

New perspectives on morphological variation in tridactyl footprints: clues to widespread convergence in developmental dynamics

Martin G. LOCKLEY



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It is well-known that the phalangeal formulae of the feet of dinosaurs and other vertebrates are relatively consistent within any given clade. Indeed, such similarities are part of the basis for alpha taxonomy (e.g., bird and non-avian theropod relationships). Developmental studies of the vertebrate foot support the view that morphological similarity owes as much to intrinsic (formal) developmental dynamics as to extrinsic (functional) influences. Thus, the morphologies of ornithopod, non-avian theropod and most bird feet are convergent (especially with respect to digits II–IV) despite significant differences in size and functional adaptation. Despite these “general” convergences, “detailed” variation in the morphology of tridactyl, mesaxonic, Triassic through recent non-avian dinosaur and bird tracks has allowed the diagnosis of hundreds of ichnotaxa, as well as the recognition of nearly continuous subtle variation in modern bird tracks. Several studies characterize this variation by measuring how far digit III projects anteriorly beyond lateral digit IV and medial digit II, creating an “anterior triangle” between the tips of digits II, III and IV (Weems, 1992). Differences in this projection of digit III highlight a polarity between strong mesaxony (strong central tendency) and weak mesaxony (weak central tendency). Early studies (Olsen, 1980) suggested that as theropod tracks in the *Grallator–Eubrontes* plexus increase in size, they shift from narrow to wide and from strongly to weakly mesaxonic. However, such polarities also reiterate (independent of size) among medium-sized and diminutive theropod tracks (e.g., *Minisauripus*). Such polarity also recurs among ornithopods, and is equally striking in extant birds (e.g., between passerines and members of the charadriiformes). Such “intrinsic” differences can only be partially attributed to functional variation in digit divarication caused by foot-substrate interaction. Moreover, such polarities in foot morphology give important clues to whole limb and whole body proportions, and suggest an intrinsic “lawfulness” to patterns of convergence.

Martin G. Lockley, Dinosaur Tracks Museum, University of Colorado at Denver, PO Box 173364, Denver, Colorado, 80217, U.S.A.; e-mail: Martin.Lockley@cudenver.edu (received: March 03, 2009; accepted: December 18, 2009).

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INTRODUCTION

Most theropod and ornithopod dinosaurs, and many terrestrial birds have functionally three-toed, tridactyl feet in which the middle toe (digit III) is the most prominent, with medial and lateral digits (II and IV respectively) often subequal and subordinate in length. This condition is referred to as mesaxonic (Fig. 1), a term which can also be applied when a hallux (digit I) is present. However, the hallux of birds, if present, is more variable in length and orientation than in dinosaurs. The most common condition in birds, with three toes directed anteriorly, and a posterior, or posterior-medial hallux, is referred to as “anisodactyl” (Fig. 1D). This modification of the simple “mesaxonic” configuration for digits II–IV creates the anisodactyl condition by incorporation of the hallux.

In perching birds (passerines) and herons (ciconiformes) the hallux may be long and posteriorly directed so as to align with the foot axis (digit III). In such cases the total length of the foot (and footprint) is considerably increased. However, in theropod dinosaurs there are no reliable reports of a fully reversed hallux and, where present, the hallux is often short and medially directed, so as to add little to overall footprint length. A hallux is also observed in some shorebirds (charadriiformes) although often, as is the case with theropods, the hallux trace is very small or not impressed at all. Most large ornithopod dinosaurs lack a hallux altogether, although some small primitive forms, like other ornithischians may have a hallux that is oriented medially or somewhat anteriorly.

For the purpose of this paper attention is focused on the typical, simple mesaxonic condition seen in so many bipedal dinosaurs and certain ground-dwelling birds, and discussion of the avian hallux and its relationship to the mesaxonic configuration

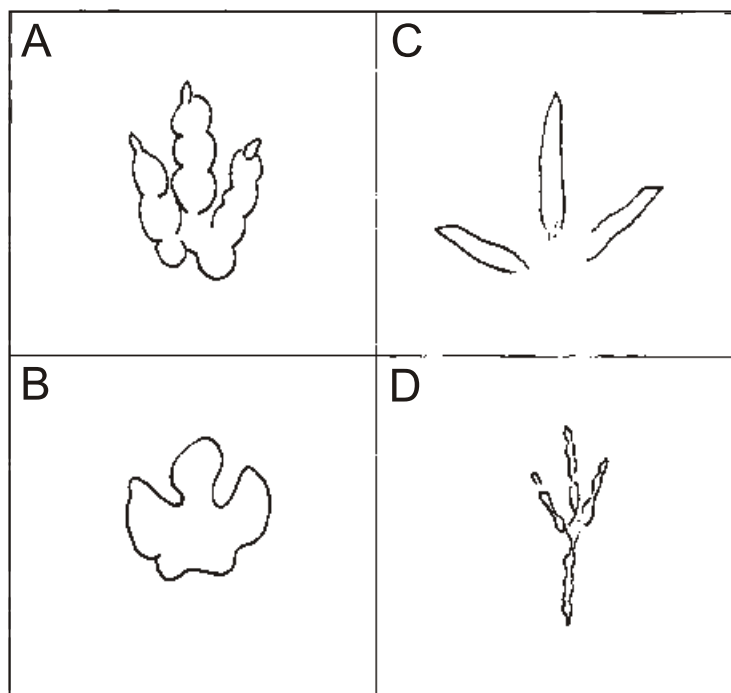


Fig. 1. Typical mesaxonid tridactyl tracks

A — a theropod; B — an ornithomimid; C — a modern shorebird; D — an anisodactyl bird track with a hallux; see Figures 3, 10 and 13 for scale

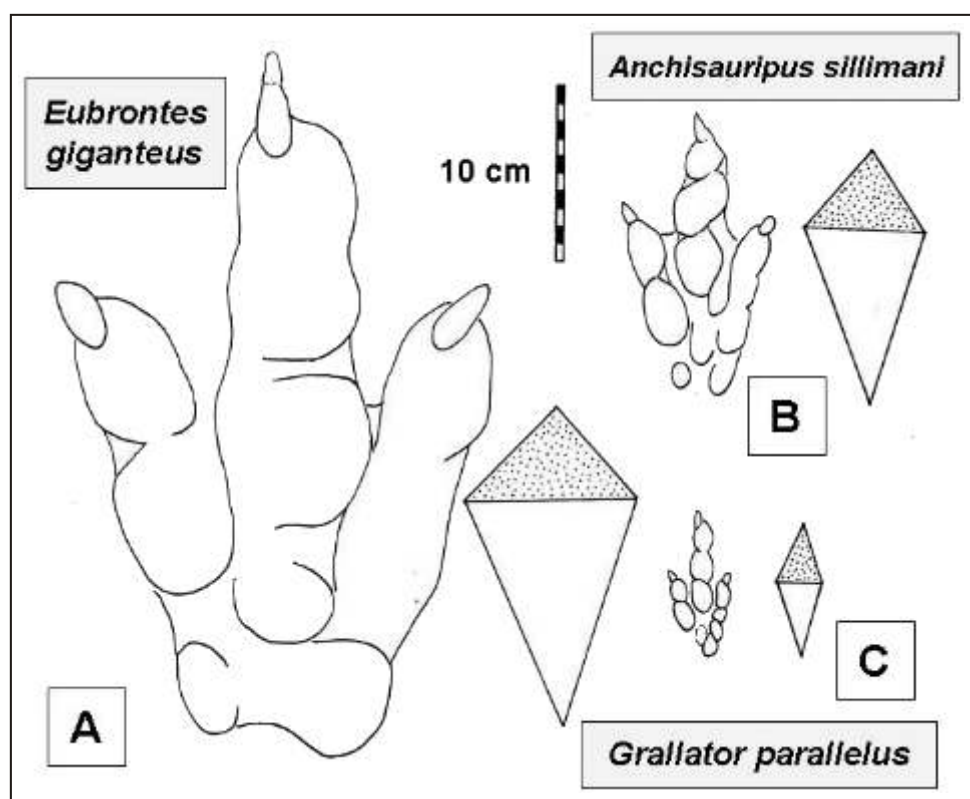


Fig. 2. The anterior triangle originally defined by Weems (1992) and redrawn to show the configuration of the type ichnospecies in the *Gallator*-*Anchisauripus*-*Eubrontes* plexus

F l/w — footprint length/width ratio and (AT l/w — anterior triangle length/width ratio) for the three ichnogenera are: A — 1.70 (0.58), B — 1.90 (0.68), C — 2.64 (1.22); all at the same scale; compare with Figure 4

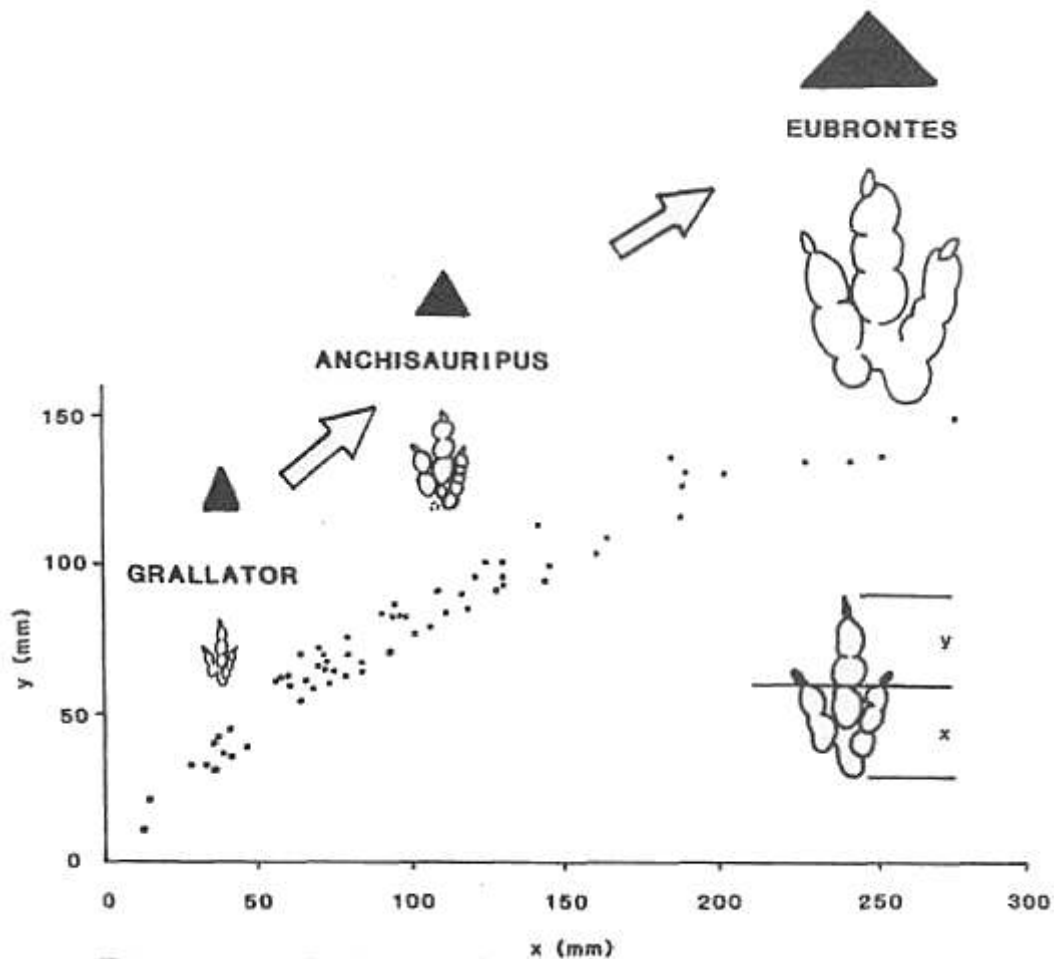


Fig. 3. The GAE plexus (modified after Olsen, 1980; Lockley and Hunt, 1995)

Note increase in width with size

of digits II–IV is limited to a few striking examples. Specifically, following the precedent of previous studies (Olsen, 1980; Weems, 1992) I examine the degree of mesaxony: that is how prominent digit III is in relation to digits II–IV. This measure defines the shape of the anterior triangle defined by Weems (1992) and illustrated herein (Figs. 2 and 3). In feet and footprints where mesaxony is “strong” (strong central tendency) the anterior apex of the triangle subtends an acute angle, but where mesaxony is “weak” (weak central tendency) and digits II–IV are almost subequal in length the anterior apex subtends an obtuse angle. Although variation in mesaxony can be influenced by variation in digit divarication, strong variation within a trackway is the exception rather than the rule. As detailed below some tracks, like *Grallator*, are inherently narrow relative to other inherently wide forms.

