidae, then it is one of the youngest. The majority of the Eustreptospondylidae are of Middle Jurassic age. *Eustreptospondylus* is found in the Callovian; *Megalosaurus bucklandi* and *Poekilopleuron* are found in the Bathonian. Assignment to Allosauroidea, if correct, would be consistent with the biochronology of the group, that is, Late Jurassic.

The genus *Hypsilophodon* is known from the Barremian and Aptian. The presence of this genus in the Jurassic of Portugal is its oldest known record but the specimen requires detailed study and review. This is possibly a different genus within the family Hypsilophodontidae.

The Amoreira Member and the Porto Novo Member are the richest in dinosaurs of the Lourinhã Formation. Both are considered Kimmeridgian-Tithonian. In Portugal, the horizon of *Ceratosaurus* and *Torvosaurus* is considered Kimmeridgian while *Allosaurus* is considered Tithonian. *Ceratosaurus* and *Torvosaurus* in the Morrison Formation are mostly Tithonian.

The genus *Ceratosaurus* has been unambiguously identified in the Morrison Formation in Colorado and Utah by three species: *C. nasicornis*, *C. dentisulcatus*, and *C. magnicornis* (Madsen and Welles, 2000). The two last species are from Brushy Member of the 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, respectively. *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 Brushy Basin Member is the most prolific producer of dinosaur sites in Morrison Formation.

Some studies (Kowallis et al., 1998; Turner and Peterson, 1999) date many of the dinosaur quarries of the Morrison to Kimmeridgian mainly based on biostratigraphic evidence (palynological, charophytes or ostracods) but ^{40}Ar/^{39}Ar isotopic dates ranges fall into the Tithonian; i.e., between 145.5 and 150.8 Ma (Gradstein and Ogg, 2004). Several ostracods (*Cetacella armata, Cetacella striata, Rhynocipris jurasica, Theriosynoecum wyomingense, Bisulcocypris pahasapensis,* and *Timiriasevia guimarotensis*), charophytes (*Echinochara pecki, Porochara fusca,*and *Porochara kimmeridgiensis*) and palynomorphs have been used to correlate the Morrison Formation and Lourinhã-Alcobaça formations and to date them as Kimmeridgian-Tithonian (Schudack et al., 1998). However, absolute dating studies with the use of the same techniques are required for both areas in order to provide rigorous correlations.

Dispersal and Colonization

Due to its geographical placement, the Iberian block may have played an important role as a dispersal passage between Gondwana and Laurasia (Fig. 5). Before the dismantling of Pangea (in the Early and Middle Jurassic), dinosaurs populated the entire supercontinent. The Iberian block was inhabited by Pangean dinosaurs but the presence of genera originating during the Late Jurassic (*Apatosaurus*, *Ceratosaurus*, *Allosaurus*, *Torvosaurus*), after the formation of the Iberian block, in Portugal and North America indicates that later dispersals occurred probably during low ocean level during regressions. This leads to the question, did the Iberian dinosaurs disperse into North America, or was it the other way around?

Little can be said with certainty about the direction of the dispersal between Late Jurassic regions. However, continents and large land masses have a higher numerical potential to populate smaller areas, such as the Iberian block. Although we cannot make rigorous conclusions, it is most probable that the main colonization routes of dinosaurs were towards Iberia and not the other way around. Due to its dimension, North America would have greater potential to host larger and healthier dinosaur communities and therefore greater potential to colonize other territories. The same argument is also valid with respect to Tendaguru dinosaurs dispersing toward Iberia, because the Gondwanan territory including Africa was vast. It is possible that dispersion between North America and Africa passed through the Iberian block. South America formed a single Gondwanan continent with Africa, suggesting that regional dispersals could have been quite complicated. There are, however, few similarities between the dinosaur faunas of Portugal and South America that can be demonstrated because of the lack of a Late Jurassic record in South America. Further uncertainties with respect to the biogeographic origins and dispersal routes of the Late Jurassic fauna are caused by the lack of informative Middle Jurassic faunas in North America and Africa.

