

Crocodylomorph Trackways from the Jurassic to Early Cretaceous of North America and Europe: Implications for Ichnotaxonomy

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Trackways described as *Batrachopus* (Batrachopodidae Lull, 1904) from the Lower Jurassic of Europe are rare and in some cases different from the type trackways from North America. Differences may be in part attributable to preservation, but current evidence suggests that there is inherent variability in Batrachopodidae morphotypes, beyond that attributable to differential preservation. Type *Batrachopus* is a stout-toed form, with minimal digit divarication (i.e., a long foot), whereas *Antipus* describes slender-toed forms with a wider foot and wider digit divarications.

Antipus is also similar to *Crocodylopodus* (ichnofamily Crocodylopodidae: Fuentes Vidarte and Mejjide Calvo, 1999) from near the Jurassic-Cretaceous boundary in Spain. *Crocodylopodus* has a relatively large manus, and a less outwardly rotated trackway, but is not sufficiently different from Batrachopodidae to warrant its own ichnofamily. Manus-pes size (area) ratios (heteropody) may also be important in differentiating different crocodylomorph ichnotaxa, as is the case with other archosaurian ichnotaxa. However, heteropody may change with size, and be less pronounced in large individuals. Manus and pes rotation patterns, and trackway width are variable and may be of use for differentiation of ichnotaxa but may also be a function of speed.

Keywords *Antipus*, *Batrachopus*, crocodylomorph tracks

INTRODUCTION

Lower Jurassic archosaur-dominated vertebrate ichnofaunas are well-known from classic sites in New England (Hitchcock, 1858; Lull, 1953) but are also well-represented in other regions including the western United States (Lockley and Hunt, 1995), Europe (Lapparent and Montenat, 1967; Demathieu, 1990; Lockley and Meyer, 2000), and southern Africa (Ellenberger, 1972, 1974).

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The dominant tracks in most regions appear to be those of saurischian dinosaurs, particularly the theropod ichnogenera *Grallator* and *Eubrontes*. The probable prosauropod ichnogenus *Otozoum* is well-known from eastern North America and is represented by similar forms, including *Pseudotetrasauropus*, in the western United States (Lockley et al., 2001) and southern Africa (Ellenberger, 1972, 1974; Lockley and Meyer, 2000; Rainforth, 2003).

Tracks assigned to the ichnogenus *Anomoepus*, and attributed to ornithopod dinosaurs, have also been reported from a number of regions and appear to be especially abundant in the type area of New England (Hitchcock, 1858; Lull, 1953). *Anomoepus* is less common in the western United States (Lockley and Hunt, 1995) and Europe (Gierlinski, 1991). Tracks assigned by Ellenberger (1972, 1974) to the ichnogenus *Moyenosauripus* from southern Africa are considered synonyms of *Anomoepus* by some authors (Olsen and Galton, 1984; Thulborn, 1990). Only one other unnamed track, from the Hettangian of France (LeLoeuff et al., 1999; Lockley and Meyer, 2000) has been attributed to an ornithischian dinosaur of possible stegosaurian affinity.

Among the non-dinosaurian vertebrate tracks reported from Lower Jurassic ichnofaunas *Batrachopus* (Fig. 1A), a purported crocodylian track, appears to be diagnostic of a non-dinosaurian archosaur. The type, originally described from New England (Hitchcock, 1845; Olsen and Padian, 1986), has many synonyms, some of which are evidently extra-morphological variants. This is the only non-dinosaurian track considered by Haubold (1986, fig. 15.10) to be characteristic of Lower Jurassic assemblages. The only other non-dinosaurian track, from the classic New England faunas, that has recently received serious scientific attention is *Antipus* (Coombs, 1996: Fig. 2 herein) though this may be a synonym of *Batrachopus* (Olsen and Padian, 1986). It is also similar to the trackway named *Stenodactylus* by Hitchcock (1858) and renamed *Sustenodactylus* by Lull (1953) (see Fig. 2), which according to Olsen and

