HETTANGIAN (EARLY JURASSIC) DINOSAUR TRACKSITES FROM THE MECSEK MOUNTAINS, HUNGARY

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Abstract—Isolated theropod dinosaur tracks were first collected in Hungary from Hettangian (Lower Jurassic) beds of the Mecsek Coal Formation in 1966 and described as *Komlosaurus carbonis* Kordos, 1983. Our study is based on newly collected material from additional track-bearing beds. The description of the two largest preserved surfaces, containing a total of 102 tracks that can be referred to 21 trackways, is provided here. This represents the first attempt to measure, map and compare the tracks of these bipedal, functionally tridactyl dinosaurs in several associated trackways. Significant morphological variability can be observed (e.g. depth, presence or absence of a metatarsal impression, digit length, digit divarication angle) that is explained by differences in physical parameters of the substrate. The mean of pes length is 16.3 cm in tracksite PB1 and 19.9 cm in tracksite PB2. Stride length of trackways usually ranges between 120 and 170 cm, the pace angulation is 160°–175°. The speed of the trackmaker is calculated to range between 6 and 14 km/h. Imprints are diagnosed by a pes length/width ratio lower than 2.0; metatarsal pads and hallux impressions are frequent. Based on the similarity of several morphological characters, the herein described tracks are referred to the ichnotaxon *Komlosaurus carbonis*, which is clearly distinct from *Grallator* and *Kayentapus*.

INTRODUCTION

Footprints of theropod dinosaurs in Lower Jurassic sediments occur in several parts of Europe (Lockley and Meyer, 2000). Such localities have been reported from France (Demathieu, 1990; 1993), Poland (e.g. Gierliński, 1991; 1994; Gierliński et al., 2004; Gierliński and Niedźwiedzki, 2005), Sweden (Gierliński and Ahlberg, 1994) and Hungary. The latter boasts one of the earliest discoveries.

The first dinosaur footprints in Hungary were found in 1966 by the geologist György Wein in an open pit coal mine of the Lower Jurassic Mecsek Coal Formation near Pécs-Vasas, Mecsek Mountains (Tasnádi Kubacska, 1967; Fig. 1A). Additional tracks were unearthed 14 years later from the same stratigraphic unit near Komló (Kordos, 1981; 1983). In 1988, during summer, the field school of geology students from the Eötvös University of Budapest discovered a new site of Lower Jurassic footprints in the open pit mine at Pécsbánya (Fig. 1A) that provided a rich assemblage footprints belonging to several trackways. During the excavation a surface area of 75 m^2 was cleaned and more than 350 tracks configuring 48 trackways, were mapped and measured (Hips et al., 1988). Beside this material collected by the student field party and the staff of the Hungarian Natural History Museum, in the same year a team of the Geological Institute of Hungary (MÁFI) collected an additional track-bearing surface of about 100 m^2 with 110 footprints in the Pécs-Vasas locality (Kordos, 1989; 2005). This latter material is housed in the Hungarian Geological Museum.

Besides numerous footprints, the outcrops of the Lower Jurassic Mecsek Coal Formation also yielded a well-preserved macroflora (Barbacka, 2000; 2001; 2002) as well as palynomorphs (Bóna, 1969; 1983; 1995). The Mecsek Coal Formation is important because it contains the Triassic/Jurassic boundary. Recent palynological studies focusing on paleoenvironmental and vegetation changes and climatic signatures within the boundary interval provided evidence for a series of cyclic, short-term paleoenvironmental changes (Ruckwied et al., 2008). Unfortunately, the lack of a continuous succession with footprint levels and the lack of any vertebrate bodyfossils prevents the evalution of a vertebrate faunal change and the known tetrapod extinction event (Olsen et al., 1987; Benton, 1994) across the Triassic/Jurassic boundary. Other bodyfossils that occur in the formation in stratigraphic proximity of the tracks are remains of different molluscs (Szente, 1992; 1993; 2000) and phyllopods (Nagy, 1960; Láda and Nagy, 1961).