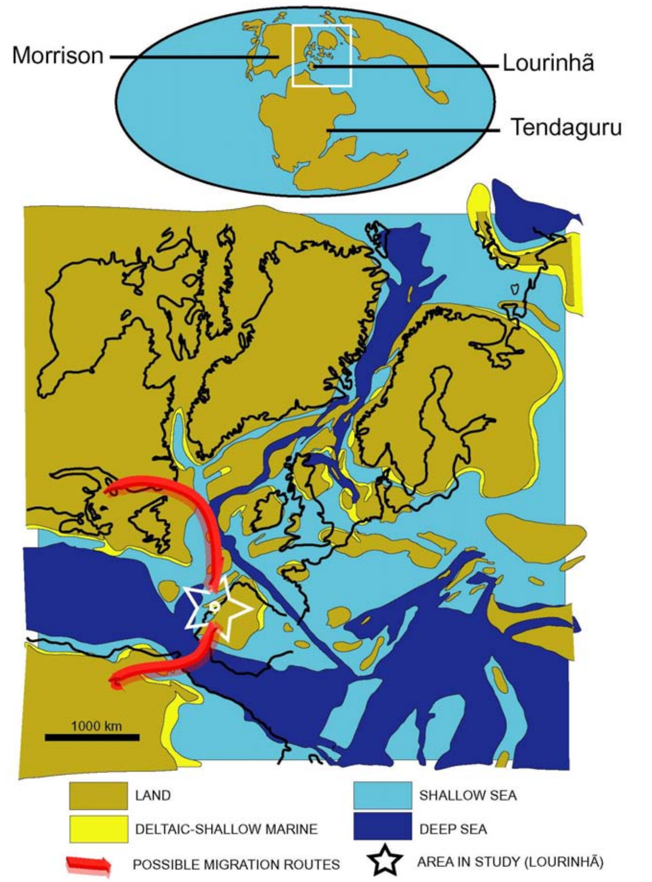

FIGURE 5. Paleogeographic maps of North Atlantic in the Late Jurassic (modified from Ziegler, 1998).

Isolation and Dwarfism

Isolation and reduced land areas such as encountered on islands tend to induce dwarfism in many large vertebrates. Body size generally is related to available land area; i.e., species restricted to smaller home ranges tend to be smaller, although ectothermic herbivores can increase in body size within smaller areas due to low food requirements (Burness et al., 2001). Island dwarfism has been suggested in dinosaurs, in particular among Late Jurassic dinosaurs from Europe, such as the case of *Europasaurus* sauropod from Germany (Mateus et al, 2004; Sander et al., 2004; Sander et al., in press) and the Late Cretaceous of Romania (Jianu and Weishampel, 1999). During the Late Jurassic, Europe was an archipelago and Iberia was an island. Taking into consideration the European scenario concerning dinosaurs at that time, dwarfism might be expected among Portuguese dinosaurs. However, that is not the case. There is no evidence whatsoever of dwarfism among the Late Jurassic dinosaurs of Portugal, although dwarfism has been suggested for Late Cretaceous Portuguese dinosaurs (Antunes and Sigogneau-Russell, 1991, 1992, 1995, 1996).

The Portuguese specimens of *Ceratosaurus*, *Torvosaurus*, *Apatosaurus* and *Allosaurus* are just as large as the North American specimens. The largest Late Jurassic theropod was *Torvosaurus*, and the Portuguese specimen, an 82 cm long tibia (ML430), is larger than specimen BYUVP 20016 (72.5 cm) of *Torvosaurus tanneri* (Britt, 1991; Mateus and Antunes, 2000). The largest known Jurassic ornithopod is *Camptosaurus* from the USA, and the largest known from Portugal is the camptosaurid *Draconyx loureiroi* (Mateus and Antunes, 2001). Neither of these reached the body size suggested by a new ornithopod footprint from Lourinhã, Portugal. The footprint (ML1000), is 70 cm long, and suggests a hip height of 2.8 m. The footprint is the only evidence for a Jurassic ornithopod of such large size (Mateus and Milàn, 2005; Mateus and Milàn, in prep.).