The purpose of this paper is to elaborate on a presentation given at Ichnia 2008 and to explore morphodynamic relationships (*sensu* Lockley, 1999, 2001, 2007) between degree of mesaxony and the size and/or shape (narrowness or breadth) of footprints associated with different groups of dinosaurs and birds, and to consider how these relationships, might be related to intrinsic, “formal” developmental dynamics or extrinsic, “functional” adaptation (*sensu* Gould, 2002).

METHODS AND MATERIALS

Following the precedent set by Olsen (1980), elaborated by Weems (1992) and discussed briefly by Lockley (2000) and Lockley *et al.* (2008). The anterior triangle was measured and drawn for tridactyl theropod, ornithopod and bird tracks from representative, well preserved holotype, paratype and topotype specimens in various collections. Most of these tracks were drawn from the original specimens, replicas or full-size tracings made by the author, and not from line drawings or photos in the literature except in cases where original material was not available. The Dinosaur Tracks Museum, University of Colorado at Denver contains a library of more than 1350 full size tracings on clear acetate film. Whenever possible, illustrations of tracks from this library are presented at the same scale. Thus, a measure of consistency is achieved in the method of tracing, illustration and morphological comparison.

The anterior triangle (AT) is measured from the distal point on the digital pads of digits II, III and IV, and not from claw marks which may be variably preserved. The maximum height of the triangle is measured, perpendicular to the transverse base of the triangle and expressed as the l/w ratio (AT l/w). Likewise maximum footprint (F) length and width were also measured

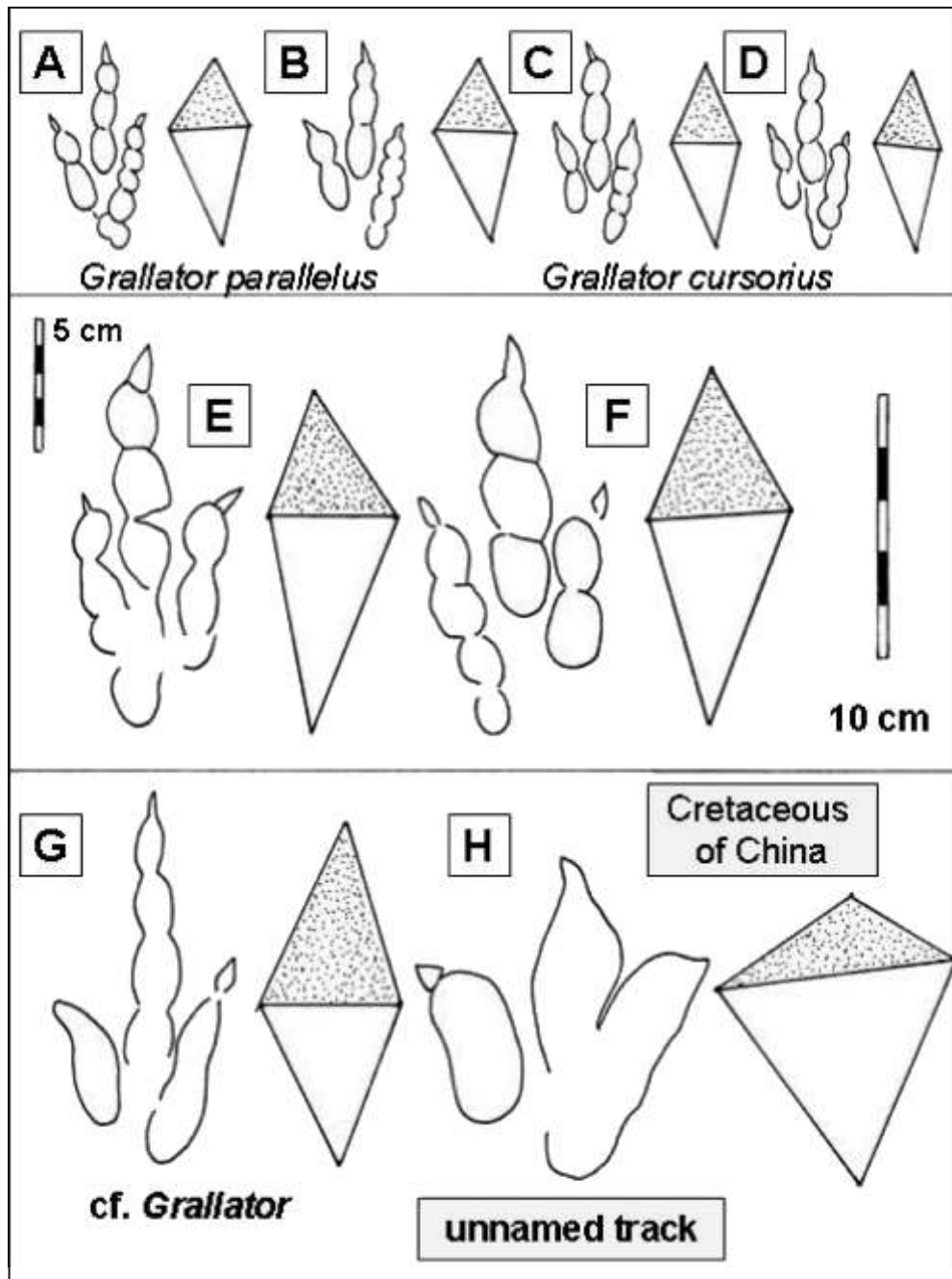


Fig. 4. Track (F l/w) and anterior triangle length/width (AT l/w) ratios for *Grallator* from the Hitchcock collection and other sites

A–D — small *Grallator*: A–B — *Grallator parallelus*, C–D — *Grallator cursorius* after Olsen *et al.* (1998, fig. 11); E–F — tracings of medium-sized *Grallator* (CU T 424), made by the author from Hitchcock collection specimen AC 9/14; G — *Grallator*-like track with strong mesaxony; H — co-occurring theropod track with weak mesaxony from the Cretaceous of Shandong Province China; F l/w (and AT l/w) for illustrated tracks are as follows: A–D mean for 4 similar tracks 2.32 (1.43), E — 2.42 (1.0), F — 2.27 (1.0), G — 2.23 (1.26), H — 1.08 (0.31); note reduced mesaxony of H; all drawn at the same scale; compare with Figures 2A, 5 and 6

and expressed as a l/w ratio (F l/w). This pair of measurements is given in the figure captions for ease of reference, and the anterior triangle, illustrated beside the track, gives a visual indication of the degree of mesaxony. See Figures 4–14.

Abbreviations: AC = Amherst College, CU = University of Colorado at Denver, Dinosaur Tracks Museum (T = tracings in CU Denver collection).

THE EUBRONTES–GRALLATOR PLEXUS

Eubrontes and *Grallator* are among the best known and first named theropod tracks, and as such are a necessary starting point in the discussion of the morphology and ichnotaxonomy of any theropod tracks. The names were originally applied by Hitchcock

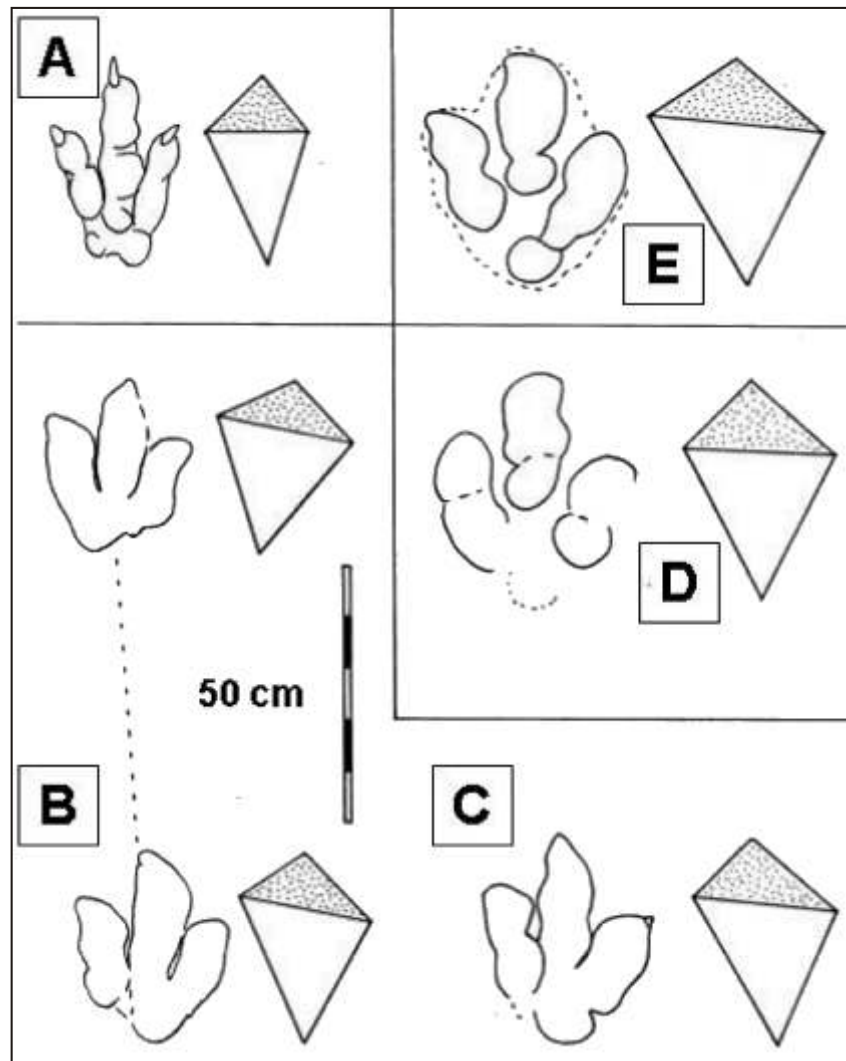


Fig. 5. Track (F l/w) and anterior triangle length/width (AT l/w) ratios for *Eubrontes* from the Hitchcock collection (A) and from the Glen Canyon Group, Utah (B–E)

A — *Eubrontes giganteus* type specimen after Olsen *et al.* (1998); B — trackway sequence based on CU 184.74 (T 928); C — track CU 184.75 (T929); D — from tracing T 935; E — CU 184.70 (T 909); F l/w and (AT l/w) for illustrated tracks are as follows: A — as in Figure 2A and B — two tracks in same trackway 1.17 (0.38) and 1.22 (0.40), C — 1.44 (0.44), D — 1.41 (0.47) and E — 1.29 (0.37); all drawn at the same scale; compare with Figures 4 and 6

(1845, 1858) to describe tridactyl tracks from the Lower Jurassic of New England. Although Hitchcock's studies of these two track types are complicated by his having previously applied other ichnotaxonomic labels to the type material and other similar tracks, these two names became widely accepted in subsequent revisions (Lull, 1904, 1915, 1953). Although Hitchcock believed that both track types were attributable to birds, ichnologists now universally accept that they are attributable to saurischian (theropod) dinosaurs, probably ceratosaurs, basal tetanurines and carnosaur. In most cases the inferred trackmakers for both ichnogenera are theropods, though Weems (2003) attributed *Eubrontes* to a prosauropod. The possibility of an ornithischian trackmaker might be considered (Smith and Farlow, 1996, 2003), but this attribution is usually reserved for the ichnogenus *Anomoepus* discussed below.

