GAIA Nº 15, LISBOA/LISBON, DEZEMBRO/DECEMBER 1998, pp. 313-337 (ISSN: 0871-5424)

MEGALOSAURIPUS AND THE PROBLEMATIC CONCEPT OF MEGALOSAUR FOOTPRINTS

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ABSTRACT: The concept of "megalosaur tracks" and the ichnogenus "*Megalosauripus*" (LESSERTISSEUR, 1955), spelled with an "i", is reviewed and is shown to have originated in connection with large theropod tracks from the Late Jurassic of Portugal, which were then thought to have been made by *Megalosaurus* BUCKLAND, 1824, or a close relative. By contrast, the ichnogenus *Megalosauropus*, spelled with an "o", (COLBERT & MERRILEES, 1967), is based on material from the Cretaceous of Australia, and can be shown to have historical priority over Late Jurassic "*Megalosauropus*" ichnites described independently from Germany (KAEVER & LAPPARENT, 1974) and Uzbekistan (GABUNIA & KURBATOV, 1982). However, because the name *Megalosauripus* (with an "i"), is a *nomen nudum*, it is available for use (LOCKLEY, MEYER & SANTOS, 1996). We argue that the use of this ichnogenus name is appropriate for the purposes of maintaining historical stability, and because it also appears probable that the tracks were made by megalosaurid dinosaurs. We herein formally transfer the German and Uzbek specimens to *Megalosauripus barkhausensis* comb. nov. and *Megalosauripus usbekistanicus* comb. nov. respectively. We also suggest that the large German and Central Asian ichnospecies are similar or identical to certain tracks found in Upper Oxfordian-Lower Kimmeridgian deposits in Portugal, Utah, Arizona, New Mexico and Oklahoma (herein also assigned to *Megalosauripus* ichnosp.), and possibly in Spain where the name *Hispanosauripus hauboldi* has been applied to similar tracks. Other tracks from Portugal that have been named *Eutynichnium lusitanicum* (NOPSCA, 1923)- a name which we retain. Current evidence suggests a widely distributed but stratigraphically restricted "*Megalosauripus*" vertebrate track assemblage. Such widespread distribution may be related to aggradation during a period of high sea level. Evidence that *Megalosauripus* track assemblages represent discrete ichnostratigraphic entities is supported by the co-occurrence, at many localities of another distinctive ichnogenus, *Therangospodus* (LOCKLEY, MEYER & MORATALLA, 1998). The use of *Megalosauropus* (or ?*Eubrontes*) for Albian tracks from Texas and Croatia is also considered invalid, on morphological, and other grounds. We suggest that these also require an alternate ichnotaxonomic label, but propose that the trivial name *glenrosenis* be preserved, because the original material, although assigned to an inappropriate ichnogenus, was adequately described in relation to a holotype. Caution should be exercised in the use of well-known, catch-all, Lower Jurassic ichnogenera such *Grallator* and *Eubrontes*, especially when applied to large, stratigraphically discrete assemblages from other epochs and periods.

HISTORICAL BACKGROUND I: JURASSIC ORIGINS

Although *Megalosaurus* was the first dinosaur ever named (BUCKLAND, 1824), the concept of megalosaurs has remained vague (WEISHAMPEL, DODSON & OSMÓLSKA, 1990). The concept of megalosaur tracks is also uncertain, though it has recently been reviewed and discussed by LOCKLEY, MEYER & SANTOS (1996). The purpose of this paper, therefore, is to extend this work, address and resolve previous taxonomic confusion through a comprehensive historical review of the problem, and apply appropriate nomenclature that will stabilize the ichnotaxonomy.

The ichnological concept of megalosaur tracks appears to originate with observations made by LAPPARENT *et al*. (1951), LESSERTISSEUR (1955), and LAPPARENT & ZBYSZEWSKI (1957) in connection with large theropod tracks from the Late Jurassic of Portugal. Many of the tracks in question had first been described by GOMES (1916), and NOPSCA (1923) subsequently attached the name *Eutynichnium lusitanicum* to this material with minimal reference to the actual material (see HAUBOLD, 1971; CHURE & MCINTOSH, 1989). Consequently the ichnospecies *Eutynichnium lusitanicum* is in need of an updated description. When LAPPARENT *et al.* (1951) made the connection between these footprints and the genus *Megalosaurus* they went so far as to claim that the skeletal remains of *Megalosaurus insignis*, a small species originally named on the basis of teeth from France (WEISHAMPEL, DODSON & OSMÓLSKA, 1990) and *Megalosarus pombali* a larger species based on "powerful" dorsal and caudal vertebrae, corresponded with very high probability (avec une très grande probabilité) with small and large tracks found at Cabo Mondego in Portugal. This conclusion prompted HAUBOLD (1971) to refer to *Eutynichnium* (*Megalosaurus*) *pombali*, despite the fact that this is a hybrid ichnological-osteological name. The intent seems clear: the tracks are thought to be of megalosaurid origin. However we should note that the term megalosaurid in this context refers to a very generalized concept of large theropod dinosaurs (cf. Megalosauroidea NOPSCA, 1928) as noted by LOCKLEY, in press. The name *Eutynichnium* can be retained for certain specimens in the Portuguese assemblage, but the name *Megalosaurus* is clearly invalid for any tracks for a variety of reasons (LOCKLEY, in press).

Following the observations of his French colleagues (LAPPARENT *et al*., 1951), LESSERTISSEUR (1955) coined the name *Megalosauripus* (with an "i") in much the same way as he coined the name *Tyrannosauripus* (also with an "i"), to illustrate the principle of naming tracks (LOCKLEY & HUNT, 1994). Thus the name *Megalosauripus*, like *Tyrannosauripus*, was a *nomen nudum*, because no species name or type specimen was designated. The name was not adopted by his colleagues, who in subsequent reference to the Portuguese footprints, continued to use the name *Megalosaurus* (LAPPARENT & ZBYSZEWSKI, 1957: fig. 8; see Fig. 1 herein), even though this is even more inappropriate.

In reference to *Megalosauripus* however, despite its *nomen nudum* status, LESSERTISSEUR (1955: fig. 64) cited a purported megalosaur track, from the Lower Cretaceous (Wealden beds of Germany), illustrated by ABEL (1935), as an example, but no description was provided, and no specific name was assigned. This particular track, later designated as *Bueckeburgichnus* (KUHN, 1958) reveals a pronounced hallux (Fig. 2) impression and could, in this respect, be considered similar to track natural casts from the Late Jurassic of Portugal, named *Eutynichnium lusitanicum* (NOPSCA, 1923) and attributed to *Megalosaurus* by LAPPARENT *et al.* (1951). However, in addition to age differences, it has been demonstrated that the track is significantly different from most Portuguese specimens in morphological details such as digit divarication, shape and width and position of hallux (LOCKLEY, in press). Even though HAUBOLD (1971) assigned *Eutynichnium lusitanicum* to the Megalosauroidea (NOPSCA, 1928) *Eutynichnium lusitanicum* (NOPSCA, 1923) might be considered a *nomen dubium*, because no type material was designated, at the time. We conclude, in this study, however, that the specimen illustrated by LAPPARENT & ZBYSZEWSKI (1957: fig. 8) from the original sample reported by GOMES (1915-1916) can effectively be considered the holotype within the assemblage of topotypes preserved at the National Museum of Natural History, Lisbon (Fig. 3). The connection of the name *Megalosauripus*, with an "i" with the name *E. lusitanicum* is tenuous, but it is clear that the intention was to imply that the tracks had megalosaurid affinity, as the concept "megalosaurid" was then understood. This raises an interesting philosophical question for ichnotaxonomy. When a track is legitimately named on the basis of a osteological taxonomic classification that is later discarded, changed or amended, the ichnotaxon appears to have its taxonomic validity diminished. However, if the name is seen in its historical context, it may be regarded as appropriate. Such considerations are important in the context of any discussion of megalosaurids and their tracks since both the track maker and its spoor are very poorly defined.

Any argument that the ichnogenus *Megalosauripus* should be applied to the Cretaceous material from Germany was obviated by the work of KUHN (1958) who formally named the German track *Bueckeburgichnus maximus* and provided a brief description. In addition there is really no evidence of megalosaurid dinosaurs in the Cretaceous of

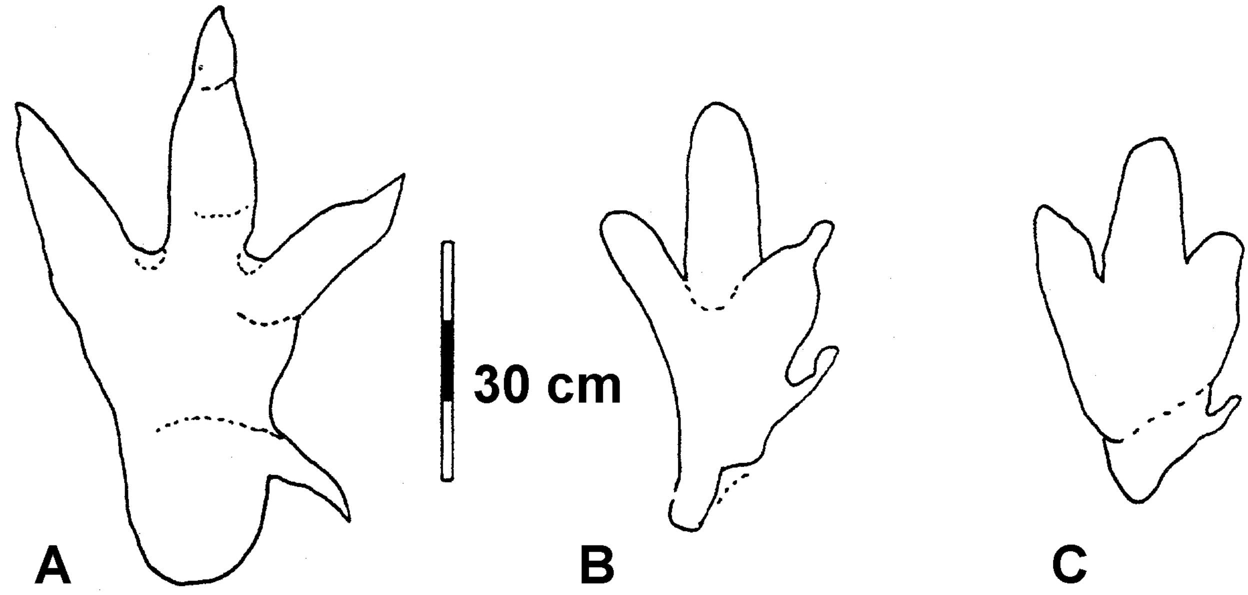

Fig. 1 - Line drawings of: **A** - "*Megalosauripus*" (right) after LESSERTISSEUR (1955); **B** - *Eutynichnium lusitanicum sensu* NOPSCA (1923) after LAPPARENT & ZBYSZEWSKI (1957), and HAUBOLD (1971); **C** - Specimen MNHN-MG-P261 of *Eutynichnium lusitanicum* (compare with Fig. 7).

Europe, or elsewhere. Detailed study of the type material of *Bueckeburgichnus* (LOCKLEY, in press) provides a detailed amended description which supports the conclusion that it is different from the Portuguese material (i.e., *Eutynichnium lusitanicum*). There is, therefore, a strong argument that there has never been any good morphological or historical reason to assign tracks from Cretaceous to the conceptual category of megalosaur (whether, *Megalosaurus*, megalosaurid *Megalosauripus* or *Megalosauropus*).

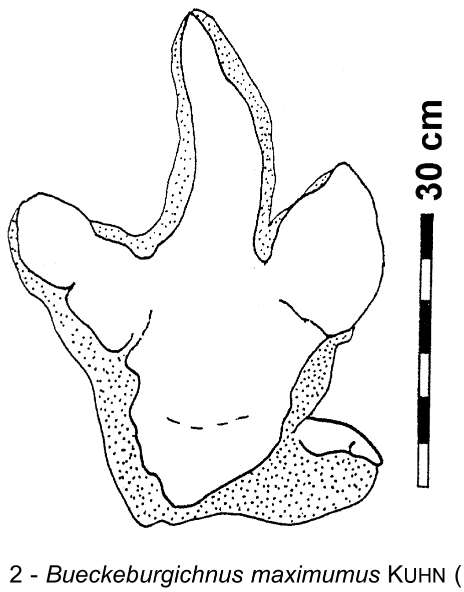

Fig. 2 - *Bueckeburgichnus maximumus* KUHN (1958), redrawn from type specimen (after LOCKLEY, in press).

