Harris et al., eds., 2006, The Triassic-Jurassic Terrestrial Transition. New Mexico Museum of Natural History and Science Bulletin 37.

EVAZOUM AND THE RENAMING OF NORTHERN HEMISPHERE "*PSEUDOTETRASAUROPUS*": IMPLICATIONS FOR TETRAPOD ICHNOTAXONOMY AT THE TRIASSIC-JURASSIC BOUNDARY

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Abstract—*Evazoum* is a new ichnogeneric name recently proposed for small, tetradactyl tracks from the Upper Triassic of Italy that can also be applied to various tracks in the Northern Hemisphere (especially western Europe and the western United States). *Evazoum* resembles the larger *Otozoum* and *Pseudotetrasauropus,* which are based on type material from the Lower Jurassic of North America and the Upper Triassic of southern Africa, respectively. Recently, the status of these ichnogenera, and related forms such as *Kalosauropus*, has been debated, and the probable prosauropod affinities of the track makers discussed. We draw attention to this *Otozoum-Pseudotetrasauropus-Evazoum-Kalosauropus* (OPEK) plexus and suggest that all of these ichnogenera can be accommodated in the previously-named ichnofamily Otozoidae Lull.

Reanalysis of the type material of *Pseudotetrasauropus* suggests that this ichnotaxon is not known from the Northern Hemisphere. Thus, *Evazoum* is arguably a distinct form, and tracks fitting its description from Europe and North America should no longer be assigned to *Pseudotetrasauropus*. However, ongoing studies suggest that there is still confusion over differences between *Otozoum* and *Pseudotetrasauropus*, both of which are large tracks that show some evidence of quadrupedal progression, and between *Evazoum* and *Kalosauropus*, both of which are small tracks that represent bipeds.

Reanalysis of the type material of *Tetrasauropus*, from southern Africa, has also led to the conclusion that this ichnogenus is rare or unknown in the Northern Hemisphere, and that somewhat similar forms referred to *Tetrasauropus* can be reassigned to the new ichnogenus *Eosauropus.* The reassignment of putative Northern Hemisphere *Pseudotetrasauropus* tracks to *Evazoum* and putative Northern Hemisphere *Tetrasauropus* tracks to *Eosauropus* has significant implications for our understanding of the differences between Southern and Northern Hemisphere tetrapod ichnofaunas during the Late Triassic and Early Jurassic.

INTRODUCTION

In this paper we address the recent proposals of Nicosia and Loi (2003) that: (1) named small, tetradactyl tracks from the Upper Triassic of Italy *Evazoum*, and (2) applied this name to other, similar tracks from the Northern Hemisphere. These small track types, which occur outside of Italy in the Upper Triassic of Europe and North America (Lockley et al., 1996 and Lockley and Hunt, 1995, respectively), had previously been compared with *Pseudotetrasauropus* from southern African (Ellenberger, 1972, 1974). Likewise, Lockley and Meyer (2000) also noted that Ellenberger's ichnogenus *Kalosauropus* is very similar to some tracks found in Europe and North America. The Italian research group (Nicosia and colleagues) has undertaken a revision of the type material of *Pseudotetrasauropus* and *Tetrasauropus* from southern Africa (D'Orazi Porchetti and Nicosia, 2004, in press), concluding that these forms are distinct from any identified with confidence in the Northern Hemisphere. We find their conclusions compelling and favor transferring most putative examples of Northern Hemisphere *Pseudotetrasauropus* tracks to *Evazoum*. However, such a transfer does not necessarily validate transfer of *all Pseudotetrasauropus* tracks to *Evazoum* without considering each individual case. It is necessary to consider the following: (1) *Evazoum* is similar to *Kalosauropus* (which is, in turn, of dubious ichnotaxonomic status [D'Orazi Porchetti and Nicosia, in press]); (2) according to Rainforth (2003), *Kalosauropus* is a synonym of *Otozoum*; and (3) there is a possibility that some putative North American *Pseudotetrasauropus* tracks are extramorphological variants of chirothere tracks (Klein et al., this volume). These factors preclude a simple transfer of all North American *Pseudotetrasauropus* to *Evazoum*. Thus, ichnotaxa included in the *Otozoum-Pseudotetrasauropus-Evazoum-Kalosauropus* (OPEK) plexus are complexly inter-related and need to be understood morphologically, extramorphologically, ichnotaxonomically, and in terms of their spatio-temporal distribution.

In a companion paper (Lockley et al., this volume), we propose the new ichnogenus *Eosauropus* for Northern Hemisphere tracks previously referred to as *Tetrasauropus*. We suggest that the present article on the "OPEK plexus" should be read in conjunction with that paper, Klein et al. (this volume), and the contributions of Nicosia and Loi (2003), D'Orazi and Nicosia, (2004, in press) and Rainforth (2003) on European, North American and southern African material. These studies introduce some significant but contradictory changes in the ichnotaxonomy of important tracks. Collectively, this flurry of ichnotaxonomic activity permits further important observations about the global distribution of these tracks and their purported track makers.

It is now becoming clear that Late Triassic and Early Jurassic ichnofaunas from Europe, North America, and southern Africa are more diverse and complex than previously assumed. This diversity, reflected in size and morphology, and, as a result, ichnotaxonomy, suggests genuine differences between Southern and Northern Hemisphere ichnofaunas that are not easily dismissed as a consequence of mere provincial ichnotaxonomy (e.g., compare Olsen and Galton [1984] with Rainforth [2003] and D'Orazi Porchetti and Nicosia [in press]). Thus, despite recent positive contributions, the ichnotaxonomy of some components of these ichnofaunas is still in a state of flux. Although many authors favor a sauropodomorph affinity for many of the track types of the OPEK plexus, this interpretation is open to question. This and other inferences are discussed below.

Institutional Abbreviations: AC, Amherst College, Amherst, Massachusetts; CU, University of Colorado at Denver Dinosaur Tracks Museum, Denver, Colorado; CU-MWC, joint CU Denver and Museum

of Western Colorado collections; NMMNHS, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico; UM, University of Montpellier, Montpellier, France.