Kordos (1983) gave the first scientific description of the Early Jurassic footprints and identified them as a new ichnotaxon, *Komlosaurus carbonis*. On the basis of newly collected material (four specimens: Muz. PIG. 1624.II.1, 1624.II.2, 1624.II.3, 1624.II.4) in the Vasas and Pécsbánya open pit coal mines, however, Gierliński (1996) regarded *Komlosaurus* as a synonym of *Kayentapus* (Grallatoridae). He distinguished two ichnotaxa and concluded that the smaller tracks can be referred to *Grallator tuberosus* (Hitchcock, 1836) Weems, 1992, whereas the larger, more slender ones can be assigned to *Kayentapus soltykovensis* (Gierliński, 1991).

The new material described here represents the first assemblage of large-scale tracksites preserving a high and representative number of tracks and trackways from the Lower Jurassic of Hungary. The aims of the present study are: (1) to provide a detailed, comparative description of the tracksites and tracks, (2) to assess the morphological variability of the tracks and trackways, permitted by a much larger material compared to that of earlier studies, (3) to discuss the ichnotaxonomic status and diversity and the validity of *Komlosaurus carbonis*, and (4) to infer the speed and behavior of the track-making theropod dinosaur.

Institutional and technical abbreviations—MGIW: Museum of Geological Institute, Warsaw; **MTM:** Hungarian Natural History Museum, Budapest; **Muz. PIG**: Geological Museum of the Polish Geological Institute; **PB**: Pécsbánya.

LOCALITY AND GEOLOGICAL SETTING

The material described here was collected in the Karolina Valley open pit coal mine at Pécsbánya in 1988 (Fig. 1A). The dinosaur footprints are preserved in the alluvial, coal-bearing deposits of the uppermost Triassic to lowermost Jurassic (Rhaetian to Sinemurian) Mecsek Coal Formation (Fig. 1B). This sequence was formed in the half-graben of the southern Mecsek (Mecsek Unit, Tisza Mega-unit; Haas and Péró, 2004) and consists of alternating sandstone, shale, and coal layers attaining a maximum thickness of 1200 m. Both litho- and chronostratigraphically, the formation is correlated to the Gresten facies of the Alp–Carpathian region. Due to its economic importance for the coal mining of the last 200 years in the district of Pécs and Komló, the Mecsek Coal Formation represents the most intensively studied occurrence of this facies (Némedi Varga, 1995).

The variable thickness of the formation indicates that the deposition of the formation took place in a strongly asymmetrical basin. The lower part of the formation was formed in the latest Triassic and is composed of siliciclastics of fluvial and lacustrine facies with thin coal seams (Nagy and Nagy, 1969). In the Early Jurassic, a relative sea-level rise occurred and the alluvial flood plain with rivers and abandoned channels was replaced by a delta with different depositional environments. The salinity fluctuated, predominantly freshwater and brackish environments were interrupted by occasional marine incursions. These deposits are commonly dark, and rich in pyrite and organic material. The track-bearing beds, described below, occur in the middle part of the formation (Hips et al., 1988; Fig. 1C) of Middle to Late Hettangian age (Nagy and Nagy, 1969). Dinosaur footprints occur in between the coal seams, in fine-grained flood plain deposits where shales and siltstones are predominant. In both the Pécsbánya and Pécs-Vasas localities, several levels with track-bearing bedding planes have been identified (Hips et al., 1988; Kordos, 2005), but previously none of them has been subjected to a comprehensive and systematic documentation.

As mining activities were terminated during the last decade, unfortunately now most of the localities in the open pit mines are covered by overburden; thus these strata are no longer available for study.

MATERIAL AND METHODS

After the discovery of the first in situ footprints in the Pécsbánya locality, the students' team cleared a large track-bearing surface. The track-bearing layer was broken up into smaller blocks and was first reassembled in the field, where detailed maps of the tracksites were made (Fig. 2) in order to permit a later reconstruction of the whole surface. Both the individual blocks and the tracks were labelled with a separate number for their later identification on the map. The blocks were transported to the Hungarian Natural History Museum. Using the original maps and documentation, a smaller part of this surface (5.7 m ×1.5 m), here referred to as PB1 (MTM V 2010.247.1.), has been reassembled and is now on display at the Eötvös University (Ősi et al., 2005). A larger slab (10 m × 2.7 m; (MTM V 2010.248.1.–MTM V 2010.282.1.), here referred to as PB2, is now also reconstructed and available for study in the Hungarian Natural History Museum, where it is planned to be part of a future exhibition. Trackways of the two slabs are from the same stratigraphic level. All mapped tracks and trackways were assigned numbers and basic measurements were obtained (Tables 1–4). Measuring of the tracks and trackways follows the method of Lockley and Hunt (1995). Standard statistical methods, including multivariate analyses, were applied to the measurement data to aid ichnotaxonomy and to reveal the possible effects of the animal's speed and firmness of substrate on track morphology. Data analysis was performed using the PAST software package (Hammer et al., 2001).