Prior to our preliminary review of megalosaurid tracks (LOCKLEY, MEYER & SANTOS, 1996), in which we noted the availability of the ichnogenus label *Megalosuripus*, the most recent reference to the subject was by MENSINK & MERTMANN (1984) who assigned both *Gigantosauripus asturiensis* and *Hispanosauropus hauboldi*, from the Upper Jurassic of Asturias, to large and small "Megalosauroidea" respectively. *Gigantosauropus* is 1.35 m long, and in the opinion of THULBORN (1990) and ourselves (LOCKLEY, MEYER & SANTOS, 1994) this gigantic footprint must be of sauropod origin. Examination of *Hispanosauropus hauboldi* from Asturias as illustrated by GARCIA RAMOS & VALENZUELA (1977, 1979) and VALENZUELA, GARCIA RAMOS & SUAREZ DE CENTI (1986,1988) reveals several tracks comparable to the morphology of *Megalosauripus* from rocks of the same age in Portugal, (especially VALENZUELA, GARCIA RAMOS & SUAREZ DE CENTI, 1988: fig. 3, 5, 16. See Fig. 4, herein). Surprisingly, even in the latter papers, no reference was made to the studies of MENSINK & MERTMANN (1984), or their introduction of the name *H. hauboldi*. From this we can infer that this name has not been adopted in this region. It could be argued that the name *H. hauboldi*, might be adopted for material assigned to *Megalosauripus* herein, but such a move would be unwise without adequate study of the *Hispanosauropus* sample. Such a move would also set the undesirable precedent of giving priority to the name most recently assigned. Moreover, to the best of our understanding, although a holotype for *H. hauboldi* was

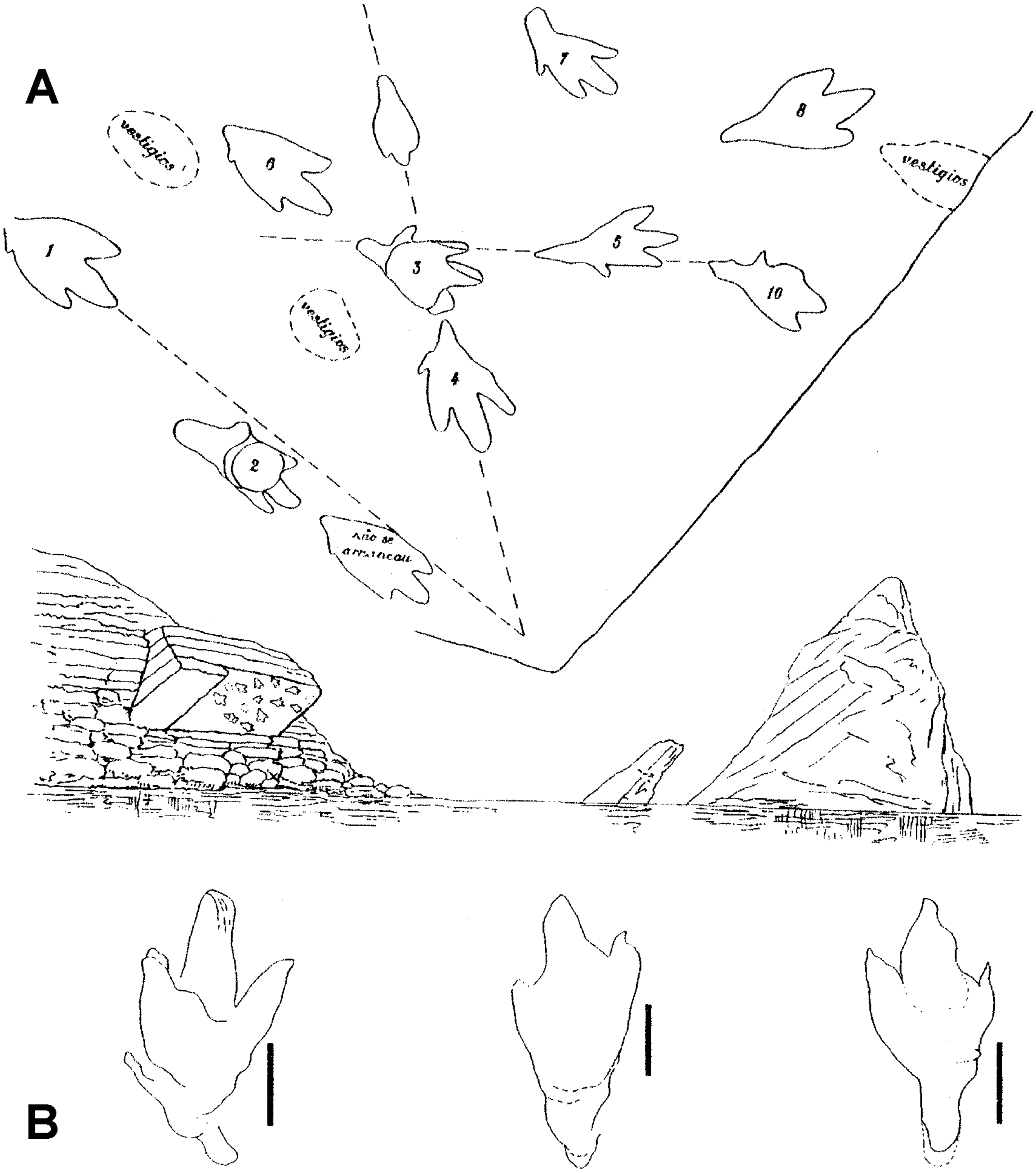

Fig. 3 - *Eutynichnium lusitanicum* specimens from the Late Jurassic of Portugal, includes material from original "type locality" at Cabo Mondego, showing outcrop and map (**A**) after GOMES (1915-1916), and (**B**) from left to right (MNHN-MG-P261, 264 and 263). Scale bar = 15 cm.

illustrated, it is a specimen at a field location, and neither an original type or a replica has been reposited in a museum. In this sense, if a type for *H. hauboldi* can not be located, it might be regarded as a *nomen dubium*. In addition, prior to this study, the connection between the Spanish material and that from the rest of the world, had not been recognized or even considered, so there has been no opportunity to make a thorough study.

HISTORICAL BACKGROUND II: CRETACEOUS APPLICATIONS

Since LESSERTISSEUR (1955) coined the name *Megalosauripus*, several papers have been published in which the name *Megalosauropus* (with an "o") has been independently introduced. These papers are as follows: COLBERT & MERRILEES (1967) described *M. broomensis* from the Lower Creta-

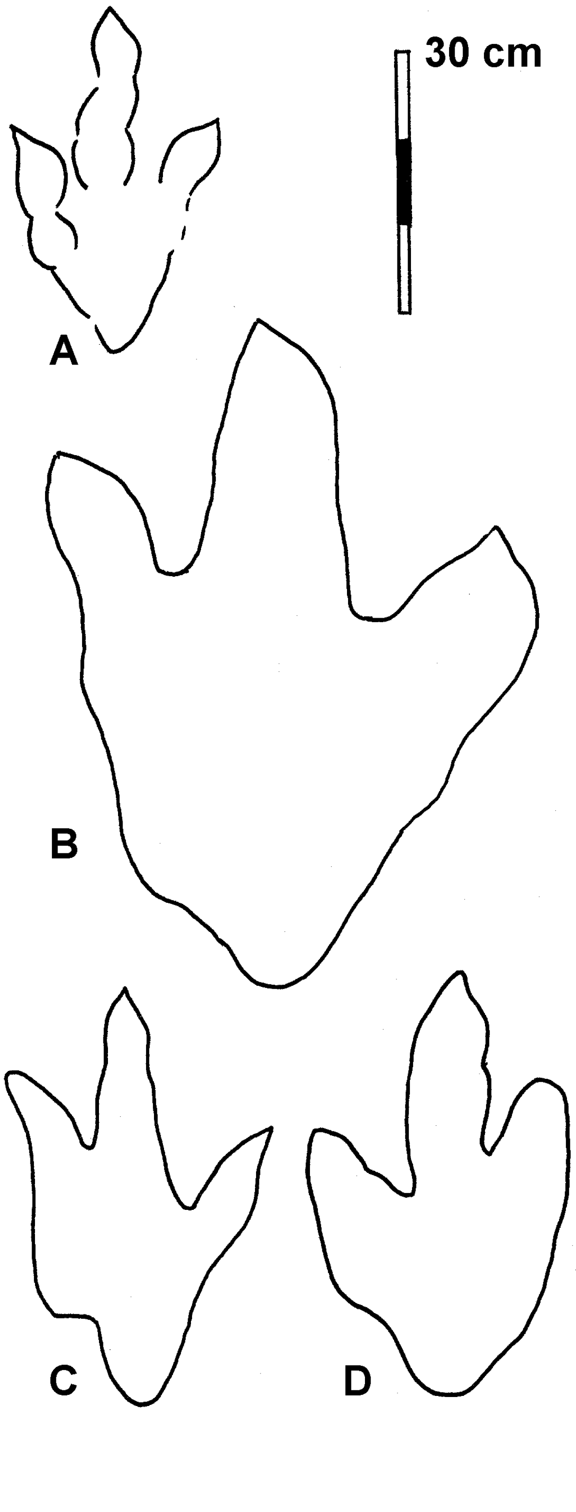

Fig. 4 - Line drawings of large elongate *Megalosauripus*-like tracks from the Upper Jurassic of Cabo Mondego (**A**) and Zambujal Quarry **B** with similar footprints (**C** and **D**) from Asturias, Spain, after VALENZUELA, GARCIA RAMOS & SUAREZ DE CENTI (1986, 1988). C and D may be compared with *Hispanosauropus* (MENSINK & MERTMANN, 1984).

ceous of Australia. HAUBOLD (1971) accepted the ichnogenus and suggested that *Eubrontes*? *titanopelobatidus* (SHULER, 1917) from the Glen Rose Formation of Texas could be assigned to *Megalosauropus* (?*Eubrontes*) *titanopelobatidus*; he also erected the new ichnospecies *M. brionensis* for Lower Cretaceous tracks from former Yugoslavia. The implication of Haubold's work is that *Megalosauropus* is temporally and geographically widespread in the Lower Cretaceous, but a close morphological match between these ichnites and the type material from Australia has not been demonstrated. On the contrary, they seem significantly different (see Fig. 5). KAEVER & LAPPARENT (1974) described *Megalosauropus teutonicus* from the Upper Jurassic of Germany, but made the mistake of referring to the ichnogenus as new, and not citing the original work of COLBERT & MERRILEES (1967). ANTUNES (1976) named *M. (?Eutynichnium) gomesi* for a lower Cretaceous theropod track from Portugal. GABUNYIA & KURBATOV (1982, 1988) described *M. uzbekistanicus* from the Upper Jurassic of Uzbekistan and also failed to cite previous work on *Megalosauropus* (see also MEYER & LOCKLEY, 1997 for further details). These studies might be taken to imply that the morphotype described by COLBERT & MERRILEES (1967) also occurs in the Upper Jurassic (Fig. 5), but this is not the case. Subsequent studies failed to make any comparisons with the Australian material, which, on the basis of the description of the type, can be shown to be morphologically distinct from all other cited examples. Such incomplete scholarship violates the "Ten paleoichnological commandments" of SARJEANT (1989: 261), especially number two, which states "no new names for footprints should be proposed until a thorough literature search has been undertaken." Although these common sense guidelines post-date the work in question, there is no justification for ignoring previous work.

Footprints referred to as "*Megalosaurus*" tracks have also been reported from the Late Jurassic of England (CALKIN, 1968) the Lower Cretaceous of England (WALKDEN & OPPÉ, 1969), the Upper Jurassic of Portugal (LAPPARENT *et al.*, 1951; LAPPARENT & ZBYSZEWSKI, 1957) and LEONARDI (1979) reported "megalosauroid" tracks from the Lower Cretaceous of Brazil. None of these names have any validity in terms of formal ichnotaxonomy. They do however indicate that in the 1950s through 1970s, there was a tendency to attribute a variety of Late Jurassic and Early Cretaceous theropod tracks to megalosaurid trackmakers, even though skeletal remains of megalosaurs had not been reported with any certainty from the Cretaceous.

Reports of footprints attributable to "*Megalosaurus*" from the Cretaceous of Spain (CASANOVAS CLA-

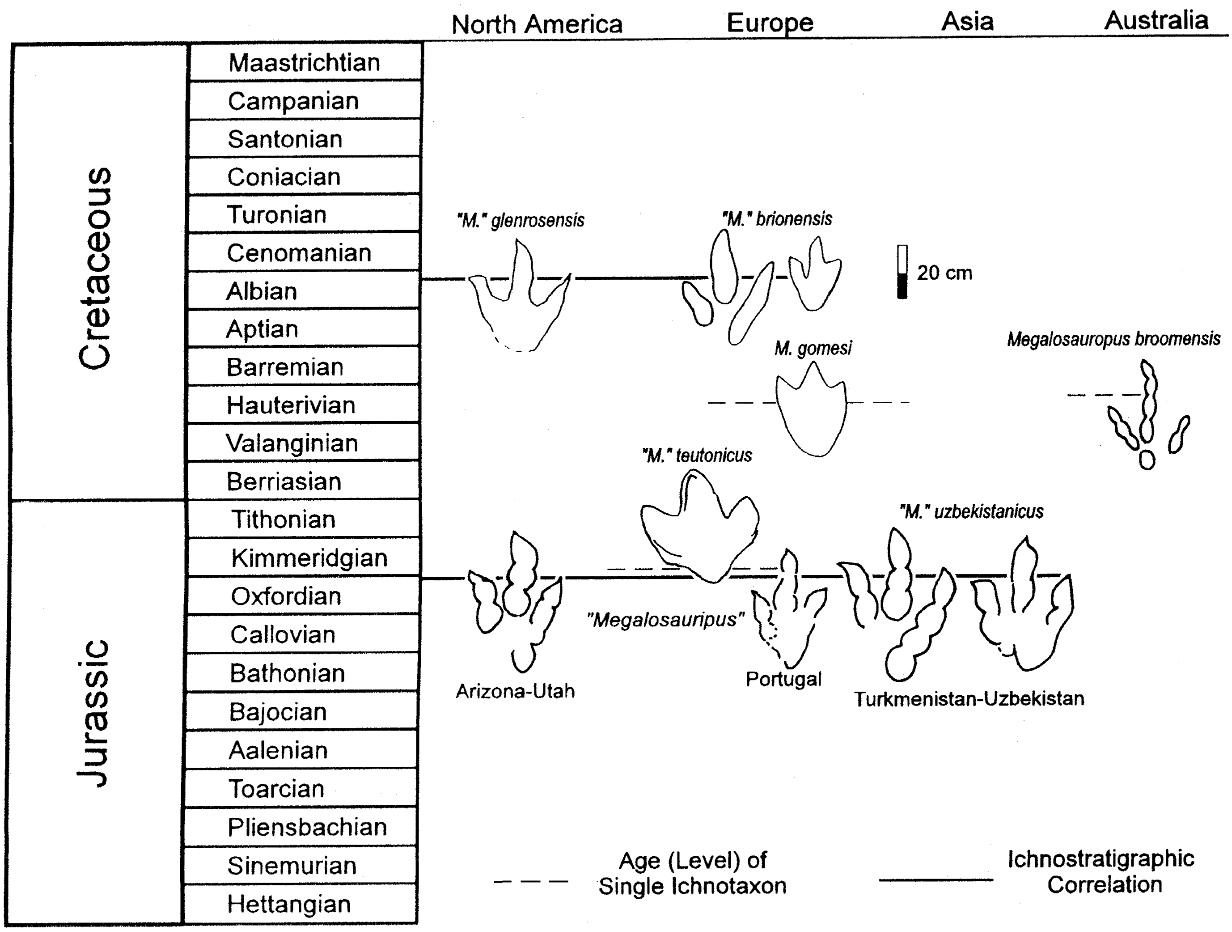

Fig. 5 - Line drawings of all purported *Megalosauropus* tracks in appropriate stratigraphic and geographic positions. After LOCKLEY, MEYER & SANTOS (1996).