HISTORICAL BACKGROUND

Although Ellenberger lacked easy access to Northern Hemisphere literature while isolated in southern Africa, he was aware, nevertheless, of the similarity between some tetradactyl footprints from southern African and those named from North America in the classic studies of Hitchcock (1858) and Lull (1953). For example, he regarded some of the southern African tracks he named *Pseudotetrasauropus* as similar to *Otozoum* (Ellenberger and Ellenberger, 1958; Ellenberger et al., 1969; Ellenberger, 1970; Rainforth, 2003; D'Orazzi Porchetti and Nicosia, 2004, in press; Lockley et al., this volume). This evident similarity prompted Olsen and Galton (1984) to revise Ellenberger's ichnotaxonomy and make extensive comparisons based on a survey of illustrations and descriptions in the literature. They synonymized many of the ichnotaxa from the two regions. For example, they inferred that *Pseudotetrasauropus* was a bipedal variant of *Brachychirotherium*. Without undertaking formal ichnological revisions, they outlined broad ichnofamilial groupings, such as the Chirotheriidae (Abel, 1935), into which they placed many of Ellenberger's ichnospecies. As noted by Lockley and Meyer (2000), Olsen and Galton adopted the "lumper" approach as a reaction to the "splitter" approach of Ellenberger.

Subsequent work on *Otozoum* and *Pseudotetrasauropus* by Rainforth (2003) suggested that the two forms are, in fact, distinct both morphologically and in their temporal distribution. She considers that *Pseudotetrasauropus* should be maintained as a valid ichnogenus, but, conversely, that it may be a junior synonym of *Brachychirotherium*. The former claim has been supported by D'Orazi Porchetti and Nicosia (in press), but the latter claim cannot be supported because the two ichnogenera are entirely different. Previously, we agreed with Rainforth (2003) that *Pseudotetrasauropus* is present in the Triassic of the Northern Hemisphere, but is distinct from *Otozoum*. In contrast, according to Nicosia and Loi (2003), Southern Hemisphere *Pseudotetrasauropus* is distinct from the Northern Hemisphere ichnogenus *Evazoum*. Both of these studies tended toward splitting rather than lumping, even though they were not in full ichnotaxonomic agreement.

Here we address the legacy of the perception that common elements exist between North American and southern African ichnofaunas. This perception encouraged ichnologists working in the western USA, such as ourselves, to apply some of Ellenberger's ichnotaxonomic labels to problematic tracks that had not previously been given names (see Lockley and Hunt, 1995 for summary). Most notable among these borrowings were the ichnogenera *Tetrasauropus* and *Pseudotetrasauropus*, which Ellenberger (1972, 1974) had split into many ichnospecies. Fortunately, given the recent revisions by Nicosia and Loi (2003) and D'Orazi Porchetti and Nicosia (in press), these southern African ichnotaxonomic names were never formally applied in North America or Europe. Thus, no new ichnospecies were named and no new type material was designated.

This cautious approach now allows us, where appropriate, to assign tracks previously compared or assigned to *Pseudotetrasauropus* (ispp.) to the new ichnogenus *Evazoum*. We generally concur with the ichnotaxonomic revisions of the Italian group, at least as they apply to *Tetrasauropus*, *Pseudotetrasauropus*, and *Evazoum* (Nicosia and Loi 2003; D'Orazi Porchetti and Nicosia, 2004, in press; Lockley et al., this volume) and provide a list of figured specimens that can be provisionally transferred to the ichnogenus *Evazoum.* We do not attempt, at this point, to ascertain whether a given specimen can or cannot be referred to the type and only described ichnospecies of *Evazoum*: i.e., *E. sirigui*.

List of North American Published Material Now Provisionally Attributable to *Evazoum* Nicosia and Loi (2003)

Pseudotetrasauropus: Lockley et al., 1992, fig. 2B

"the first recognition of the purported prosauropod track *Pseudotetrasauropus* in the Chinle Group": Lockley and Hunt, 1993, p. 283

Possible prosauropod footprint (*Pseudotetrasauropus*): Farlow and Lockley, 1993, fig. 5

Pseudotetrasauropus?: Lockley et al., 1996, fig. 7 (left and center)

Pseudotetrasauropus: Hunt et al., 2000, fig. 1

Kalosauropus (cf. *Pseudotetrasauropus*): Lockley and Meyer, 2000, fig. 4.9

Pseudotetrasauropus: Lockley et al., 2000, figs. 2, 3 and 5

Pseudotetrasauropus: Lucas et al., 2001, figs. 2D, E and 4A-C

Pseudotetrasauropus: Lockley et al., 2001, fig. 2A.

Pseudotetrasauropus: Lockley and Peterson, 2002, p. 51.

Pseudotetrasauropus-like tracks: Gaston et al., 2003, fig. 8.

Evazoum Nicosia and Loi, 2003, figs. 7-9.

Pseudotetrasauropus: Rainforth, 2003, pl. 1, figs. 4-5.

"*Pseudotetrasauropus*": D'Orazi Porchetti and Nicosia, in press, fig. 22b-d.

DISCUSSION

As knowledge of tracks from the Upper Triassic of the western United States and Europe grew, and the names *Tetrasauropus* and *Pseudotetrasauropus* were adopted, questions concerning the meaning and validity of these labels came under increased scrutiny. Lockley et al. (2001) noted that North American specimens of "*Tetrasauropus*" differ from southern African specimens of *Tetrasauropus* and that this ichnotaxon was in need of revision; this has been undertaken by Lockley et al. (this volume). Likewise, various authors have examined Ellenberger's collection of replicas in the University of Montpellier (Lockley and Meyer, 2000; Rainforth, 2003; D'Orazi Porchetti and Nicosia, in press) to try to better understand tracks belonging to what we call the OPEK plexus. As a result, advances have been and are being made in our understanding of these ichnotaxa that are leading to a series of formal and informal ichnotaxonomic revisions and interpretations, including those proposed here. Examples of such revisions and interpretations include:

1) the formal revision of *Tetrasauropus* and *Pseudotetrasauropus* and a few other associated ichnotaxa (D'Orazi Porchetti and Nicosia, in press) based on significant but incomplete type material in the Montpellier collections, plus confirmation that *Tetrasauropus* and *Pseudotetrasauropus* are quite different from each other and that the latter is similar to, but not necessarily identical to, *Otozoum* (Lockley and Meyer, 2000; Rainforth, 2003; D'Orazi Porchetti and Nicosia, in press). Despite these differences, it has been suggested that both may represent sauropodomorphs, but this is not universally agreed upon;

