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# *KAYENTAPUS* REVISITED*:* NOTES ON THE TYPE MATERIAL AND THE IMPORTANCE OF THIS THEROPOD FOOTPRINT ICHNOGENUS

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**Abstract—***Kayentapus* is the ichnogenus name applied to relatively large (pes length ~35 cm) tridactyl tracks of a bipedal theropod dinosaur, originally described by Samuel Welles, in 1971, based on a trackway with long steps from the Lower Jurassic Kayenta Formation of Arizona. In his original description, Welles designated the type trackway on the basis of five consecutive track casts in the University of California Museum of Paleontology collections (UCMP 83668-1 to 83668-5) illustrating track UCMP 83668-1 with a line drawing and tracks UCMP 83668-2 to 4 with field photographs. Although the line drawing of track UCMP 83668-1 has often been reproduced, it does not represent the actual footprint morphology accurately. Based on a re-study of duplicates of all five UCMP casts in the University of Colorado Denver (UCD) collections, we supplement Welles' description by re-illustrating the tracks that comprise the trackway. This exercise allows us to describe the morphology of *Kayentapus* in greater detail. This re-evaluation includes estimation of trackmaker speed from the type trackway (~14.5 km/hr) and a referred trackway (~19.8 km/hr) suggesting an agile, fast trackmaker.

Although some vertebrate ichnologists have suggested that *Kayentapus* might be a synonym of *Eubrontes*, in the four decades since Welles completed his study, *Kayentapus* has been identified at 11 locations in North America and Europe, in the Late Triassic and Early Jurassic, and has quite consistently been regarded as a distinct and important ichnogenus, that may also occur in Africa. In fact, it is the only theropod footprint ichnogenus from these epochs, other than *Eubrontes* and *Grallator*, that has in recent decades been seriously studied and widely regarded as valid by numerous workers.

## INTRODUCTION

Late Triassic and Early Jurassic theropod tracks are among the best known of all tridactyl tetrapod tracks. The ichnogenera *Eubrontes* Hitchcock (1845) and *Grallator* Hitchcock (1858) have been known for more than a century and a half and are among the most frequently identified and documented ichnogenera from the Late Triassic and Early Jurassic epochs. Prior to the third revision of Hitchcock's collection by Lull (1953), few tracks that could be considered synonyms of these two ichnogenera had been formally named or referred to repeatedly in the literature. However, following the naming of Early Jurassic theropod tracks from Europe, (Lapparent and Montenant, 1967), as well as *Kayentapus* and *Dilophosauripus* from Arizona (Welles, 1971) and numerous tracks from southern Africa (Ellenberger, 1972, 1974), vertebrate ichnologists began to suspect that a number of newly introduced ichnogenera were probable synonyms of *Eubrontes* and *Grallator*. As a result, Olsen (1980) and Olsen and Galton (1984) suggested synonymizing many of the newly introduced ichnogenera. Olsen (1980) even suggested that all North American theropod tracks, and many from southern Africa could be synonymized under the single 'super-ichnogenus' *Grallator* (but see Piubelli et al., 2005, for an alternate view). Olsen (1980) argued that most theropod track morphologies represent end members of a *Grallator-Anchisauripus-Eubrontes* plexus, and that ichnologists could use the double barreled "ichnogenus" labels *Grallator (Grallator), Grallator (Anchisauripus) and Grallator (Eubrontes)*. Lucas et al. (2006) summarized this idea as an "ichnologically-unprecedented scheme… has some merit for fans of allometry, and has been accepted by some authors and discussed by others (Gierlinski, 1991; Gierlinski and Ahlberg, 1994; Weems, 1992; Lockley, 2000)." Nevertheless some authors, notably Rainforth (2005) and Lucas et al. (2006) still consider or suspect that *Kayentapus* may be a synonym of *Eubrontes*. Ostensibly, the implications of this proposal were that almost all Lower Jurassic theropod tracks could be subsumed under a single ichnogenus: *Grallator*. Although the details of these numerous, suggested synonymies need not concern us here, it is germane to point out that Olsen et al. (1998) subsequently abandoned this nomenclature when re-describing the type material of the three ichnogenera *Grallator, Anchisauripus* and *Eubrontes* as distinct morphotypes. Such vacillation between the lumping and splitting philosophy, which is inherent in taxonomic debates, has been particularly acute in theropod track ichnotaxonomy. As a postscript to this debate over theropod track nomenclature in North America and Europe, it is worth noting that there is also a suspicion that many names applied to broadly coeval (Lower-Middle Jurassic) theropod tracks from East Asia are also suspect, and likely synonyms of *Grallator*, *Eubrontes* and perhaps also *Kayentapus* (Lockley and Matsukawa, 2009).

What concerns us here is the status of *Kayentapus* as documented in the vertebrate ichnology literature and used as a formal label to describe theropod tracks from many localities around the world (Fig. 1). Most authors acknowledge that *Kayentapus* is more gracile (slender-toed) and manifests greater digit divarication than the holotype of *Eubrontes* (Fig. 2), an inference that was first suggested by Welles (1971). Despite a few adherents to the Olsen school of synonymy (Rainforth, 2005), numerous authors regard *Kayentapus* as a valid ichnogenus distinct from *Eubrontes* and *Grallator* (Weems, 1987, 1992, 2003, 2006; Lockley and Hunt, 1995; Gierlinski, 1996, Piubelli et al., 2005; Lockley, 2009; Xing et al., 2009).