The brachiosaurid sauropod *Lusotitan* (Antunes and Mateus, 2003) was the largest European dinosaur for its time. The humerus is 205 cm and the femur is 200 cm (Lapparent and Zbyszewski, 1957), almost as large as *Brachiosaurus altithorax* (femur up to 203 cm) or *B. brancai* (femur MNB XV1, 214 cm long). With a 174 cm long femur, the Portuguese sauropod *Lourinhasaurus* was not much smaller. The evidence of one of the largest Jurassic sauropods is a huge *Supersaurus* ("*Ultrasaurus*") partial tibia - stored at BYU- collected by Jim Jensen, and named *Ultrasaurus*. Carpenter (this volume) points to a 2.7 meter tall *Amphicoelias fragillimus* dorsal vertebra from the Morrison at Garden Park.

In summary, the Late Jurassic dinosaurs from Portugal do not show evidence of dwarfism. Most dinosaurs are similar in size to comparable specimens from Dry Mesa Quarry (see Britt, 1991) or the Cleveland-Lloyd Quarry (Madsen, 1976), and larger than the dinosaurs from the Howe Ranch Quarry (Ayer, 2000). Despite being an island during the Late Jurassic, the Iberian block was probably larger than the critical minimal area and richer in resources than necessary to induce dwarfism.

CONCLUSIONS

In sum, the conclusions are:

- The Lourinhã and Alcobaça Formations (in Portugal) are comparable with the Morrison Formation (in North America), and Tendaguru Beds (in Tanzania), regarding paleoenvironments and sedimentology.
- The three areas are contemporaneous: Late Jurassic, Kimmeridgian to Tithonian.
- Nearly all families of dinosaurs from the Lourinhã and Alcobaça Formations are present in the Morrison Formation, and the Tendaguru Beds

contain 38% of the familial dinosaur diversity known from the Morrison Formation.

- Every family of dinosaurs known from Tendaguru also occurs in both the Morrison Formation and in Portugal.
- Portugal shares with the Morrison Formation four dinosaur genera (*Allosaurus, Ceratosaurus, Torvosaurus* and *Apatosaurus*).
- Taxa in common with Portugal and the Morrison include plants, palynomorphs, charophytes, ostracods, squamates, choristoderes, crocodiles, dinosaurs and mammals
- Tendaguru also shares with the Morrison Formation four (possibly six) dinosaur genera: *Allosaurus*, *Ceratosaurus*, *Brachiosaurus*, *Dryosaurus*, *Elaphrosaurus*(?), and *Barosaurus*(?).
- *Allosaurus* and *Ceratosaurus* are known from all three areas.
- Portugal shows proportionally more theropods and fewer sauropod taxa than either the Morrison or Tendaguru.
- There was dinosaur faunal exchange between North America, Iberia and Africa in the Late Jurassic.
- The Late Jurassic dinosaurs from Portugal do not show evidence of dwarfism and comparable taxa are of similar size to the Morrison specimens from Dry Mesa Quarry, Como Bluff or Cleveland-Lloyd Quarry, and larger than the ones from Howe Ranch Quarry.

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APPENDIX

TABLE 1. Distribution of major clades of flora and fauna among the continental Lourinhã and Alcobaça Formations (Late Jurassic of Portugal), and presence in Morrison Formation, North America, and Tendaguru Beds, Tanzania. The Late Jurassic of Portugal shows more brackish/marine influence. The table shows the occurrence of suprageneric clades of organisms. Most are by "family" ranking, but for simplicity of comparison not all groups are depicted by the same ranking, and they are arranged accordingly with the diversity of taxa. More detailed comparisons will be possible when the systematics of the species from each of the three areas are better understood.