SYSTEMATIC ICHNOLOGY

Ichnofamilia incertae sedis

Ichnogenus *Komlosaurus* Kordos, 1983

Komlosaurus carbonis Kordos, 1983

Holotype: Geological Institute of Hungary (MÁFI) V12692. (Vt. 88.). a slab with two positive imprints.

Referred material: MTM V 2010.247.1. on slab PB1 with 27 tracks in 7 trackways; and MTM V 2010.248.1.–MTM V 2010.282.1. on slab PB2 with 75 tracks in 14 trackways.

Locality: Pécsbánya, Karolina Valley open pit mine, Hungary.

Age and horizon: Early Jurassic (Hettangian), Mecsek Coal Formation, between coal seams No. 8 and 11.

Revised diagnosis (based on the type material, supplemented by 102 tracks of 21 trackways of slabs PB1 and PB2): functionally tridactyl tracks of a biped with the following combination of traits: foot length/width ratio lower than 2.0; digit impressions slender and elongate (compared to *Grallator* and *Kayentapus*); digit impressions frequently curved; digit divarication angles high with an average angle of 72° between digits II–IV; metatarsal pad and hallux impressions frequent; metatarsal impression confluent with proximal digit impressions.

Description and interpretation of tracksites

Two large, independent tracksites, referred to as Pécsbánya tracksites 1 and 2 (PB1 and PB2; Figs. 3A, B), and from the same stratigraphic level, were collected, mapped and measured. Originally, at the locality, both slabs were part of a single, steeply-dipping indurated siltstone bed (dip 44° to the SE; Fig. 2).

The *Pécsbánya tracksite 1 (PB1)* is 5.7 m long and 1.3–1.5 m wide. It contains 27 footprints representing at least seven trackways of theropod dinosaurs (A–G; Fig. 3A, Tables 1–2). Trackways C and D are from larger individuals (pes length ~ 19 cm) approximately parallel with each other, heading NNE. Trackways B and E, although both are composed of only three tracks, appear to be oriented in a similar direction as C and D. Trackway F is oriented with an angle of approximately 45° and trackway G is oriented with an angle of approximately 70° relative to the direction of B–E trackways. The tracks are not deep but their quality of preservation is generally good. The tracks are commonly tridactyl, in some cases with the impression of the distal end of the metatarsals. This style of preservation appears to be related to the relatively firm substrate as the pes was implanted. Some footprints are fragmentary, they were damaged during collection, and only the impression of one or two digits can be seen (e.g. tracks A1, C6, E2). Trackway A is oriented in the opposite direction compared to B–E, and consists of two successive incomplete footprints.

Trackway A is from a smaller individual (pes length 11 cm) and the pace length is shorter relative to those of the other trackways. Trackway B is formed by three incomplete footprints with longer pace length compared with trackway A. Trackway C is one of the longest with 7 successive tracks. Here the pace length increases toward the end of the trackway (C4–C5: 95 cm, C5–C6: 86 cm) compared to the first steps (C1–C2: 64 cm), indicating accelerating movement of the trackmaker. Tracks C1 and C4 show impressions of the distal ends of the metatarsals. Pace angulation (Thulborn, 1990), in agreement with other trackways from Pécsbánya, ranges between 160° and 170°. Trackway D is composed of seven footprints and has similar stride lengths and pace angulation as trackway C. A shallow oval depression seems to be track D1 and probably overlaps the first preserved track of trackway E. Thus, the different impressions of the digits are hardly distinguishable. Footprints of C and D trackways are well preserved and they are similar to those of *Komlosaurus carbonis* illustrated by Kordos (2005: fig. 4b). Footprints of trackway E are slightly different in morphology from those of the other trackways (see below), also the pace length is much higher (E1–E2: 112 cm). Trackways F and G are incomplete and composed of only two successive tracks with high pace length in F (F1–F2: 100 cm).