To date, almost all references to the type material of *Kayentapus hopii* (the type ichnospecies) have focused on the first track in the sequence (UCMP 82668-1), which was only illustrated as a line drawing (Figs. 2-4). Unfortunately, this drawing, which has been reproduced many times (e.g., Irby, 1993, fig. 5.3; Lockley and Hunt, 1995, fig. 4.12; Piubelli et al., 2005, fig. 3c) is rather inaccurate. Weems (1992, fig. 6) adapted the drawing so that it more closely resembles the actual specimen, which we illustrate as an outline drawing in Figure 3 and as a photo

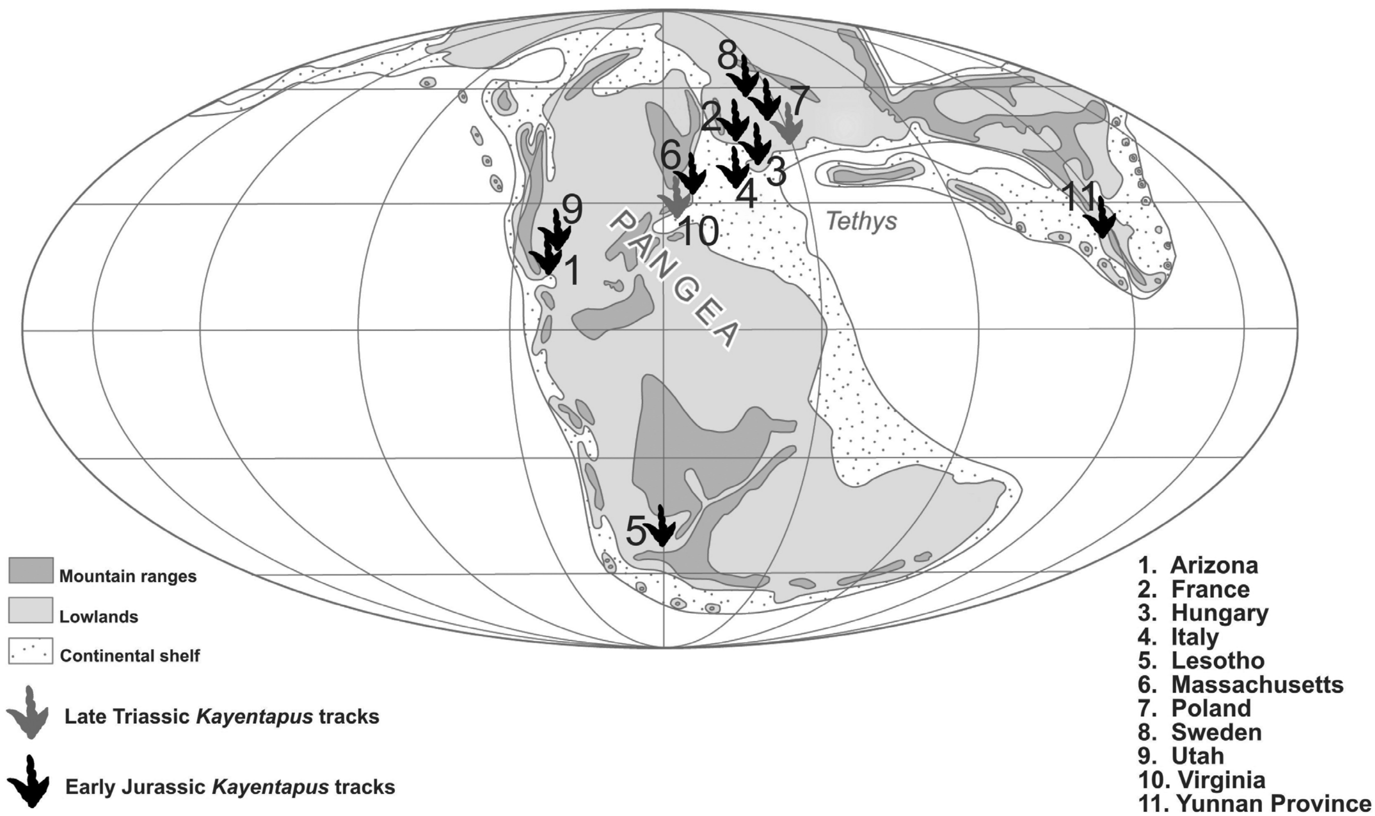


FIGURE 1. Localities from which *Kayentapus* and *Kayentapus*-like tracks have been reported. See text for details.

in Figure 4. For these reasons we take another look at the ichnogenus and supplement the original description given by Welles (1971). We also briefly review other reports of the ichnogenus and the implications for its wide distribution, as suggested by Piubelli et al. (2005).

**Institutional abbreviations:**UCMP refers to the University of California, Museum of Paleontology (Berkeley, California); CU refers to the University of Colorado at Denver (Denver, Colorado); PIG refers to the Polish Geological Institute (Warsaw, Poland); ROLM refers to Rovereto Lavini de Marco collections (Italy); and VRBL refers to Verona Bella-Lasta collections (Verona, Italy).

