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Crouching Theropods in Taxonomic Jungles: Ichnological and Ichnotaxonomic Investigations of Footprints with Metatarsal and Ischial Impressions

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Tracks and traces of crouching theropods are rare, known from only three specimens from the Lower Jurassic of New England and the Lower to ?mid Jurassic of China. The New England specimens reveal manus, metatarsal and sub-crescentic ischial callosity impressions associated with *Grallator*-like tracks. The Chinese traces reveal metatarsal traces and a sub-triangular ischial callosity impression associated with *Eubrontes*-like tracks. All reveal symmetrical crouching postures. Theropod crouching traces should not be confused with ornithopod crouching traces, often assigned to *Anomoepus*. The ichnotaxonomy surrounding all these traces and associated footprints is very complex, and over split. Suggestions for simplification allow recognition that the North American and Chinese ichnofaunas have many similarities. The ichnotaxonomy is not as complex and confused as it may at first appear.

Keywords Lower Jurassic, crouching theropod traces, metatarsal traces, ischial callosity traces

INTRODUCTION

There are a number of well-known examples of tracks that are associated with metatarsal impressions, and in some cases with traces of the pelvic girdle. The best and historically most famous specimens (AC 1/1 and 1/7) are probably *Sauropus barrattii* (Hitchcock, 1837; 1841) refigured by Lull (1953), with a reconstruction of the animal in a "seated," or crouching position, showing the location of an inferred ischial callosity, centrally located behind the metatarsal impressions. This reconstruction has attracted the attention of other researchers and has been recycled into other publications (e.g., Lessertisseur, 1955; Thulborn, 1990), some of which incorrectly inferred that the traces represent ornithopods (ichnogenus *Anomoepus*). This misconception is understandable given the later assignment of the specimens to this ichnogenus by Hitchcock (1858). As explained by Lull (1953, p. 205), the ichnotaxonomy of this track type is complex with manus and pes tracks having received as many as 10 different names. However, the specimens are readily "distinguished from *Anomoepus*" (Hitchcock, 1848) because of "greater size . . . (and) . . . less divarication of the digits." Lull (1953) also added that the track "resembles *Anchisauripus*" which is typically inferred to imply theropod affinity. This interpretation is strongly supported by the work of Gierlinski (1994), who places *Sauropus barrattii* (specimens AC 1/1 and 1/7) in the ichnospecies *Grallator (Eubrontes) tuberosus* and *Grallator (Eubrontes) minisculus*, respectively (Fig. 1).

As specimens AC 1/1 and AC 1/7 are the only theropod tracks with paired metatarsal and ischial callosity impressions, reported prior to those described herein from Sichuan Province, China, it is helpful to review the debate surrounding their interpretation. It is impossible to completely disentangle the debate about the behavior indicated by such crouching traces from the ichnotaxonomic implications. For example, if the tracks represent ichnogenus *Grallator*, does this imply a need to expand the description of this ichnogenus to include details of the metatarsal and ischial callosity impressions?

In our opinion the first step is to provide a description of available material, and review the status of ichnotaxonomic usage. The purpose of this paper therefore threefold: 1) to out-

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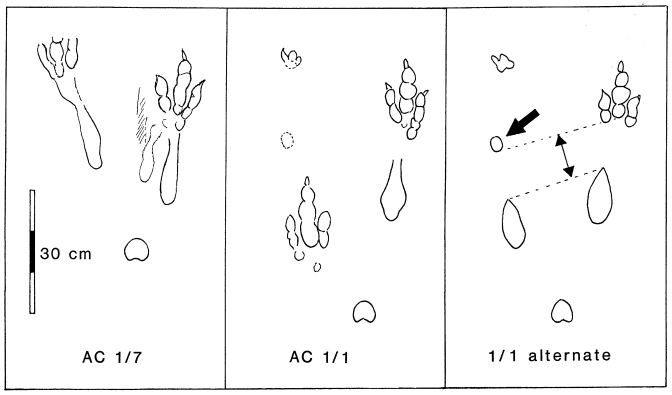

FIG. 1. *Sauropus barrattii* (Lull, 1953) has since been assigned to *Grallator (Eubrontes) tuberosus* (specimen AC 1/1) and *Grallator (Eubrontes) minisculus* (specimen AC 1/7) by Gierlinski (1994). Note that our interpretation of AC 1/1 (right) differs from Gierlinski's (center) in inferring a symmetric posture as seen in AC 1/7. Large arrow indicates position of proximal pad, digit III left pes. Double arrow indicates consistent length between metatarsal and proximal digit III impressions. (Based on tracing T 715 in the University of Colorado at Denver collection).

line historical discussion and debate about the tracks and traces produced by crouching bipedal dinosaurs, 2) to outline the taxonomic problems that arise from the discovery of new crouching traces in China where an entirely different provincial ichnotaxonomy has arisen, and 3) to suggest probable ichnotaxonomic solutions.

PREVIOUS INTERPRETATIONS OF CROUCHING DINOSAUR TRACES

As noted above, the classic work of Hitchcock (1858) and Lull (1953) confirms that tracks assigned to both *Grallator* (a presumed theropod) and *Anomoepus* (a presumed ornithopod) have associated paired metatarsal impressions associated with a single ischial callosity impression Figs. 1 and 2, respectively. The non-specialist, or even the specialist, may find it hard to differentiate these two track types if preservation is sub-optimal. The preservation of these "type" specimens of crouching dinosaurs from the Hitchcock collection is quite good, but by no means optimal. As indicated in Figs. 1 and 2, the preservation is sufficiently imperfect to allow to for differences of interpretation as outlined below. Lull (1953) also had the habit of idealizing trackways as shown in Fig. 2.