The *Pécsbánya tracksite 2 (PB2)* is 10 m long with an average width of 2.7 m. It contains 75 tracks representing 14 trackways (A–N; Fig. 3B, Tables 3–4). Similarly to PB1, some footprints or blocks in PB2 were damaged during collection, thus they are not complete, and some of the tracks are missing (e.g. tracks I5, K2, K3). Among the 14 trackways, A and B are the longest, including 10 and 11 tracks, respectively. Trackways C, D, F, G, H, M, N are composed of 2–6 tracks and they are more or less perpendicularly directed to trackways A–B and I–K. Pace angulation is similar to that measured in PB1. Some differences in the style of preservation of the tracks can be observed. In some trackways (e.g. trackway N), similarly to those of PB1, tracks are tridactyl, shallow and have a medium to good preservation. Trackways F and I are composed of tetradactyl footprints where the quality of the hallux impression is variable. In trackway H, the four preserved tracks are slightly deeper and possess elongated metatarsal impressions. Here, besides similar footprint measurements, the pace length is one of the longest among the trackways (Table 4).

As it was suggested for tracks with similar style of preservation from the Lower Jurassic Kayenta Formation of the Colorado Plateau (USA), these animals moved on a softer substrate and thus “their progression was slower than that of same-sized animals on a firmer substrate” (Lockley et al., 2006: p. 271). These differences are related to the nature of the substrate and indicate that tracks were made at different times on this surface. Of the 14 trackways of PB2, A–B and I–K are approximately parallel. Similarly to trackways C and D of PB1, these trackways are also closely associated with each other. They show similar stride lengths and estimated speed (see below), and the tracks are characterized by similar preservational types (see below). These features suggest that these theropod dinosaurs might have moved in herds, as was also suggested for other theropod trackmakers (Ostrom, 1972; Olsen, 2002; Lingham-Soliar et al., 2003; Lockley et al., 2006).

Description and interpretation of tracks

Of the 102 tracks, 68 specimens were suitable for measuring the length (although 3 of them yielded excessive lengths see footnote of Table 3), 63 specimens yielded width measurement, and 56 yielded both, allowing calculation of the length/width ratio. Track lengths range between 9.5 and 26 cm with a mean value of 19 cm, whereas track widths range between 7 and 16 cm with a mean value of 12.5 cm. The size distribution of track lengths is shown on a histogram (Figure 4A).

All tracks on slabs PB1 and PB2 are from functionally tridactyl, bipedal animals, as it was also interpreted for similar tracks collected earlier from the Mecsek Mts. (Kordos, 1983; 2005; Gierliński, 1996). Footprints of the two tracksites are mostly tridactyl, with digit III being longest. The impression of the distal end of the metatarsals is more frequent on PB2. Numerous similar tracks have been documented but were not removed from the locality (K. Hips pers. comm.). The angle between digits II and III is always smaller (typically varies between 30° and 40°) than that of digits III and IV (typically 40°–50°). However, in some tracks angles between digits II and III are much smaller (10°–20°, e.g. trackway PB2-E). The impression of digit III is commonly straight, but in some tracks it is slightly curved medially (Fig. 6B) similarly to the track figured by Gierliński (1996: fig. 2). This phenomenon reflects the rotation of the foot axis toward the midline. Due to the shallow nature of most tracks, the individual phalanges of the digits are barely distinguishable. The distal ends of the digit impressions are shallow and thin. They were made by the horny claws that are frequently oriented in a different angle compared to the digits. The shape and depth of the metatarsal impression may be highly variable even in a single trackway (e.g. trackway PB1-C; Figs. 5 and 6A). In some tracks, especially on the slab of PB1, the metatarsal impression is shallow and in most of these cases only the digits can be observed. Metatarsal impressions are typically short and rounded, but they may be elongated anteroposteriorly (e.g. in trackway PB2-H; Fig. 3B). In some of the tracks the impression of the hallux is also preserved but its position relative to digits II–IV varies slightly. Track PB2-K5 shows an exceptionally preserved hallux impression (Fig. 6A) which is shifted farther backward than that seen in others, e.g. PB2-A3. This is most likely related to the different properties of the sediment during implantation of the foot and/or later diagenetic alterations.