## METHODS

Using the plaster casts in the CU Denver collection, each cast was traced and photographed in the lab using low-angle illumination to show individual pad and claw traces (Figs. 3-4). The original tracks were preserved in concave epirelief, which appear as convex hyporelief in the casts. These casts show the difference between the main, exposed surface on which the track is most clearly seen and the remnants of a thin underlying layer (preserved in the cast as apparent convex hyporelief, and shown in stipple in Fig. 3). The five tracings were then superimposed, using the method of Baird (1957) to create a composite (Fig. 5).

## REDESCRIPTION OF THE TYPE MATERIAL OF *KAYENTAPUS HOPII*

Welles (1971) description of the type trackway of *Kayentapus hopii* is fairly thorough. He followed the guidelines of Peabody (1955) in selecting a type trackway with a minimum of three consecutive footprints, as was later recommended by Sarjeant (1989). This trackway, designated as UCMP 83668, consists of five consecutive tracks (four steps = three strides), designated UCMP 83668-1 to 83668-5, and preserved as plaster casts, hereafter referred to as tracks 1-5. Duplicates of these plaster casts are preserved as specimens CU 124.11- CU 124.15, respectively. However, although Welles illustrated track 1 in a line drawing and tracks 2-4 as small photographs, as well as giving measurements and details of individual tracks, he did not illustrate the trackway, and in some cases his illustrations lack necessary detail. He also did not discuss the preservation. We therefore supplement the original descriptions as follows:

**Track 1 (UCMP 83668-1 = CU 124.11):** This is the track Welles illustrated as a line drawing (1971, fig. 2). However the tracing we obtained is significantly different (Fig. 3). The trace of digit II shows two phalangeal pad impressions, more or less as shown by Welles. We agree with Welles that the trace of digit III is weak, but the distal pad traces are quite recognizable, though our tracing is significantly different from his. Among all the tracks this one shows the best detail of digit IV, which reveals four pads, including the proximal pad referred to as the 45 mm diameter metatarsal pad by Welles (1971, p. 34). Again our interpretation, showing four pad traces, is different from that of Welles. Thus, we can unequivocally determine the 2-3-4 phalangeal formula corresponding to digits II-III-IV. This was not explicitly stated by Welles.

**Track 2 (83668-2 = 124.12):** This track clearly shows all digital pad traces except for the proximal "metatarsal" or metatarsal phalangeal pad of digit 1V.

**Track 3 (83668-3 = 124.13):** This track clearly shows all digital pad traces except for the proximal "metatarsal" or metatarsal phalangeal pad of digit 1V.

**Track 4 (83668-4 = 124.14):** This track shows digital pad traces less clearly than in tracks 1-3. Two pad traces are weakly discernable in digit II, and the digit III trace is fusiform with the proximal and distal pad appearing less well-impressed than the central one between these two. However, the digit IV trace shows the proximal "metatarsal" or metatarsal- phalangeal pad of digit 1V, even though the distal pad traces are less clearly differentiated.

**Track 5 (83668-5 = 124.14):** Although this track is rather poorly-preserved, it is possible to discern the pad traces on digits II and III.

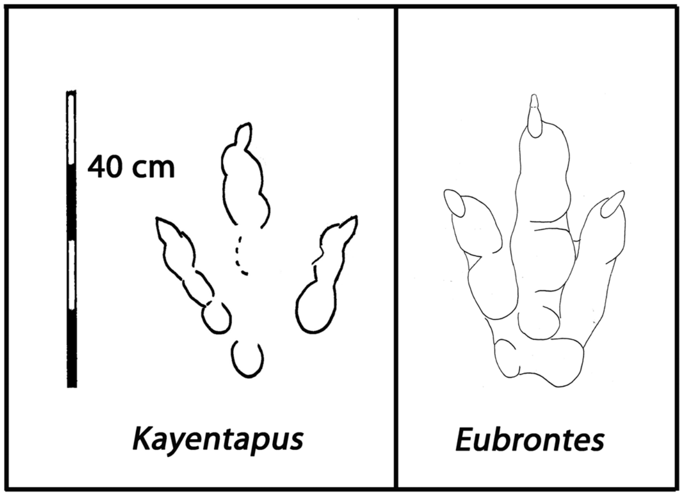


FIGURE 2. Comparison between type specimens of *Kayentapus* and *Eubrontes*.