Gierlinski (1994) has achieved a certain notoriety by suggesting that specimen AC 1/7 shows traces of feather impressions. In our opinion these fine parallel striations (Fig. 1) are probably traces of scales that appear elongate as a result of the motion of the integument (skin) against the substrate. We also disagree with Gierlinski's interpretation of AC 1/1, in which he shows the right foot and metatarsus impression with the ischial callosity almost directly behind it, and the purported left pes impression situated about 20 cm to the left of the right metatarsus impression. We consider this left side impression to be the left metatarsus impression, though we admit that there are a few rather indistinct indentations around it that might be mistaken for phalangeal pad impressions, perhaps caused by a footprint that was impressed earlier.

Our interpretation is supported by three observations: 1) the greater symmetry of the metatarsal impressions in relation to the ischial impression, and 2) the presence of a rounded impression that appears to represent the proximal pad of left pes digit III, which is normally the deepest point on a theropod track. The distance between this pad impression and the metatarsus impression is exactly the same as the distance measured on the right side. (cf. Fig. 1 for alternate interpretations), and 3) Hitchcock, (1858, pl. VIII) illustrated the same specimen (1/1), which, although labeled *Anomoepus major*, is correctly interpreted with respect to pes and pelvic trace configurations, despite idealization of the manus impressions. Given that we arrived at our interpretation of this specimen (Fig. 1) independently, prior to noting it illustrated under *Anomoepus major* in Hitchcock (1858), we regard the convergence of interpretation as significant in rejecting Gierlinski's interpretation. It also suggests that the natural crouching posture for theropods was symmetric—not asymmetric.

To the best of our knowledge, these two examples (AC 1/7 and 1/1) are the only two hitherto reported that show a pair of tracks "side by side" with both metatarsal impressions and ischial callosity impressions. Thus, the Chinese example, presented herein in association with a *Eubrontes*-like track is only the third to be reported (Matsukawa et al., 2002; Figs. 3 and 4). As noted below, there are a number of examples of isolated

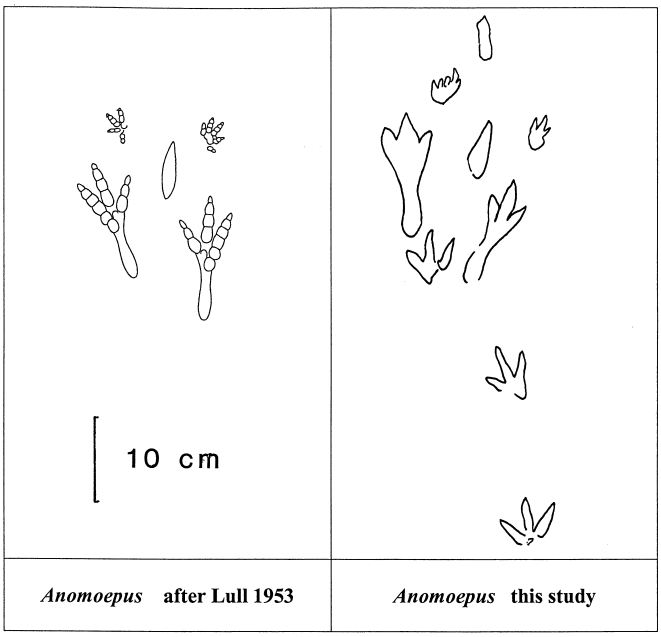

FIG. 2. Left: *Anomoepus* (idealized by Lull, 1953, p. 154) with our revised interpretation (right) based on tracing in University of Colorado at Denver collection.

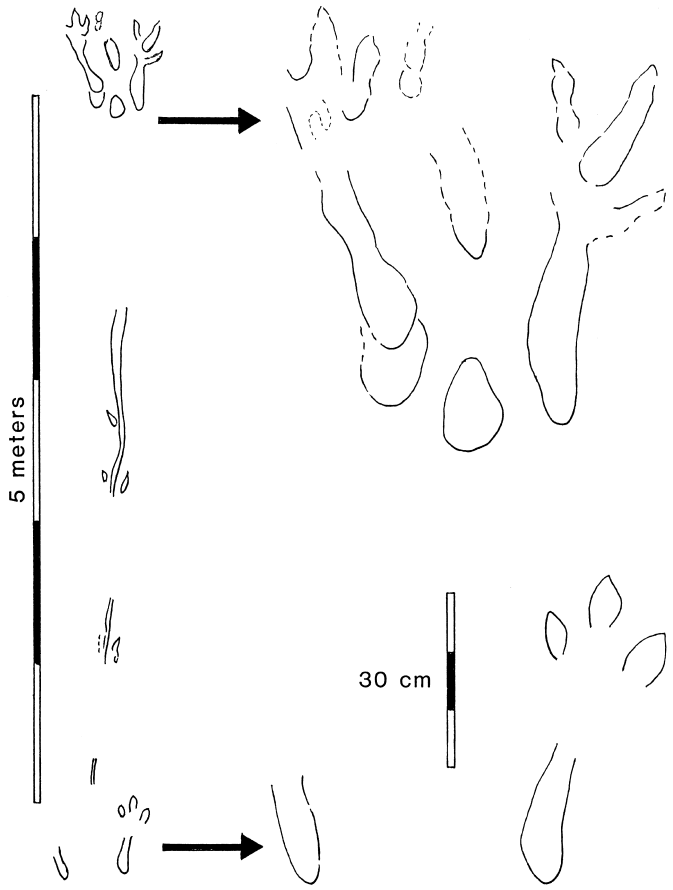

FIG. 3. Two Lower, or early Middle Jurassic pairs of crouching traces occur in the same trackway: Wu Ma Cun site A (Sichuan, China).

theropod tracks, and some associated in trackways, with metatarsal impressions. Similarly, there are also several known examples of probable ornithopod tracks (*Anomoepus*) with metatarsal impressions, and rarely with pelvic impressions (cf. Lull, 1953, p. 194; Fig. 2 herein).