DELLAS & SANTAFE LLOPIS, 1971,1974: 90) are interesting for the statement that they can be attributed to "un carnisaurio tipo *Megalosaurus* de gran talla. Se trataria, pues del Ichnogenero *Megalosauripus* segun la moderna nomeclatura Ichnologica." To the best of our knowledge this is the only case of the use of the ichnogenus name *Megalosauripus* (spelled with an '"i") and the first explicit statement that, at the time, this usage was fashionable in ichnology. Subsequent work on these same ichnofaunas, culminating in the studies of MORATALLA (1993) has not adopted this name, but instead has used *Bueckeburgichnus*, again stressing the Cretaceous affinity of this ichnite, and the reluctance to adopt the ichnogenus *Megalosauripus* for footprints of this age or from this region. Note however that the use of *Bueckeburgichnus*, which is a Berriassian ichnogenus, for significantly younger ichnites from Spain has recently been questioned (LOCKLEY, in press).

All "formally" named ichnospecies with the *Megalosauropus* label are illustrated for comparison in Figure 5, though this does not imply that the names are all valid. Several of the other purported "*Megalosaurus*" tracks were illustrated by FARLOW (1987). CHURE & MCINTOSH (1989: 173) correctly pointed out that "this ichnogenus was proposed independently" in the studies by COLBERT & MERRILEES (1967) and KAEVER & LAPPARENT (1974). They also cited the naming of *M. brionensis* and the transfer of *Eubrontes titanopelobatidus* to *Megalosauropus* by HAUBOLD (1971). CHURE & MCINTOSH and (1989) also cited the naming of *M. gomesi* by ANTUNES (1976) for tracks from the Lower Cretaceous of Portugal (Figure 5), but did not mention the naming of *M. uzbekistanicus* by GABUNIYA & KURBATOV (1982) based on material from Central Asia. We have examined this material first hand (LOCKLEY *et al.*, 1996; MEYER & LOCKLEY, 1997).

HAUBOLD (1971) was, in our opinion (LOCKLEY & MEYER, 1999), correct in inferring that the Yugoslavian (Croatian) tracks *M. brionensis* are theropodan in origin- as confirmed by DALLA VECCHIA, TARLAO & TUNIS (1993). As noted by LOCKLEY *et al.* (1994b), it is also possible that these tracks (Fig. 6) are similar to tracks from the Glen Rose Formation named

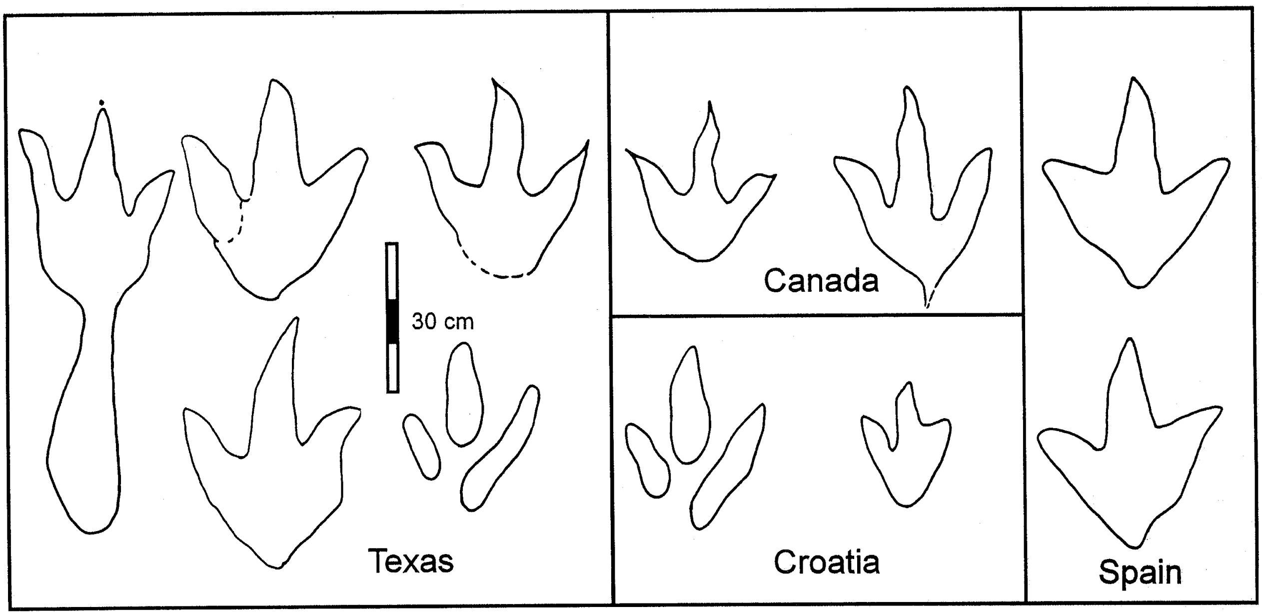

Fig. 6 - Comparison of tracks from the Albian of Texas (after FARLOW, 1987 & PITTMAN, 1989, Aptian of Canada (after STERNBERG, 1932), Croatia (MEYER & LOCKLEY, unpublished data), and ?Aptian of Spain (after MORATALLA, 1993).

Eubrontes (?) *titanopelobatidus* (SHULER, 1917). FARLOW (1987) noted however that the lack of a type specimen for *E.* (?) *titanopelabatidus* means that the name has no validity, but he did not comment on the transfer of the ichnospecies to *Megalosauropus* by HAUBOLD (1971). FARLOW (1987) also noted that the famous footprint mounted in the Glen Rose bandstand had been named *Eubrontes? glenrosensis* by SHULER (1935), but did not dismiss this name as invalid. He observed that there is little question that this is a carnosaur footprint. He thought however, that is was premature to give formal names to the Texas theropod tracks and referred to them simply as "grallatorids," but gave no reason for this assignment. This statement requires further examination and qualification. What FARLOW (1987) evidently meant was that it was premature for **him** to give **additional formal or formally amended** names to the Texas theropod tracks" (our emphasis), since the tracks already have various labels dating back to studies in 1917, 1935 and 1971.

We argue that Farlow is correct in drawing attention to the lack of a type specimen for *Eubrontes (?) titanopelobatidus* (SHULER, 1917), and that consequently it is a *nomen nudum*. The specific name *Eubrontes* ? *glenrosensis* (SHULER, 1935) can not be so easily dismissed because a valid type specimen, and meaningful description exists. The pertinent ichnotaxonomic issue becomes whether the track is assigned to an appropriate ichnogenus. In our opinion it is not. The type specimens of *Eubrontes*, from the Lower Jurassic of New England, has recently been restudied, OLSEN, SMITH & MCDONALD (1998) and it appears that this ichnogenus is marked by distinctive digital pads, not seen in the Glen Rose ichnites. In the entire scattered literature on Glen Rose tracks we can not find any good illustrations of the large theropod tracks that show more than a hint of distinct pad traces (cf. FARLOW & CHAPMAN, 1997: fig. 36). We therefore conclude that lack of well-defined, discrete pads is a primary morphological feature in this track assemblages, as suggested by SHULER (1935). This is not to say that a few tracks might not indicate faint pads in rare cases. As for *Grallator* and "grallatorids" these highly distinctive small, Lower Jurassic tracks (OLSEN, SMITH & MCDONALD,1998) with very well-defined pad impression are not in the least similar to the type of *Eubrontes* ? *glenrosensis*.

PITTMAN (1989, 1992) adopted a similar approach to FARLOW (1987) in naming the Texas tracks, when he referred to them as *Grallator* sensu lato. As indicated above, we strongly disagree with Farlow and Pittman that the Texas tracks resemble *Grallator*, which, based on the type material is a small narrow highly segmented Lower Jurassic track (HITCHCOCK, 1858). In fact the introduction of this term, without reference to the ichnotaxonomic literature for the region (SHULER, 1917, 1935; HAUBOLD, 1971) further confuses the issue. Since the transfer of the Texas material to *Megalosauropus* (*sensu* HAUBOLD, 1971) was ignored by FARLOW (1987) and PITTMAN (1989,1992) we must assume they regarded it as an inappropriate ichnogenus for the large Texas tracks, and that they considered them close to *Eubrontes* (?) as indicated by SHULER (1917, 1935). Despite a significant body of literature on the subject of theropod tracks from the Glen Rose, the footprints still lack an appropriate name, and have not been given further formal ichnotaxonomic treatment since SHULER (1935) and HAUBOLD (1971). As discussed below we think the ichnospecies "*glenroensis*" is valid, but can not be accommodated either in question *Eubrontes* or *Megalosauropus*. Retaining the name "*glenroensis*" is recommended and can be justified on the grounds of historical precedent and taxonomic stability.

The fashion of applying the name *Megalosauropus* to Cretaceous tracks continued when ANTUNES (1976) applied the name *Megalosauropus* (*Eutynichnium*) *gomesi* to Cretaceous footprints from Portugal. We have examined these footprints and conclude that they are not diagnostic beyond the descriptor "theropod tracks". They can not be placed in either the ichnogenus *Megalosauropus*, which should be restricted to the Australian material, or in *Eutynichnium*. MADEIRA & DIAS (1983) also attributed Portuguese Albian theropod tracks to *Megalosaurus*.

HISTORICAL BACKGROUND III: THE OVERVIEW

From a historical perspective, the concept of megalosaur tracks in general (LAPPARENT *et al*., 1951; LAPPARENT & ZBYSZEWSKI, 1957) and "*Megalosauropus*" *sensu* (KAEVER & LAPPARENT, 1974; GABUNIYA & KURBATOV, 1982) has been based to a significant extent on Late Jurassic tracks from Europe, as the age (Middle Jurassic) and origin (England) of the purported trackmaker *Megalosaurus*, and relatives would imply. A similar number of reports, however, indicate that comparable tracks occur in the Lower Cretaceous, sometimes near the Jurassic-Cretaceous boundary (LESSERTISSEUR, 1955; COLBERT & MERRILEES, 1967; CALKIN, 1968; WALKDEN & OPPÉ, 1969; CASANOVAS CLADELLAS & SANTAFE LLOPIS, 1971,1974; ANTUNES, 1976; LEONARDI, 1979). However, such identifications are not often supported by compelling evidence that the tracks were made by megalosaurids or that they have been compared ichnologically with the original material formally described in the ichnological literature.

Our primary reason for addressing this problem is the recognition of the chaotic state of affairs surrounding the ichnotaxonomy of *Megalosauropus*. We are also interested in the subject as the result of a study of a large sample of well-preserved "*Megalosauropus*" *uzbekistanicus* trackways from Uzbekistan and Turkmenistan (LOCKLEY *et al*., 1996; LOCKLEY, MEYER & SANTOS, 1996), and the realization that a very similar ichnites are also found in North America and Europe (Spain and Portugal). In order for clear scientific communication, it is essential that each of these different ichnotaxa be clearly defined and labeled for unambiguous comparison with other ichnotaxa.

In view of the historic uncertainty regarding the ichnogenus it is desirable to review the current state of affairs. We have reservations about the continued use of generalized categories (*Grallator* and *Eubrontes*), based on Early Jurassic ichnogenera, for Late Jurassic and Cretaceous tracks, unless evidence is presented that they are indistinguishable from these ichnogenera. In this regard lack of morphological studies that help determine degree of similarity between such samples is not adequate justification for the application of these Lower Jurassic names, and it would be better simply to use a label such as "theropod tracks," to avoid implied similarity or dissimilarity. The use of the term "grallatorid" is also not helpful since it is not precisely defined in the ichnological literature.