The application of the labels *Eubrontes* and *Grallator*, although widespread in the ichnological literature, especially with reference to Early Jurassic theropod track dominated assemblages, is by no means universally agreed. For example, Lull (1904) introduced the ichnogenus *Anchisauripus*, which due to the widespread dissemination of subsequent revisions of his work (Lull, 1953) was initially accepted as an important addition to lexicon of theropod track names. This led to the suggestion by Olsen (1980) that all the type species assigned to the ichnogenera *Grallator*, *Anchisauripus* and *Eubrontes* form an allometric plexus (GAE) best characterized by reducing all three ichnogenera to the status of sub-ichnogenera under the umbrella of *Grallator*: i.e. *G.* (*Grallator*), *G.* (*Anchisauripus*) and *G.* (*Eubrontes*).

In this plexus Olsen (1980) noted that large forms (*Eubrontes*) showed significantly less mesaxy than small

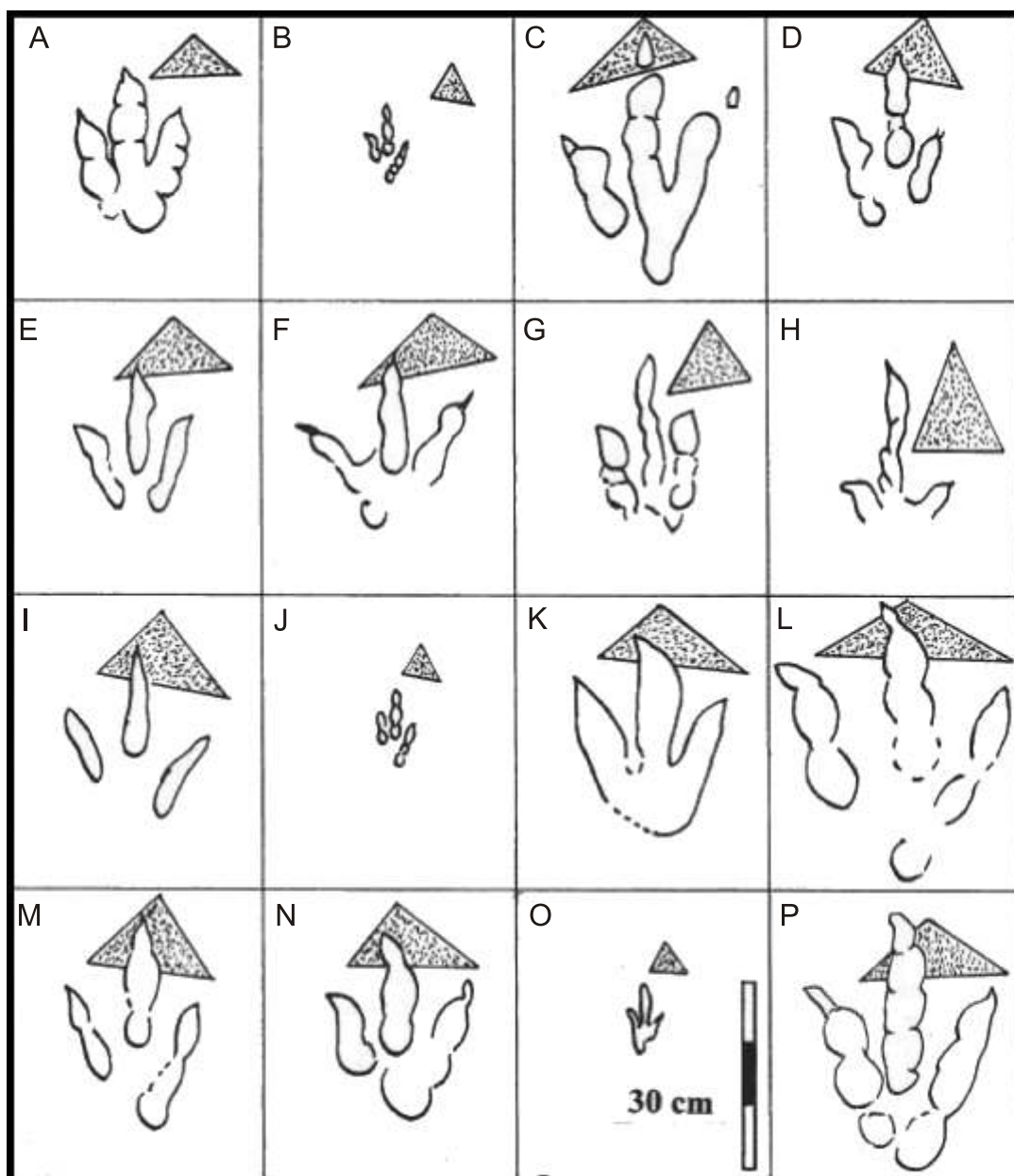


Fig. 6. Track (F l/w) and anterior triangle length/width (AT l/w) ratios for *Grallator*- and *Eubrontes*-like tracks from the Lower–Middle Jurassic of China

A — *Eubrontes* Hitchcock 1845; B — *Grallator* Hitchcock 1858; C — *Changpeipus carbonicus*, after Young (1960); D–H after Zhen *et al.* (1983, 1996): D — *Grallator limosus*, E — *Paracoelurosaurichnus monax*, F — *Schizograllator xiaohabaensis*, G — *Youngichnus xiyangensis*, H — *Zhengichnus jinningensis*; I–O after Yang and Yang (1987): I — *Zizhongpus wumanensis*, J — *Chongqingpus microiscus*, K — *Tuojiangpus shuinanensis*, L — *Chonglongpus hei*, M — *Megaichnites jizhaishiensis*, N — *Jinlijingpus nianpanshanensis*, O — *Chuannchengpus wuhaungensis*; P — *Weiyuanpus zigongensis* (after Gao, 2007); C–P are all very similar to *Eubrontes* Hitchcock 1845 (A) and *Grallator* (B) Hitchcock 1858; F l/w and (AT l/w) for illustrated tracks are as follows: A — 1.48 (0.44), B — 2.10 (1.0), C — 1.47 (0.40), D — 1.65 (0.66), E — 1.23 (0.48), F — 1.03 (0.38), G — 1.74 (0.8), H — 1.43 (1.18), I — 1.18 (0.5), J — 2.0 (0.71), K — 1.32 (0.37), L — 1.21 (0.30), M — 1.56 (0.61), N — 1.30 (0.48), O — 2.0 (0.92), P — 1.34 (0.38); note that small tracks B, J and O have *Grallator*-like proportions, large tracks A, C, E, I, K, L, N and P have *Eubrontes*-like proportions; the remaining tracks have intermediate proportions; all tracks (except for I and K) drawn by the author from type material and redrafted to the same scale

forms (*Grallator*): i.e. the projection of digit III beyond digits II and IV decreased with size. Weems (1992) took this measure of “anterior projection” (= y in Fig. 2, lower right) as the basis for measuring and anterior triangle between the three digits tips. This triangle is clearly wider in larger forms (Fig. 3) and can be compared with the posterior triangle (*sensu* Weems, 1920 which

is another measure of the projection of digit III relative to track length. This plexus scheme, which elevated *Grallator* to a super-ichnotaxon status, was initially accepted by some workers (Gierli ski, 1991) but ironically was abandoned by Olsen *et al.* (1998) and others (Gierli ski, 1996) in later analyses. Thus ichnotaxonomic opinion returned to that of the initial pre-1980

status and *Eubrontes* and *Grallator* continued to be regarded by most ichnologists as distinct ichnogenera. Nevertheless, few workers have used the “intermediate” ichnotaxon *Anchisauripus*, and it is now rarely mentioned, and is considered by many as a synonym of *Grallator*. Meanwhile, although the GAE plexus is reduced to its two end members (*Grallator* and *Eubrontes*), the ichnogenus *Kayentapus* (Welles, 1971) has been distinguished from *Grallator* and *Eubrontes* by morphometric analysis (Weems, 1992) and accepted as a distinct form by Lockley and Hunt (1995); Gierli ski (1996); Piubelli *et al.* (2005); Xing *et al.* (2009).

It is easy to demonstrate that Olsen’s 1980 claim is correct: large *Eubrontes* are consistently wider than *Grallator* and this greater width is also manifest in the relatively greater width of the anterior triangle: i.e., weaker mesaxony (compare Figs. 4 and 5). In the case of representative *Grallator* specimens from the Hitchcock collection, and *Grallator*-like tracks from a Cretaceous site in Shandong Province, China, the footprint length/width (F l/w) ratio of the track is consistently between about 2.2 and 2.4 (Fig. 4), and the anterior triangle (AT l/w) ratio is between 1.0 and 1.5. By contrast the l/w ratios for a co-occurring wide track from the same Shandong site are quite different (1.08 and 0.31) and *Eubrontes*-like. As discussed below, this suggests that there are also medium-sized tracks with weak mesaxony, which do not fit the GAE plexus.

F l/w and AT l/w ratios for type *Eubrontes* from the Hitchcock collection (Fig. 2A) of 1.70 and 0.58 respectively suggest a track that is slightly more elongate than large *Eubrontes* from the western USA which have F l/w ratios of between 1.17 and 1.44 and AT l/w ratios of between 0.37 and 0.47 (Fig. 5). This suggests that the larger wider, and more robust *Eubrontes* (Fig. 5B–E) may be significantly different from the type specimen (Fig. 5A).

Measuring the differences in shape between *Eubrontes* and *Grallator* does not however, lead to any definitive ichnotaxonomic conclusions as Olsen’s own ambivalent lumper *v.* splitter inferences indicate (comp. Olsen, 1980 *v.* Olsen *et al.*, 1998 respectively). Herein no attempt is made to resolve the lumper *v.* splitter debate. Rather, an attempt is made to consider whether F l/w and AT l/w relationships hold true for other tridactyl dinosaur and bird tracks. The *Grallator*–*Eubrontes* plexus indicates a positive correlation between elongation of the track and the elongation of the anterior triangle. As noted below, this positive correlation is typical of other, but not all tridactyl trackmakers, and to a large extent independent of preservational factors.