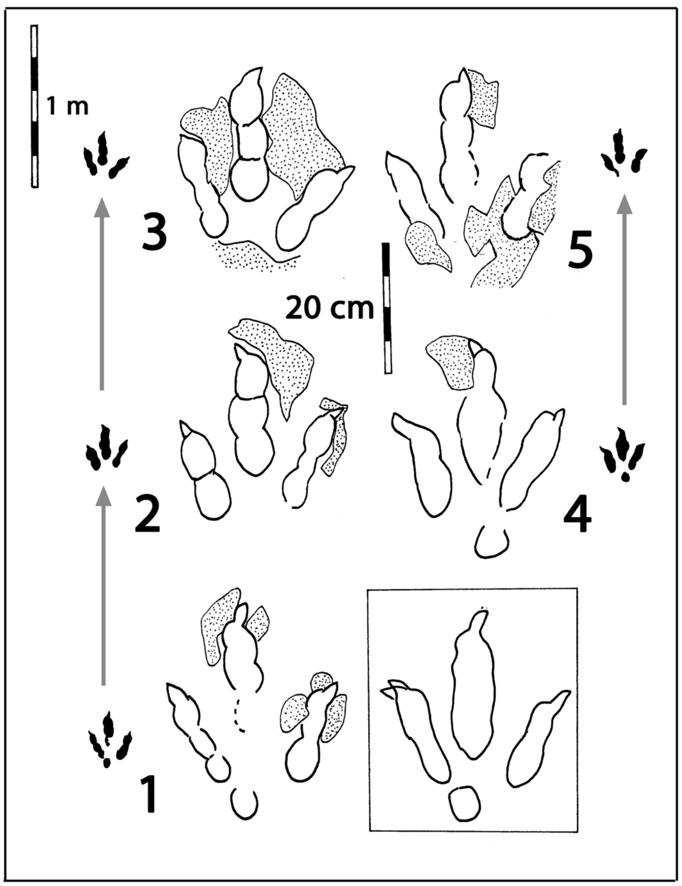


FIGURE 3. The type *Kayentapus* trackway redrawn based on all five casts of tracks in the UCMP collection: i.e., 83668-1 to 83668-5, also preserved as duplicate casts CU 124.11- CU 124.15. Compare with Fig. 4.

The composite track (Fig. 5) is a sharp-toed tridactyl footprint with a long, highly projected (strongly mesaxonic) middle digit, which indicates its theropod affinity. This specimen shows four important features. First, in all cases, the claw trace of digit III is oriented anteromedially. This characteristic of theropods as noted by Thulborn (1990), is common among bird tracks, and also observed in prosauropod tracks (*Evazoum, Otozoum* and *Pseudotetrasauropus*) and several types of the ornithischian footprints (e.g., *Anomoepus*, *Moyenisauropus* and *Dinehichnus*). Despite been common, this feature is particularly strong in *Kayentapus*. Second, there appears to be significant variation in the orientation of the distal traces of digit II (Fig. 5), although the location of the proximal pad of digit II is quite consistent. This suggests that the distal portion of digit II was quite flexible. Third, widely divaricated digits, that appear convergent with ornithischian track configurations, stand out as a distinctive feature among Late Triassic-Early Jurassic theropod footprints. Fourth, the footprint is lily-shaped (V-shaped) posteriorly.

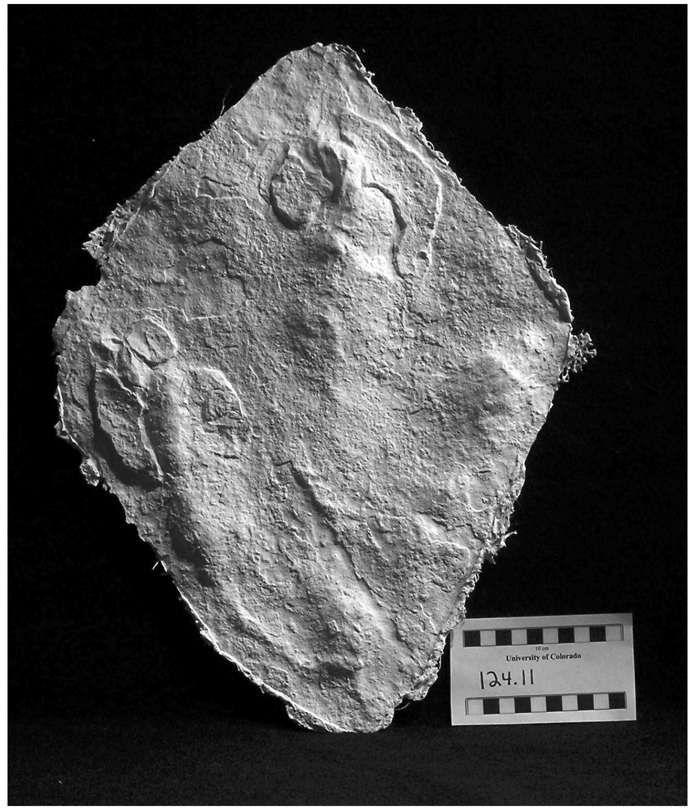


FIGURE 4. Photograph of a duplicate of UCMP 3668-1 (= CU 124.11), which is the first track in the five track sequence in the type *Kayentapus* trackway. This is the one track that Welles (1971) did not illustrate photographically, choosing instead to illustrate it based on line drawings. Nevertheless, in subsequent publications, it is the specimen most often illustrated, as representative of the type. Compare with Fig 3.

The trackway is narrow (pace angulation about 174-175° according to Welles) and characterized by a long step (188-191 cm in the holotype and as much as 234-239 cm in the referred trackway), which Welles (1971) regarded as significant in distinguishing it from Early Jurassic trackways from the Connecticut Valley. Based on these measurements we illustrate the trackway configuration (Fig. 3).

## INTERPRETATION OF THE TRACKS AND TRACKWAY

Welles (1971) noted that the lack of a consistent trace of the proximal “metatarsal” digit or metatarsal phalangeal pad of digit IV, together with the aforementioned long step made the trackmaker species “advanced over any of the Connecticut Valley trackways in having developed an isolated tarsal pad, a considerably longer pace:pes ratio and a greater divarication of digits II and IV” (op cit., p. 35-36). He also adds that there is no hallux trace. Although Welles (1971) did not name the Connecticut Valley trackways with which he was making comparisons, it is probable that he relied primarily on Lull’s (1953) monograph, which he cites. In this much used, but not always accurate, revision of Hitchcock’s work, the most frequently cited theropod ichnogenera are the aforementioned members of the *Grallator*, *Anchisauripus* and *Eubrontes* plexus.