2) rejection of some *Pseudotetrasauropus* ichnospecies as unlike the type material; these "atypical" ichnospecies represent other, quite different ichnotaxa, such as chirotheres (Lockley and Meyer, 2000; D'Orazi Porchetti and Nicosia, in press; Klein et al., this volume);

3) recognition that small, *Pseudotetrasauropus*-like ichnites of previously uncertain ichnotaxonomic assignment, including a southern African form named *Kalosauropus*, are distinct from large *Pseudotetrasauropus*, *Otozoum* and *Brachychirotherium*, and that these small forms occur in both North America and Europe;

4) the formal naming of *Evazoum* (Nicosia and Loi, 2003) for small, tetradactyl tracks from Europe that had previously been informally labeled as resembling *Pseudotetrasauropus*, *Kalosauropus* or *Otozoum*;

5) synonymy of *Kalosauropus* with *Otozoum* (Rainforth, 2003), implying that the former is not congeneric with *Pseudotetrasauropus* (or *Evazoum*);

6) the naming of *Eosauropus* to describe North American tracks previously labeled as *Tetrasauropus* (Lockley et al., this volume); and

7) recognition that an *Evazoum*-like, "didactyl" morph is known

from several localities in the Gateway area of Colorado (previously referred to as "*Pseudotetrasauropus*-like": Gaston et al., 2003). This track morph resembles tracks reported by Olsen and Gore (1989) from the Upper Triassic Wolfville Formation of Paddy Island, Nova Scotia, originally referred to *Coelurosaurichnus* sp. B (Olsen et al., 1989, fig. 10.2B). This same track type in the Passaic Formation of New Jersey was referred to as "?saurischian dinosaurian track 'new genus 1'" (Olsen and Rainforth, 2003, fig. 51E, p. 140). We agree that these tracks require a new ichnotaxonomic designation, and the material is presently under study (Olsen and Lockley, in preparation). As noted below, preliminary observations (Olsen and Lockley, unpublished data) suggest that this track type is similar to *Evazoum* except that in addition to the absence of an impression of digit I, digit II is not impressed distally, or represented only by a claw trace, thus strongly emphasizing the digits III and IV.

The ichnotaxonomy of the OPEK plexus is complex. There are many arguments that support some degree of synonymy among these four ichnogenera (OPEK plexus), and for this reason we propose that they all be included in the existing ichnofamily Otozoidae (Lull, 1904), which originally contained only the ichnogenus *Otozoum*. The revised diagnosis for this ichnofamily, given below, accommodates the four OPEK plexus ichnogenera and demonstrates the complexity of the ichnofamily that is now evident from the diversity of morphologies described in recent years. Several authors have argued for taxonomic differences between the ichnogenera based on morphological criteria such as the number of pad impressions in digit IV. Likewise, some ichnogenera have associated manus prints, whereas others do not. In addition, the type specimens of these ichnogenera have different geographic and stratigraphic contexts that convey interesting evolutionary and paleobiogeographical information. In order to clearly frame these issues, we offer the following summaries of the relevant ichnogenera.

Otozoum (Hitchcock, 1847)

Otozoum was the first named OPEK plexus track; the type material consists of large (pes length 49 cm) tracks from the Lower Jurassic Portland Formation of the eastern USA. In a recent review of the ichnogenus, Rainforth (2003) recognized the type species (*O. moodii*) as the only valid Northern Hemisphere ichnospecies of this ichnogenus. However, she based her description on a pes specimen (lectotype, AC 4/1) from one trackway, and a manus specimen (AC 5/14) from a different trackway (Fig. 1). A specimen from the Lower Jurassic of Utah (CU 184.41, Fig. 2) reveals new information about the *Otozoum* manus, i.e., indicating that it is pentadactyl, not tetradactyl. Rainforth proposed that the southern African ichnospecies *Kalosauropus pollex* (Ellenberger, 1970, 1972) should be transferred to *Otozoum*, thus producing the new combination *O. pollex*.

Pseudotetrasauropus (Ellenberger, 1972)

This ichnogenus was based on large tracks (pes length 40-50 cm) from the Upper Triassic Molteno Formation of southern Africa (Fig. 3). Originally consisiting of eight ichnospecies, of which six were purportedly bipeds and two quadrupeds, the type material has since been emended and consolidated by D'Orazi Porchetti and Nicosia (in press) into a single ichnospecies: *P. bipedoida* although some forms were originally attributed to quadrupeds, as the ichnospecies name implies, the revised description omits any mention of an associated manus trace.

Kalosauropus (Ellenberger, 1970, 1972)

Erected for a small track (foot length 7-9 cm, based on UM2 LES232-3, LES233 and LES234; Fig. 4) from the Lower Jurassic Clarens Formation of Lesotho, this ichnogenus was regarded as similar to *Pseudotetrasauropus* (Lockley and Meyer, 2000) and synonymized with *Otozoum* by Rainforth (2003) in part because of her claim that the name is a *nomen nudum*.

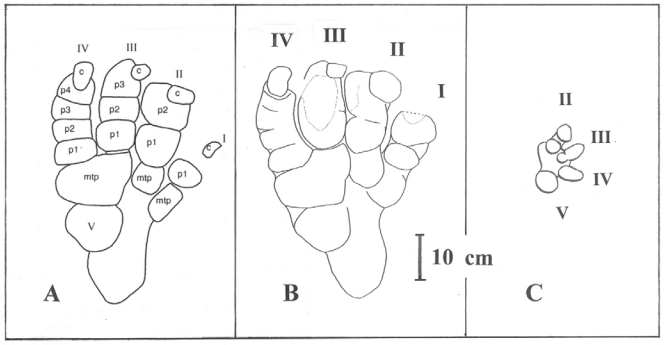

FIGURE 1. **A**, Stylized *Otozoum*, after Rainforth (2003, fig. 2A) showing interpretation of arrangement of digital phalangeal and metatarsal-phalangeal pads. **B**, Type *Otozoum* pes AC 4/1, after Rainforth (2003, fig. 3D). **C**, Type *Otozoum* manus AC 5/14, after Rainforth (2003, fig. 3D).