There is little doubt that *Anomoepus* is attributable to an ornithopod dinosaur, based on the five toed manus, as well as the short step and inward rotation of the pes as seen in virtually all other ornithopod trackways. As pointed out by Gierlinski (1991) it is not too hard to distinguish between typical *Anomoepus* and *Grallator* or *Grallator*-like tracks with or without metatarsal and associated crouching impressions. Following the morphodynamic arguments presented by Lockley (1999a,b, 2000a), *Anomoepus* tracks are typically short and wide in comparison with elongate (longer than wide) theropod tracks such a *Grallator*. This applies not only to the plantar surface of the foot (footprint) but also to the metatarsus (see Figs. 1 and 2). Here we have confined ourselves to the description of inferred theropod tracks with crouching traces. Detailed comparisons of anomoepid and grallatorid crouching traces will be dealt with elsewhere.

Crouching traces recently recognized at the Lower-Middle Jurassic site at Wu Ma Cun in Sichuan Province, China (Matsukawa et al., 2002: Figs. 3 and 4 herein) are the only complete crouching theropod traces (i.e. paired metatarsal impressions and an ischial callosity) other than the two Connecticut Valley examples. Due to the complex ichno-taxonomy that surrounds tracks from this site (Yang and Yang, 1987) we have had to outline the ichnology of the site in order to determine the possible ichnotaxa to which the crouching traces might be assigned.

The remainder of this paper briefly lists examples of theropod tracks with metatarsal impressions reported from sites in the Jurassic of southern Africa (Ellenberger, 1972, 1974), the Cretaceous of Texas (Kuban, 1989), the Jurassic of China (Zhen et al., 1989), the Jurassic of Poland (Gierlinski, 1994) and the Jurassic of Utah (Lockley et al., 1998).

AGE, ICHNOTAXONOMY, GEOLOGICAL CONTEXT AND PRESERVATION OF IMPORTANT JURASSIC SPECIMENS

Lower Jurassic tracks from the Portland Sandstone at Gill, Massachusetts were originally assigned to *Sauropus barrattii* (Lull, 1953) but have since been assigned to *Grallator (Eu-*

FIG. 4. Photograph of second pair of crouching traces from Wu Ma Cun site A (Sichuan, China). Tape measures 50 cm. Compare with Fig. 3.

brontes) tuberosus (specimen AC 1/1) and *Grallator (Eubrontes) minisculus* (specimen AC 1/7) by Gierlinski (1994). The footprints are quite well preserved as natural impressions and include so-called ischial callosity pads as well as metatarsal and manus impressions. The purported manus impression (AC 1/1) is faint (see Fig. 1), and as indicated above, our interpretation of AC 1/1 differs from Gierlinski (1994).

Lower, or early Middle Jurassic tracks from the Wu Ma Cun site (Sichuan, China) are associated with massive sandstone of the Xin Tian Gou Formation. There are two sites at Wu Ma Cun, herein labeled A and B. Site A, where the crouching traces are found (Figs. 3 and 4), is the type locality for tracks assigned to the ichnospecies *Zizhongpus wumanensis*, *Chonglongpus hei*, *Tuojiangpus shuinanensis* and *Chuannchengpus wuhuangensis* (Yang and Yang, 1987: Figs. 5 and 6 herein). Generally these tracks, which consist of natural impressions, are not well preserved. In addition, many have been removed for museum collections (in Chongqing and Zigong, both in Sichuan Province). However, one-track type, *Chonglongpus hei*, and the

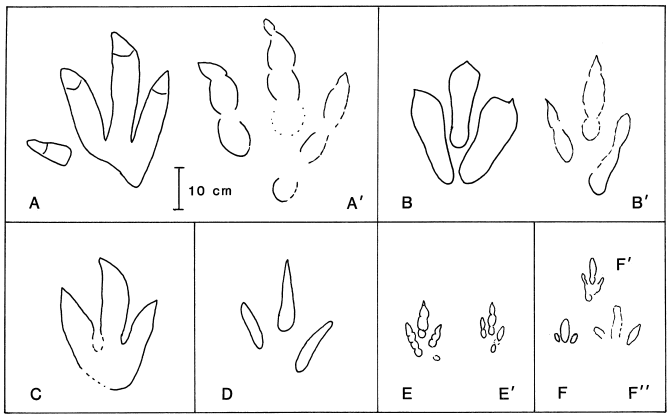

FIG. 6. Detail of tracks assigned to **A.** *Chonglongpus hei*, **B.** *Megaichnites jizhaishiensis*, **C.** *Tuojiangpus shuinanensis*, **D.** *Zizhongpus wumanensis*, **E.** *Chongqingpus microiscus*, and **F.** *Chuannchengpus wuhuangensis* after Yang and Yang, (1987), with reinterpretations A', B', E', F' and F'' based on tracings made during the current study. See text for details.