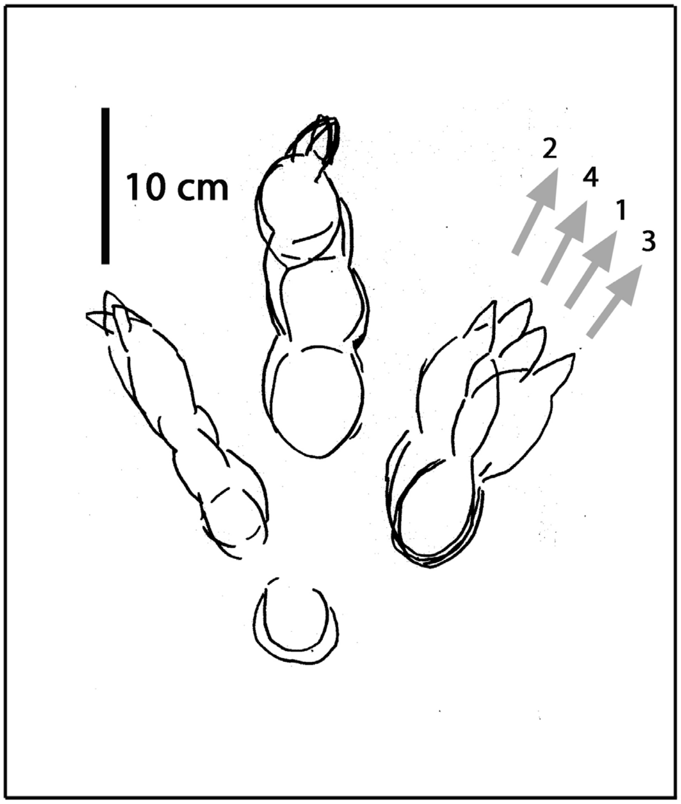


FIGURE 5. Composite track based on all five track casts (CU 124.11- CU 124.15) from the type *Kayentapus* trackway. Compare with Figure 2.

While Welles is more conscientious than many ichnologists in enumerating the diagnostic features of *K. hopii* that differentiate it from other Early Jurassic theropod trackways from the Connecticut Valley, it is possible that some of the features he describes are the result of differential preservation. It is evident that the tracks are "slight" undertracks, impressed or transmitted on the sandstone surface through a thin overlying layer of shale, and thin layers of sandstone (Fig. 3). Thus, the lack of a metatarsal impression in some cases may be an extra-morphological feature: in this case negative evidence "could" have a preservational interpretation, as is common in the fossil record. However, as is often the case in ichnology, such inferences are not certain, and it may be, as Welles (1971) implies, that the *Kayentapus* trackmaker was indeed more digitigrade than other theropod trackmakers of similar size, and this in turn may be a function of gait, as noted below.

When compared with the type of *Eubrontes* the type *Kayentapus* has more slender digits and wider divarication angles (Fig. 2). This latter attribute was identified by Welles (1971) as diagnostic. In other words, *Eubrontes* is more tulip-shaped (U-shaped posteriorly) than lily-shaped (V-shaped posteriorly) than *Kayentapus*. The same *Kayentapus*-like, lily-shaped pattern appeared again convergently in the Cretaceous theropod ichnites named *Irenesauripus* Sternberg, 1932.

The long pace (step) relative to pes length of the type trackway of *Kayentapus hopii* allows us to calculate speed ($v$) using the formula of Alexander (1976):

$$v = 0.25g^{0.5} \cdot SL^{1.67} \cdot h^{-1.17}$$

where g is the gravitational acceleration in m/sec, SL = stride length and h = hip height, estimated as 4.9 times foot length (FL), using the ratio for large theropods proposed by Thulborn (1990). Based on the measurements given by Welles (1971, table 1), where footprint length is 0.34 m and stride length is 3.82 m (i.e., pace length of 1.91m x 2): we estimate a speed of ~4.03 m/sec or ~14.51 km/hr. According to Welles (1971, table 1) the referred trackway has an even longer step (up to 239 cm) and stride (up to 473 cm) relative to pes length. This allows us to calculate a speed of ~5.5 m/sec or ~19.8 km/hr. The trackway of *Schizograllator xiaohebaensis* from Sichuan, China (Zhen et al., 1986) interpreted as a possible example of *Kayentapus* (Lockley and Hunt, 1995; Piubelli et al., 2005) gives an estimated speed of ~12.0 km/hr. Hamblin et al. (2006) report a *Eubrontes* trackway with a step of 2.56 m which gives and estimated speed of 11.38 m/s or 41 km /hr.