Similarly, justification must be given for transferring tracks from one generalized ichnogenus to another (cf. HAUBOLD, 1971). It is our view that perceived general similarities are in part due to a lack of comparative studies, perhaps resulting from reluctance to tackle a revision of the material studied by HITCHCOCK (1858) and LULL (1953). Such reluctance to study this material is perhaps understandable in the context of the perceived over-split ichnotaxonomy, and the specialized nature of vertebrate ichnology, but it does not help solve the problem. Moreover, casual use of these ichnogenera for a wide variety of post-Late Jurassic tracks creates exactly the same problem as has arisen with the catch-all ichnogenus *Megalosauropus*. It does not help to transfer tracks from one catchall ichnogenus to another- unless some clear, explicitly stated, ichnological precedent favors such a move.

CURRENT STATUS, USAGE AND ASSUMPTIONS.

Clearly the name *Megalosauropus broomenis* (COLBERT & MERRILEES, 1967) has historical priority over *M. teutonicus* (KAEVER & LAPPARENT, 1974) as implied by HAUBOLD (1971) who erected further *Megalosauropus* ichnospecies with full knowledge of the original definition of COLBERT & MERRILEES (1967). Thus, unless the material described by KAEVER & LAPPARENT (1974) can be shown to be congeneric or conspecific with the type *Megalosauropus* material from Australia, the ichnotaxonomy and descriptions must be amended. The same applies to the material described by GABUNIYA & KURBATOV (1982), and to material transferred or added to the ichnogenus by HAUBOLD (1971).

Megalosauropus is not a particularly well-known ichnogenus. Consequently, even after the observations made by HAUBOLD (1971) that ichnospecies assignable to this ichnogenus exist in Europe, and the introduction of additional, but invalid descriptions for the ichnogenus by KAEVER & LAPPARENT (1974) and by GABUNIYA & KURBATOV (1982), no one other than CHURE & MCINTOSH (1989) and more recently (LOCKLEY, MEYER & SANTOS, 1996) had noted the duplication of names or taken issue with the current unacceptable state of ichnotaxonomic confusion.

In a strict sense none of the existing descriptions are truly adequate, if judged by the standards of the "Ten paleoichnological commandments" proposed by SARJEANT (1989). In each case however ichnotaxonomic names refer to particular material that must be studied and understood before discarding or introducing ichnotaxonomic labels. We must accept the diagnosis and description of COLBERT & MERRILEES (1967), despite lack of detailed illustration of the holotype in their paper, because a type specimen is reposited in the Western Australia Museum, and an illustration is provided by HAUBOLD (1971: 78-79, fig. 48.1). A ruthless interpretation of this paper might argue that *Megalosauropus broomenis* (COLBERT & MERRILEES, 1967) is a *nomen dubium*, because the material, as presented is undiagnostic beyond the descriptor "theropod tracks." But such an approach should not be undertaken without careful scrutiny of the type material, nor does it remove the name. Besides, dinosaur tracks from this area are currently being reexamined (cf. THULBORN, HAMLEY & FOULKES, 1994), so it is hoped that this ichnotaxon will be among those amended and reevaluated.

Megalosauropus teutonicus (KAEVER & LAPPARENT, 1974) previously lacked an adequate description (see below), and so was somewhat problematic. HAUBOLD (1984: fig. 122) provided additional information and illustration of the material. Given that the description of the Australian *Megalosauropus* refers to a relatively elongate, slender-toed footprint with a purported, and rather extra-ordinary, phalangeal formula of 3, 4 and 5 for digits II, III and IV (Fig. 5, herein), it is easy to argue that the German "*Megalosauropus*", as a wide, broader-toed form, without distinct digit pad impressions is fundamentally different and can not be placed in the same ichnogenus with any confidence. Based on rexamination of the type material by one of us (M.G.L) it appears that *M. teutonicus* is a large theropod track even though it has been illustrated to look very much like a typical large Early Cretaceous ornithopod track (Fig. 5). Thus we suggest the expedient of removing the ichnospecies *M. teutonicus* from *Megalosauropus* and placing it in *Megalosauripus* (with an "i" - see systematic section).

It is also clear that *M. brionensis* and *M. titanopelobatidus* (HAUBOLD, 1971; Fig. 5-6 herein) are not closely related to the Australian material, and that the validity of the latter name is in dispute (FARLOW, 1987). Thus we propose to abandon the use of ichnogenus *Megalosauropus* in reference to Glen Rose theropod tracks previously assigned to *Eubrontes*? (SHULER, 1917, 1935). However the Texas ichnospecies should not revert by default to *Eubrontes* (?) *glenrosensis sensu* SHULER (1935), unless it can be demonstrated, that the track really has affinities with true *Eubrontes* (*sensu* HITCHCOCK, 1845; and subsequent revisions). In our opinion the Texas tracks are currently orphaned with respect to their ichnogenus name. It is therefore necessary to introduce an appropriate (new) ichnogenus. In view of the fact that these tracks are also being investigated (Farlow, pers. comm.), we make no formal assignment.

We regard Cretaceous *Megalosauropus* (*Eutynichnium*) *gomesi* (ANTUNES, 1976) as different from the Australian material, and again not an example of *Megalosauropus* sensu stricto. The material is poorly preserved, from a small sample and essentially a *nomen dubium*. By using a combination of two ichnogenus names ANTUNES (1976) followed HAUBOLD (1971) in implying a possible connection between *Eutynichnium* and *Megalosauropus*, (see NOPSCA, 1923; HAUBOLD, 1971, 1984 and CHURE & MCINTOSH, 1989 for further reference to this ichnotaxon). To date *Eutynichnium* has been used only to describe the Portuguese material, with a distinctive hallux (Fig. 1-3), and we suggest retaining this usage for historical consistency. Nopsca's original description however is invalid because it does not refer to a type specimen, and so must be considered a *nomen dubium*. However specimens do exist in the collections of the Portuguese Geological Survey (Instituto Geológico e Mineiro) and the National Natural History Museum (Museu Nacional de História Natural da Universidade de Lisboa) from which we select a holotype (strictly lectotype) for the purposes of providing the formal description given below.

Except for *Bueckeburgichnus* (KUHN, 1958; LOCKLEY, in press; Fig. 2 herein) virtually none of the other material discussed herein reveals a hallux trace. But the presence or absence of a hallux is dependent to a large degree on depth of tracks or mode of preservation. The original discoveries of Portuguese tracks (GOMES, 1915-1916; NOPSCA, 1923) pertained exclusively to material preserved as deep natural casts. Almost all subsequent discoveries of tracks from this stratigraphic level in Portugal, and elsewhere, have been shallower impressions revealing only the impression of the tridactyl portion of the footprint.

Regardless of the complexities of the preceding ichnotaxonomic history, all evidence suggests that *Megalosauropus* (with an "o") has repeatedly been used as a "catch-all" or "dustbin" ichnogenus, with little regard for the existing ichnological literature or the development of a careful, morphologically based ichnotaxonomy. Moreover it was "independently introduced" three times on three different continents! Hence the whole ichnotaxonomy surrounding purported megalosaurid tracks is in need of revision. We argue therefore that for taxonomic stability it is necessary to confine the use of *Megalosauropus* (with an "o"), which may prove to be a *nomen dubium*, or in need of amendment, to the first formally named sample, from Australia (COLBERT & MERRILEES, 1967). Thus the Jurassic material, which is the primary focus of this study is in need of taxonomic redefinition. Again in the interests of ichnotaxonomic stability we return to the original concept of "*Megalosauripus*" with an "i", redefine this "available" ichnogenus, on the basis of abundant and often well-preserved tracks that are widely distributed in Late Jurassic rocks.

SYSTEMATIC DESCRIPTIONS

PRELIMINARY DISCUSSION

The name *Megalosauripus* (with an "i") is not preoccupied, and so may be applied to another appropriate (i.e., megalosaurid or theropod) ichnite without violation of ichnotaxonomic rules. [Although the introduction of similar sounding names is not encouraged by the ICZN for species names, there is no prohibition for genus names. Moreover the ICZN encourages taxonomic stability. Furthermore, in this case, the name *Megalosauripus* already exists and was introduced into the literature prior to the name *Megalosauropus* with an "o". Thus we are not introducing any new names]. Evidence also suggests that large theropod tracks are abundant in the Late Jurassic and that various authors have attributed the trackmakers to "megalosaurs."

Since the ichnospecies *Eutynichnium lusitanicum* can be connected with certain tracks from Portugal we propose, for historical continuity, to retain the name, only for the sample in question (GOMES, 1915-16), which we redescribe. We also propose to adopt the *nomen nudum* "*Megalosauripus*" (with an "i") to label certain tracks that were incorrectly labeled *Megalosauropus*. These are re-described and amended herein, thus providing a formal diagnosis of *Megalosauripus* based on several large samples of tracks from the Upper Jurassic of several localities in Asia, Europe and the western United States. In this process we transfer *Megalosauropus uzbekistanicus* and *Megalosauropus teutonicus* to the ichnogenus *Megalosauripus*. We considered the option of the new combination: *Megalosauripus lusitanicum* (cf. LOCKLEY, MEYER & SANTOS, 1996: fig. 2) which would not be without ichnological precedent, since there has been a tradition of transferring ichnospecies into megalosaurid categories (cf. HAUBOLD, 1971). However we do not consider this is a well-conceived taxonomic procedure in this case.

After transferring *Megalosauripus teutonicus* and *Megalosauripus uzbekistanicus* from the preoccupied ichnogenus *Megalosauropus* (*sensu* KAEVER & LAPPARENT, 1974, and GABUNIYA & KURBATOV, 1982, respectively), it may be necessary to consider the relationship of these ichnotaxa to *Hispanosauropus hauboldi* (MENSINK & MERTMANN, 1984), and to other coeval theropod tracks from Europe and north America which we label as *Megalosauripus* sp.

All samples are based on abundant and/or diagnostic material that has been described to some degree in the ichnological literature, and includes adequate supplies of well preserved material (BAIRD, 1957; SARJEANT, 1989; TABLE I-III herein). In view of the theropodan affinity of these trackmakers, the history of reference of these tracks to megalosaurs, megalosaurids or to *Megalosauropus*, and the close age of the tracks to strata yielding type *Megalosaurus* material (Mid-late Jurassic: Bathonian-?Oxfordian, according to WEISHAMPEL, DODSON & OSMÓLSKA, 1990), retention of the name *Megalosauripus* (with an "i") for some of this widely distributed material is considered appropriate. In this regard recent, unpublished studies of Bajocian-Bathonian tracks in Portugal and England reveal large (up to 70 cm long tracks) that appear to fit the description of most examples of *Megalosauripus* given herein (LOCKLEY, MEYER & SANTOS, 1996; LOCKLEY & MEYER, 1999).

AMENDED ICHNOTAXA

Eutynichnium lusitanicum Amended

Fig. 3, 7

Referred material:

GOMES, 1916: pl. I-II.
NOPSCA, 1923.
LESSERTISSEUR, 1955.
LAPPARENT & ZBYSEWSKI, 1957: fig. 7, 8.
HAUBOLD (1971): fig. 48.7.
LOCKLEY & MEYER, 1999: fig. 7.1, 7.2 right, 7.3 right.

Type ichnospecies: MNHN-MG-P261 (Fig. 3, 7 and TABLE III) with topotypes MNHN-MG-P262-264 and an unnumbered specimen from Cabo Mondego Portugal.

TABLE I
Megalosauripus track measurements from sites in North America.

TRACKWAY NUMBER	LENGTH	WIDTH	DEPTH	STEP	STRIDE	T. W.
BULL 1	45.00	39.00			205.00	
BULL2	45.00	39.00				
BULL4	42.00	34.00		115.00	217.00	
BULL5	44.00	32.00		130.00		
BULL6	42.00	33.00				
MMA-1	48.00	36.00	3.00	120.00	235.00	58.00
MMA-2	53.00	38.00	3.00	130.00	263.00	73.00
MMA-6	43.00	37.00		120.00	225.00	70.00
MMB-1	51.00	39.00	3.50	148.00	289.00	70.00
MMB-4	51.00	46.00	5.00	132.00	266.00	48.00
MMC-1	44.00	30.00	7.50	135.00	242.00	79.00
MMC-3	44.00	35.00	2.50	133.00	270.00	59.00
MMC-5	46.00	38.00	3.00	130.00	240.00	77.00
MMC-6	45.00	39.00	8.00	129.00	244.00	84.00
MME-6	46.00	36.00	7.00	123.00	245.00	55.00
MMG-11	40.00	33.00	3.00	110.00	229.00	47.00
MMG-6	50.00	30.00	4.00	125.00	238.00	69.00
MMG-7	43.00	30.00	3.00	107.00	245.00	63.00
MMH-3	40.00	34.00	3.00	115.00	214.00	59.00
MMI-1	48.00	37.00	6.00	129.00	255.00	68.00
MML-1	47.00	36.00	5.00	122.00	231.00	66.00
MML-2	45.00	34.00	4.00	112.00	207.00	92.00
MML-3	43.00	34.00	2.00	130.00	255.00	71.00
MML-4	45.00	29.00	2.00	121.00	240.00	
MMO-1	40.00	30.00	3.00	130.00	243.00	60.00
MMQ-1	48.00	31.00	4.00	151.00	297.00	35.00
MMQ-2	44.00	29.00	2.00	148.00	290.00	62.00
MMQ-3	47.00	35.00	2.00			
MMR-1	41.00	32.00	2.00	125.00	246.00	46.00
MMR-2	42.00	32.00	2.00	125.00	249.00	35.00
MMW-1	45.00	37.00	7.00	118.00	221.00	50.00
MMW-2	49.00	40.00	8.00	115.00	219.00	71.00
MMX-1	45.00	32.00	0.50	130.00	258.00	47.00
MMX-2	48.00	37.00	3.50	131.00	250.00	56.00
WEST	48.00	32.00		125.00		

T.W. = trackway width. BULL = Bull Canyon Site; MMA-MMX prefixes = Moab Megatracksite, Utah. WEST = Westwater site.