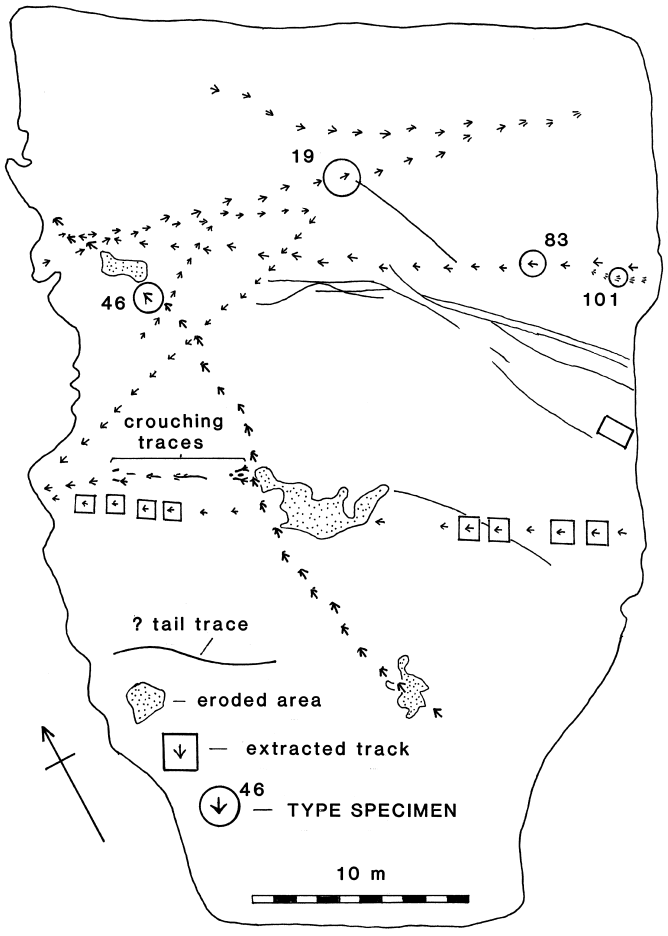

FIG. 5. Map of the Wu Ma Cun site showing the location of the crouching dinosaur trackways shown in Fig. 2 and the purported location of tracks assigned to ichnospecies *Zizhongpus wumanensis* (#19), *Chonglongpus hei* (#46) *Tuojiangpus shuinanensis* (#83) and *Chuannchengpus wuhuangensis* (#101), after Yang and Yang (1987).

crouching dinosaur traces are sufficiently well preserved to reveal accurate morphological detail. Moreover, the crouching traces reveal a distinctive triangular ischial callosity impression and probable tail traces. To compound the ichnotaxonomic complexity the second Wu Ma Cun locality (site B), according to Yang and Yang (1987) is also the type locality for *Megaichnites jizhaishiensis* and *Chongqingpus microiscus* (Fig. 7). Here, the tracks are somewhat better preserved.

As discussed below, we infer that several of the many of the Wu Ma Cun ichnospecies may be junior synonyms of better-known ichnotaxa such as *Eubrontes* and *Grallator*. One of the challenges faced in understanding this site is to know how many track types are really represented, and to attempt to correlate the crouching traces with a specific, named ichnotaxa. This is not easy, because, as noted below, there are at least two other sites in the general Wu Ma Cun region where we find additional theropod tracks, at the same stratigraphic levels that have been given new ichnospecies names in a addition to the six cited above!

Ellenberger (1972) illustrated a single distinctive theropod track with metatarsal impression from the Upper Stormberg "Transition beds," (Cave Sandstone, stage B/5). This track is probably Lower Jurassic in age and has been assigned to the ichnospecies *Megatrisauropus malutensis* (Fig. 8A). It is a large track with distinct pad impressions, but no sign of manus or pelvic traces.

Another large track with a metatarsal impression is known from the ?Middle or Upper Jurassic Moab Tongue Member of the Entrada Formation where it passes into the upper tongue of the Summerville Formation on the eastern flank of the Salt Valley Anticline just north of Arches National Monument, near Moab, Utah. This track has not previously been described. It is preserved, like other tracks in the region as a series of distinctive concentric markings in a massive sandstone. However the