Absolute speed of the Mecsek theropods

Applying the method of Alexander (1976), the following equation was used to estimate the speed of the Mecsek dinosaurs:

$$V=0.25g^{0.5}SL^{1.67}h^{-1.17} \quad (1)$$

This equation is appropriate for animals that used a walking gait and the SL/h ratio (stride length/hip height) is lower than 2.0 (Thulborn, 1990). In trackways with this ratio higher than 2.9 (i.e. for running animals), the equation of Thulborn and Wade (1984) was used:

$$V=[gh(SL/1.8h)^{2.56})^{0.5} \quad (2)$$

In cases where the SL/h ratio falls between 2.0 and 2.9, a mean of the values calculated from the two equations was used. Most of the trackways provide more than one stride and the associated foot length, thus an average value for the absolute speed can be calculated for every trackway. Based on these calculations, the speed of the track-making theropods ranges between 6 to 14 km/h (Tables 2 and 4). As it is expected, comparison of different trackways shows correlation between track morphology and estimated speed. For example, based on the measured associated strides, trackway PB1-C provided one of the highest values (13.96 km/h). This trackway is mainly composed of tridactyl footprints without impression of the distal end of the metatarsals. Here, the estimated speed suggests a slowly running animal. This is further supported by other features of trackway C. At the medioproximal ends of digits II and IV in C3 the sediment became creased into low bumps (Fig. 5B) when the foot left the substrate. In addition, the pace angulation is low (160°–165°) compared to other trackways (170°–178°) which has been also observed in modern birds when running (Milàn, 2003). On the other hand, trackways A, B, E, and I with frequently preserved distal metatarsal and hallux impressions indicate a slower velocity of the animal between 8–12 km/h.

However, speed does not appear to exert a primary control on the overall shape of the tracks, as expressed in morphometric measurements. We found no statistical support for any significant correlation between calculated speed and either the L/W ratio or the II–III and III–IV divarication angles. Pace angulation is another parameter that might be expected to correlate with speed. The mean pace angle in 8 trackways with at least three measurable paces is plotted against the estimated speed in Figure 4B. The lack of a clear trend and the large spread at the most commonly observed angle (170–175°) and calculated speed (12–14 km/h) suggest that it is not speed but rather some other parameter, most likely the firmness of substrate, which primarily controls the pace patterns.

Movement of the track-making theropods in herds is further supported by closely similar values of inferred speed of parallel trackways, e.g. PB1-C and PB1-D (13.9 and 13.6 km/h, respectively), PB2-A and PB2-B (12.8 and 11.9 km/h) and PB2-D and PB2F (12.1 and 12.4 km/h).

DISCUSSION

The general morphology of the studied Hungarian tracks, i.e. the angle between the digits, and the number and thickness of digit impressions (Tables 1, 3), permits the distinction of several loosely defined footprint types. This was also pointed out in other specimens from the Mecsek Mountains by Kordos (2005: figs. 4–5). Such morphological diversity appears to be a general feature of theropod tracks (Thulborn, 1990). The 21 described trackways clearly reveal that most of the morphological variation is represented by the range in some parameters, i.e. the angle between the digits, the thickness of digit impressions, the shape of the metatarsal impression, the presence/absence of a hallux impression (Fig. 5C, 6A). The variability occurs even within single trackways. This observation is most likely caused by (1) the slightly different physical properties (e.g. fluid content) of the sediments at the time when the tracks were made (extramorphological variation)(Milàn, 2003; Milàn and Bromley, 2006), (2) anatomical/ functional criteria as the variable gait and posture of the foot relative to the surface during implantment, (3) the degree of erosion after the track was made, and (4) diagenetic processes, mainly the compaction of sediments (Aplin and Vasseur, 1998; Mondol et al., 2007; and references therein).

Bivariate and multivariate statistical techniques were used to test whether morphometrics support the presence of distinctive ichnotaxa. Principal component analysis (PCA) on all simple morphometric measurements (track length and width, digit lengths, divarication angles) show significant scatter on a plot of the first two principal components (Fig. 4C). No distinct grouping of morphotypes is apparent, therefore we found no multivariate morphometrical ground for separating different ichnotaxa in our material.