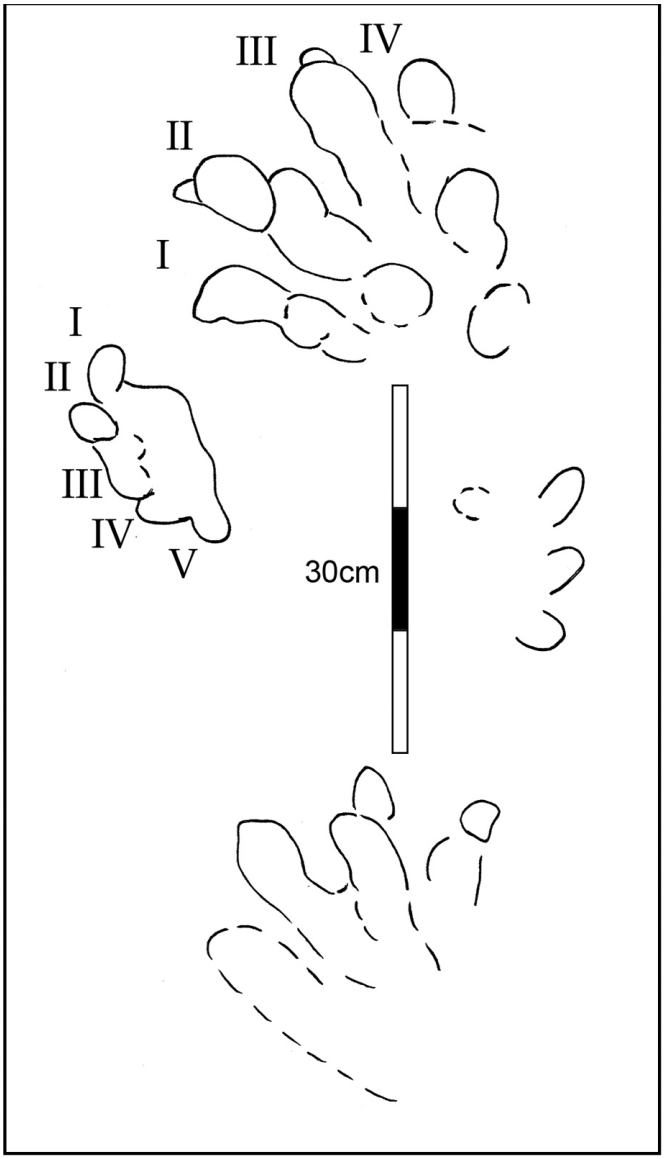

FIGURE 2. *Otozoum* trackway, based on specimen CU 184.41 from the Navajo Sandstone near Moab, Utah, showing a pentadactyl manus and moderately divergent pedal digit impressions.

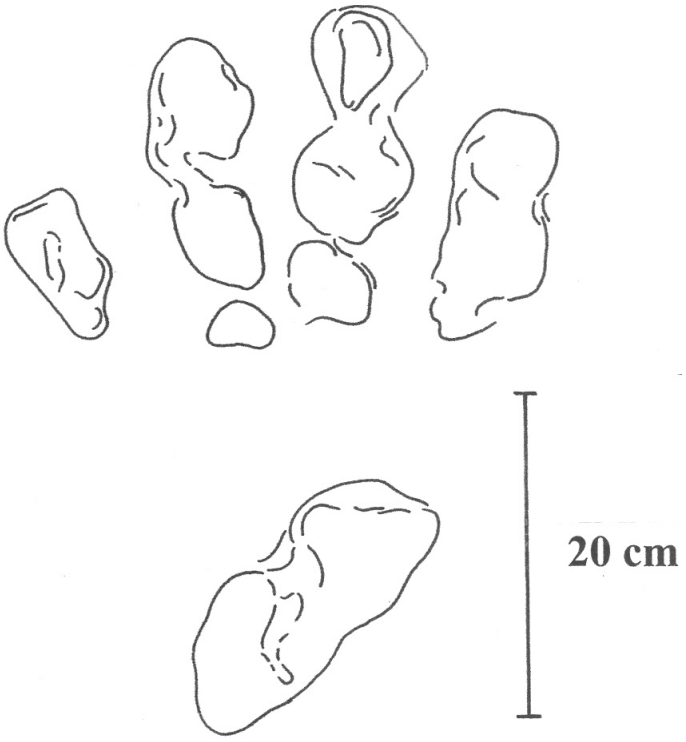

FIGURE 3. Type *Pseudotetrasauropus bipedoida*, after D'Orazi Porchetti and Nicosia (in press).

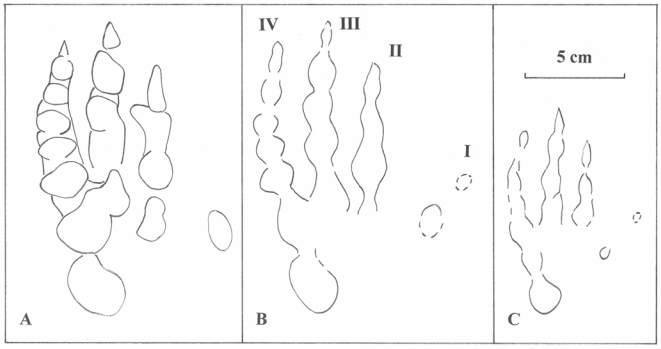

FIGURE 4. Type *Kalosauropus pollex*. **A**, UM2 LES232-3 after Rainforth (2003). **B**, UM2 LES232-3 after Lockley and Meyer (2000). **C**, UM LES234 after Lockley (unpublished data).

Evazoum (Nicosia and Loi, 2003)

Evazoum is based on small tracks (footprint length 10.5 cm) from the Upper Triassic (Carnian) Montemarcello Formation of northern Italy (Fig. 5). Nicosia and Loi (2003) acknowledged that the track is very similar to *Kalosauropus* and similar-sized small tracks referred to *Pseudotetrasauropus* in the Northern Hemisphere, particularly in the western United States (Lockley and Hunt, 1995; Lockley and Meyer, 2000), including at least two examples of trackways (Fig. 6) and one possible trackway segment with what appears to be an isolated manus track (Fig. 7). However, Hendrik Klein (personal commun.) and Klein et al. (this volume) infer that this is an artifact of preservation and not a true manus track. *Evazoum* ostensibly differs from *Kalosauropus* and *Otozoum* by having more splayed digits and having a larger trackway width, and from *P. bipedoida* in the shapes of the digits and presence of claw impressions (Nicosia and Loi, 2003).