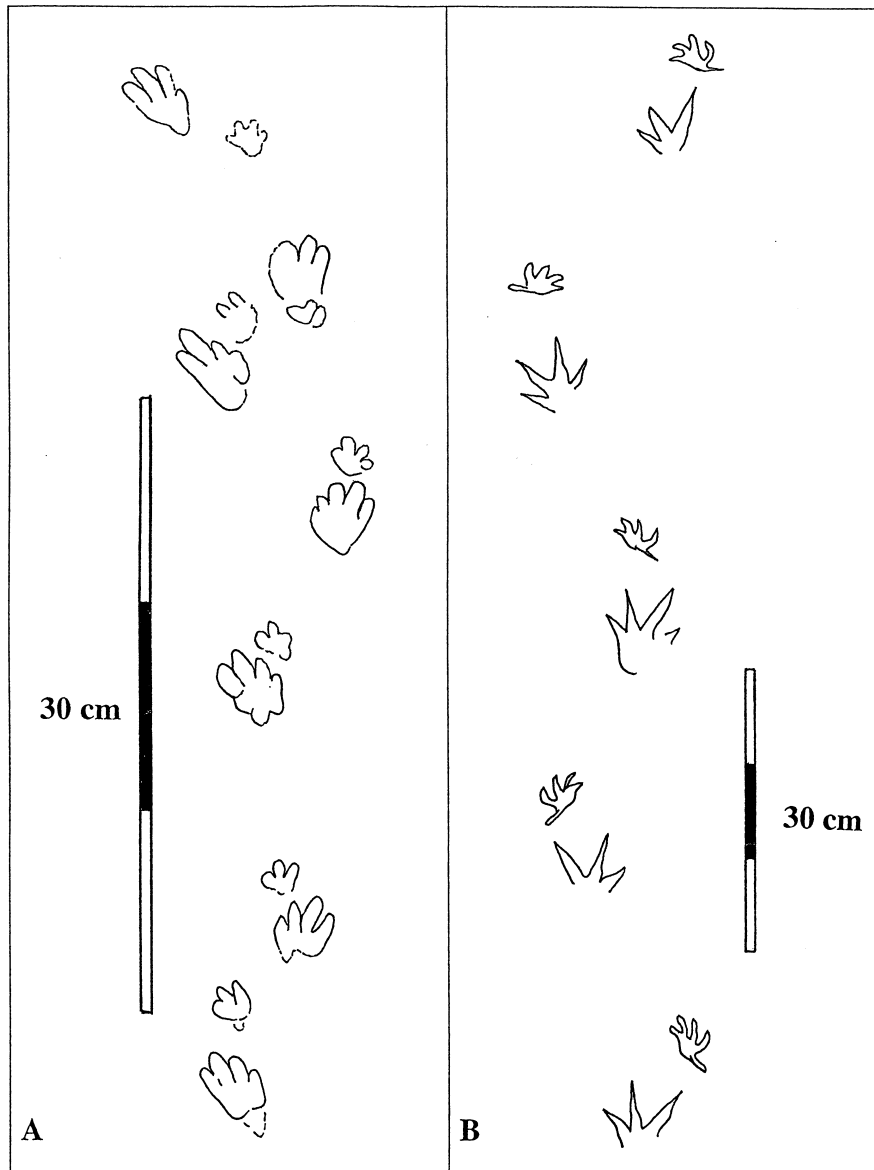


FIG. 1. A. Type specimen of *Batrachopus* (*B. deweyi*) from New England (traced from the type specimen 26/5 in the Pratt Museum, Amherst College) with *Batrachopus* from the Causses region of France for comparison.

Padian (1986) is probably one of many synonyms of *Batrachopus*. As reported elsewhere in this volume (Lockley et al.,) Olsen and Padian (1986) counted 27 ichnospecies in 14 ichnogenera that they regarded as a mixture of objective, and probable subjective synonyms of ichnogenus *Batrachopus*.

Reports of *Batrachopus* outside New England are scattered and brief. For example, the ichnogenus appears to be present in western United States (Olsen and Padian, 1986; Lockley et al., this volume) though some reports may be better interpreted as *Brasilichnium*-like mammal-like reptile tracks (Schultz-Pittman et al., 1996; Lockley and Hunt, 1995). The tracks occur sporadically in Europe, in the Le Veillon ichnofaunas (Lapparent and Montenat, 1967; Fig. 3 herein), and are also reported from the

Causses region (Demathieu and Sciau, 1995; Fig. 1B herein). Although this latter report was accepted by Lockley and Meyer (2000), we have re-examined similar material from this region (Figs. 4 and 5) in the Natural History Museum of Basel, and pose the question as to whether it more closely resembles *Antipus* (compare Figs. 2 and 4). If this is the case, it would be the first report of this ichnogenus in Europe, or indeed anywhere outside the type area.