ASIA ICHNOTAXA ATTRIBUTED TO THE *EUBRONTES*–*GRALLATOR* PLEXUS

In recent years, study of *Eubrontes*- and *Grallator*-like tracks from the Lower–Middle Jurassic of Asia have suggested that despite the assignment of diverse ichnotaxonomic names, most tracks are indistinguishable from *Eubrontes* and *Grallator* (and *Kayentapus*) from North America (Lockley *et al.*, 2003; Lockley and Matsukawa, 2009). Measurements of the F l/w and AT l/w ratios (Fig. 6) confirms this inference.

Thus in Figure 6 (modified after Lockley and Matsukawa, 2009) small tracks B, J and O have *Grallator*-like proportions and large tracks A, C, E, I, K, L, N and P have *Eubrontes*-like proportions. The remaining tracks have intermediate proportions, but some including D, G and H are compromised by poor preservation. *Schizograllator* (Fig. 6F) has been compared with *Kayentapus* (Zhen *et al.*, 1989; Matsukawa *et al.*, 2005).

MINIATURE THEROPOD TRACKS

A recent study of the miniature theropod track *Minisauripus*, which co-occurs with the smallest named *Grallator* track (*Neograllator emeiensis*) in the Cretaceous of China (Zhen *et al.*, 1995; Lockley *et al.*, 2008) indicates that the positive correlation between track and anterior triangle l/w ratio holds true even in diminutive tracks (Fig. 7). Thus, while the respective values for *N. emeiensis* of 2.18 and 1.38 are in the range of larger *Grallator*, indicating strong mesaxony (Fig. 4), the values are quite different for *Minisauripus* (1.5 and 0.4 respectively) which falls in the weak mesaxony range cited for the medium-sized Shandong track (Fig. 4H) and for large *Eubrontes* (Fig. 5). This convergence of shape between diminutive *Minsauripus* (length 3 cm) the medium-sized Shandong tracks (length 12 cm) and large *Eubrontes* (length ~30–40 cm) may be explained as a heterochronic phenomenon (Lockley *et al.*, 2008) and is further discussed below. It appears that convergence with the *Eubrontes* morphotype is independent of size in some cases.

PROBABLE COELUROSAUR TRACKS: *ORNITHOMIMIPUS*, *IRENICHNITES*, *COLUMBOSAURIPUS* AND *MAGNOAVIPES*

There are significant differences between the feet and footprints of different groups of theropods. For example, Late Triassic and Jurassic theropod trackmakers mostly belong are to the Ceratosauria and basal tetanurines (including Carnosauria), whereas in the Cretaceous the Coelurosauria are also widely represented (*sensu* Holtz and Osmólska, 2004). As noted above, most pre-Cretaceous theropod tracks are quite elongate, and large forms like *Eubrontes* are quite robust. However in the Cretaceous slender-toed forms appear with wider digit divarications (Fig. 8). These include *Ornithomimipus* (Sternberg, 1926), *Irenichnites* and *Columbosauripus* (Sternberg, 1932) and *Magnoavipes* (Lee, 1997; Lockley *et al.*, 2001). As the former name suggests, the inferred trackmakers for this group are ornithomimisaur-like coelurosaurs and their close relatives (i.e., Maniraptoriformes, *sensu* Holtz and Osmólska, 2004). In comparison with the aforementioned theropod tracks of probable ceratosaurian, basal tetanurine and carnosaurian affinities these maniraptoriform tracks are significantly wider (Fig. 8). *Ornithomimipus* is significantly more elongate and strongly mesaxonic than the other three ichnogenera which are all wide with similar degrees of mesaxony. In comparison with the widest theropod tracks in GAE plexus (i.e., *Eubrontes* morphotypes), *Columbosauripus*, *Irenichnites* and

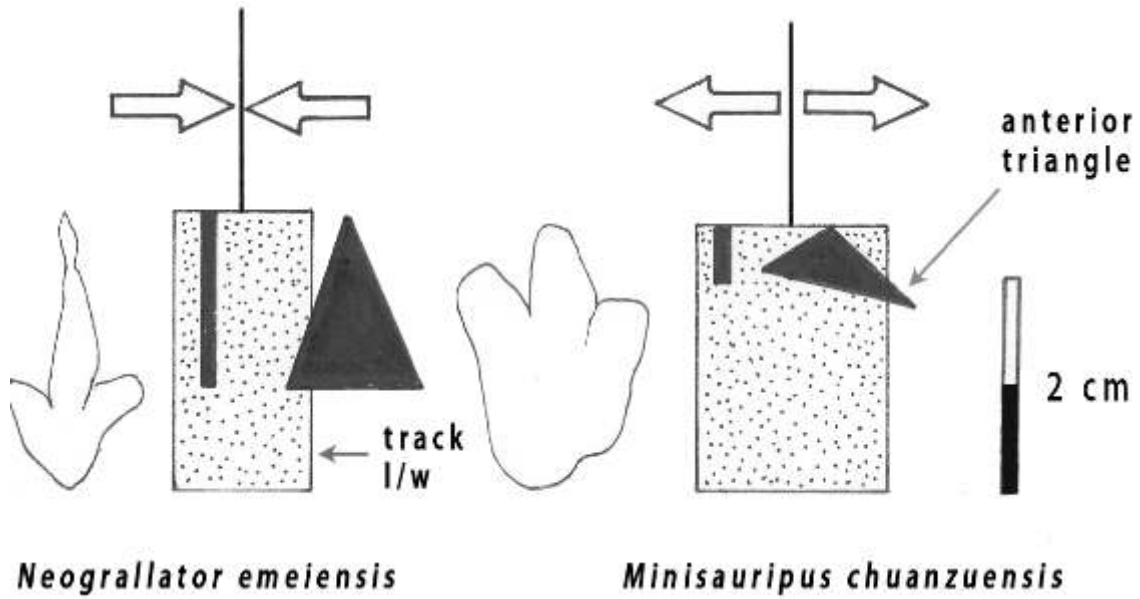


Fig. 7. Track (F l/w) and anterior triangle length/width (AT l/w) ratios for *Neograllator emeiensis* (2.18 and 1.38) and *Minisauripus* (1.5 and 0.4) from the Cretaceous of China (modified after Lockley *et al.*, 2008)

Note the extreme variation in the anterior triangle despite similar size; both drawn at the same scale

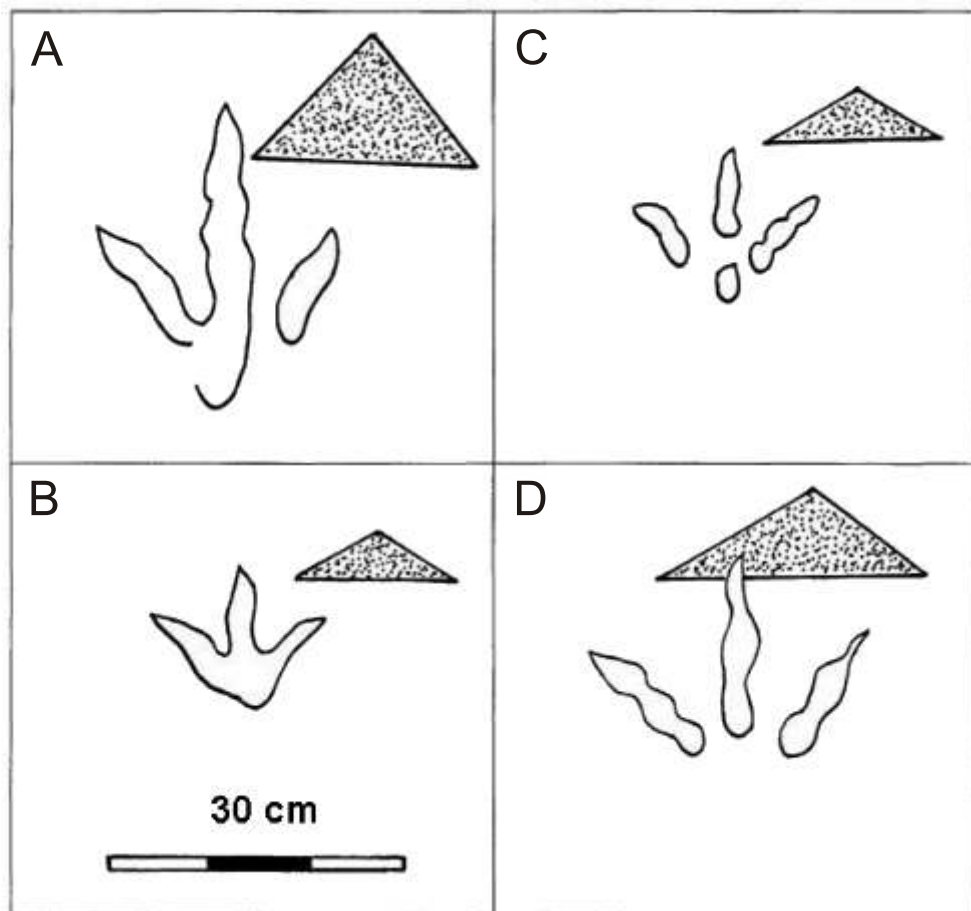


Fig. 8. Track (F l/w) and anterior triangle length/width (AT l/w) ratios for slender-toed non-avian dinosaur tracks of probable coelurosaurian affinity

A — *Ornithomimipus*; B — *Columbosauripus*; C — *Irenichnites*; D — *Mugnoavipes*; F l/w and (AT l/w) for A–D are as follows: A — 1.29 (0.55), B — 0.78 (0.30), C — 0.85 (0.30), D — 0.74 (0.38); all drawn at the same scale