Collectively, these observations suggest that these OPEK ichnospecies can be divided into large (O and P) and small (E and K) forms. The large forms may include both manus and pes prints, but, based on described specimens, the small forms were exclusively made by bipeds.

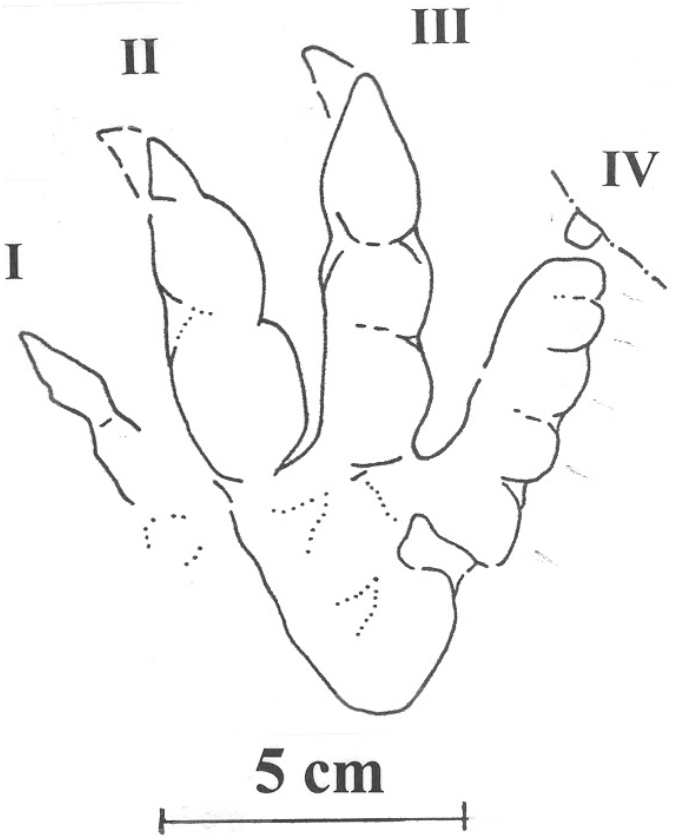

FIGURE 5. Type *Evazoum sirigui,* after Nicosia and Loi (2003).

According to Lockley and Meyer (2000), at least two small Upper Triassic tracks from Colorado (Fig. 8) are similar to *Kalosauropus*, and comparable to the European tracks formally named *Evazoum* by Nicosia and Loi (2003). These Colorado tracks were transferred to *Otozoum* by Rainforth (2003). These same tracks, and additional specimens from Colorado and New Mexico, were referred to as "*Pseudotetrasauropus*-like" didactyl tracks by Gaston et al. (2003). Strictly speaking, these are not fully didactyl in all cases. However, they apparently show retraction of digit II, which has a distinctive, enlarged proximal pad (Fig. 8), and digit I is not impressed. Although these tracks have already been compared to all the OPEK plexus ichnogenera, it is outside the scope of this paper to give these tracks a formal ichnotaxonomic label. However, as noted above, very similar tracks have been reported from the Upper Triassic of Nova Scotia and New Jersey and are currently under investigation. Because of their relationship to the OPEK plexus, these tracks are illustrated for comparative purposes (Fig. 8).

Some authors have suggested that *Otozoum* and *Pseudotetrasauropus* are synonymous (e.g., Haubold, 1971; Gand et al., 2000). For example, Lockley and Meyer (2000, p. 89) inferred that "*Pseudotetrasauropus* is essentially identical to *Otozoum*," but did not propose a formal synonymy. However, this position was not supported by Rainforth (2003), who claimed four means of distinguishing the two ichnogenera:

(1) Rainforth (2003, p. 823) argues that "in contrast to *Otozoum*, *Pseudotetrasauropus* has 4 rather than 5 phalangeal (including claw) pads on digit IV." There is no unequivocal support for this claim; the revised description of *Pseudotetrasauropus* (D'Orazi Porchetti and Nicosia, in press) contains no mention of digit IV pads (see discussion below);

(2) "the metatarsal-phalangeal pads on digits III and IV in

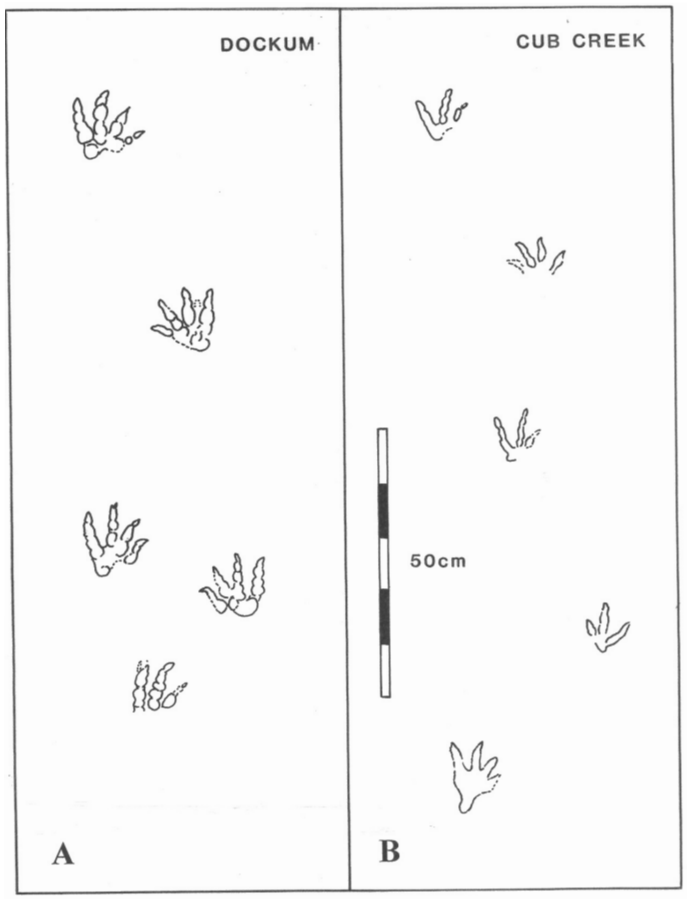

FIGURE 6. *Evazoum* trackways previously referred to as *Pseudotetrasauropus* (*sensu* Lockley and Hunt, 1995), from the Chinle Group of New Mexico and Utah.