At first sight it appears that there may be two distinct Lower Jurassic morphotypes: the blunt-toed *Batrachopus* and the slender-toed *Antipus*, both of which could be accommodated in the long-standing ichnofamily Batrachopodidae (Lull, 1904). However, the question is complicated by the recent report

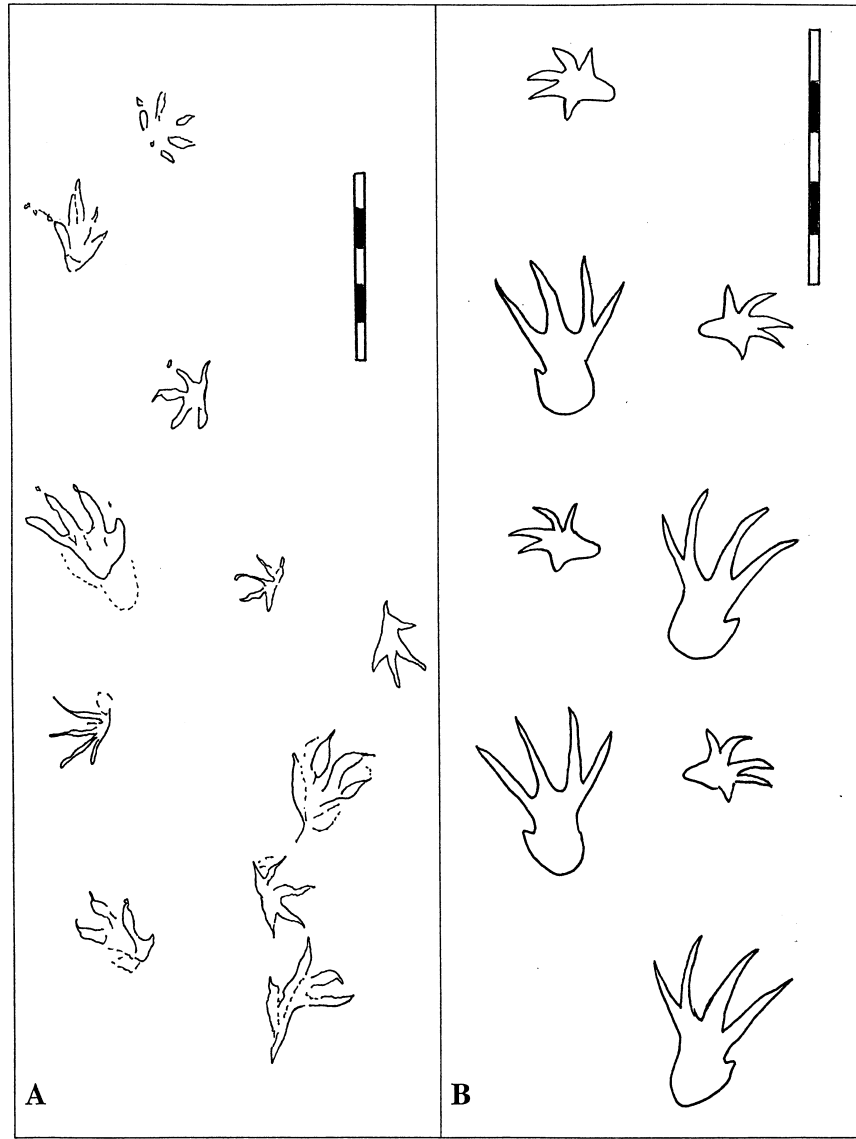


FIG. 2. A: Type specimen of *Antipus* (*A. flexiloquus*) and B: type of *Sustenodactylus* (*Stenodactylus*) for comparison. Both ichnotaxa were originally named by Hitchcock (1858), though Lull 1953 reassigned *Stenodactylus* to *Sustenodactylus*. Scale bars 5 cm.

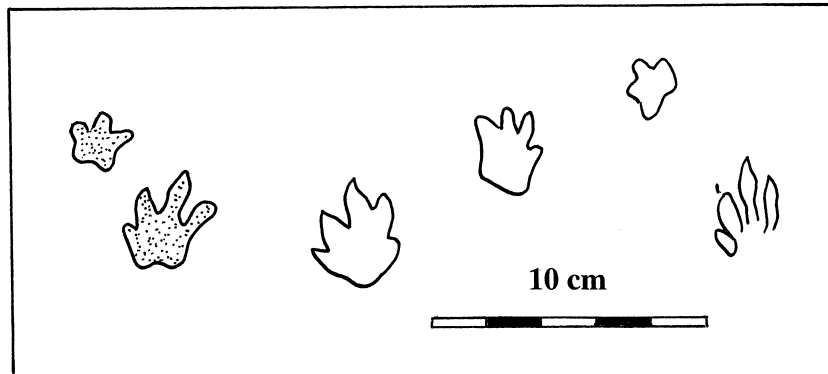


FIG. 3. *Batrachopus* from Le Veillon, drawn from original specimens in collection at Albert Lapparent Institute of Geology, Paris. Stippled pair (left) represent a manus pes set.