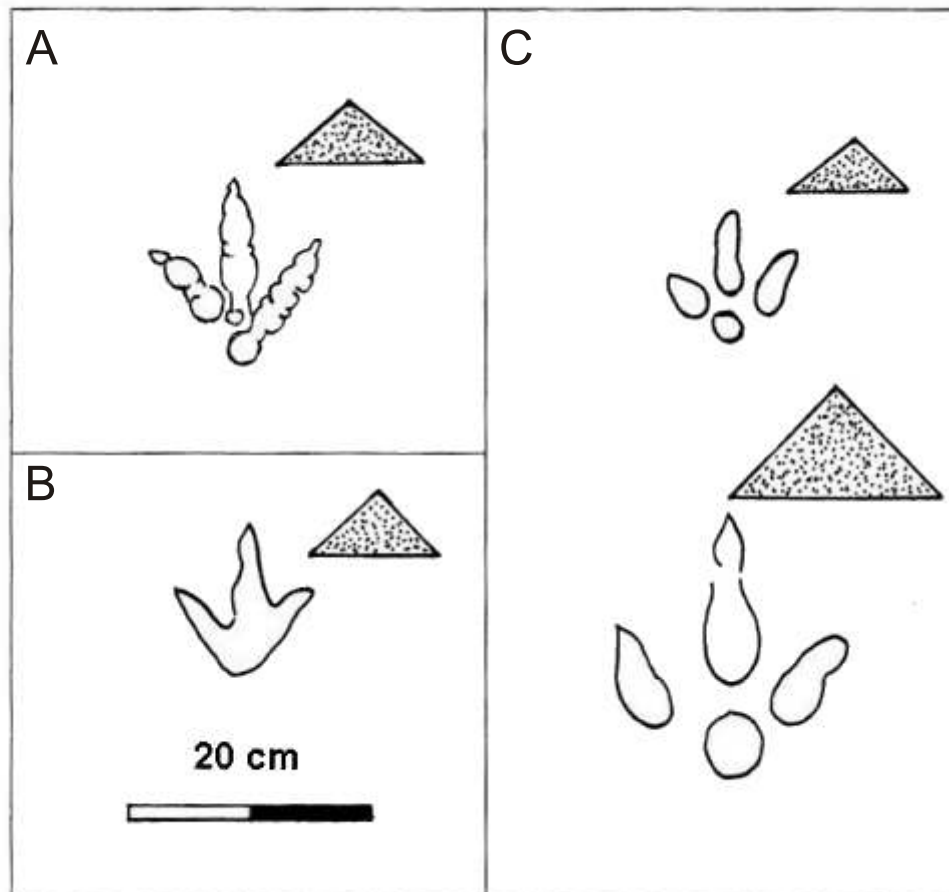


Fig. 9. Track (F l/w) and anterior triangle length/width (AT l/w) ratios for *Anomoepus*, *Neoanomoepus* and *Dinehichnus*, modified after Lockley *et al.* (2009)

F l/w and (AT l/w) for A–C are as follows: A — 1.07 (0.42), B — 1.04 (0.48), C — large track 1.13 (0.51), small track 1.0 (0.45); all drawn at the same scale

Magnovipes are significantly wider, but the degree of mesaxony (AT l/w) is similar. The relative proportions of these presumed coelurosaurian tracks are also convergent with many ornithopod tracks and shorebird tracks, illustrated below. However, it should be stressed that the trackway patterns are quite different. Coelurosaurian trackways, like theropod trackways in general, are narrow with long steps and little or no rotation of the foot axis, whereas ornithopods typically have wider trackways, short steps and strong inward rotation of the foot axis: compare Figure 8 with Figures 9 and 10.

ORNITHOPOD TRACKS

Most unequivocal, tridactyl ornithopod pes tracks are relatively large iguanodontid and hadrosaurid tracks known from the Cretaceous. Many of these are associated with a small triangular to sub-oval hoof-like manus trace, which proves ornithopod affinity rather than affinity with some other ornithischian group. By contrast probable small ornithopod tracks from the Early Jurassic include *Anomoepus*, which has a pentadactyl manus, which suggests the possibility that this

ichnogenus is attributable to some other ornithischian (Olsen and Rainforth, 2003; Lockley and Gierli ski, 2006). As shown in Figure 9 the track and anterior triangle l/w ratios for *Anomoepus* are 1.07 and 0.42 respectively. *Dinehichnus*, from the Upper Jurassic is also a probable ornithopod track with F l/w ratios between 1.0 and 1.13 and AT l/w ratios of 0.45–0.51. Likewise *Neoanomoepus* from the basal Cretaceous (Lockley *et al.*, 2009) is also of probable ornithopod affinity and has respective ratios of 1.04 and 0.48 (Fig. 9). Almost invariably ornithopod tracks have a slight to pronounced inward rotation of the pes axis (digit III), and most large forms (foot length >30 cm) lack discrete pad impressions.

Most typical Cretaceous ornithopod tracks (Fig. 10) are about as wide or wider than long (track l/w ratios between 0.92 and 1.17), with anterior triangle ratios between 0.28 and 0.47, although the relatively small and gracile morphotype from the Jurassic–Cretaceous boundary site at Cerradicas, Spain has a l/w ratio of 1.36, an anterior triangle ratio of 0.47. The Cerradicas trackways also reveal distinct digital pad impressions and were it not for the manus traces, they could easily be mistaken for theropod tracks. Generally speaking, therefore, there is a tendency for smaller ornithopod tracks to be more elongate than large robust forms.

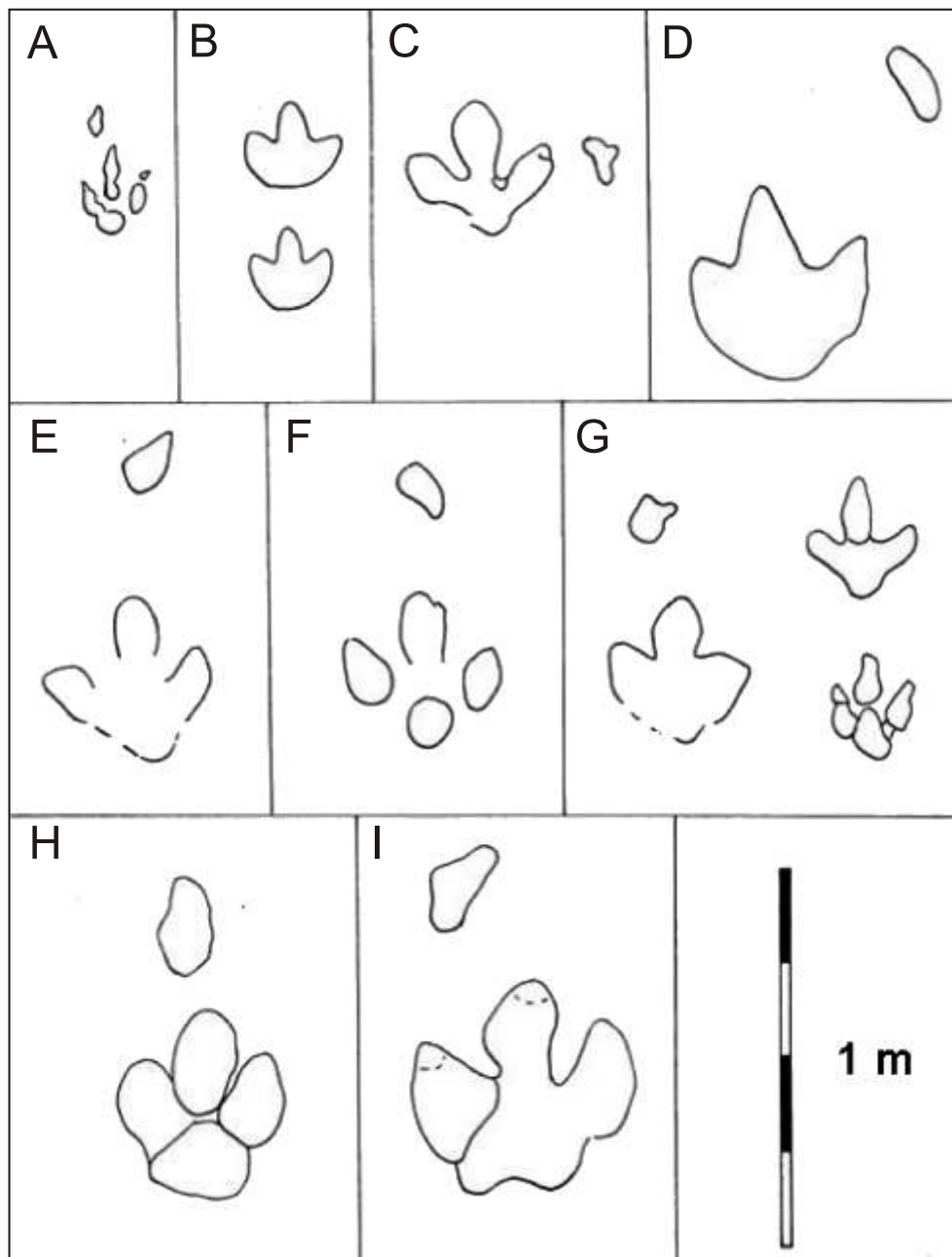


Fig. 10. Track (F l/w) and anterior triangle length/width (AT l/w) ratios for typical Cretaceous ornithopod tracks show great consistency

A — unnamed track from Cerradicas site, Spain; **B** — *Iguanodontipus*, England; **C** — iguanodontid tracks from Munchehagen, Germany; **D** — iguanodontid tracks from Cabezon de Cameros, Spain; **E** — iguanodontid tracks from Regumiel de la Sierra; **F** — iguanodontid tracks from the Lakota Group, South Dakota; **G** — *Caririchnium* tracks from Dinosaur Ridge, Colorado; **H** — *Caririchnium* tracks from Brazil; **I** — *Hadrosauropodus* from the St. Mary River Formation, Canada; F l/w and (AT l/w) for A–I are as follows: A — 1.36 (0.47), B — 0.92 and 0.92 (0.39 and 0.40) for two tracks, C — 0.93 (0.41), D — 1.07 (0.41), E — 1.0 (0.43), F — 1.0 (0.41), G — for three track in decreasing order of size: 1.0 (0.44), 1.09 (0.51) and 1.29 (0.44), H — 1.14 (0.42), I — 1.0 (0.28); all drawn at the same scale; modified after Moratalla *et al.* (1994), Sarjeant *et al.* (1998), Lockley and Wright, (2001) and Lockley *et al.* (2004)

There are a number of large Cretaceous ornithopod tracks that show very weak mesaxony: i.e., on simple inspection the tracks have very short middle digits (III) relative to the medial and lateral digits (II and IV). As shown in Figure 11 these tracks have low l/w ratios (0.82–0.94) and extremely low anterior triangle l/w ratios

(0.19–0.28). Two of the four examples cited here have been described in detail and assigned names that have yet to appear “formally” in the literature. These are “Ornithopodichnus” from Korea (Kim *et al.*, in revision) and “Brachyguanodonipus” named in a Ph.D. Thesis by Moratalla (1993).