## COMPARISON WITH OTHER *KAYENTAPUS* MORPHOTYPES

Following the erection of ichnogenus *Kayentapus* by Welles (1971), based on the type ichnospecies *K. hopii*, from the Lower Jurassic Kayenta Formation, Weems (1987) transferred the ichnospecies *Apatichnus minor* (*sensu* Lull, 1953), which was in turn based on *Gigantitherium minus* (Hitchcock, 1858) from the Upper Portland Series of Massachusetts, to *Kayentapus minor* (comb. nov.). Incidentally, in so far as Lull (1953) regarded *A. minor* as having ornithischian affinity, he clearly regarded the ichnospecies as distinct from theropod morphotypes in the *Grallator*, *Anchisauripus* and *Eubrontes* plexus. Weems (1987, 1992, 2003) justified transfer of *A. minor* to *Kayentapus* on the basis of a number of morphometric characters, but in particular on the basis of the ratio of the anterior triangle to the posterior triangle (Fig. 6), which is a measure of mesaxony (*sensu* Lockley, 2009). These studies were supported by Gierlinski (1996) who concurred with Weems that the two ichnospecies were distinct, and Lockley (2000) pointed out that Weems is one of the few theropod track researchers to present significant data on which ichnotaxonomic conclusions can be based.

Consequently, the ichnospecies *Grallator (Eubrontes) slotykovensis* described by Gierlinski (1991) and Gierlinski and Ahlberg (1994) from Poland and Sweden, respectively, was transferred to *Kayentapus slotykovensis* by Gierlinski (1996). There has been a relatively consistent rationale applied to the morphometric analysis of the three named *Kayentapus* ichnospecies: thus, the diagram presented by Weems (1992) to show anterior and posterior triangle configurations and relationships was first modified by Gierlinski (1996), then by Piubelli et al. (2005), and is again reproduced here (Fig. 6).

Lockley and Hunt (1995) were the first to suggest that there were Asian ichnospecies comparable to *Kayentapus*, notably the ichnogenus *Schizograllator* (Zhen et al., 1986; Lockley and Matsukawa 2009). This inference is further supported by the comparisons made by Xing et al. (2009) between *Kayentapus* and various Asian theropod tracks.

Piubelli et al. (2005) were the first authors to devote a whole paper to the ichnogenus *Kayentapus*, which they characterize as "one of the most important tridactyl dinosaur ichnogenera" (op cit., p. 259). They identified the ichnogenus in the Lower Jurassic of Italy, and following the suggestion of Lockley (2000) that the ichnogenus "may" occur in the Lower Jurassic assemblages identified by Ellenberger (1972) from southern Africa. They pursued this line of enquiry to the point where they identified and illustrated four different Ellenberger ichnotaxa (the ichnogenera *Deuterotrisauropus, Kleitotrisauropus* and two ichnospecies of *Neotrisauropus*), which they consider as possible synonyms of *Kayentapus* (Fig.7).

## POSSIBLE TRACKMAKERS

There is a general, but unproven assumption that *Eubrontes* tracks were made by a large theropod such as *Dilophosaurus*. For example, abundant *Eubrontes* tracks in the East Berlin Formation and Dinosaur State Park in Connecticut are exhibited with a large *Dilophosaurus* model (Farlow and Galton, 2003). Welles (1971) was clearly partly responsible for this inference, because he named the track *Dilophosauripus,* which was found in the Kayenta Formation in close geographic and stratigraphic proximity to the skeletal remains of several *Dilophosaurus* specimens (Welles, 1984). Based on a comparison of *Dilophosauripus* and *Kayentapus* footprints, the former may be considered *Eubrontes*-like in so much as it represents a robust trackmaker, as noted by Welles (1971). By contrast, the ichnogenus *Kayentapus* represents a more gracile