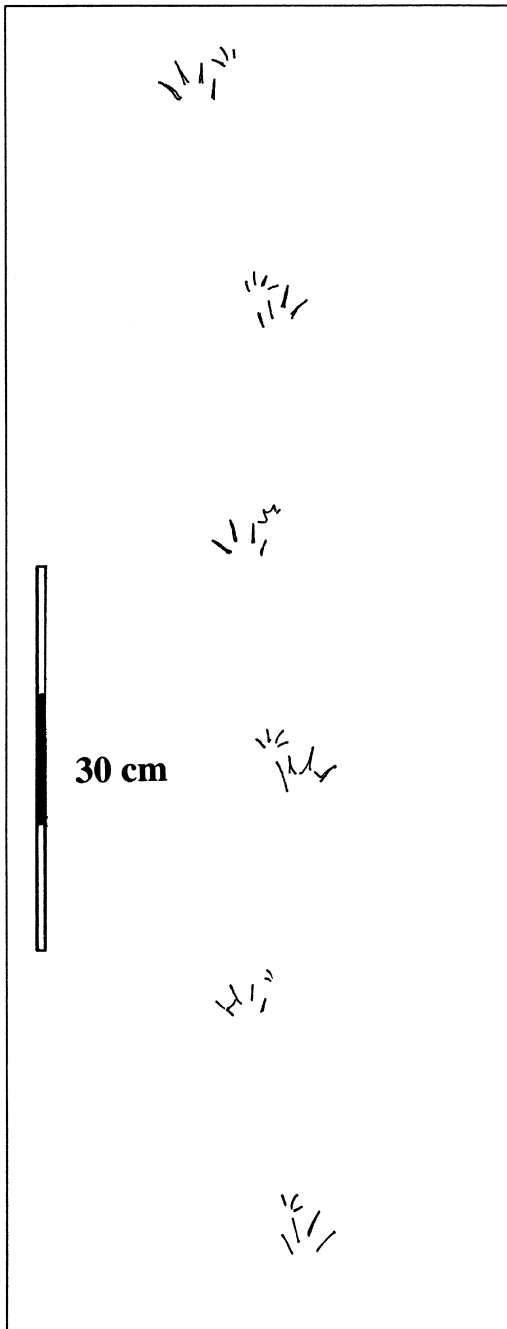


FIG. 4. Basel Museum of Natural History trackway of “*Batrachopus*” from the Les Causses region of France. Note that manus digits point anteriorly, not laterally. Compare with Figs. 1B and 2A.

of a slender-toed crocodylian morphotype (*Crocodylopodus*) from near the Jurassic Cretaceous boundary of Spain which has been placed in the new ichnofamily *Crocodylopodidae* (Fuentes Vidarte and Mejjide Calvo, 1999). This extends any discussion of the *Batrachopodidae* into the Cretaceous and raises doubts as to whether it is a single ichnofamily.

The purpose of this paper therefore is to evaluate European crocodylian tracks assigned to *Batrachopus* and *Crocodylopo-*



FIG. 5. Photo Basel Museum of Natural History trackway of “*Batrachopus*” from the Les Causses region of France.

dus and compare them with the *Antipus* and *Batrachopus* type material and other similar track types (e.g., *Sustenodactylus*) to determine whether the differences warrant the establishment of the new ichnofamily *Crocodylopodidae*. We also consider

whether differences are morphological or extramorphological (i.e., preservational).

DESCRIPTIONS OF *BATRACHOPUS* AND *ANTIPUS*

Olsen and Padian (1986) gave a detailed description of *Batrachopus*, with an emended diagnosis of the type species *B. deweyi*. Under the ichnogenus *Batrachopus* they list 15 ichnotaxa (ichnogenera) that are purported synonyms: 13 named by E. Hitchcock (1845, 1858), including *Antipus*, one by C. H. Hitchcock (1871), and one by Lull (1942). Coombs (1995) evidently did not agree that *Antipus* should be assigned to *Batrachopus*, since he re-described the type material under its original name, arguing that trackway patterns that showed greater spacing between manus and pes tracks, rather than partial overlap, suggested that “the *Batrachopus* track-maker had limbs that were longer relative to its glenoacetabular length than were the limbs of the *Antipus* trackmaker.” This, he argued, provided “evidence for a morphological difference between the trackmakers . . . [thus] . . . the proposed synonymy of *Antipus flexiloquus* with *Batrachopus deweyi* is rejected” (Coombs, 1995, p. 330).