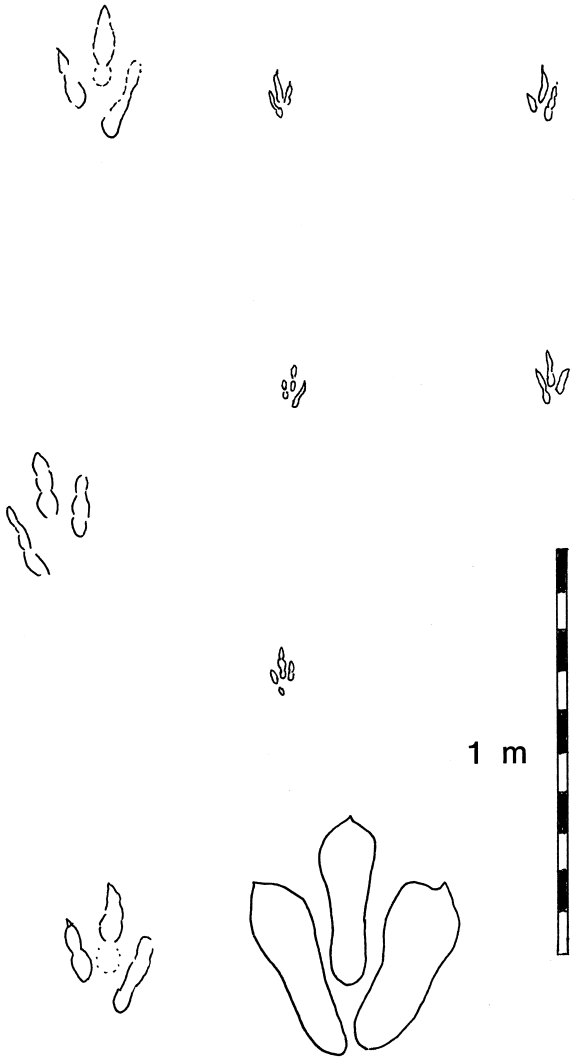

FIG. 7. Wu Ma Cun locality (site B) showing the type material for *Megaichnites jizhaishiensis* and *Chongqingpus microiscus* in trackway configurations based on tracings made during the current study. See text for details.

outline is clear and allows the dimensions of the metatarsal impression to be measured. Other large tracks from the region have been assigned to *Megalosauripus* sp. (Fig. 8B). The track is not associated with manus or pelvic traces.

A well-preserved track from the Upper Jurassic Penglaizhen Formation of Sichuan province China has been assigned to the ichnospecies *Jialingpus yuechiensis* (Zhen et al., 1983, 1989; Fig. 7C herein). In the latter paper the track was included in the ichnofamily Anomoepodidae (Lull, 1904). We infer that this is incorrect. The track is narrow and elongate with typical theropod morphology. It is part of a well-preserved assemblage of natural casts assigned to this ichnospecies. Many specimens are preserved in collections at the Chongqing and Beijing museums. However, none of the specimens are preserved in trackways or with associated manus or pelvic traces.

OTHER JURASSIC SPECIMENS

There are few other Jurassic tracksites that have yielded well-preserved theropod tracks with metatarsal impressions or other evidence of crouching behavior. Lockley et al. (1998) described a poorly preserved trackway from the Glen Canyon Group (Kayenta Formation) of the Lake Powell area, Utah. This trackway, however, lacks the detail necessary for yielding reliable measurements. Kuban (1989, Fig. 7.17) illustrated an example from the Middle Jurassic of Morocco taken from the work of Shinibou Ishigaki. He also cited a second example from the Upper Jurassic of Brazil taken from the published work of Leonardi (1979), but the wide digit divarications suggest that this might be a track of ornithopod affinity.

CRETACEOUS SPECIMENS

The work of Kuban (1989) on the Cretaceous (Albian) Glen Rose Formation, Texas, can be considered something of a landmark in the analysis of "elongate" dinosaur tracks, because his objectives were to assess the claims of creationists that such tracks were "man tracks." He was successful in demonstrating that many such elongate man tracks were simply theropod tracks in which the posterior metatarsal impressions were preserved behind recognizable tridactyl track impressions, many

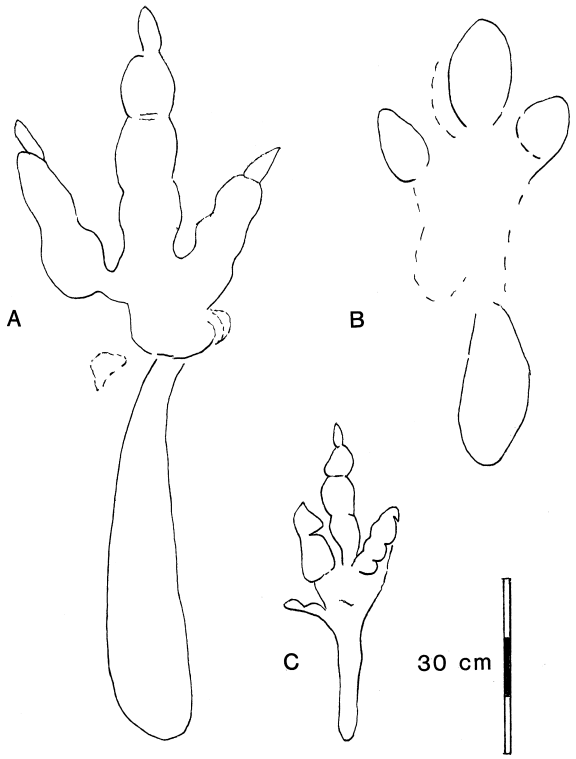

FIG. 8. Miscellaneous Jurassic tracks with metatarsal impressions. **A.** The Lower Jurassic ichnospecies *Megatrisauropus malutensis* southern Africa (after Ellenberger, 1972); **B.** *Megalosauripus* sp. From the ?Middle or Upper Jurassic of Utah, C. *Jialingpus yuechiensis* from the upper Jurassic of Sichuan, China after Zhen et al. (1983, 1986).