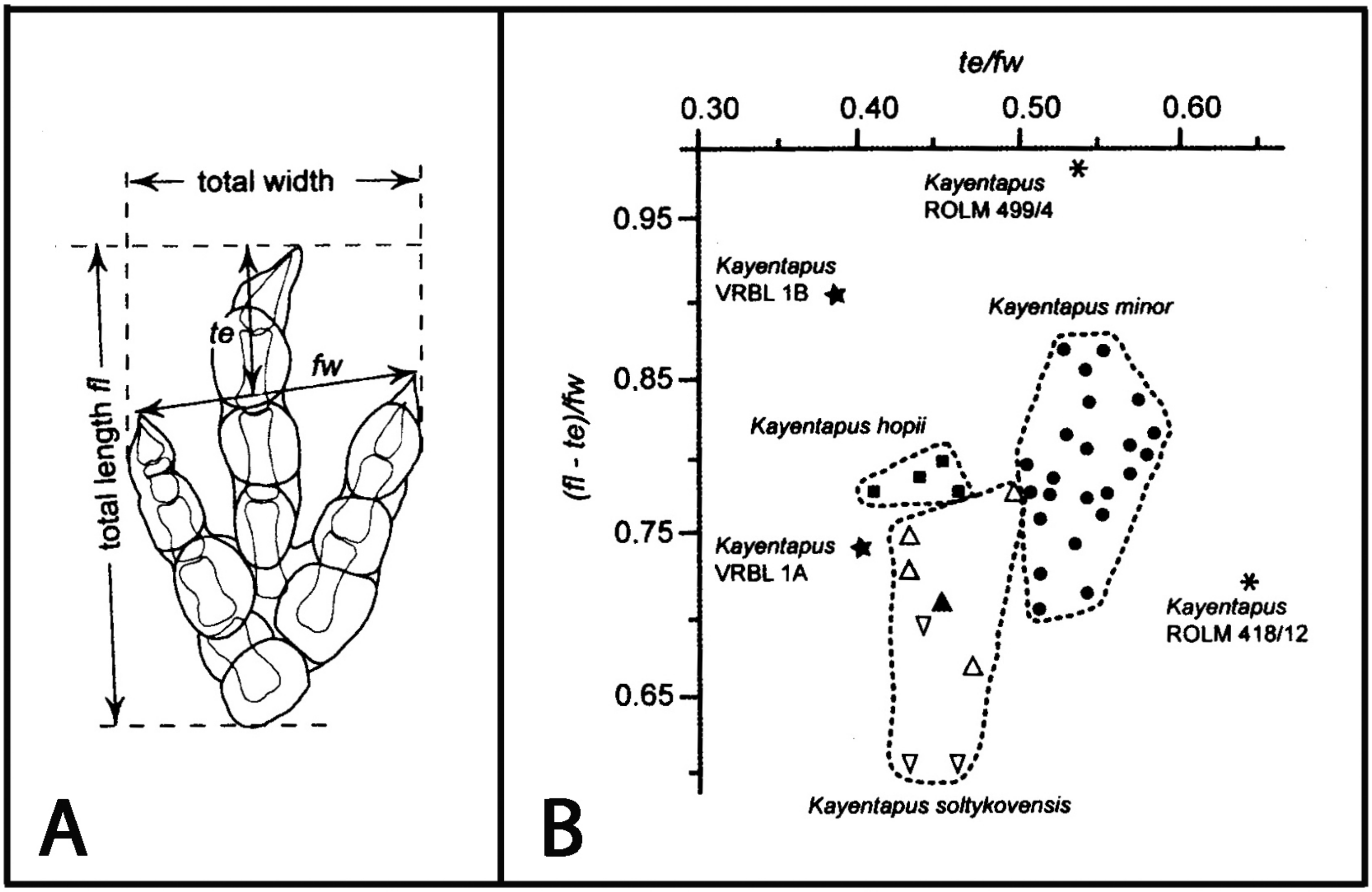


FIGURE 6. Comparison of the morphology of the three named ichnospecies of *Kayentapus* based on measurement of anterior and posterior triangles (modified after Gierlinski, 1996, and Piubelli et al., 2005). Data points for unnamed *Kayentapus* ichnites (ROLM and VRBL) from Italy are also shown.

trackmaker, which according to Welles, was unlike the maker of tracks from the Connecticut Valley (i.e., by inference, the *Eubrontes* trackmaker). Weems (2003, p. 305) offers a dissenting view and suggests that *Eubrontes* was more likely made by the prosauropod *Plateosaurus* and that it was *Dilophosaurus* that provided the best available match for the *Kayentapus hopii* trackmaker. He also claimed that the much smaller track *Kayentapus minor* may have been made by a small theropod the size of *Liliensternus*.

## DISCUSSION

Despite the growing number of reports of *Kayentapus*, or *Kayentapus*-like tracks from North America, Europe, southern Africa and Asia, most vertebrate ichnologists are aware that it is difficult to distinguish and label Lower Jurassic theropod tracks confidently. Lockley (2000) commented on the lack of consistent approaches to morphometric studies on theropod tracks, and this sentiment is reiterated in Xing et al. (2009). Many of the illustrations that appear in the papers cited herein are not associated with any discussion of the preservation of the tracks. It is often not possible to determine the details of footprint morphology from small photographs. Although line drawings have the advantage of presenting clearer outlines of features, they also have significant drawbacks, especially if they have been derived from poorly preserved material. In the absence of opportunity to study original tracks, or good casts in detail, the researcher must have faith in the quality of interpretative diagrams produced in the published record. As we have seen such diagrams, copied from primary sources, often convey subjective, dubious or misleading morphological information. Moreover, once a line drawing is published there is a tendency to copy it repeatedly: indeed without re-examining and re-illustrating a given track, one is obliged to refer to the original source illustration, if only for consistency. However, as shown by Lockley et al (2003) there can be considerable variation in the morphological representation presented in line drawings when different authors illustrate the same tracks.

At the present time there are few documented *Kayentapus* trackways. For this reason we present a fuller account of the *K. hopii* trackway (Fig. 3) and for the first time illustrate the cast of the first specimen (UCMP 83668-1 = CU 124.11), which was not photographed by Welles. Based on data given in Welles (1971) the trackway suggests an animal moving at 14.5 km/hr, and an associated trackway indicating a speed of almost 20 km/hr. This compares with an estimated speed of ~5.8 km/hr for *Eubrontes giganteus* from New England which, according to Lull (1953) had a foot length of 37 cm and a step of 109-117 cm. As noted above Hamblin et al. (2006) report a *Eubrontes* trackway giving an estimated speed of 11.38 m/s or 41 km /hr. Gierlinski and Pieńkowski (1999) illustrate a *K. slotykovensis* trackway that has an estimated speed of about 5 km/hr.

This small database is of limited utility in differentiating *Kayentapus* trackways from other theropod trackways or allowing convincing inferences about the trackmaker. One can only infer that the trackmaker was an erect biped capable of significant speed, and that some *Kayentapus* trackmakers were moving more rapidly that *Eubrontes* trackmakers and vice versa. Such differences in estimated speeds may be attributed to variation in behavior among individuals of different sizes rather than as a characteristic gait of different species. Thus, until more data are systematically gathered it is difficult to say whether *Kayentapus* trackways consistently show longer steps and strides than those measured in *Eubrontes* trackways.