Taxonomy	Portugal	Morrison Fm.	Tendaguru Beds
Fungi			
Ascomycetes	-	X	-
Basidiomycetes	-	X	-
Charophyta	X	X	X
Rhodophyta	-	X	-
Plantae			
Bryophyta	-	X	-
Sphenopsida			
Equisetales	X	X	X
Pteridophyta			
Dipteridaceae	-	X	-
Dicksoniaceae	-	X	-
Lycopodiaceae	X	X	
Osmundaceae	X	X	
Gleicheniaceae	X	X	
Schizaeacea	X	X	
Matoniaceae	X	X	
Cyatheaceae	X	X	
Gimnospermae			
Caytoniales	X	X	
Bennettitales	X	X	
Cheirolepidiaceae	X	X	X
Taxodiaceae	X	X	
Protopinaceae	X	X	
Czekanowskiaceae	-	X	-
Ginkgoatae	X	X	X
Podocarpaceae	-	X	-
Pinaceae	-	X	-
Araucariaceae	-	X	X
Gnetales	-	X	-
Animalia			
Bivalvia			
Pterioida	X	-	X
Mytiloida	X	-	X
Trigonioida	X	-	X
Unionoida	X	X	
Veneroida	X	-	X
Myoida	X	-	?
Gastropoda			
Archaeogastropoda			
Neritinidae	X	X	-
Mesogastropoda			
Cyclophoridae	-	X	-
Pleuroceridae	-	X	-
Bithyniidae	-	X	-
Valvatidae	-	X	-
Naticidae	X	-	-
Pulmonata			
Ellobiidae	X	X	
Lynmaeidae	-	X	-
Otinidae	-	X	-
Planorbidae	-	X	-
Littorinimorpha			
Vitrinellidae	X	-	
Cerithiodea	X	-	
Arthropoda			
Crustacea			
Cyzicidae	-	X	X
Ostracoda			
Cypridacea	X	X	X
Cytheracea	X	X	X
Darwinulacea	X	X	X
Dryelbidae	-	X	-
Malacostraca	-	X	
Echinodermata			
Cidaroida	X	-	-
Chondrichthyes			
Hybodontoidea	X	-	X
Orectolobiformes	X	-	
Lonchidiidae	-	-	X
Orthacodontidae	-	-	X
Batoidea	-	-	X
Osteichthyes			
Pycnodontidae	X	X	X
Semionotidae	X	X	X
Ionoscopidae	X	-	-
Macrosemiidae	X	-	-
Amiiformes	X	X	-
Teleostei	X	X	-
Coccolepididae	-	X	-
Halecostomi	-	X	-
Ceratodontidae	-	X	-
Amphibia			
Albanerpetontidae	X	-	-
Caudata	X	X	-
Anura	X	X	X
Discoglossidae	X	X	?
Chelonia			
Plesiochelyidae	X	-	-
Pleurosternidae	X	-	-
Platychelyidae	X	-	-
Glyptopsidae	-	X	-
Baenidae	-	X	-
Squamata			
Paramacellodidae	X	X	X
Scincoidea	X	-	-

Table 1. contd.

Taxonomy	Portugal	Morrison Fm.	Tendaguru Beds
Dorsetisauridae	X	X	-
Choristodera	X	X	-
Sphenodonta			
Sphenodontidae	X	X	X
Crocodyliformes			
Teleosauridae	X	-	
Atoposauridae	X	X	
Goniopholididae	X	X	X
Pterosauria			
Rhamphorhynchidae	X	X?	X
Pterodactyloidea	X	X	X
Dinosauria			
Coeluridae	-	X	-
Ceratosauridae	X	X	X
Eustreptospondylidae	X	X	X
Allosauridae	X	X	X
Tyrannosauridae	X	X	-
Dromaeosauridae	X	X	-
Troodontidae	X	X	-
Aves	X	-	-
Diplodocidae	X	X	X
Camarasauridae	X	X	-
Brachiosauridae	X	X	X
Heterodontosauridae	-	X	-
Hypsilophodontidae	X	X	-
Fabrosauridae	X	X	-
Dryosauridae	X	X	X
Iguanodontia	X	X	
Stegosauridae	X	X	X
Nodosauridae	X	X	-
Ankylosauridae	-	X	-
Mammaliaformes			
Docodontidae	X	X	
Mammalia			
Amphilestidae	-	X	-
Triconodontidae	-	X	X
Multituberculata			
Plagiaulacidae	-	X	-
Paulchoffatiidae	X	-	-
Albionbaataridae	X	-	-
Haramiyida	-	-	X
Symmetrodonta			
Amphiodontidae	-	X	-
Eupantotheria			
Paurodontidae	X	X	X
Dryolestidae	X	X	
?Peramuridae	-	-	X
Zatheria	X	-	

Source: Portugal (Antunes and Mateus, 2003; Martin and Krebs, 2000; Pais, 1998); Morrison (Chure et al., 1998; Chure et al., this volume); Tendaguru (Aberhan et al., 2002; Heinrich, 1998; Schudack and Schudack, 2002).