There are six trackways where at least three tracks in each yielded reliable length/width ratios. A one-way ANOVA test applied to this subset of data suggests that the null hypothesis of all these samples representing the same population, i.e., all tracks belonging to the same ichnotaxon, cannot be rejected (p=0.296). A bivariate scatter plot with convex hulls to envelope data points from individual trackways is shown in Fig. 4E, to help visualize the significant overlap in tracks made by different individuals. The PCA analysis repeated on a subset of these data (four trackways with at least five tracks in each) reveals that gradual morphometric differences do exist among sets of tracks from separate trackways (Fig. 4D). However, both the areal extent of and the amount of overlap between these sets of tracks from individual trackways is variable within the PC1-PC2 morphospace. Thus we conclude that the 102 tracks preserved on the slabs PB1 and PB2 were made by multiple individuals of a single taxon.

Among the bipedal, functionally tridactyl theropod tracks, *Eubrontes* differs from those of *Komlosaurus carbonis* in its much larger size and more robust digit impressions (Fig. 7A).

On the basis of their size, the angle between the digits II–III and III–IV, and the contour of the II–IV digit impressions, the studied tracks are readily comparable to those of *Komlosaurus carbonis* (Kordos, 1983; 2005) described from the same stratigraphic unit. Gierliński (1996) described two different types of tracks from the Mecsek Mountains and he identified the smaller tracks as *Grallator tuberosus* (Hitchcock, 1836) Weems, 1992. Comparison of different *Grallator* tracks described from various localities (Hitchcock, 1858; Lockley and Hunt, 1995; Olsen et al., 1998; Hunt et al., 2000; Lockley and Meyer, 2000; Haubold and Klein, 2002) with the functionally tridactyl tracks from the Mecsek Mountains (type specimens of *Komlosaurus* and the tracks of PB1 and PB2) reveals at least three important differences. *Grallator* ichnites possess wider, more robust digit impressions, and digit divarication angles are narrower (Lockley et al., 1992, Fig. 7C). According to Olsen et al. (1998), the track length/width ratio is near or greater than 2.0. However, the average length/width ratio of the PB1 and PB2 tracks is 1.4 and 1.7, respectively. In addition, tracks referred to *Grallator* are usually smaller than 15 cm (Fig. 7C), whereas the average length of the Hungarian tracks is 16.3 cm (PB1) and 19.9 cm (PB2). It is important to note that most of the tracks in PB1 are digit imprints only. Based on these features and measurements, the presence of *Grallator* tracks within the Pécsbánya tracksites can be excluded.

Apart from "*Grallator*" tracks, Gierliński (1996) described a larger, more slender footprint morphotype as *Kayentapus soltykovensis* (Gierliński, 1991) from the Lower Jurassic of the Mecsek Mountains. The identification of Gierliński raises two questions: (1)

whether the differentiation of these two ichnotaxa (i.e. *Kayentapus* and *Komlosaurus*) is well-established, and (2) whether there are true *Kayentapus* footprints present in the Mecsek material? One of the most important advantages of the here described Pécsbánya tracksites is that the tracks can be studied and compared in relatively long trackways. Thus slight differences within track morphology, stride and pace length, and pace angulation can be observed and characterized. As it was pointed out above, our study reveals the morphological variability of tracks even within a single trackway. One of the main factors that controls the preservation of foot impressions is the fluid content of the sediments (Milàn and Bromley, 2006). Trackway PB1-C and several trackways in PB2 clearly contain tracks with slightly different morphology. Animals that moved on a wet and soft substrate left deeper and longer footprints (Milàn and Bromley, 2006), usually with hallux and metatarsal impressions (e.g. trackways PB2-H, I, K). These tracks generally show higher digit divarication angles, thus these tracks could be readily compared to those described by Gierliński (1996) as *Kayentapus soltykovensis*. On a firm substrate, the animals' feet sank less deeply into the substrate and digits were less spread. This resulted in smaller divarication angles and less common preservation of the impression of the hallux and metatarsals (e.g. trackways PB1-C, D). Furthermore, the track morphology is also influenced by the speed of the animals. Thus, our observations allow a conclusion that the two morphotypes described by Gierliński (1996) as different taxa probably represent a single taxon. The differences are simply due to variation in the physical parameters of the sediment, the animal's speed, and subsequent diagenetic alteration of the tracks (extramorphological variation).