Derivation of name: Meaning originally reported from Lusitania (the name of the Roman Province corresponding to modern Portugal).

Type horizon and locality: (For holotype and topotypes) Cabo Mondego (GOMES, 1915-1916); LAPPARENT *et al*. (1951), LAPPARENT & Zbyszewski (1957): Stratigraphic position: Cabaços Formation (Upper Oxfordian).

Description: Medium-sized tetradactyl theropod footprint with three large functional digits II-IV and small slender, antero-medially directed hallux (digit I). Size range: length excluding hallux 37-40 cm (with hallux 46-58 cm); width 26-27 cm. Digits II-IV relatively wide and non tapering, without clearly defined pad impressions. Step short (less than 100 cm) and trackway narrow (Fig. 3).

Discussion: Tracks from Cabo Mondego in the Gomes collection, preserved in the Portuguese National Museum of Natural History, constitute a historically important sample, since they are among the first Jurassic tracks ever reported from Europe, and have been known since the 1880s (GOMES, 1915-1916). All are natural casts preserved in a relatively coarse sandy matrix, indicating that the original tracks were deep before they were filled in with sand. The depth of the tracks, on the order of 10-15 cm, presumably accounts for the preservation of hallux traces. The relatively short step may also be attrib-

Fig. 7 - *Eutynichnium lusitanicum* (MNHN-MG-P261). See TABLE III for measurements.

uted to progression of the trackmaker over a soft substrate.

Other tracks from Cabo Mondego, including a sample in the collections of the Portuguese Geological Survey, are preserved as impressions, and appear to be somewhat different from *Eutynichnium lusitanicum*, both in size and morphology. However it is not clear whether these differences are related to preservation or to morphology of the trackmakers. We know however that similar track impressions are still found in situ at Cabo Mondego (LOCKLEY & MEYER, 1999: fig. 7.3 left). These tracks are about 60 cm long, and 50 cm wide with a step of 1.50 m. They appear to have wider digit divarication angles and more strongly tapering digits than *Eutynichnium lusitanicum*. They are more similar in size to tracks from other sites in Portugal which we label *Megalosauripus* sp.

Megalosauripus ichnogen. nov.

Fig. 4-5, 8-9

Ichnological discussion: The ichnogenus *Megalosauripus* (LESSERTISSEUR, 1955) is not occupied and so is adopted to describe certain ichnites in the large compound sample of track material found in Europe, North America and Asia. The type ichnospecies is designated as *M. uzbekistanicus* and is recognized in Central Asia (Uzbekistan-Turkmenistan-Tadjikistan). Similar ichnites are recognized in Germany, Portugal, Spain, Utah, Arizona, New Mexico and Oklahoma where they have variously been referred to *Megalosauripus teutonicus* or simply to "*Megalosauripus*" sp. *Hispanosauropus* may be hard to distinguish from *Megalosauripus* as re-defined herein.

Megalosauripus Amended

Diagnosis: Medium to large, elongate tridactyl tracks with phalangeal pad formula of 2, 3 and 4 corresponding to digits II, III and IV. Elongate heel, relative to length of digit III impression. Trackway very variable ranging narrow to moderately wide, with pace angulation values as low as 120º.

Derivation of name: Meaning large saurian footprints and deriving historically from an archaic and generalized concept of megalosaurid dinosaurs (cf. Megalosauroidea, NOPSCA, 1928, cited in HAUBOLD, 1971). The name may coincidentally, but by no means certainly, imply a relationship to dinosaurs similar to *Megalosaurus* and its relatives.

Ichnogenotype:

Megalosauripus uzbekistanicus comb. nov. Amended

Fig. 5, 8; TABLE II

Note that the species "*Megalosauropus*" *uzbekistanicus* GABUNIYA & KURBATOV (1982), spelled with an "o" is transferred to the ichngenus *Megalosauripus* (spelled with an "i").

Type material: Specimen 8/849. Tashkent Geological Museum. Belonging to a trackway with average footprint length of 53 cm and width of 36 cm, and a variable step (alternating long and short steps: 120-160-130-150-130-155-130 cm; LOCKLEY *et al.*, 1996)

Type locality and Horizon: Upper Oxfordian-Lower Kimmeridgian limestones of the Kurek Suite (Kuritang Series), Mergandava Creek, Yakkabag Mountains, near Tashkurgan, Uzbekistan.

Paratype Locality: Kodja Pil Ata, Turkmenistan (LOCKLEY *et al.*, 1996).

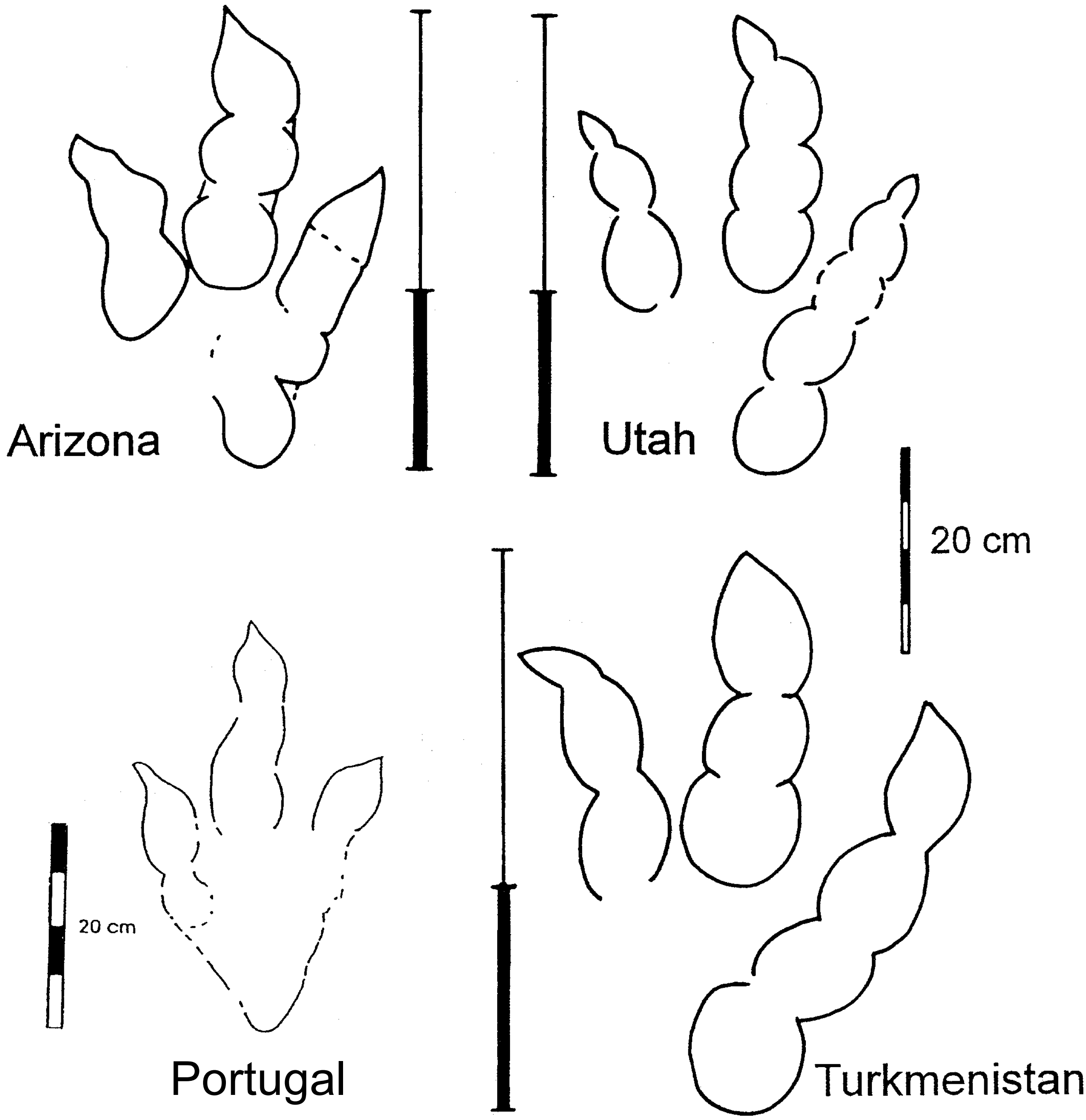

Fig. 8 - Comparison of *Megalosauripus* from Portugal (Cabo Mondego), North America (Arizona and Utah) and Asia (Turkmenistan). Wide and narrow bars respectively indicate segments of footprint length posterior and anterior to proximal pad on digit III.

Synonomy and referred material:

Megalosauropus uzbekistanicus GABUNIYA & KURBATOV (1982).

Khodjapilosaurus krimholz AMMANIAZOV (1985).

Turkmenosaurus kugitanensis AMMANIAZOV (1985).

Mirosauropus tursonzadevi NOVIKOV (1991).

Shirkentosauropus shirkentensis NOVIKOV (1991).

Karkushosauropus karkushensis NOVIKOV & DZHALILOV (1993).

Megalosauropus uzbekistanicus (LOCKLEY, MEYER & SANTOS, 1996: fig. 3-5).

Megalosauropus uzbekistanicus (LOCKLEY, HUNT & LUCAS, 1996: fig. 3-4).

Megalosauropus uzbekistanicus (LOCKLEY *et al.*, 1996: fig. 2).

Megalosauropus uzbekistanicus (MEYER & LOCKLEY, 1997: fig. 3).

Megalosauropus uzbekistanicus (LOCKLEY, 1999: fig. 5.1).

Description: Large elongate, asymmetric tridactyl tracks, ranging from 39 by 29 cm up to 72 by 65 cm (length-width): see TABLE II. Phalangeal pad impressions only well-defined in well preserved specimens, showing the typical theropod formula (2, 3, and 4 corresponding to digits II, II and IV). Trackway irregular with steps alternating between about 120 and 160 cm. Pace angulation also variable ranging from about 125-175º.

Discussion: The type specimen of *Megalosauripus uzbeckistanicus* forms part of an irregular sequence of 32 tracks arranged in alternating short and long steps; such irregularity is typical of *Megalosauripus* trackways. *M. uzbekistanicus* is also representative of a large sample of trackways from Late Jurassic (Oxfordian-Kimmeridgian) carbonates in Central Asia. The best preserved sample has been recorded from a site at Khodja-Pil Ata in eastern Turkmenistan. We use this sample to describe the range of known footprint morphology and to outline the variation in size (from 39 by 29 cm to 72 by 55 cm), trackway width and pace angulation (TABLE II).

The name *Megalosauropus uzbekistanicus* was coined by GABUNIYA & KURBATOV (1982) to describe distinctive large theropod tracks from Late Jurassic limestones at a site near Tashkurgan, Uzbekistan. However, as noted above, we must transfer the name to *Megalosauripus*. Following the report of GABUNIYA & KURBATOV (1982) there have been a number of additional discoveries and descriptions of large theropod tracks from Tadjikistan and Turkmenistan, and at least five other names have been coined for similar tracks from strata of the same age and facies (see synonomy above). In many cases these names are *nomina dubia* (Novikov, pers. comm., 1995) because the tracks they purported to describe were not diagnostic, lacked unambiguous type material, or were obvious synonyms of *M. uzbekistanicus*.

It is clear that there is very little difference between *M. uzbekistanicus* and some of the material, described below, from deposits of the same age in Europe and North America. In fact the similarities outweigh the differences. The size range of material from Europe (approx. 50 by 30 cm up to 77 by 60 cm length width), North American (40 by 30 cm to 53 by 38 cm) and Asia (from 39 by 29 cm to 72 by 55 cm), is remarkably similar except that the North American sample lacks truly gigantic tracks. The two largest measurements cited (77 by 60 and 72 by 55) are the largest theropod tracks known from the Jurassic. The former of these tracks from Zambujal Quarry in Portugal was destroyed when the sub-vertical track-bearing surface collapsed (SANTOS, CARVALHO & SILVA, 1995: fig. 1-2, 4) but photos and tracings remain. Finally we note that all tracks assigned herein to the ichnogenus *Megalosauripus* are larger that those assigned to *Eutynichnium*, and moreover they consistently lack hallux impressions.

Megalosauripus *tracks from Barkhausen, Germany.*

KAEVER & LAPPARENT (1974: 524) described tridactyl tracks from the Barkhausen site (*Megalosauropus teutonicus*) as "large tridactyl tracks, with large and powerful digits, with claws present: digitigrade progression and long step (140 to 160 cm)". [non-literal translation by authors]. They referred in this description to the trackway labeled "g" which was the only tridactyl trackway then known to them at the site.