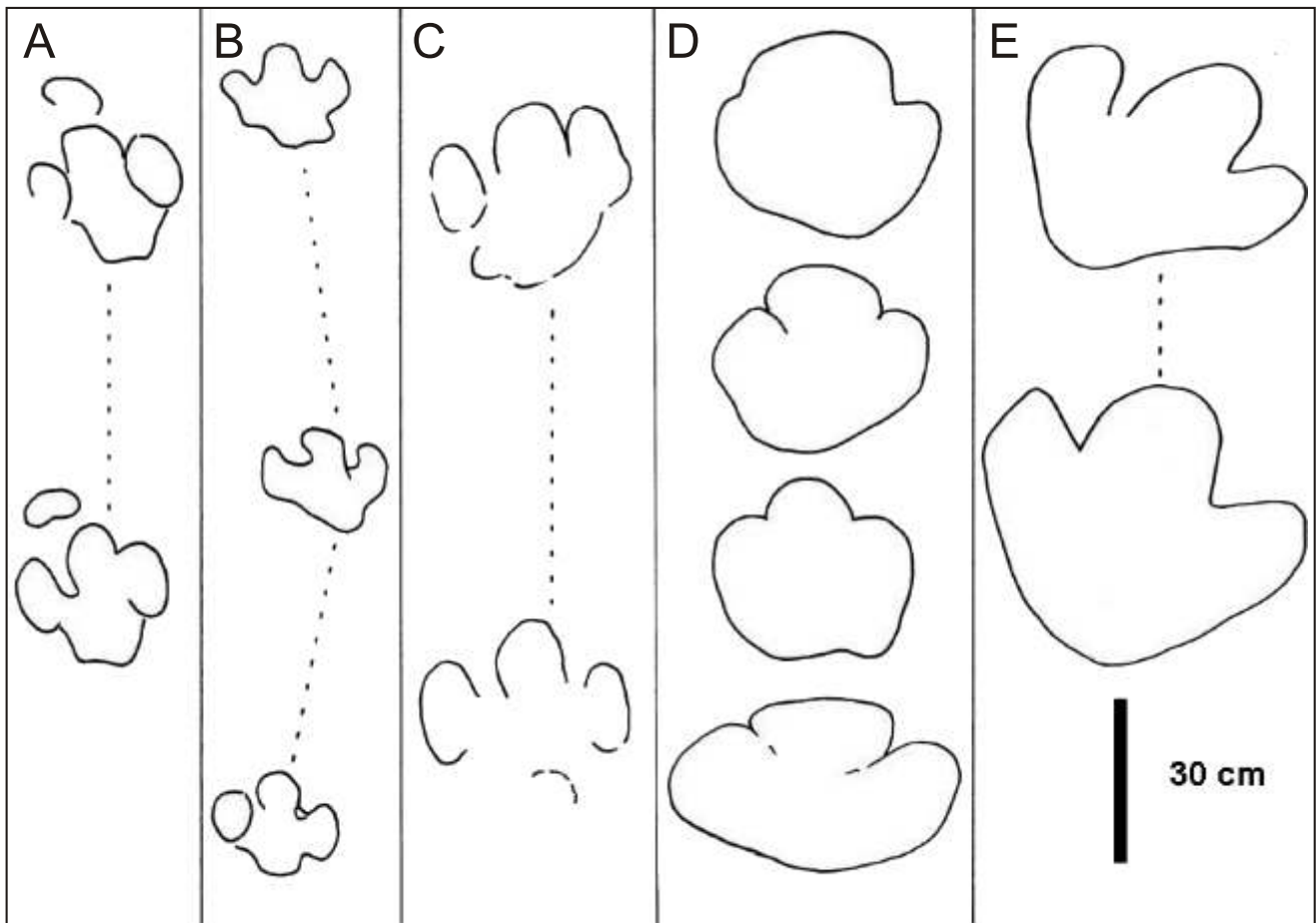


Fig. 11. Track (F l/w) and anterior triangle length/width (AT l/w) ratios for unusually wide ornithopod tracks

A and B — ornithopod tracks from the Houzuoshan Dinosaur Park, Shandong Province, China; C — unamed tracks from the Hwasun tracksite, Korea; D — “*Ornithopodichnus*” from the Cretaceous of Korea; E — “*Brachyguanodontipus*” from the Cretaceous of Spain (after Moratalla, 1993); F l/w and (AT l/w) for A–E are as follows: A — 0.94 (0.23), B — 0.84 (0.20), C — 0.93 (0.19), D — 0.82 (0.28), E — 0.82 (0.22); all drawn at the same scale

Comparing these forms with the typical ornithopod tracks described above, it appears that there is again a positive correlation between track size, track width and anterior triangle width among ornithopods. These “extra wide” ornithopod tracks were probably made by large taxa like *Zhuchengosaurus* (Zhao *et al.*, 2007) in which pes digit III is very short (weak mesaxony).

BIRDS

Lockley (1999, 2007) noted that there is a striking polarity between the feet and footprints of perching birds (passerines) and shorebirds (charadriiformes). The former typically have narrow, anisodactyl footprints with a long reversed hallux, whereas the latter have wide tridactyl footprints and usually no hallux or one that is very short (Fig. 12). For the purposes of comparison with theropods and ornithopods, representative F l/w and AT l/w ratios are presented (Fig. 13) for various extant bird tracks illustrated by Elbroch and Marks (2001). They show that although the reversed hallux makes passerine tracks are very long (F l/w 2.08–3.36, N = 8), the anteriorly oriented

digits (II–IV) show relatively weak mesaxony (AT l/w, 0.36–0.64, N = 8). So while F l/w ratios fall well outside the range of any dinosaur tracks the AT l/w ratios fall in the range of *Eubrontes*, coelurosaurs and ornithopods. By contrast typical shorebird tracks are wide (F l/w 0.68–1.00, N = 7) with wide anterior triangles (AT l/w 0.32–0.52). Thus shorebirds appear most convergence with the coelurosaur group (Fig. 8), and perching birds appear to be the exception to the rule, because their high l/w track ratios are negatively correlated with low anterior triangle l/w ratios.

Among large, extant and recently extant ground dwelling flightless birds, such as the moa, emus and rheas most have tridactyl feet which permit morphological comparison with large ground dwelling dinosaurs (theropods and ornithopods), as done by Padian and Olsen (1989) and Lockley *et al.* (2007). As shown in Figure 14 there is a strong tendency for these forms to have wide feet (F l/w 0.70–1.04) and wide anterior triangles (AT l/w 0.25–0.52). These values are convergent with coelurosaurian and shorebird tracks, although the tracks are mostly more robust, with wide, fleshy digits. The larger more robust forms tend to be wider, with weaker mesaxony than the smaller forms. This polarity is seen in the moa group: compares Figures 14A and B (after Lockley *et al.*, 2007).

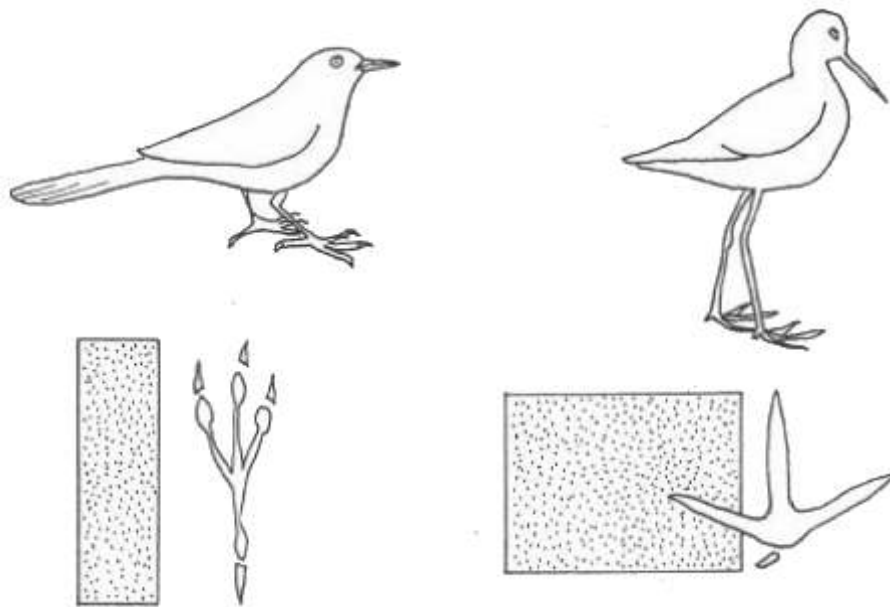


Fig. 12. Comparison between representative extant perching bird (passerine) and shorebird (charadriiform) tracks and trackmakers; after Lockley (1999)

DISCUSSION CONCERNING RECURRENT PATTERNS OF MORPHOLOGICAL ORGANIZATION

INTRA-TAXON VARIATION: THE INFLUENCE OF DIGIT DIVARICATION

Ichnologists understand that track variation is the result of both morphological and extramorphological (or preservational influences). Thus, tracks made by the same track maker may appear significantly different as a result of substrate conditions, or variation in digit divarication (Gatesy *et al.*, 1999). In most cases ichnologists select well preserved tracks as the basis of any serious ichnotaxonomic work, as common sense guidelines recommend (Sarjeant, 1989). However, the digit divarication represents an aspect of track morphology that is hard to interpret unequivocally. Track morphology may be well preserved in a trackway while digit divarication varies as the result of substrate conditions. Obviously as digit divarication increases the length of the anterior triangle (or degree of mesaxony) will increase. In order to measure the influence of divarication on apparent mesaxony, and the F l/w and AT l/w ratios, a range of values consistent with the natural range seen in tridactyl tracks was considered (Fig. 15). Two different models were used to represent differences in morphology resulting from differential digit length. Model A is a strongly mesaxonic track with digit III twice the length of digits II and IV (Fig. 15A). The alternate model (Fig. 15B) is one in which all three digits are of equal length. As shown, variation in divarication angle between 30° and 150° has much less influence on l/w ratios than digit length. Thus the intrinsic factor of basic morphology can not be obscured by the extrinsic variable of divarication. For example, there is virtually no overlap in the F l/w and AT l/w ratios between the strong mesaxony and weak mesaxony morphologies even when divarication varies by as much as 100°.

Clearly this modelling could be tested with a variety of different parameters to represent a range of variation in digit lengths and divarication angles. However, preliminary indications from this survey indicate that digit divarication is of secondary importance in defining track morphology, including mesaxony, whereas relative digit length is of primary importance. In the two models presented here, an interesting polarity, is observed. In the strongly mesaxonic tracks the anterior triangle is most elongate when the divarication is least. This configuration is typical of *Grallator* (Fig. 4). In contrast in the weakly mesaxonic tracks the anterior triangle is most elongate when the divarication is greatest, resulting in morphologies that closely mirror those found in coelurosaurian dinosaurs, extant shorebirds and large ground dwelling birds (Figs. 8 and 13 respectively). Figure 16 also shows this polarity.

INTRINSIC INTER-TAXON MORPHOLOGICAL VARIATION

Having assessed the role of digit divarication as an extrinsic (non-morphological) variable we can consider the importance of intrinsic morphological variation in defining distinct track types that can be distinguished using formal ichnotaxonomic approaches (Fig. 16).