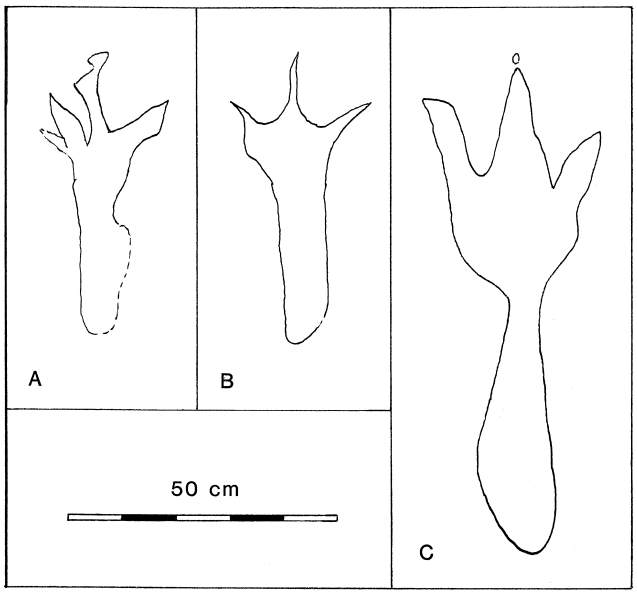

FIG. 9. Cretaceous tracks with metatarsal impressions from the Glen Rose Formation Texas. **A.** and **B.** redrawn after Kuban (1989, Figs 7.5 B, C); **C.** redrawn after Pittman (1989, Fig. 15.8E).

of which occurred as part of distinct trackways. However, in many of these tracks the anterior tridactyl portion of the track was obscured, either by the slumping of sediment into the digit impressions or by subsequent erosion. Thus the utility of the tracks for accurate morphological measurement of footprint and metatarsal dimensions is compromised. The best examples, in which a reasonably clear track with metatarsal impressions is provided, with accurate scale are probably those illustrated by Kuban (1989, Figs. 7.5 B, C) and a track from the same formation illustrated by Pittman (1989, Fig. 15.8E). These three examples are compared at the same scale in Fig. 9.

UNDERSTANDING THE WU MA CUN ICHNOTAXONOMY

The Wu Ma Cun sites are both intriguing and problematic owing to the profusion of new ichnotaxa (six ichnogenera and species!) reported by Yang and Yang (1987) and the crouching traces and probable tail traces. Current evidence suggests that only the Connecticut Valley and Wu Ma Cun sites reveal "complete" crouching theropod traces (with paired metatarsal and pes impressions and ischial/pelvic traces). If this is so we must ask whether this crouching behavior is characteristic of particular Lower Jurassic species, genera or higher-level clades, or whether the co-occurrence of such traces in rocks of about the same age is merely fortuitous. The sandstones of the Xin Tian Gou Formation are probably late Early Jurassic in age, based on a classic *Anomoepus-Grallator-Eubrontes* track assemblage found at several sites in the formation in the Sichuan Basin (Matsukawa et al., 2002). Though the age is often given as basal Middle Jurassic in the Chinese literature (e.g., Yang and Yang, 1987) there is no compelling, independently derived fossil evidence that this age determination is correct.

We should also note that the Wu Ma Cun crouching traces (Figs. 3 and 4) are significantly larger than the Connecticut Valley traces. This would tend to argue in favor of the traces being associated with a large *Eubrontes*-like ichnospecies rather than with a smaller *Grallator*-like form as in the latter case. The shape of the ischial callosity is also different being sub-triangular rather than sub crescentic or heart-shaped (compare Fig. 1 with 3 and 4). The anterior pelvic, presumably pubic, trace is poorly defined in both the Connecticut and Sichuan samples. The only observable difference apart from size is that the relative distance between the two pelvic traces is slightly less in the larger, Chinese specimen. Similarly, the Chinese specimen is evidently associated with tail traces. Though preservation of many of the traces at the site is indistinct, the crouching traces and apparent associated tail and foot traces are reasonably clear, and were recorded at 1:1 scale by tracing a six-meter segment with clear acetate film.

Based on the map of the site (Fig. 5), the crouching traces are associated with a trackway that runs from northwest to southeast. It is interesting to note that the original map (Yang and Yang, 1987) reveals a normal walking trackway leading up the crouching traces, but no continuation of tracks beyond that point. This evidence is open to either preservational or behavioral interpretation. Also of interest is that there is a second trackway parallel to the crouching traces. Eight of the tracks from this trackway have been removed to local museums. There are four other trackways with this general NW-SE or SE-NW trend. These may be indicative of a shoreline trend. We should also note that the Wu Ma Cun site is quite a large area on the order of 30 x 40 m of sub-horizontal bedding plane. It is situated in a humid subtropical latitude. Three factors have contributed to the deterioration of the site: first, the removal of original specimens, second the subtropical weathering, and third, the habit of using the large flat surface as a threshing floor for the drying and processing of rice and other grains.

As noted above the Wu Ma Cun site is the type locality for tracks assigned to the ichnospecies *Zizhongpus wumanensis*, *Chonglongpus hei*, *Tuojiangpus shuinanensis* and *Chuannchengpus wuhuangensis* (Yang and Yang, 1987). In order to give the reader a clear indication of the quality of material used as the basis of these ichnotaxa, they are all illustrated (Fig. 5) at the same scale, along with the two ichnotaxa (*Megaichnites jizhaishiensis* and *Chongqingpus microiscus*) from nearby Wu Ma Cun locality B.