Pseudotetrasauropus remain discrete, rather than coalesced," a contention supported by D'Orazi Porchetti and Nicosia (in press). We consider that this distinction may be valid, but it could equally well be a function of differential preservation.

(3) greater digit divarication of digits III and IV in *Pseudotetrasauropus*; and

(4) a relatively longer digit I in *Otozoum*.

Criteria (3) and (4) could be attributed to differential preservation or individual variation, although D'Orazi Porchetti and Nicosia (in press) support the third criterion and suggest that differences in weight distribution and track depth can be discerned. Again, we consider that this distinction may be valid, but advocate caution in the use of such subtle criteria. In our opinion, given that type *Otozoum* (with skin impressions) is much better preserved than type *Pseudotetrasauropus* (*sensu* D'Orazi Porchetti and Nicosia, in press), such criteria are tenuous, especially as the basis for ichnotaxonomic differentiation at the ichnogenus level. Indeed, we know of no compelling example of a tetrapod ichnogenus that is differentiated from a separate but purportedly similar ichnogenus on the basis of differential track depth. Likewise, regarding Rainforth's fourth criterion, Lockley (2005) has argued that the relative length of digit I varies in size systematically within the Saurischia, and Gaston et al. (2003) have shown that the preservation and configuration of the inner digits (both I and II) are variable, depending on the ontogenetic state of the track maker, sexual dimorphism, interspecific variation, etc. Of course, we acknowledge that some ostensible morphological variation may be attributed to extramorphological factors pertaining to variable preservation: see Milàn (2006) for a recent discussion.

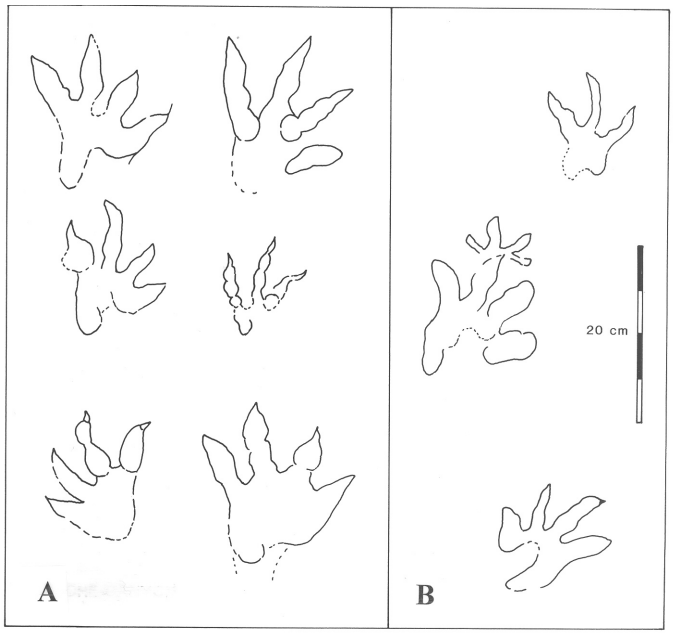

FIGURE 7. *Evazoum* tracks previously referred to as *Pseudotetrasauropus* (Lockley and Hunt, 1995) from the Chinle Group of New Mexico. **A**, Six specimens in the NMMNHS, clockwise from top left: MV 2002, MV 2004 (L 445), MV 2250 (P 14334), no number, PV 14151 (89-63) and MV 2000. **B**, Trackway segment L 446. (MV refers to Mesozoic vertebrate).

Despite these reservations, most authors have regarded *Otozoum* and *Pseudotetrasauropus* as separate but similar ichnogenera if only because of the difficulty of comparing the types, which come from different continents, formations, and collections, and that have been described using different ichnotaxonomic approaches. Based on recent publications (Lockley and Meyer, 2000; Rainforth, 2003; D'Orazi Porchetti and Nicosia, in press), tentative support is granted for maintaining a distinction between *Otozoum* and *Pseudotetrasauropus*, with the proviso that the criteria for doing so have as much to do with preservation, and the subtleties and subjectivity of perceived criteria as they do with unambiguous morphological features. Thus, the presence or absence of a manus, or proposed differences in metatarsal-phalangeal pad impressions and their possible relation to subtle differences related to weight distribution in a living organism, could be entirely preservational, sedimentological, and/or locomotory in origin.

The rarity of manus impressions associated with *Otozoum* (or *Pseudotetrasauropus*) has also been a source of confusion. The purportedly quadrupedal *Otozoum grandcombensis* (Gand et al., 2000), from the Upper Triassic of France, has been reinterpreted as having been made by a bipedal track maker by Rainforth (2003) and D'Orazi Porchetti and Nicosia (in press). We agree with this interpretation but, due to the quality of preservation of the French tracks, we cannot make a compelling argument that the ichnospecies should be transferred to *Pseudotetrasauropus*, as these authors proposed. However, based on the possibility that subtle metatarsal-phalangeal pad and digit coalescence criteria are diagnostic, we tentatively accept the formal reassignment to *P. grandcombensis* (Rainforth, 2003).

The result of these interpretations is that, based on present knowledge, *Pseudotetrasauropus* and *Otozoum* can be only subtly differentiated morphologically. However, there are stratigraphic and paleobiogeographic differences to be considered. Stratigraphically, *Pseudotetrasauropus* is found in the Upper Triassic and *Otozoum* in the Lower Jurassic. Furthermore, they occur in different hemispheres. These clear cut distinctions are convenient, if not strongly compelling as a basis