The concept of a morphological plexus or continuum involving the related “theropod” ichnotaxa *Grallator*, *Anchisauripus* and *Eubrontes* is based on the holistic assumption that there is an inherent organizational principle at work that manifests in a discernable allometric pattern or plexus. It is therefore not surprising that the GAE plexus is interpreted as an ontogenetical phenomenon. Thus, the extreme lumpers’ view, implied by Olsen (1980) and Rainforth (2005) is that *Grallator* could simply be a small (or juvenile) expression of *Eubrontes* which represents a large or adult morphotype, that can be derived from *Grallator* by ontogeny. Such a rationale justifies placing these different morphotypes in the same taxon (in this

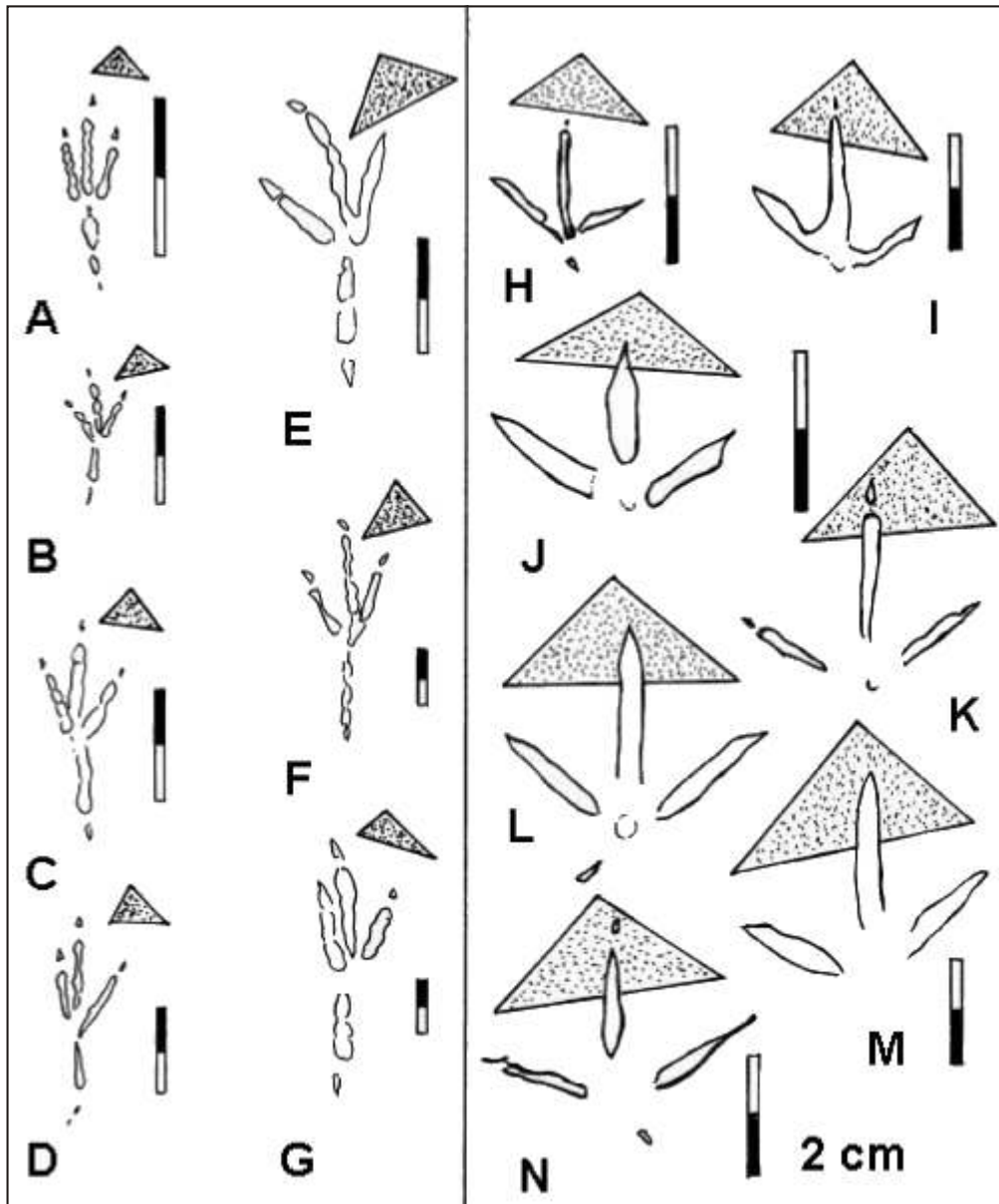


Fig. 13. Track (F l/w) and anterior triangle length/width (AT l/w) ratios for typical extant perching bird (passerine A–G) and shorebird (charadriiform H–N) tracks

Bird name, F l/w and (AT l/w) for A–N are as follows for perching birds (passerines): **A** — Yellowthroat, 3.36 (0.5), **B** — Brewers Sparrow, 2.08 (0.5), **C** — Gray Catbird, 2.60 (0.50), **D** — Red Wing Blackbird, 2.85 (0.64), **E** — European Starling, 2.24 (0.5), **F** — Boat-tailed Grackle, 2.53 (0.65), **G** — American Crow, 3.20 (0.36), and for shorebirds (charadriiformes): **H** — Least Sandpiper, 1.00 (0.40), **I** — Spotted Sandpiper, 1.00 (0.50), **J** — Sanderling, 0.68 (0.32), **K** — Killdeer, 0.89 (0.52), **L** — Ruddy Turnstone, 1.00 (0.45), **M** — Black-bellied Plover, 0.80 (0.50), **N** — Short-billed Dowitcher, 0.83 (0.43); scale bars 2 cm; redrawn after Elbroch and Marks (2001)

case the “super-ichnogenus” *Grallator*), albeit with the tacit implication that the ichnotaxon displays wide variability. The alternate view is that the (GAE plexus) represents different but related ichnospecies that share common morphological characteristics due to their close evolutionary relationships. In the case of the GAE plexus, the concept of allometry is equally amenable to a phylogenetic, as well as ontogenetic interpretation: i.e., the different track types correspond to a multi-taxon theropod clade, showing a spectrum of morphological variability convergent with the variability seen within the ontogenetic series of a single species. This concept of a clade wide

allometric series, has much the same connotation as the concept of a morphodynamic series or “movement” (Lockley, 2007): and, in a developmental sense, is inseparable from the concept of heterochrony (McNamara, 1997), which is essentially required as an explanatory principle in order to interpret how differential growth allows one parameter (e.g., length) to grow at a differential rate from another (e.g., width) either in individuals within a species, or species/taxa within a larger natural group/clade. Lockley (2007) has pointed out that it is possible to recognize large scale recurrent patterns of “morphodynamic” organization across multiple dinosaur clades, and

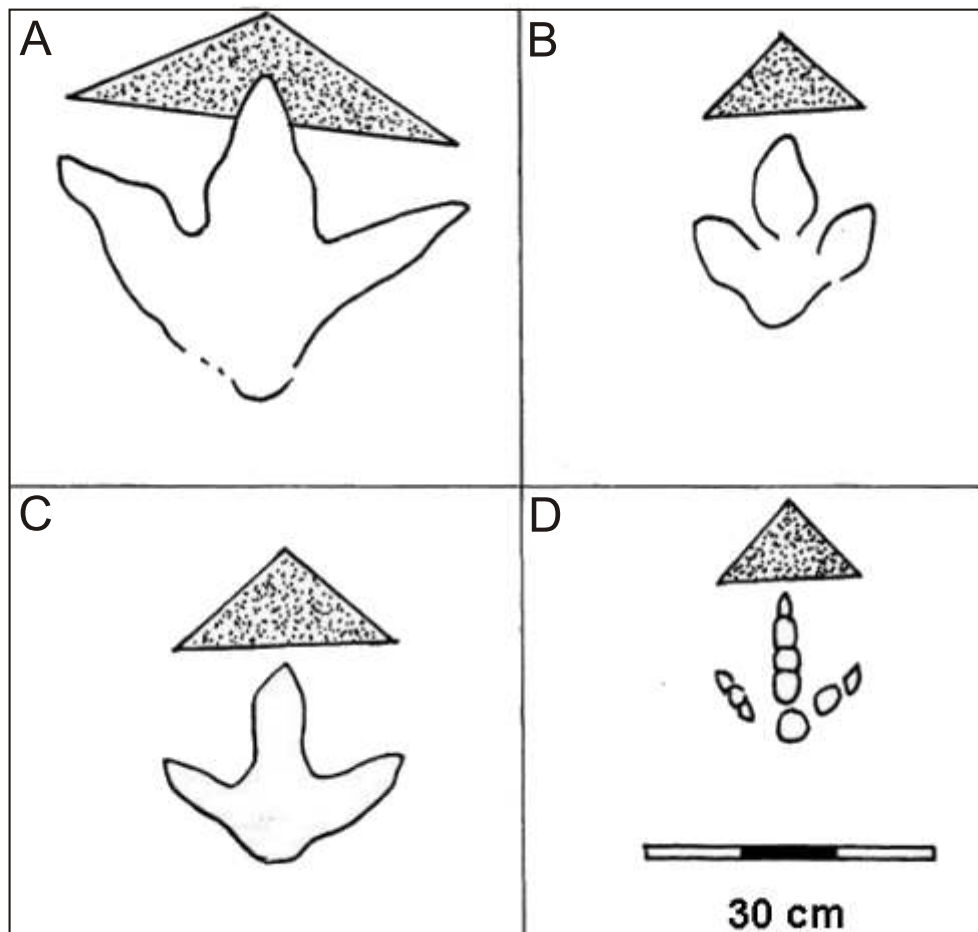


Fig. 14. Track (F l/w) and anterior triangle (AT l/w) ratios for large ground dwelling birds

Bird name, F l/w and (AT l/w) for A–D are as follows: **A** — a large moa, 0.70 (0.25), **B** — a small moa, 1.04 (0.46) after Lockley *et al.* (2007); **C** — Dromornithid, 0.82 (0.41) after Rich and Green (1974), **D** — Rhea 1.00 (0.52) after Padian and Olsen (1989)

that in essence this pattern recognition is similar to the identification of convergence or correlated progressions (*sensu* Kemp, 1982, 1999).

The allometric GAE spectrum provides a model for variation in tridactyl track shape for the Lower Jurassic (Olsen, 1980), in which small tridactyl tracks (*Grallator*) are the most elongate (high F l/w) and strongly mesaxonic, and larger tracks (*Eubrontes*) are the most transverse (low F l/w) and weakly mesaxonic (Fig. 16). As yet no tracks are known from the Jurassic which depart significantly from this allometric trend. However, in the Cretaceous while the small *Grallator* and large *Eubrontes* morphotypes persists, there are both medium- and small-sized tracks which are convergent with *Eubrontes* (Figs. 4H and 7). This suggests that the *Eubrontes* morphotype although initially expressed dominantly in clades consisting of large forms, was later also expressed, albeit less frequently, in clades consisting of small- and medium-sized forms.

The broader question here is, can we identify similar trends to those seen in the GAE plexus, in other dinosaur groups. As noted by Lockley (2000) the application of analytical techniques in the study of theropod tracks has been inconsistent and rarely with a few exceptions (Demathieu, 1990; Weems 1992) applied in conjunction with formal attempts at revision of

theropod track ichnotaxonomy. The same shortcomings can be noted for the study of ornithopod and bird tracks. However, Weems (1992) deserves credit for taking the brief speculations of Olsen (1980) regarding a positive allometric correlation between size increase and width increase, and the corresponding increase in relative transverse width of the anterior triangle, and analyzing the *Eubrontes*–*Grallator* plexus and related forms statistically. In the process he noted that the relative length of digit III (degree of mesaxony) is in fact useful for discriminating ichnotaxa. In fact he was one of the first ichnologists to base his taxonomic conclusions on morphometric analysis, and in the process he distinguished *Kayentapus* as a distinct ichnogenus.

The morphological information presented above clearly show that there are size-related polarities between “small” long narrow, and “large” short wide feet in theropods, ornithopods and birds (Fig. 16). Moreover, these polarities repeat in a regular fashion between these clades, so that small tracks are consistently narrower, and less mesaxonic than large track regardless of the group in question. The question arises, however, as to what this, recursive or fractal repetition of allometric or morphodynamic trends means, or what it might tell us about the morphology and/or function of the whole animal.