Although the name *Megalosauropus* was preoccupied when this description was written (COLBERT & MERRILEES, 1967), the possibility of a distinctive morphotype (ichnospecies *teutonicus*) is implied by reference to the Barkhausen trackway. Owing to the poor quality of the maps and tracings of the Barkhausen trackiste, the published information is misleading. For example, the map reproduced by HAUBOLD (1971), from various previous sources, indicates that the tracks are wider than long, with a short step of about half the distance recorded by KAEVER & LAPPARENT (1974). Even the description given by these authors indicates tracks that are wider (60 cm) than long (56 cm), whereas according to our measurments the reverse is true. The tracks, from two discernable trackways (not one) reveal tracks that are longer (63 cm) than wide (53 cm): see LOCKLEY & MEYER (1999) for further details.

There has arisen an incorrect, word of mouth perception that the tracks might be those of ornithopods (compare with so called "Iguanodon" tracks from the Wealden of England; (DELAIR, 1989; WOODHAMS & HINES, 1989 and references therein). Note that following the present interpretation, the length/width ratio changes from 0.93 to 1.18, a difference of 25% as a result of substituting our measurements for those of KAEVER & LAPPARENT (1974). We therefore revise the description based on reexamination of the actual site, by one of us (M.G.L.) The appropriate diagnosis and description is as follows:

Megalosauripus teutonicus KAEVER & LAPPARENT (1974) Amended

Fig. 5, 9

Note that the species "*Megalosauropus*" *teutonicus*, KAEVER & LAPPARENT (1974), spelled with an "o" is transfered to the ichnogenus *Megalosauripus* (spelled with an "i").

Referred material:

Megalosauropus teutonicus, KAEVER & LAPPARENT (1974: fig. 1-4). Trackway "g".

TABLE II
Megalosauripus track measurements from Khodja-Pil Ata sites in Turkmenistan.

Trackway	Length	Width	Depth	Orient.	Step	Stride	P.A.	T'way Width	T'Way Length (m)	nº Track
1	-	-	w	210	160-170	310-320	-	-	12.5	9
2	(50)	(40)	-	200	-	-	-	-	-	1
3	50	48	w	190	160	297	123	127	-	3
4	(45)	36	5	225	150	300	138	95	12.1	8
5	(22)	19	3	50	91-101	200	(180)	(20)	9.8	10
6	(50)	(45)	w	223	avg 145	260	130	105	7.5	6
7	50	42	3	195	180	310	123	127	123	(65)
8	58	48	7.5	70	165	310	132	100	118	(67)
10	58	48	w 4	208	148	365	135	110	52	40
12	46	35	w 4	250	155-163	310	155	75	23	14
13	39	29	5	170	145-160	304	165	50	58	25
14	53	44	5.5	192	162	315	150	83	184*	113
16	26	22	w 4.5	355	96-102	198	176	28	105	82
17	58	46	6	208	177	321	130	136	195*	110
18	52	42	5	200	160	300	148	95	226*	161
A	50	40	3	225	170	-	-	-	-	2
B	42	35	-	215	165	355	-	-	128	67
C	72	55	3	90	109-118	212	145	110	26.2	18
20	52	45	4	330	175-185	355	160	75	18	11
21	45	35	4	200	144	274	145	75	311*	141
22	52	40	4.5	214	171-161	285	122	123	266*	104
23	60	50	3.5	250	145	287	164	80	12	9
24	60	50	4	260	132-152	250	125	130	62	27
25	27	22	3	260	98	198	170	28	45	37
26	50	44	12	(193)	140-150	250	110	120	32	18
27	(28)	22	w 4	255	110	212	152	43	31	28
28	55	48	w 4	280	125	238	145	90	98	40
29	62	52	3.5	90	120-125	217	122	106	105	50
30	27	22	w 2.5	60	90	181	170	35	50	26
31	55	48	w 4	(180)	142-150	257	130	125	157	91
32	40	30	w	200	160	310	160	70	113	

P.A. = Pace angulation; No. Track = number of tracks in trackway. Trackways 5, 16, 25, 27 and 30 are assigned to *Therangospodus*.

Megalosauropus teutonicus HAUBOLD (1984: fig. 122).
Megalosauropus teutonicus THULBORN (1990: 306).
Megalosauropus teutonicus LOCKLEY & MEYER (1999).

Description: Trackway of a large tridactyl biped with footprints, slightly longer (63 cm) than wide (53 cm) based on type trackway labeled "g" by KAEVER & LAPPARENT (1974) and one other of similar size. Trackway relatively narrow, with step of 155-160 cm, pace angulation of about 160-170º, and little or no rotation of the axis of digit III relative to the trackway mid line (Fig. 9). Tracks about 10 cm deep (based on number 47 of KAEVER & LAPPARENT, 1974). Digit impressions broad and short, deeply impressed anteriorly. Heel large, but less deeply impressed than digit traces. Preservation of discrete phalangeal pad impressions not visible.

Discussion: Comparison of the maps of the trackway published by KAEVER & LAPPARENT (1974: fig. 4) and (HAUBOLD, 1984: fig. 122), suggest that there is a need for a reinterpretation of the site. To this end a new map has been prepared (LOCKLEY & MEYER, 1999) which demonstrates that the sauropod trackways have the opposite orientation to those suggested by KAEVER & LAPPARENT (1974: fig. 3). Also a second *Megalosauripus* trackway has been recognized. It should be noted that these *Megalosauripus* trackways do not indicate a wide gauge at this site.

Megalosauripus ichnosp.

Fig. 4A,B, 8, 10-12.

Referred material:

MENSINK & MERTMANN, 1984: fig. 4, 5.
VALENZUELA, GARCIA RAMOS & SUAREZ DE CENTI, 1986: fig 2, numbers 4 and 5, top right block.
LOCKLEY, 1986: fig. 18, pl 2. top left.

TABLE III
Eutynichnium lusitanicum, *Megalosauripus* and *Hispanosauropus* track measurements from sites in Portugal and Spain.

Eutynichnium lusitanicum				
SPEC. NUMBER	LENGTH	LENGTH WITH HALLUX	WIDTH	STEP
MNHN-MG-P261	37	46	27	-
MNHN-MG-P262	39	58	26	-
MNHN-MG-P263	39	53	26	-
MNHN-MG-P264	39	56	26	-
No number	40	-	26	-
Megalosauripus				
Zambujal Quarry	77	-	60	-
Praia do Cavalo	67	-	56	193
Cabo Mondego	60		50	150
Hispanosauropus				
Hispanosauropus	52	-	36	-
Ribadessella 1	44	-	29	-
Ribadessella 2	49	-	31	-

VALENZUELA, GARCIA RAMOS & SUAREZ DE CENTI, 1988: fig. 3, 5-16.
FARLOW & LOCKLEY, 1989: fig. 4.1.
LOCKLEY, 1991a: fig. 2.3.
LOCKLEY, 1991b: fig. 5.
GOODKNIGHT & ERTEL, 1991: fig. 19.8a.
LOCKLEY, 1993a: fig. 2.3.
LOCKLEY, 1993b: fig. 2.3.
LOCKLEY *et al.*, 1991: 18.
LOCKLEY *et al.*, 1992: fig. 34.
LOCKLEY *et al.*, 1994a: fig. 1.
DANTAS *et al.*, 1994: fig. 1.
LOCKLEY & HUNT, 1995: fig. 4.38.
SANTOS, CARVALHO & SILVA, 1995: fig. 2.
LOCKLEY, MEYER & SANTOS, 1996: fig. 3-5.
LOCKLEY, HUNT & LUCAS, 1996b: fig. 3-4.
LOCKLEY & MEYER, 1999: fig. 7.2-7.7.

Descriptive notes: Medium to large elongate, asymmetric tridactyl tracks, ranging from 44 by 29 cm up to 77 by 60 cm (length width) excluding metatarsal impression, in Iberian samples (TABLE III). Size range of tracks from largest North American sample is 40 by 30 cm to 53 by 38 cm (see TABLE I). Phalangeal pad impressions well-defined in well preserved specimens, showing the typical theropod formula (2, 3, and 4 corresponding to digits II, II and IV: Fig. 7-9). Length of digit III impression comprising about 60 % of footprint length (Fig. 8). Proximal edge of metatarsal phalangeal pad on digit three, anterior to posterior part of second phalangeal pad on digit IV. Trackway narrow to moderately wide with pace angulation values ranging from about 125-175º.

Representative North American specimen: CU-MWC 188.25 (Fig. 10).

Locality and Horizon for representative specimen: (CU-MWC 188.25) Upper Summerville, Formation, Late Jurassic, Northwest Carrizo Mountains Arizona. See appendix, for other paratype material.

Other significant localities and stratigraphic positions: Region 1: Portugal: Zambujal Quarry (LOCKLEY *et al.*, 1994a: fig 1; SANTOS, CARVALHO & SILVA, 1995: fig. 2), Stratigraphic position: micritic limestone Oxfordian-Lower Kimmeridgian (LOCKLEY *et al.*, 1992). Also Praia do Cavalo (DANTAS *et al.*, 1994: fig. 1), purportedly Portlandian A (but may Kimmeridgian): Region 2: Western USA: Moab Megatracksite (LOCKLEY, 1991a,b; LOCKLEY & HUNT, 1995a): stratigraphic position at contact between Moab Tongue member of the Entrada and the Upper Summerville Formation; Kenton, Oklahoma (LOCKLEY, 1991a; LOCKLEY, HUNT & LUCAS, 1996b): stratigraphic position, Bell Ranch Formation considered equivalent to the Summerville Formation; Chama New Mexico (LOCKLEY, HUNT & LUCAS, 1996b): stratigraphic position the Summerville Formation. Upper part of Entrada Formation, Escalante region, Utah (FOSTER, HAMBLIN & LOCKLEY, in press).

Discussion: *Megalosauripus* sp. is known from many localities in the western United States. It is found in the Summerville formation and equivalents in Utah, Arizona, New Mexico and Oklahoma. In the Moab region of Utah it is one of two track types associated with the Moab Megatrackiste (LOCKLEY,

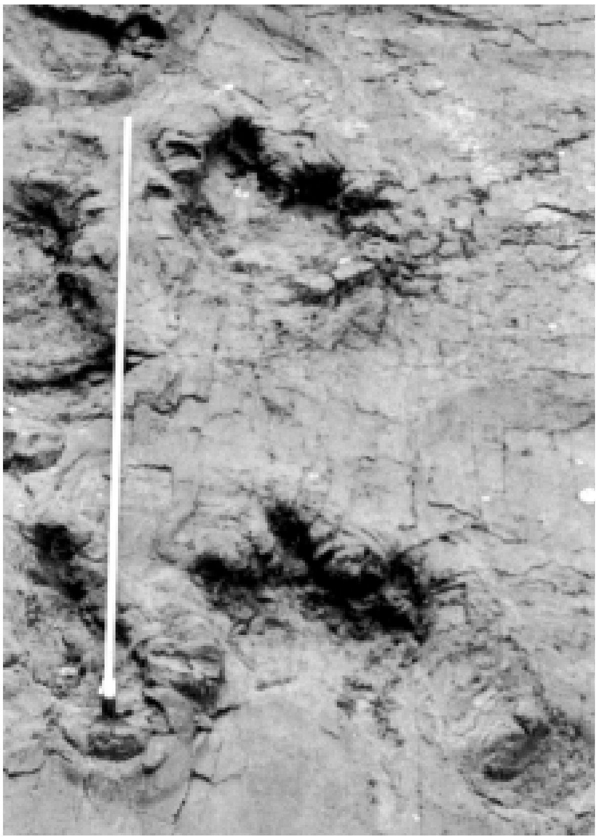

Fig. 9 - *Megalosauripus teutonicus*, from the Barkhausen site, Upper Jurassic (Germany). Scale 2 m.

1991a, b; LOCKLEY & HUNT, 1995). Consequently it is very widely distributed, and large trackway samples are available for study (TABLE I). In view of the large size of samples from North America and Asia, and the fact that, with the exception of Therangospodus (LOCKLEY, MEYER & MORATALLA, 1998), it is not possible to differentiate different tracks within these samples into distinctive morphologies, it is appropriate to apply the consistent label ?*Megalosauripus* sp., in recognition of the aforementioned ichnological history on the subject. The impressions of large theropods from Zambujal Quarry and Praia do Cavalo, and Cabo Mondego, in Portugal, as well as certain tracks from Asturias, Spain, might tentatively be assigned the label ?*Megalosauripus* (see Referred Material above, and TABLE III).

GENERAL DISCUSSION OF *MEGALOSAURIPUS* ICHNOSPECIES.

One of the most distinctive features of *Megalosauripus* trackways is they are irregular and variable. Trackways are characterized by relatively short steps, wide pace angulation (Fig. 12) and in some cases by alternating long and short steps (limping pattern *sensu* DANTAS *et al.*, 1994; LOCKLEY *et al.*, 1994a). Thus the trackmaker had a variable locomotor repertoire (BAKKER, 1996) and did not habitually walk fully erect with one foot in front of another like most theropods. Their body form is inferred to have been "more primitive' than allosaurs with a "longer, more flexible torso", and "shorter hind legs." (op cit.: 43). The trackmaker was also generally large. Tracks from Asia and Portugal exceed 70 cm in length, and are the largest theropod tracks known from the Jurassic (Fig. 4, 8, and TABLE I, III).

Careful comparison of the Late Jurassic Asian material with well know forms such as Lower Jurassic *Eubrontes*, shows that there are significant morphological differences that preclude the lumping together of such taxa. For example when comparing *Eubrontes* with *Megalosauripus* (Fig. 11) it is clear that the relative length of digit III is much greater in the former ichnotaxon. The position of the posterior (proximal) margin of metatarsal phalangeal pad III in relation to pads on digit IV is also quite different between *Megalosauripus* and *Eubrontes*. The impression of digit III in *Eubrontes* is also spindle shaped in relation to parallel-sided impression seen in *Megalosauripus*.