The type species of *Kayentapus* is *Kayentapus hopii* Welles, 1971. Its type material exhibits more similarities to the Hungarian tracks than to tracks of *Grallator*, such as having relatively slender digit imprints, wider angles of digit divarication, and thus a lower length/width ratio (cf. Weems, 1992; Lockley and Hunt, 1995). On the other hand, several differences are also recognized. Beside their different size—*K. hopii* tracks are 1.5–2 times larger than the Hungarian tracks—the digit impressions of *Kayentapus* are more robust, and especially the imprint of the proximal part of digit III is weak or missing if a metatarsal pad is present (cf. Welles 1971, Fig. 7B). In the Hungarian tracks, in cases where no metatarsal pad is observed, the imprint of the proximal part of digit III still reaches the level of those of digits II and IV (Figs. 5 and 6C). Otherwise, the Hungarian tracks frequently possess metatarsal pad impressions which are not separated from the proximal end of the digit imprints, in contrast to that described for *Kayentapus* (Welles, 1971). Gierliński (1991) described *Grallator soltykovensis* from the Lower Jurassic of Holy Cross Mountains, Poland, and later he referred it to the genus *Kayentapus* (Gierliński, 1996). In the latter work it was concluded, on the basis of some isolated tracks from the Mecsek Mountains, that the *Komlosaurus* footprints are *Kayentapus soltykovensis* ichnites. In a recent study Milàn and Bromley (2006: fig. 1D, F) presented two different horizontal sections of modern emu footprints. Following their model, the general preservation of the two type specimens of *K. soltykovensis* (Muz. PIG 1560 II.10, 1560 II.12) fits well with different depth of the tracks as it was described also by Gierliński (1991). This indicates that the paratype specimen (Gierliński, 1991: fig. 2b) represents the deeper section which exhibits the maximum width of the digit impressions. This footprint, however, possesses relatively thick digit impressions similar to that of *Kayentapus hopii* (Fig. 7B). In the case of *Komlosaurus*, the digit impressions are much more slender, even for the deepest tracks (trackways PB2-H and K). Additionally, they show a hallux impression (Fig. 6A).

The Hungarian footprints are closely similar to some bird-like footprints as described by Lockley and Hunt (1995) and Lockley and Meyer (2000). Indeed, the most diagnostic features of these bird-like tracks, such as the slender, elongate digit impressions and the great divarication angles, are present in various Early Jurassic tracks from Morocco (Ishigaki, 1988:fig. 1, 14) or in that of *Shizograllator* from China (Zhen et al., 1986:fig. 3). In addition, *Shizograllator* shows similar digit divarication angles (II–III: 30°; III–IV: 45°) as were observed in the Hungarian tracks. The confluent metatarsal–digit impressions, and the presence of a hallux usually medially to the imprint exclude the avian affinity of the tracks, at least from Hungary and Morocco.

A rich material of Early Jurassic bird-like footprints has long been known from the Newark Basin (e.g. Hitchcock, 1836, 1858). Rainforth (2005) carried out a detailed study of this classical material and concluded that a major revision of bipedal theropod tracks is needed. Comparable ichnogenera described from the Newark Basin include *Platypterna*, *Sauroidichnites*, and *Sillimanius*. A future revision of such forms is necessary to clarify the taxonomic relationships of bird-like, bipedal, functionally tridactyl theropod tracks but this is beyond the scope of this study.

In summary, our observations on the tracks of PB1 and PB2 demonstrate that the Hungarian footprints show numerous morphological differences compared to grallatorid tracks. On the other hand, we could not find any convincing difference between the tracks of PB1 and PB2, and those of *Komlosaurus carbonis* Kordos, 1983. Thus, the tracks described by Kordos (1983) and those of the PB1 and PB2 tracksites are best referred to the same ichnotaxon, i.e. *Komlosaurus carbonis*.