According to Weems (2006) there is one example of *Kayentapus minor* that can be interpreted as representing a quadrupedal animal that

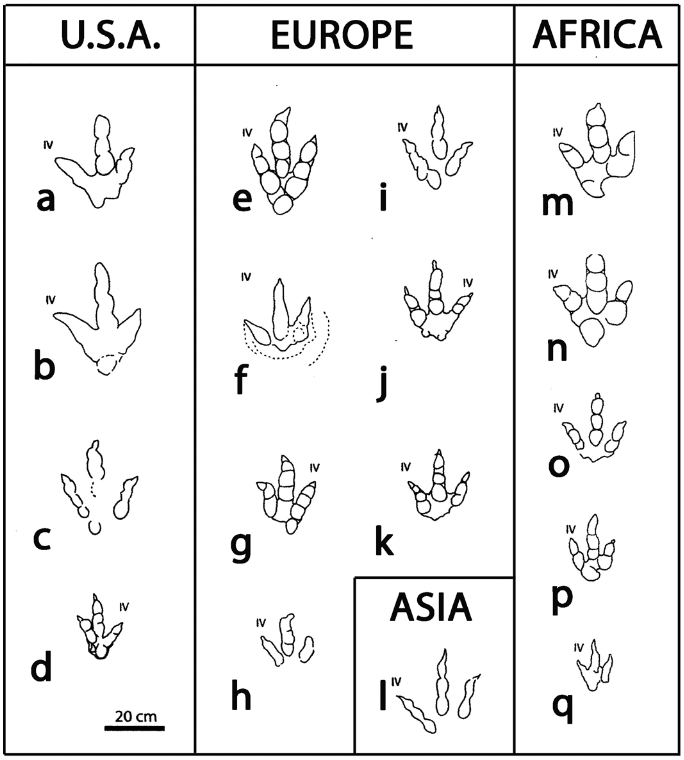


FIGURE 7. Comparison of the morphology of *Kayentapus* and *Kayentapus*-like tracks from the USA, Europe, Asia and Africa (modified after Piubelli et al., 2005): **a-d**, from the U.S.A: **a-b**, unnamed tracks from the Navajo Formation, Utah, **c**, *Kayentapus hopii* (compare with Figs. 2-3), **d**, *Kayentapus minor* (after Lull, 1953; Weems, 1992), **e-k**, from Europe: **e-h**, *Kayentapus* tracks from Lavini de Marco, Italy (after Piubelli et al., 2005), **i**, *Grallator lescurei* from France (after Demathieu, 1990), **j**, *Kayentapus slotykovensis* from Poland (after Gierlinski, 1991), **k**, *Kayentapus slotykovensis* from Sweden (after Gierlinski and Ahlberg, 1994), **l**, from Asia: **l**, *Schizograllator* (after Zhen et al., 1989), **m-q**, from Africa (after Ellenberger, 1972); **m**, *Deuterotrisauropus socialis*, **n**, *Neotrisauropus leribeensis*, **o**, *Neotrisauropus deambulator*, **p**, and **q**, *Kleitotrisauropus shososhoei*.

registered an inferred manus track. In our opinion this interpretation is dubious. Weems (2003) confesses that the purported manus traces are non-descript ovals that lack any diagnostic digit traces. Reservations regarding Weems interpretations are further discussed by Milner et al. (2009).

## CONCLUSIONS

Since first described by Welles (1971) *Kayentapus* has become one of the most widely recognized Early Jurassic theropod track ichnogenera. It may occur in the Late Triassic also (Weems, 1987; Gierlinski and Sabath, 2005; Niedzwiedzki, 2005).

In comparison with other theropod track ichnogenera, particularly the well-known *Eubrontes* and *Grallator*, *Kayentapus* has been fairly thoroughly studied in recent decades. However, this does not mean that there is universal agreement on how *Kayentapus* differs from other theropod track ichnotaxa.

The differences between *Kayentapus* and *Eubrontes* are inferred on the basis of both general and specific characteristics. General features include the inference that *Kayentapus* is more gracile, with wider digit divarication and possibly a tendency to longer step, which gives higher speed estimates. However, to date the fastest speed estimates are derived from a *Eubrontes* trackway (Hamblin et al., 2006). *K. hopii* may be slightly more digitigrade than *Eubrontes*. Specific features used to differentiate *Eubrontes* and *Kayentapus* include relatively subtle differences in the anterior and posterior triangle configurations that measure mesaxony and digit divarication.

Three *Kayentapus* ichospecies have been formally described: *K. hopii* from Arizona, *K. minor* (formerly *Apatichnus minor*) from Connecticut, and *K. slotykovensis* from Poland, Sweden and Hungary. However, *Kayentapus*-like tracks are known from elsewhere in the USA, Europe, Asia and Africa, and there is growing consensus that the ichnogenus is of global importance.

Available information on formally-named *Kayentapus*, should not be taken to indicate that the many variously named *Kayentapus*-like tracks, especially from Africa and Asia, can be referred confidently to *Kayentapus* without detailed restudy.

It remains the case that theropod tracks are difficult to differentiate, owing to a multiplicity of factors such as variable preservation, lack of strong consensus on the application of consistent morphometric methods of analysis, and complex ichnotaxonomic history. Thus, inferences about the distribution and significance of *Kayentapus* and our ability to differentiate it from other theropod ichnites should be approached with caution.

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