It is also of interest that well preserved Late Jurassic large theropod tracks from the Summerville Formation of eastern Utah and Arizona (Fig. 11) are essentially indistinguishable from the Central Asian material, and derive from strata that is exactly the same age. Moreover they occur in assemblages that are dominated by this large theropod track type. The only other recognizable morphotype occurring in Asia, western North America and Europe is a smaller morphotype that lacks discrete phalangeal pad impressions (labeled *Therangopodus* by MORATALLA, 1993; LOCKLEY, MEYER & MORATALLA, 1998). Such co-occurrences of distinctive morphotypes, can only be adequately described and understood, if appropriate ichnotaxonomic labels are applied. This has been suggested in preliminary studies (LOCKLEY, MEYER & SANTOS, 1996; LOCKLEY, HUNT & LUCAS, 1996 and LOCKLEY *et al.*, 1996).

*Informal description of purported "*Megalosauropus*" or "*Eubrontes*" tracks from the Cretaceous of Texas.*

Eubrontes (?) *glenrosensis* SHULER (1935)

Fig. 5-6 herein.

As indicated by the use of a question mark following the ichnogenus name *Eubrontes*, and the reassignment of the ichnospecies to *Megalosauropus* by HAUBOLD (1971) there is clearly uncertainty about the taxonomic status of this ichnospecies "*glenrosensis*"). We argue that it can not be assigned to either of these ichnogenera on morphological or ichnotaxonomic grounds and so is an orphan ichno-

Fig. 10 - *Megalosauripus* from North America, (CU-MWC 188.25). See TABLE I for measurements.

species in need of an ichnogenus. In deference to ichnologists who are still actively working this area, we refrain from erecting a new ichnogenus. However, this study highlights the ichnotaxonomic vacuum created by demonstrating that both the ichnogenus labels applied in the past are probably incorrect.

Referred material:

Eubrontes titanopelobatidus SHULER, 1917.
Eubrontes (?) *glenrosensis* SHULER, 1935: fig. 1.
Megalosauropus glenrosensis HAUBOLD, 1971.
FARLOW, 1987: fig. 3B, fig. 32.
Eubrontes (?) *glenrosensis* THULBORN, 1990: pl. 4.
FARLOW & CHAPMAN, 1997: fig. 36.5.

Ichnological discussion: Tracks referred to as *Eubrontes?* by SHULER (1917, 1935) and later partially transferred to *Megalosauropus* by HAUBOLD (1971) are not similar to the type material of the latter ichnogenus (COLBERT & MERRILEES, 1967) based on published descriptions, and differ from type *Eubrontes* (HITCHCOCK, 1845) in being much larger, and lacking distinct pad impressions in almost all known examples. In comparison with *Eubrontes* many appear to be much larger (foot length 64-65 cm for the "*glenrosensis*" "type specimen") have elongate, tapering digit impressions, rather than the spindle-shaped digit impressions (cf. Fig. 5, 6).

Eubrontes titanopelobatidus is a *nomen dubium* due to lack of a designated type specimen, and formal ichnological description (cf. FARLOW, 1987). *Eubrontes* (?) *glenrosenis* however is based on a known specimen (SHULER, 1935). Moreover, this latter specimen appears to be representative of many other tracks, many in trackways, from the Glen Rose Formation (FARLOW, 1987; PITTMAN, 1989, 1992). We consider that the track should be named. In the tradition of suggesting an appropriate label, as done by Roland Bird when he informally suggested the sauropod tracks be named *Brontopodus* - a name now formally adopted. (FARLOW, PITTMAN & HAWTHORNE, 1989), we suggest at least that a name like *Shulerpodus* is preferable to the present lack of nomenclature and applications of inappropriate and invalid names. Other creative possibilities, include "*Texipes*" "*Texipus*" or "*Texapodus*", since they are among the best know tracks from Texas. Even a name based on the possibility that the trackmaker was an *Acrocanthosaurus* (or a relative), as often claimed, might be considered, if evidence can be presented to support such a case. In the interest of caution we refrain from formally applying any such label, but we offer these suggestions with the accompanying summary of known descriptive information on these tracks to encourage future researchers to describe these tracks in their proper historical context.

We make these suggestions because, unless convincing evidence can be presented that the tracks should be assigned to an existing ichnogenus, we contend that a new one must be established. To date, Our surveys of various Jurassic and Cretaceous theropod track assemblages suggest that we have not overlooked any well-known ichnogenus in which the Texas tracks obviously belong. In the interests of erring on the side of caution, we again stop short of providing a formal description of these tracks. However, as it is necessary to demonstrate how we consider these tracks as different from the other theropod tracks under discussion, the following descriptive notes are included:

Tracks similar to the type of ichnospecies *E. (?) glenrosensis* are large, slightly asymmetric and tridactyl, longer than wide, with inward curve of tip of impression of digit III. Long metatarsus impression, without recognizable hallux trace, preserved in

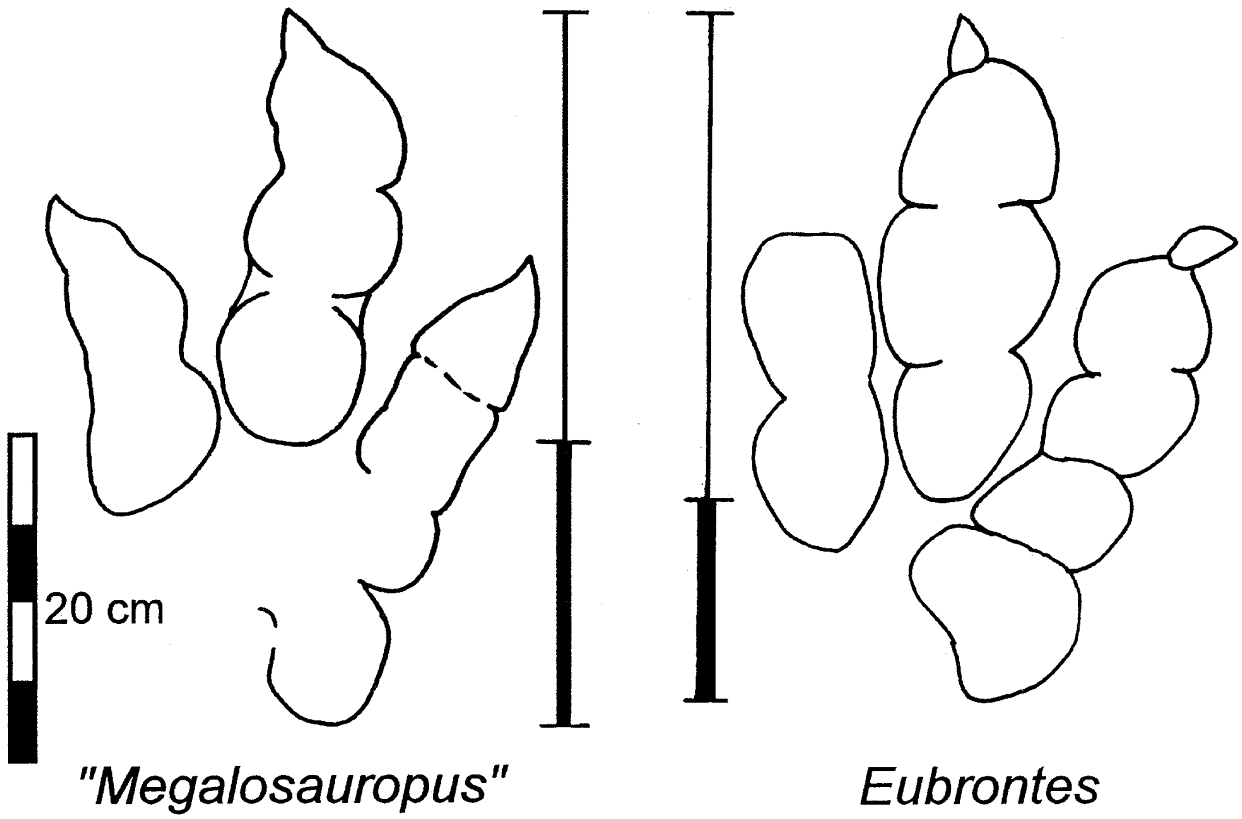

Fig. 11 - Comparison of a Late Jurassic theropod track (*Megalosauripus*) from Arizona with *Eubrontes* from the Early Jurassic of Utah.

some examples (PITTMAN, 1989: fig. 15) and posterior heel "projection" *sensu* SHULER (1935: fig. 1-2) corresponding to posterior margin of digit IV also preserved in some specimens. Tracks typically "indicate that the under surface of the toes was not developed into pads but was flat" (SHULER, 1935: 10).

Since SHULER (1917, 1935) first named tridactyl tracks from the Glen Rose of Texas, there has been general agreement that this track type is theropodan in origin, and widely distributed in Albian sediments. All subsequent illustrations of the material have shown, a conspicuous absence of well-defined pad impressions- exactly as indicated by SHULER (1935) in the quotation cited above. Some illustrations and reports (PITTMAN, 1989: fig. 15.8; KUBAN, 1989) indicate that this track type sometimes displays metatarsus impressions, evidently without hallux traces. In this regard the track type can be considered different from *Bueckeburgichnus* and *Eutynichnium* which both display a hallux trace, and different shaped digit impressions.

Theropod tracks from the Albian of Croatia may also be "similar to those found in the Glen Rose Formation of Texas" (i.e. *glenrosensis*; see LOCKLEY *et al*., 1994b: 240; Fig. 6 herein). This conclusion was predicted by HAUBOLD (1971) when he assigned both Croatian and Texan material to *Megalosauropus*, thus implying some degree of similarity or correlation. These samples are currently being studies by DALLA VECCHIA and colleagues (pers. comm., 1997-1999)

It is also important to compare the Texas (and Croatian) tracks with those, of approximately the same age, that comprise the very large samples from the Lower Cretaceous (?Aptian-Albian) of Spain (MORATALLA *et al*., 1988; MORATALLA, 1993 and references therein). These were assigned by MORATALLA (1993) to the ichnospecies *Bueckeburgichnus maximus* (ABEL, 1935), see Figure 6 herein. We consider that this assignment is incorrect owing to the considerable morphological differences between the type of *Bueckeburgichnus* (Fig. 2) and the Spanish material (LOCKLEY, in press). In addition the age of these tracks is significantly different. However the Spanish tracks do resemble the Texas tracks in lacking any clear pad impressions in the large sample described by MORATALLA (1993).

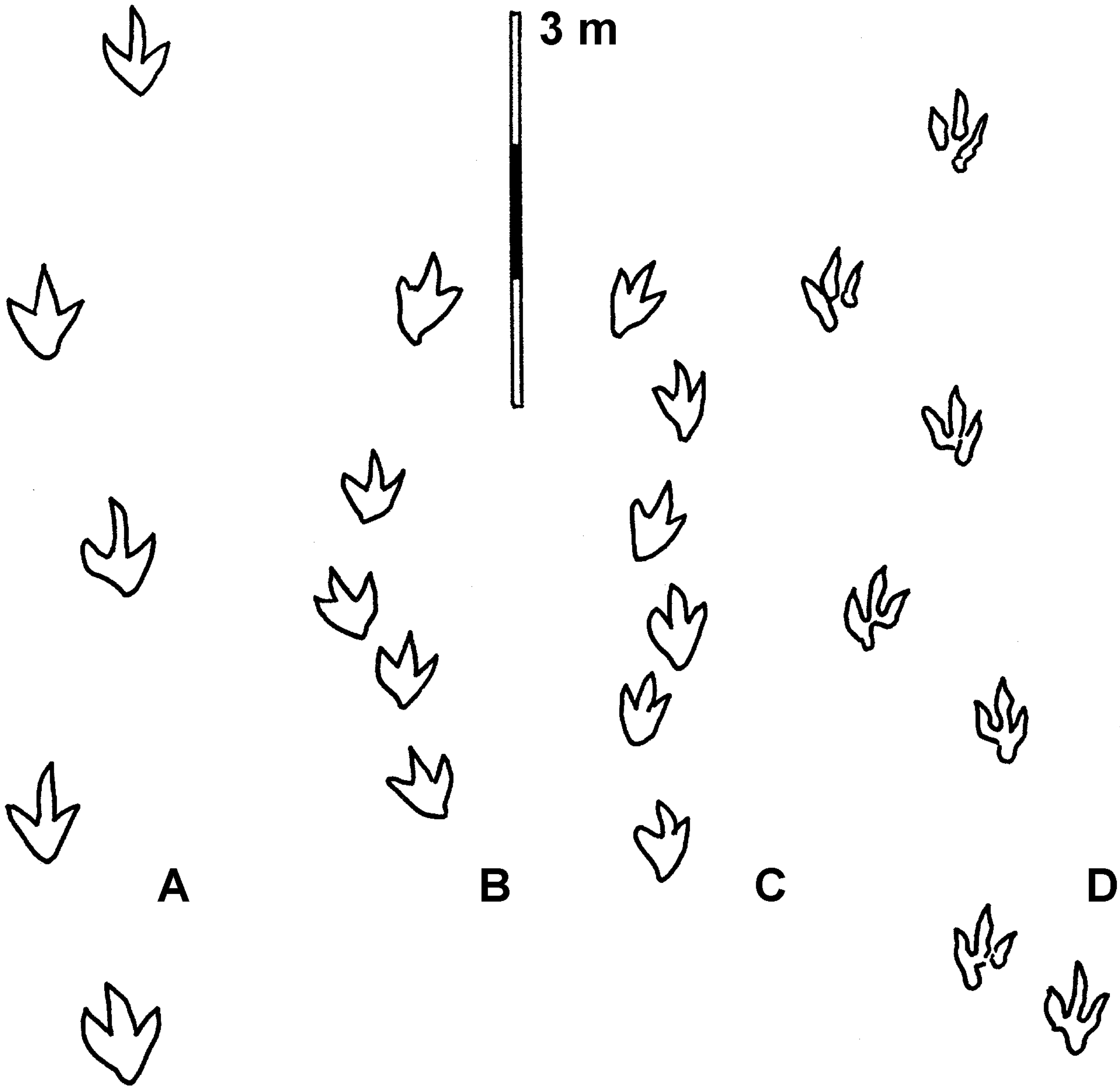

Fig. 12 - Pronounced irregularity has been noted in trackways attributed to *Megalosauripus*, as examples from Portugal (**A**), North America (**B** and **C**) and Asia (**D**) show.