TABLE 2. The dinosaur genera and species from the Late Jurassic of Portugal, Morrison Formation and Tendaguru Beds:

Late Jurassic of Portugal (Antunes and Mateus, 1998)	Morrison Formation (Britt, 1991: 2; Carpenter, 1998; Carpenter et al., 1998; Foster, 2003 ; Weishampel et al., 2004)	Tendaguru Beds (Janensch, 1925, 1935/36, 1950; Maier, 1997; Bonaparte et al., 2000; Weishampel et al., 2004)
	THEROPODA	
	Allosaurus (*A. fragilis, A. maximus = Saurophaganax [?]*)	
	Ceratosaurus (*C. nasicornis , C. dentisulcatus, C. magnicornis*)	
Ceratosaurus cf. *dentisulcatus*	*Coelurus* (*C. agilis, C. fragilis*)	
Torvosaurus tanneri	*Edmarka rex [=Torvosaurus?]*	*?Allosaurus tendagurensis*
Lourinhanosaurus antunesi	*Elaphrosaurus sp.*	*Ceratosaurus* sp. (= *C. roechlingi*
Allosaurus europaeus	*Hypsirophus discurus*	
Cf. *Compsognathus*	*Koparion douglassi*	*Labrosaurus stechowi*
Aviatyrannis jurassica	*Marshosaurus bicentesimus*	*Elaphrosaurus bambergi*
Aff. *Paronychodon* sp.	*Ornitholestes hermanni*	
Cf. *Richardoestesia*	*Saurophaganax maximus [=A. maximus?]*	
Cf. *Archaeopteryx*	*Stokesosaurus clevelandi (=Aviatyrannis)*	
	Torvosaurus tanneri	
	Tanycolagreus topwilsoni	
	SAUROPODA	
Dinheirosaurus lourinhanensis	*Amphicoelias (*2 spp: *A. altus* and *A. fragillimus)*	*Barosaurus gracilis*
Lusotitan atalaiensis	*Apatosaurus* (4 spp: *A. ajax, A. excelsus, A. louisae, "A." minimus*)	*Brachiosaurus brancai*
Lourinhasaurus alenquerensis	*Barosaurus lentus*	*Dicraeosaurus (D. hansemanni D. sattleri)*
Apatosaurus sp.	*Brachiosaurus altithorax*	*Janenschia robusta*
	Camarasaurus (4 spp.: *C. grandis, C. lentus, C. lewisi, C. supremus*)	*Tendaguria tanzaniensis*
	Diplodocus (3 spp: *D. carnegii, D. hayi, D. longus*)	*Tornieria africanus*
	Dystrophaeus viamalae	
	Dystylosaurus edwini	
	Haplocanthosaurus (*H. delfsi, H. pricus*)	
	Seismosaurus hallorum (=Diplodocus)	
	?Eobrontosaurus yahnahpin	
	Supersaurus vivianae	
	ORNITHISCHIA	
Dracopelta zbyszewskii	*Camptosaurus (C.dispar, C. amplus, ?C. depressu)*	
Dacentrurus armatus	*Drinker nisti*	
Phyllodon henkeli	*Dryosaurus altus*	
? *Hypsilophodon* sp.	*Gargoyleosaurus parkpinorum*	
Trimucrodon cuneatus	*"Laosaurus" celer*	*Dryosaurus lettowvorbecki*
Draconyx loureiroi	*Mymoorepelta maysi*	*Kentrosaurus aethiopicus*
	Nanosaurus agilis	
	Othnielia rex	
	Stegosaurus (*S. armatus, S. longispinus, S. stenops*)	
	Hesperosaurus mjosi	