Although it is probable that all of these ichnotaxa can be assigned to *Grallator*, *Eubrontes* or some similar, well-known ichnotaxon such as *Anchisauripus* or *Kayentapus*, the Chinese names, although unfamiliar to many ichnologists cannot be dismissed. There has been a tradition, especially in reference to Lower Jurassic ichnofaunas, of attempting to synonymize such

relatively obscure and recently proposed names with better-known ichnotaxa from the Connecticut Valley (Hitchcock, 1858; Lull, 1953, and reference therein). For example, Olsen and Galton (1984) attempted to synonymize many of Ellenberger's southern Africa ichnotaxa with those from the Connecticut Valley region, though this "broad-brush stroke" approach has been criticized (Lockley and Meyer, 2000) for failing to look at the actual southern African material. Similarly Gierlinski (1994) synonymized 39 ichnogenera (representing a considerably larger number of ichnospecies) under the single ichnogenus *Grallator*. This is again too broad a brush-stroke approach and is not valid without some level of comparative study of diagnoses and descriptions. Although these "lumping" approaches acknowledge the widely recognized fact that all theropod tracks are somewhat similar, it can be shown to be patently selective and unrigorous in attention to detail. For example, all six ichnogenera from Wu Ma Cun are missing from Gierlinski's list though some (notably *Chongqingpus microiscus*) are very obviously synonyms of *Grallator*. The reason for this omission appears to be that the relevant literature (Yang and Yang, 1987) is in Chinese, whereas other Chinese tracks, described in papers in the English language, are included. As noted by Lockley (2000), there has been considerable variation and inconsistency in the scientific approach adapted to the study of theropod footprints.

Owing to the necessity to at least be aware of tracks that may be relevant to a study such as this, and that fact that several (highlighted in **bold**) have metatarsal impressions, discussed herein, a complete list of the 39 purported *Grallator* synonyms cited by is given below (see Gierlinski and references therein, 1994)

Abelichnus, Anchisauripus, Apatichnus, Bressanichnus, Byakudansauripus, Columbosauripus, Coelurosaurichnus, Changpeipus, Defferrariichium, Deuterotrisauropus, Dilophosauripus, Eubrontes, Gigantipus, Hyphepus, Irenesauripus, Itsukisauropus, ***Jialingpus****, Kayentapus, Kleitotrisauropus, Komlosaurus, Kuwajimasauropus, Masitisauropus, Megalosauropus,* ***Megatrisauropus****, Neotrisauropus, Otouphepus, Paracoelurosaurichnus, Picunichnus, Platytrisauropus, Prototrisauropus, Qemetrisauropus, Saltopoides, "Sauropous," Schizograllator, Skartopus, Stenonyx, Talmontopus, Youngichnus, and Zhengichnus.*

For the purposes of this paper it is only necessary to discuss the characteristics and validity of the six ichnotaxa from the Wu Ma Cun area (which are not included in Gierlinski's list). As shown in Fig. 6, the original illustrations show a range of size and morphology that can be related to varying degrees to better know ichnotaxa such as *Grallator* and *Eubrontes*. Dealing with each ichnospecies in turn we reach the following conclusions:

Chonglongpus hei from Wu Ma Cun site A (Fig. 6A) is a large, *Eubrontes*-like track that sometimes shows a medially directed hallux. For this reason the tracks are comparable to the ichnogenus *Gigandipus*, which also has a hallux in a similar position, and is included in the ichnofamily Gigandipodidae by Yang and Yang (1987). Our tracing of the best-preserved tracks (Fig. 6A′) indicates that the tracks show a typical 2-3-4 phalangeal formula for digits II, III, and IV. This highlights the similarity with *Gigandipus* and perhaps suggests that the new combination *Gigandipus hei* might be appropriate.

Megaichnites jizhaishiensis from Wu Ma Cun site B (Fig. 6B) is drawn as a wide-toed track with digit width expanding anteriorly, and included in the ichnofamily Eubrontidae by Yang and Yang (1987). Our tracings indicate an entirely different and more typical theropod track configuration, with phalangeal pad impressions. The track resembles that of a large grallatorid, eubrontid or possibly *Kayentapus*.

Tuojiangpus shuinanensis from Wu Ma Cun site A (Fig. 6C) was included in the ichnofamily Anchisauropodidae by Yang and Yang (1987). We were unable to locate the type of this tridactyl track, but we consider that without details of pad configuration, it does not warrant being recognized as a new ichnogenus. We therefore consider it similar to *Eubrontes* and refer to it herein as *Eubrontes* sp.

Zizhongpus wumanensis from Wu Ma Cun site A (Fig. 6D) is poorly preserved and was included in the ichnofamily Anchisauropodidae by Yang and Yang (1987). The type material consists of three narrow digit impressions without traces of phalangeal pads. The general configuration is similar to so called *Megaichnites jizhaishiensis*, which in turn we consider indistinguishable from a large grallatorid or *Kayentapus* like form.

Chongqingpus microiscus from Wu Ma Cun site B (Fig. 6E) is in our opinion a classic example of a small *Grallator* (foot length 9–12 cm). It was included in the ichnofamily Anchisauropodidae by Yang and Yang (1987).

Chuannchengpus wuhuangensis from Wu Ma Cun site A (Fig. 6F) is too poorly preserved to be diagnostic, though it was included in the ichnofamily Anomoepidae by Yang and Yang (1987). The photograph provided by Yang and Yang (1987) shows that the diagram (Fig. 6F) is an inaccurate representation. It can be clearly seen that the type specimen has the typical outline of a *Grallator* track (Fig. 6F'). However *Anomoepus* tracks are also known from this horizon at several sites in the region (Fig 6F'').