PALICHNOSTRATIGRAPHIC CORRELATIONS AND PALEOECOLOGICAL OBSERVATIONS

A major incentive for careful ichnotaxonomic description and discrimination of track assemblages arises from the growing evidence that distinct ichnotaxa characterize particular stratigraphic units (and facies) and can be used for palichnostratigraphic correlation (HAUBOLD & KATZUNG, 1978; HAUBOLD, 1986; LOCKLEY, 1993a, b; LOCKLEY *et al.*, 1994c; LOCKLEY & HUNT, 1995a). Such correlations are still severely hampered by invalid ichnotaxonomy, and the incorrect assignment of poorly defined ichnites to catch-all catagories, as in the case of the example of "*Megalosauropus*," which we now hope is partially resolved. However, it is important to stress that terrestrial vertebrate biostratigraphy is very crude in most regions, and it is possible to use tracks to help refine it somewhat. For example LOCKLEY, MEYER & MORATALLA (1998) present evidence to suggest a change in Spanish ichnofaunas close to the Jurassic-Cretaceous boundary, that may shed light on a sequence of rocks that is otherwise very poorly dated.

Although we must be careful not to undertake ichnotaxonomic revision with stratigraphic preconceptions in mind, it is indeed recognition of morphologically distinctive, and stratigraphically constrained ichnofaunas, that alerts us to problems with the dating of certain terrestrial sequences, and highlights the archaic state of vertebrate ichnotaxonomy and the unsatisfactory lumping of many ichnospecies into catch-all ichnogenera such as *Megalosauropus*. Moreover we expect all manner of fossils to have stratigraphic ranges that are restricted to some degree, and we would consider it odd to find terrestrial vertebrate track assemblages that have ranges extending through several epochs or periods. It is therefore desirable to attempt to separate the distinct morphotypes as done here. Even if all taxonomic issues are not fully resolved, at least explicit labels are used to distinguish tracks with different morphologies.

The alternate argument that all theropod tracks look alike is a weak one based largely on lack of detailed work (LOCKLEY & HUNT, 1995a, b; LOCKLEY, 1998). The fact that only one worker (LULL, 1904, 1915, 1953) has undertaken any significant revision of Hithcock's classic work (1836-1858) underscores this point. OLSEN, SMITH & MCDONALD (1998) and Olsen (written communication, 1998) indicate that Lull's revisions leave much to be desired. Farlow (personal communication) is working on a quantitatively based osteometric analysis of the foot bones of tridactyl track makers. Such work may have implications for our understanding of classic ichnofaunas, but we worry that not enough is being done to describe ichnofaunas in their stratigraphic context, and that it is highly improbable that studies of foot bones, however revealing will be useful to ichnology before the actual track record is adequately described in its own right.

The osteometric approach (FARLOW & LOCKLEY, 1993) is not a panacea for resolving ichnological problems, because it can only go so far in helping us understand the morphology of the fleshy part of the foot, represented in footprints. The morphological disparity between bones and flesh is particularly important in the case of large trackmakers of the type discussed herein, and track morphology should be described first for what it is, not what it might represent (see LOCKLEY, 1998).

Though Lull continued to use Hitchcockian labels such as *Grallator* and *Eubrontes*, he did so only to describe Lower Jurassic tracks. To the best of our knowledge no workers have extended the use of ichnospecies, of these two ichnogenera, outside the Lower Jurassic, even though the generic names have been used very casually outside this epoch. This implies that all workers, recognize some differences between Early Jurassic theropod tracks and those from other epochs, at least at the specific level. Despite degrees of similarity, conservatism and convergence among theropod tracks, there are a variety of distinct morphotypes, so no compelling evidence exists that well-defined ichnotaxa have long ranges outside the age or epoch where the type material occurs.

The current revision allows us to propose that *Megalosauripus* is a distinctive large theropod track type, distinguishable from forms such as Lower Jurassic *Eubrontes* and *Grallator*, Upper Jurassic *Eutynichnium*, and Lower Cretaceous *Megalosauropus* (with an "o") and *Bueckeburgichnus*. Moreover *Megalosauripus* is currently only known with certainty from a relatively restricted stratigraphic interval (Late Oxfordian- Kimmeridgian) in Europe, Asia and North America. It is probable that the widespread preservation of these tracks in this restricted stratigraphic interval is due to aggradation during a period of high sea level (LOCKLEY *et al.*, 1994b).

Concerns about the extent to which *Megalosauripus* tracks are different from other theropod tracks can be addressed, at least partially, by listing distinguishing features as follows:

1) *Megalosauripus* (or *Megalosauropus*) ichnospecies have been recognized by previous workers as distinct from *Eubrontes*, *Grallator* and other ichnogenera.

2) Tracks from *Megalosauripus* assemblages are larger than any known from the Jurassic.

3) *Megalosauripus* trackways are unusually wide (low pace angulation values).

4) *Megalosauripus* tracks are associated with a relatively restricted stratigraphic interval. (This conclusion requires qualification, see below).

5) *Megalosauripus* tracks are morphologically distinct from *Eubrontes* in a number of respects (Fig. 11)

6) *Megalosauripus* tracks are associated, in many areas with another theropod track type (*Theragospodus*) that is also restricted to the same stratigraphic levels.

The implications of this latter discovery are significant. Ichnological evidence establishes the existence of two trackmakers on three continents at a restricted interval in time (Oxfordian-Kimmeridgian). Moreover such evidence sheds light on faunal interchange between North America, Europe and Asia during the Late Jurassic, when the Atlantic ocean was already opened. The same potential for correlation may apply to tracks from the Albian of Texas and Croatia.

Very recent research, conducted while this paper was in review, has demonstrated that large, wide gauge, trackways resembling *Megalosauripus*, as defined herein, are emerging from the late Middle

Jurassic of Portugal (SANTOS, 1998) and England (LOCKLEY & MEYER, 1999). This is significant in suggesting that megalosaurid tracks may really have a late Middle Jurassic to early late Jurassic range, coinciding very nicely with the known range of skeletal remains. However, this suggests that the *Megalosauripus* track zone may be somewhat longer in duration than previously supposed (item 4 above). What this conclusion, if correct, also implies is that we have redefined and amended the concept of megalosaurid (*Megalosauripus*) tracks on the basis of material from the latter part of the megalosaurid "era" and that more important information is about the emerge regarding the early ichnological history of this group.

Given that the occurrence of large, wide gauge "megalosaurid" or *Megalosauripus*-like tracks are first associated with Middle Jurassic carbonate facies in which the only other tracks are those of sauropods, we consider that such occurrences represent an early expression of the low latitude, sauropod-theropod ichnofacies refered to in many areas as the *Brontopodus* ichnofacies (LOCKLEY, HUNT & MEYER, 1994; LOCKLEY & MEYER, 1999). A similar association of sauropod and *Megalosauripus* tracks appears to be recognizable in the Upper Jurassic carbonate facies of Portugal and Central Asia, though in the latter region sauropod tracks are rare. In North America *Megalosauripus* tracks, as here defined are, associated with arid siliciclastic eolian and marginal marine deposits, in which sauropod tracks are rare [see FOSTER, HAMBLIN & LOCKLEY (in press) for the only known occurrence]. We suggest that further attempts understand the distribution of purported megalosaurid tracks, in addition to focussing on understanding details of morphology, may benefit, at least to some degree from considering the ichnoassemblage and ichnofacies context in which they are found.

This study would not have been possible without access to type and "paratype" material, much of it in situ in Portugal, Germany, Uzbekistan, Turkmenistan, Utah, Arizona and Oklahoma. To date, the only material that we have not examined first hand is that reported from Spain. It has became clear to us that it is easy to be misled about track morphology if one relies too heavily on illustrations, especially line drawings, or fails to examine actual specimens (tracks and trackways) in different regions. We nevertheless consider that our contribution only begins to describe and constrain the megalosaurid tracks problem, and that future ichnological studies are needed to understand more about intra and inter-sample variation. The historical information, specimen descriptions and measurements provided, should help in such endeavours.

CONCLUSIONS

1) The concept of Late Jurassic megalosaur tracks dates back to the 1950's, but has become confused by inconsistent usage and lack of comparative studies, and so has also been casually applied to Lower Cretaceous tracks, despite the lack of evidence for megalosaurid dinosaurs at this time.

2) The name *Megalosauripus* (with an "i") is a *nomen nudum* and so available for use (LOCKLEY, MEYER & SANTOS, 1996). We have adopted it to describe three of the largest, best- preserved and most widely-distributed track samples currently known, namely Late Jurassic assemblages identified in Asia, Europe and North America. Three closely related ichnotaxa (*Megalosauripus uzbekisanicus*, *M. teutonicus* and *Megalosauripus*, respectively) are described and amended on the basis of existing type and topotype material. Further study is needed to describe these samples in more detail and establish the extent to which they can be differentiated.

3) The name *Megalosauropus* (with an "o") currently refers only to tracks described from the Lower Cretaceous of Australia, that are neither the same age, nor, according to formal descriptions, the same morphology as other tracks subsequently and incorrectly assigned to this ichnogenus. Hence all other tracks assigned to this ichnogenus become orphaned unless assigned to an alternate or new ichnogenus. Tracks in this category include the famous Cretaceous tracks from the Glen Rose Formation in Texas, and suggest the designation of an alternate ichnogenus name is overdue.

4) Recognition of distinctive stratigraphically restricted track assemblages provides an incentive to reexamine theropod track ichnotaxonomy, and evaluate the extent to which distinctive morphotypes can be identified and placed in stratigraphic context. New discoveries however suggest that the early history of megalosarid trackmaking has yet to be documented. Such exercises in ichnotaxonomic revision are necessary and long overdue, and should be conducted with careful consideration of as much of the sample as can be realistically observed, reference to the entire literature, and careful consideration of the morphology and stratigraphic ranges of the ichnotaxa under consideration.

ACKNOWLEGMENTS

Research on tracks in Utah and Arizona was supported mainly by National Science Foundation grants to the senior author at the University of Colorado at Denver. Research in Central Asia was supported by a grant to the senior author from the National Geographic Society. We also thank the Navajo Nation for prior written permission to study in Arizona. We also thank the Luso American Foundation, the municipality of Sesimbra, and António Marcos Galopim de Carvalho for support of our research efforts in Portugal. We thank Spencer Lucas and Adrian Hunt for reading earlier versions of this manuscript and suggesting significant improvements, based on their firsthand knowledge of such ichnites. Tom Holtz, Joaquin Moratalla, and Carlos Marques da Silva, provided helpful reviews and editing suggestions. We thank Dr. Wolfgang Schad, Universitat Witten-Herdecke, for arranging a visit to Barkhausen, and we thank Alex Burton and David Norman (Cambridge University), Phillip Powell and Juliet Hay (Oxford University) and Robert Bakker, (Boulder Colorado) for valuable discussion of the subject of megalosaurid tracks and trackways.

APPENDIX: MATERIAL

Specimens attributable to *Eutynichnium lusitanicum* from National Museum of Natural History, Lisbon, Portugal.

MNHN-MG-P261, natural cast of *Eutynichnium lusitanicum* with metatarsal impression and hallux trace.

MNHN-MG-P262, natural cast of *Eutynichnium lusitanicum* with metatarsal impression.

MNHN-MG-P263, natural cast of *Eutynichnium lusitanicum* with metatarsal impression.

MNHN-MG-P264, natural cast of *Eutynichnium lusitanicum* with metatarsal impression.

Specimens attributable to *Megalosauripus* from University of Colorado at Denver- Museum of Western Colorado collection.

185.1-2, Natural casts of tridactyl tracks from Entrada-Morrison Formation contact, near Arches National Monument, Utah. From sites H and K.

186.3, Natural cast from site O.

187.1-5, Natural casts from site X.

187.6, replica of track from Bull Canyon site, La Sal locality.

188.25, replica of Megasalosauripus track from Bluff-Summerville beds, Carrizo Mountains, northeastern Arizona.

188.26, replica of theropod track (same type and locality as 188.25).

188.27, replica of theropod track (same type and locality as 188.25).

188.30, replica of theropod track, (same type as 188.25, but locality about one mile to the east).

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