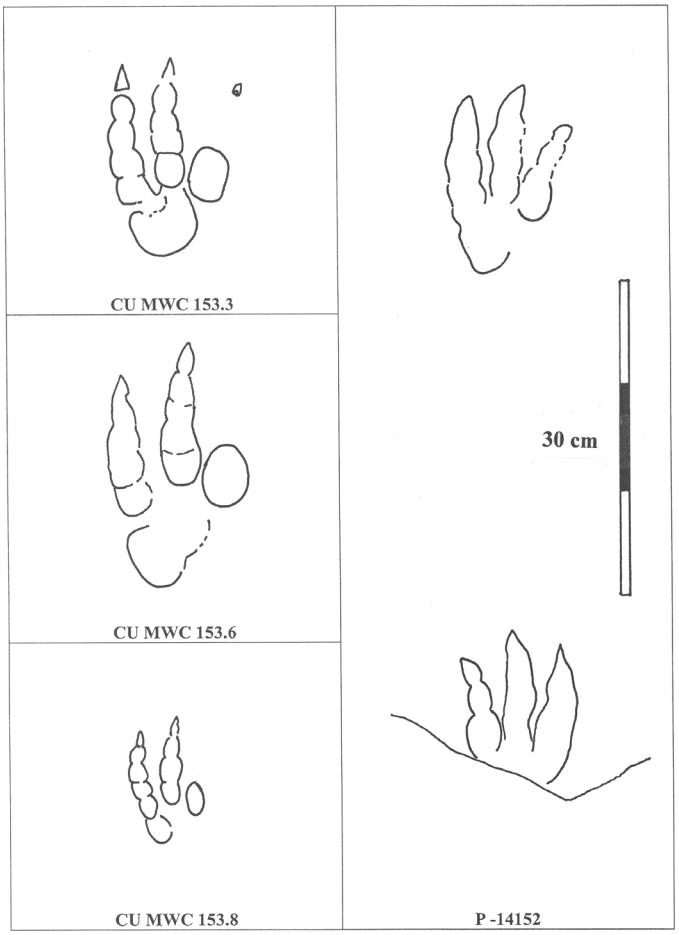

FIGURE 8. Predominantly "didactyl" tracks from the Upper Triassic of Colorado (CU-MWC specimens) and a tridactyl track from New Mexico (P-14152) (after Gaston et al., 2003, fig. 8) have variously been compared to, or labeled as, *Pseudotetrasauropus*, *Kalosauropus* and *Otozoum*. However, they may be assigned to a new ichnogenus. See text for details.

for ichnotaxonomic separation. We can now turn to the small ichnogenera *Kalosauropus* and *Evazoum* to see what morphological criteria exist to justify their recognition as distinct ichnotaxa, and to evaluate their distribution in space and time.

Kalosauropus and *Evazoum* are both small tracks. The number of phalangeal pads on digit IV, including the terminal claw, total six in the type specimens of each, so they are very similar (Figs. 3-4).

Based on type specimen UM 232-3, *Kalosauropus* (Ellenberger, 1970, 1972), as re-illustrated by Lockley and Meyer (2000, fig. 4.9) and Rainforth (2003, figs. 5A-C and 6A), clearly exhibits five phalangeal pads plus a claw impression associated with digit IV. *Evazoum*, as illustrated by Nicosia and Loi (2003, fig. 7), shows the same digit IV configuration (Fig. 3). Nicosia and Loi (2003, p. 131) stated that "At first…it seemed simple to classify these footprints" as *Kalosauropus*. But, on encountering "much difficulty, confronting some of the major problems in ichnosystematics…we decided to apply a different philosophy." In short, they named a new ichnogenus (*Evazoum*) despite acknowledging similarities to *Kalosauropus* (that they, like Rainforth [2003], referred to as a *nomen nudum*) and *Pseudotetrasauropus bipedoida*. They explicitly stated (p. 132) that they were avoiding "a systematic arrangement within a higher level taxon" pending "a paper on the systematics of this group…in preparation" (D'Orazi Porchetti and Nicosia, in press). They compared *Evazoum* with the small tracks found in the USA and Wales labeled *Pseudotetrasauropus* (Lockley and Hunt, 1995; Lockley et al., 1996), and subsequently with *Kalosauropus* (Lockley and Meyer, 2000). They noted that Lockley et al. (1996, p. 30) had specifically made a comparison with existing labels to avoid "premature erection of new ichnotaxa."

Rainforth (2003) implicitly disagreed with previous authors by assigning *Kalosauropus pollex* to *Otozoum pollex* (new combination). This assignment, if valid, has considerable influence on the taxonomic status of both *Kalosauropus* and *Evazoum*. For example, if *Evazoum* is indistinguishable from *Kalosauropus* and *Otozoum*, then only one ichnogenus is necessary. This would simplify matters, and for the first time confirm the presence of *Otozoum* (albeit a small variety) in the Upper Triassic. Likewise, if *Kalosauropus* is a *nomen nudum*, as both Nicosia and Loi (2003) and Rainforth (2003) assert, and is thus suppressed, the question arises as to whether *Evazoum* is distinct and deserving of status as a distinct ichnogenus or ichnospecies. According to Nicosia and Loi (2003), there are many similarities between *Kalosauropus* and *Evazoum* but also some differences, such as greater digit divarication in the latter form and different relative positions of the metatarsal-phalangeal pads. They suggest that *Kalosauropus* resembles *Otozoum* (*sensu* Rainforth, 2003) and that *Evazoum* is more like *Pseudotetrasauropus*, as suggested by Lockley and Meyer (2000), though ultimately admitting (p. 137) that this makes "the problem more complex and circular"!

However, as indicated above, there is a major objection to subsuming *Kalosauropus* into *Otozoum*: *Kalosauropus pollex* possesses six phalangeal pads (including the claw), not five, as in *Otozoum*. Thus, *contra* Rainforth (2003), we infer that *Kalosauropus* should not be synonymized with *Otozoum*. Using the same argument, the ichnogenus cannot be synonymized with *Pseudotetrasauropus*, if that ichnogenus really does consistently show five digit IV phalangeal pads as claimed by Rainforth (2003).

In the final analysis, *Kalosauropus* has been identified in the University of Montpellier collections (as noted by Lockley and Meyer, 2000; Nicosia and Loi, 2003; Rainforth, 2003 and D'Orazi Porchetti and Nicosia, in press). Although Nicosia and Loi (2003) labeled both *Pseudotetrasauropus* and *Kalosauropus nomina nuda*, they relented in their emendation of *Pseudotetrasauropus* and established *P. bipedoida* as the type. They noted (Nicosia and Loi, 2003, p. 136) that in "the spirit of the [International] Code [of Zoological Nomenclature] on stability and with respect to Ellenberger's wishes, we believe that most of the taxa can hardly be defined as *nomina nuda*." For consistency, we consider that *Kalosauropus* should be treated in the same manner. This means (*contra* Rainforth, 2003) that *Kalosauropus pollex* should be neither suppressed nor assigned to *Otozoum* because there is morphological evidence that they are not the same.