In the final analysis it is clear that Yang and Yang (1987) recognized that the tracks from Wu Ma Cun (sites A and B) represent representatives of the theropodan ichnofamilies Anchisauripodidae (*Grallator* and cf. *Kayentapus*), Eubrontidae (*Eubrontes*) and Gigandipodidae (*Gigandipus*). We also recognize the ornithopod ichnofamily Anomoepididae (cf. *Anomoepus*). Thus, this ichnofauna is similar to classic Liassic faunas from around the world such as the well-known Connecticut Valley assemblage. It also means that most of the tracks from Wu Ma Cun are probably junior synonyms of better-known taxa, or *nomina dubia* because they are not diagnostic beyond the level of being considered of theropod affinity.

To summarize we suggest the following synonymies:

Chonglongpus hei (ichnofamily Gigandipodidae) = *Gigandipus hei* (comb nov.)
Megaichnites jizhaishiensis (ichnofamily Eubrontidae) = cf. *Kayentapus* sp.
Tuojiangpus shuinanensis (ichnofamily Anchisauropodidae) = cf. *Eubrontes* sp.
Zizhongpus wumanensis (ichnofamily Anchisauropodidae) = cf. *Kayentapus* sp.
Chongqingpus microiscus (ichnofamily Anchisauropodidae) = *Grallator* sp.
Chuannchengpus wuhuangensis (ichnofamily Anomoepidae) = *Grallator* sp.
cf. *Anomoepus* also identified in the region

This ichnotaxonomic discussion is a necessary prerequisite to understanding the Wu Ma Cun ichnofauna in its global context, and, moreover, it allows us to conclude that the crouching dinosaur must be associated with one of the larger theropod ichnogenera (i.e., with *Kayentapus*, *Eubrontes* or *Gigandipus*). We stress, however, that formal revision of the Chinese ichnotaxa, like our preliminary conclusions, should be based on a case-by-case examination of the type material.

DISCUSSION AND CONCLUSIONS

The nomenclature surrounding classic Connecticut Valley tracks is complex. As pointed out by Lull (1953) the original specimens of crouching bipedal dinosaurs, which Lull finally assigned to *Sauropus barrattii*, underwent as many as ten name changes prior to the work of Gierlinski (1994) who assigned the two different specimens (AC 1/1 and 1/7) to *Grallator (Eubrontes) tuberosus* and *Grallator (Eubrontes) minisculus* respectively (Fig. 1). We leave the question of nomenclature open, but agree with Gierlinski that the tracks are of theropodan **not** ornithopodan affinity (i.e., they are not of the *Anomoepus* type), as suggested by many authors (Thulborn, 1990). However, we disagree with Gierlinski (1994) regarding the crouching posture of specimen AC 1/1 (Fig. 1), and infer that it must have been symmetric not asymmetric.

There are a number of examples of crouching ornithopod tracks assigned to *Anomoepus* in North America (Lull, 1953) and to *Moyenisauripus* in southern Africa (Ellenberger, 1974). *These should not be confused with crouching theropod tracks*, especially if there are associated manus impressions, or where the pes pad impressions and digit divarication patterns are well preserved. Theropod metatarsal impressions, like the footprint itself are generally more elongate that those associated with ornithopod ichnites. This follows a morphodynamic (or heterochronic) rule (*sensu* Lockley 1999,a, b, 2000a) involving is a compensation between long feet and short legs (in theropods) and shorter feet and longer legs (in ornithopods) as also indicated by Thulborn (1990).

The Wu Ma Cun crouching theropod is the first known example reported since the work of Hitchcock, and hence only the third on record. It provides evidence that large theropods exhibited crouching behavior, and that at least one type produced ischial callosities with sub triangular rather than sub crescentic or heart-shaped outlines. The ichnotaxonomy surrounding early-mid Jurassic Chinese theropod tracks is also complex, at least at the ichnogenus level, though Chinese workers have recognized similarities between Chinese and North American footprints at the ichnofamily level (Yang and Yang, 1987). However, like the ichnotaxonomy of the Connecticut Valley, Chinese theropod track ichnotaxonomy appears to be largely resolvable into a small number of well-known ichnogenera such as *Grallator* and *Eubrontes* and related forms such as *Anchisauripus* and *Gigandipus*. Thus the Wu Ma Cun crouching theropod may be allied to the well-known ichnogenus *Eubrontes*, or perhaps *Gigandipus*. Further study of the Wu Ma Cun site would be desirable before it is further deteriorated and damaged by erosion.

The behavior of theropod dinosaurs that left metatarsal impressions has been discussed by Kuban (1989) who suggested that the trackmakers may have been stalking or crouching close to the ground as part of their hunting or stalking behavior. However, Kuban (1989) dealt primarily with dinosaurs that were walking (i.e., in continuous motion) over soft substrates. Crouching evidently represents a different form of behavior, associated with firmer substrates in known examples, which would have brought the dinosaur to rest, at least temporarily. Such behaviors might indicate resting or possibly crouching to drink or feed. Traces created by theropod manus tracks are rare, even in association with crouching traces (Fig. 1), though McCrea et al. (2002) cite a recent discovery from the Cretaceous of Canada. The possibility of finding additional crouching traces may shed light on morphology of the manus, metapodium and pelvis and perhaps to give further insight into theropod behavior. Ultimately such trace fossil evidence of morphology proximal to the foot of bipedal dinosaurs has the potential to add to our knowledge of morphology of the trackmakers, and also to expand or amend the ichnotaxonomic descriptions of such footprints.

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