CONCLUSIONS

The Pécsbánya tracksites (PB1 and PB2) represent the largest suite of tetrapod ichnofossils from the pre-Cenozoic of Hungary. The studied material is the most complete among the Early Jurassic dinosaur tracksites. The 21 trackways described here show slight differences regarding pace angulation, stride length, and individual footprint shape which can be related to different extramorphological influences on a surface with varying physical properties. On the basis of similar orientation, stride length, track morphology, and inferred speed, some of the trackways in both PB1 and PB2 suggests that these animals might have moved in herds. Estimated absolute speed calculated from the trackways ranges between 6 and 14 km/h. Analysis of individual tracks and comparison with those of modern animals clearly demonstrate that morphological variation represented by the ranges in some parameters (i.e. angle between the digits, thickness of digit impression, shape of the impression of distal metatarsals) occurs even in a single trackway. The study of 102 tracks in PB1 and PB2, supported by bi- and multivariate statistical analyses, indicates the presence of a single ichnotaxon, *Komlosaurus carbonis* that clearly differs from the more robust tracks of *Grallator* and *Kayentapus*.

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FIGURE CAPTIONS

Figure 1. Location and geological setting of the Pécsbánya tracksite. A, Geographical position of the site and other localities (indicated by track symbol) where Lower Jurassic tracks have been found. B, Geological overview map of the Mecsek Mountains. C, Geological profile through the Pécsbánya open pit mine (L. Németh pers. comm.).

Figure 2. Photograph of Early Jurassic trackways (MTM 2010.247.1. and MTM 2010.248.1–MTM 2010.282.1.) in their original position in the Pécsbánya open pit mine, after their discovery in 1988.

Figure 3. Slabs collected from the Lower Jurassic Mecsek Coal Formation in the Pécsbánya open pit mine. A, from Pécsbánya tracksite 1 (PB1, MTM 2010.247.1.), exhibited in the Eötvös University, Budapest, Hungary. E1 and D1 are most probably overlapping tracks that form a rounded depression. B, from Pécsbánya tracksite 2 (PB2, MTM 2010.248.1.–MTM 2010.282.1.), assembled at the Hungarian Natural History Museum. Dark grey areas are missing blocks. Rose diagrams show the direction of trackways. Numbered circles refer to the number of trackways oriented in a similar direction.

Figure 4. Statistical data analysis of tracks and trackways from tracksites PB1 and PB2. A, Histogram of track length distribution in tracksites PB1 (black bars) and PB2 (light grey bars). B, Bivariate scatter plot of estimated speed vs mean pace angulation in 8 trackways with at least three paces. C, Principal component analysis of morphometric data of all measurable tracks in tracksites PB1 and PB2. First two axes explain 87.8% of variance in data (PC1 = 69.6%, PC2 = 18.2%). D, Principal component analysis of morphometric data from four trackways with at least five measurable tracks in each (PB1-C, PB1-D, PB2-C and PB2-D). First two axes explain 93.9% of variance in data (PC1 = 79.0%, PC2 = 14.9%). E,

Bivariate scatter plot of track length vs width from six trackways with at least three tracks in each. Note overlap in morphological ranges, emphasized using convex hulls to envelope data points from individual trackways.

Figure 5. Tracks and trackways from the tracksite PB1 (MTM 2010.247.1.). A, track C4. B, track C3. Arrow shows the creased deposits behind the second digit, formed when the foot left the substrate. C, Section of PB1 showing parts of trackways C and D. Note the medially oriented third digit impressions and the lack (C3) and presence (C4) of metatarsal impressions. Roman numerals refer to the digits.

Figure 6. Tracks from the tracksite PB2. A, track K5 (MTM 2010.272.1.). B, track B7 (MTM 2010.264.1.). C, track N3 (MTM 2010.263.1.). D, track E1 (MTM 2010.265.1.). Note impressions of metatarsals (arrow) and hallux in A.

Figure 7. Comparison of different ichnotaxa of bipedal, functionally tridactyl Early Jurassic theropods. A, *Eubrontes giganteus* (redrawn from Olsen et al. 1998: fig. 5A). B, *Kayentapus hopii* (redrawn from Welles 1971: fig. 2). C, *Grallator parallelus* (redrawn from Olsen et al. 1998: fig. 11A). D, *Komlosaurus carbonis* (drawn from this study, fig. 6A).