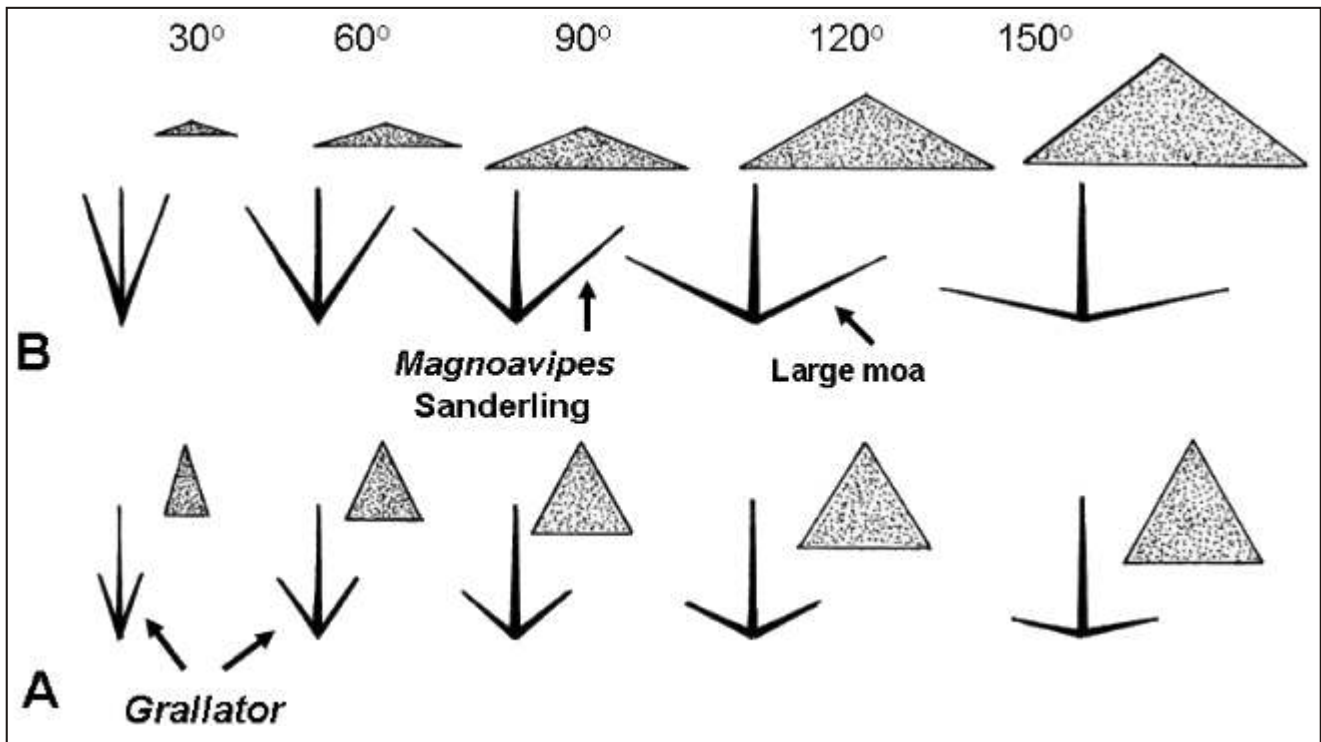


Fig. 15. Influence of digit length and divarication on variation in tridactyl track morphology

A — hypothetical tracks with digits II and IV half the length of digit III; B — hypothetical tracks with three digits of equal length; note morphologies that are closest to actual avian and non-avian dinosaur tracks; F l/w and (AT l/w) for series A, from left to right are as follows: 3.33 (1.67), 1.88 (1.06), 1.36 (0.86), 1.11 (0.85) and 1.03 (0.93); F l/w and (AT l/w) for series B, from left to right are as follows: 1.76 (0.11), 1.00 (0.14), 0.71 (0.30), 0.58 (0.32) and 0.51 (0.41)

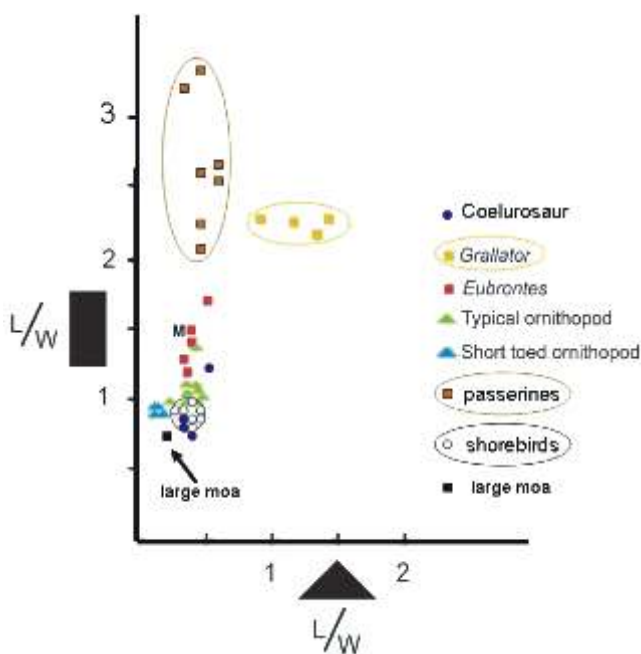


Fig. 16. Plots of foot l/w against anterior triangle l/w

Note relative elongation of either or both parameters in *Grallator* and passerines, and relative width of one or both parameters in large ornithopods, shorebirds and large moa; M — *Minisauripus*

FROM FEET TO LIMBS: THE IMPLICATIONS OF UNDERSTANDING VARIATION IN TRACK MORPHOLOGY

The present study suggests that the GAE plexus, provides us with a working ontogenetic and phylogenetic model which should encourage us to take a broader “allometric” or “morphodynamic” view of variation in tridactyl foot morphology. Understanding variation in foot morphology does not just help differentiate footprints, it also provides us with important clues to limb and whole body morphology, which is useful not just for the difficult, and often conjectural problem of track-maker identification, but also for reconstructing animals from incomplete skeletal remains.

The evolution of theropods shows a polarity between Late Triassic and Early Jurassic ceratosaurs with narrow feet and strong mesaxony and larger pre Cretaceous theropods (ceratosaurs, basal tetanurians and carnosaurs) with wider feet and less pronounced mesaxony. Although trackmakers with both these characteristics persisted into the Cretaceous, they appear to have been less common and replaced to a significant degree by wide-footed gracile trackmakers of probable coelurosaurian affinity. Thus the trend towards widening of the foot and shortening of the anterior triangle is evidently emphasized through time in different theropod clades. This shortening and widening of the foot, with reduced mesaxony is probably related to an increase in relative length of the leg, and shortening and widening of the body, in theropods as size increases (Thulborn, 1990; Lockley 2001, 2007; Bakker and Bir, 2004).

Thulborn (1990) used a leg length/foot length (LL/FL) ratios of 4.5 and 4.9 respectively to distinguish small theropods from large theropods, and LL/FL of 4.8 and 5.9 respectively to distinguish small ornithopods from large ornithopods. This implies that, as a general rule the foot gets shorter (and wider) as the limb gets longer. Thus one would predict that ornithopods would have shorter, wider feet than theropods and that the shortening (widening) would increase in larger forms. This is exactly what happens, and as a result we can draw the following conclusions:

- not only do foot l/w and anterior triangle l/w ratios decrease with size in theropods, reducing the degree of mesaxony, but...;
- foot l/w and anterior triangle l/w ratios and mesaxony also decrease with size in ornithopods. Also...;
- in both groups, as well as in birds (Fig. 12) there is evidence that this morphodynamic increase in l/w ratios with size is related to increase in limb length.

As noted by Lockley *et al.* (2008) the polarity between very small Cretaceous *Neograllator*, and the distinctive ichnogenus *Minisauripus* (Fig. 7) gives an interesting indication of the extent to which these patterns can be modified. Diminutive *Neograllator* shows typical *Grallator* morphology and close to the maximum degree of mesaxony for the ichnogenus and for theropods generally, but co-occurring *Minisauripus*, despite its small size has *Eubrontes*-like l/w track and anterior triangle and proportions. This could be interpreted to suggest that the “growth program” that leads to size-dependent increase l/w ratios, can be modified to operate size-independently, at least in a minority of cases. Such a conclusion suggests that not all size-related increases in foot width have a functional explanation. An alternative “formal” explanation allows intrinsic growth programs to operate independently: i.e., a given program might have differential paedomorphic and a peramorphic expressions in large and small taxa. One may consider this possibility in relation to birds.

It is already established that LL/FL ratios in theropods and ornithopods indicate a compensation between long feet and short legs, or the reverse short feet and long legs (Thulborn, 1990; Lockley, 1999, 2001, 2007). Thus, the evidence that the same general relationships hold true in birds (Fig. 12) indicates that morphodynamic relationships indicate a recursion in foot-limb morphological relationships, in most theropods, ornithopods and birds. Or, as the title of this paper suggests, widespread convergence in developmental dynamics: i.e., the operation of intrinsic or “formal” developmental programs (*sensu* Gould, 2002).

The limb-foot relationships are not the same as inter-digital relationships within the foot. However, based on the work of Shubin and Albrech (1986) one can assume a repetition of similar developmental dynamics during foot development in verte-

brates. Thus it is reasonable to infer that differential digit development is coupled in ways similar to the coupling of foot limb relationships. Slight “heterochronic” modification of the timing of these dynamics in different individuals and species gives us a universal “mechanism” for both intra- and inter-taxon variation. Viewed from this perspective, which demonstrates a general consistency, modified by slight variation in the fractal repetition or “recursion” of developmental systems (*sensu* Bird, 2004), we should expect to observe clade-wide convergence at many levels of organization: i.e. in interdigital, foot-limb and whole body proportional relationships. In short the evolution of development (evo-devo) paradigm anticipates convergent, “recursive” organization at the clade-wide level. Ironically such thinking brings us full circle in the taxonomic sense that it is the inherent repetition of organizational patterns in nature, that allows us to classify similar forms in the first place, and then to recognize wider evolutionary trends such as convergence, allometric/morphodynamic series and correlated progression (Kemp, 1982, 1999).

Convenient as it is to recognize convergent evolutionary trends, and recognize the stability of “gradual” correlated progressions within the majority of members within any given clade, there are cases where groups prove the exception to the rule. *Minisauripus* is one example where the track and anterior triangle l/w ratios obey the same rule as *Eubrontes*, but do so independent of size. It appears that the morphology of bird feet and footprints may provide another example of how some developmental dynamics may depart from general trends while others do not. For example, the convergence between the tracks of small shorebirds and presumed coelurosaurs is striking, but size-independent, and it is interesting that shorebird-like tracks appear in the track record at much the same time (Basal Cretaceous) as the larger coelurosaurs tracks. However, there are significant differences in the average size of feet and tracks between these two groups, and one might infer that these results indicate that similar developmental dynamics “programs” played out at different heterochronic time scales to produce convergent morphological plexuses of significantly different sizes. Conversely however, the typical passerine foot requires a somewhat different explanation. While it is narrow and elongate (even without the hallux) as is predicted for small feet, the anterior digits (II–IV) which comprise the tridactyl portion of the foot, display reduced mesaxony. How this is related to the developmental dynamics of the passerine foot, in comparison with the other groups discussed herein is uncertain. However, given that digit development proceeds from IV>III>II>I in most vertebrates (Shubin and Alberch, 1986) is possible to suggest that the development of digit III was reduced in order to allow, or compensate, for the subsequent development of digit I, the hallux, which is relatively “overdeveloped” in comparison with all other groups discussed here.

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