DISTRIBUTION OF "OPEK PLEXUS" TRACKS IN SPACE AND TIME: EVOLUTIONARY IMPLICATIONS

It is unnecessary to review the spatial and temporal distribution of *Otozoum*, *Pseudotetrasauropus*, *Evazoum*, and *Kalosauropus* in detail because this has been done elsewhere (Gand et al., 2000; Lockley and Meyer, 2000; Nicosia and Loi, 2003; Rainforth, 2003; D'Orazi Porchetti and Nicosia, in press). Nevertheless, some general observations are useful. Large tracks assigned to *Pseudotetrasauropus* were previously thought to have appeared in the Southern Hemisphere in the Upper Triassic, long before any tracks confidently assigned to *Otozoum* appeared in the Lower Jurassic of the Northern Hemisphere. According to Rainforth (2003) and D'Orazi Porchetti and Nicosia (in press), Late Triassic tracks originally assigned to *Otozoum* from Wales and France (Lockley et al., 1996 and Gand et al., 2000, respectively) are better assigned to *Pseudotetrasauropus.* This indicates that the ichnogenus occurs in both the Northern and Southern hemispheres, but not in what is now North America. If there is an evolutionary relationship between older *Pseudotetrasauropus* and younger *Otozoum*, it may involve the reduction in number of the phalanges of digit IV and in digit divarication, changes in the metatarsal phalangeal pad configuration, and a possible increased tendency toward quadrupedal progression.

The smaller OPEK plexus tracks *Evazoum* and *Kalosauropus* appear to have six digit IV phalangeal pads. Based on the latest ichnotaxonomic revisions and arguments, the former appears to be confined to the Northern Hemisphere during the Late Triassic and has not yet been reported from the Jurassic (see Lucas et al., this volume). In contrast, *Kalosauropus* is found only in the lowermost Jurassic of the Southern Hemisphere. If there is an evolutionary relationship between the track makers of older *Evazoum* and younger *Kalosauropus*, it is not apparent in the phalangeal pads of digit IV and must be inferred from other features, such as digit divarication and metatarsal-phalangeal pad configurations. If there is an evolutionary relationship between smaller *Evazoum* and *Kalosauropus* and larger *Pseudotetrasauropus* and *Otozoum*, it may also be manifest in the reduction of the phalangeal pads of digit IV. If this is the case, the small tracks can perhaps be considered more primitive.

According to Shubin and Alberch (1986), the first vector of growth in vertebrate digit development is in digit IV. Subsequent growth shifts progressively to digits III, II, and I. Thus, with prolonged growth, the relative size of digit I may increase, giving rise to differences in foot morphological polarity such as are seen between theropods and sauropods (Lockley, 2005, in press). Prosauropods represent an intermediate condition with respect to digit I development (Lockley, 2005, in press), and are generally considered the best fit for OPEK plexus track makers (Gand et al., 2000; Lockley and Meyer, 2000; Nicosia and Loi, 2003; Rainforth, 2003; D'Orazi Porchetti and Nicosia, in press). However, other track makers have been proposed (e.g., Gierlinski, 1995).

SYSTEMATIC ICHNOLOGY

The following ichnofamily and ichnogenus diagnoses are based on the type specimens and supplemental material discussed and illustrated in the text. The diagnosis of the type ichnogenus of the Ichnofamily Otozoidae (Lull, 1904) is modified after Rainforth (2003). The diagnoses for *Pseudotetrasauropus* (D'Orazi Porchetti and Nicosia, in press) and *Evazoum* (Nicosia and Loi, 2003) have not been emended.

Otozoidae Lull, 1904

Revised ichnofamily diagnosis: Tetradactyl pes track with four anteriorly-directed digit impressions; digit III slightly longer than subequal digits II and IV, all of which are longer than digit I, which may be weakly impressed; digit V impression absent or obscure and more or less coalesced with posterolateral margins of footprint; digits III and IV often curved, showing lateral convexity and medial concavity; manus rarely preserved but may appear pentadactyl or tetradactyl with short, blunt digits; trackway very variable, usually with a short step and moderately wide pace angulation in the range of 100° to 170°.

Otozoum Hitchcock, 1847

Type ichnospecies: *Otozoum moodii* Hitchcock, 1847

Revised ichnogeneric diagnosis: Pes pentadactyl with four anteriorly-directed digit impressions; digit III slightly longer than subequal digits II and IV, which are longer than digit I; digit V impression interpreted as a subrounded pad posterior to the coalesced metatarsophalangeal pads of digits III and IV; digits II-IV subparallel,laterally convex, and blunt, anteriorly or medially directed claw impressions; digit I impression less curved and slightly divergent medially with respect to digit II; ichnophalangeal formula (including claw marks) 2-3-4-5-1; manus pentadactyl, much smaller than pes, outwardly rotated, with short digit impressions; digit I impression slightly longer and more prominent than digit II-V impressions.

Pseudotetrasauropus Ellenberger, 1972

emended D'Orazi Porchetti and Nicosia, in press

Type ichnospecies: *Pseudotetrasauropus bipedoida* Ellenberger 1972

Revised ichnogeneric diagnosis: Trackway of a large biped; digitigrade; four straight, anteriorly oriented digit impressions; clear basal pad, related to the presence of an ubiquitous fifth digit on the posterolateral margin; digits almost completely separate along their lengths; foot axis orientation slightly variable from inward to outward.

Kalosauropus Ellenberger, 1970

Type ichnospecies: *Kalosauropus pollex*, based on series emended by Rainforth (2003).

Revised ichnogeneric diagnosis: Small, gracile footprint ranging from 7.0-9.0 cm in length; digits II-IV anteriorly directed, subparallel, and slightly curved with laterally convexity but not in contact along their lengths; digit III longer than II and IV, which are subequal in length; digit I not impressed except for a distal claw impression located on the medial side of digit II about midway along the track length.

Evazoum Nicosia and Loi, 2003

Type ichnospecies: *Evazoum sirigui* Nicosia and Loi, 2003.

Ichnogeneric diagnosis: Medium-sized bipedal tetradactyl footprints, ectaxonic to mesaxonic; functionally tridactyl; nearly as wide as long; first digit forwardly oriented; digits evenly splayed, giving an overall fan-shaped impression; rounded metapodial pad below digits II and IV; second and fourth digits subequal in length, while the third is the longest; relatively fleshy digits show well developed pads; long, triangular, slightly smooth, claw marks on all digits; trackways variable but with quite wide pace angulations ranging between 140° and 170°.

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