Here we try to distinguish between *Batrachopus* (Hitchcock, 1843) and *Antipus* (Hitchcock, 1858) and evaluate the extent to which they are taxonomically distinct. Based on the type material, and the emended diagnosis (Olsen and Padian, 1986, p. 261) *Batrachopus* is the track of a small quadruped with functionally tetradactyl pes and pentadactyl manus (Fig. 1A). Purportedly “digit V of the pes, when impressed, is reduced to an oval pad posteriorly.” The pes length ranges from 2 cm to as much as 8 cm. Based on the type specimen both the manus and the pes have relatively broad fleshy digits with recognizable patterns of transverse segmentation. Pes digit I is shorter than II, which is shorter than III. Pes digit IV is about the same length as, or slightly longer than digit II. Digits are straight and width is more or less constant throughout the length of the digit, with little or no evidence of sharp claw impressions. Digit divarication is low, so that there is rarely separation between the digits. Total divarication between digits I and IV is only about 25–30° in the type specimen. This is considerably less than in some of the European specimens described below, where divarication angles are as high as 70°.

Although the general pes and manus morphology of *Antipus* is similar to *Batrachopus* (tetradactyl and pentadactyl, respectively), *Antipus* by contrast to *Batrachopus* has much more slender, tapering and widely-divaricating digits, that terminate in narrow claw impressions. In addition to being far more slender, manus digit impressions seem to be much longer in *Antipus* than they are in *Batrachopus* (compare Figs. 1A and 2A). The digits were evidently quite flexible as indicated by strong curvature that gives the type ichnospecies its name: *A. flexiloquus*. *Antipus* is similar to *Batrachopus* in having a strong outward rotation to the pes (34° N = 4, measured between the trackway midline and the axis of pes digit III). Another feature not mentioned by Coombs (1996) is trackway width or straddle. In *Antipus* about 4 cm separated the inside of the right and left

pes tracks, whereas they touch the trackway midline in *Batrachopus* (compare Figs. 1A and 2A). This difference could be a function of the speed of the trackmaker: i.e., *Antipus* may have been moving more slowly.

Since ichnotaxonomy should be based strictly on differences in track and trackway morphology, not inferred differences between trackmakers, we regard the criteria for track differentiation proposed by Coombs (1996) as somewhat dubious. His criteria might be considered to have more merit if one could demonstrate that the differences in trackway configuration are consistent, which is not possible with only one specimen as in the case of the *A. flexiloquus* type. However, we must also consider the significant differences that he overlooked. Based on the aforementioned length of the manus digit impressions, the slenderness and curvature of the *Antipus* digit impressions, and the trackway width, we are inclined to accept Coombs’ conclusions. Thus, we cautiously treat the two ichnogenera separately but for *different reasons*.

THE A-B-C OF CROCODYLOMORPH TRACKWAYS: THE AFFINITIES OF *ANTIPUS*, *BATRACHOPUS* AND *CROCODYLOPODUS*

The traditional view is that *Batrachopus* (Batrachopodidae Lull, 1904) represents a crocodylian trackmaker (Olsen and Padian, 1986). Coombs (1996, p. 330) suggested that “*Antipus flexiloquus* has several characters typical of quadrupedal trackways called “crocodyloid” by Padian and Olsen (1984).” We agree with this general assessment. Thus, both ichnogenera must be compared with *Crocodylopodus meijidei*, a recently described a crocodyloid trackway from near the Jurassic-Cretaceous boundary of Spain, assigned to the new ichnofamily Crocodylopodidae by Fuentes Vidarte and Meijide Calvo (1999). *C. meijidei* is similar to *A. flexiloquus* in most important respects including the slenderness of the digits and the relative positioning and rotation of the manus and pes prints, and the length of the manus digits. Differences include the relatively large manus in *C. meijidei* in comparison with *A. flexiloquus* and the tendency of the pes digits to rotate inwards in the former ichnospecies.

A number of difficult questions arise. First, is *Antipus* similar to *Batrachopus* (ichnofamily Batrachopodidae) as implied by Olsen and Padian (1986), or are the differences in manus size, digit length and overall digit slenderness significant? We regard these as potentially significant differences, especially given the fact that several archosaurian groups divide into large and small manus morphotypes (Peabody, 1948; Tresise, 1996; Lockley, 1999, 2001; Avanzini and Lockley, 2002). Second, if *Antipus* and *Batrachopus* are different, to what extent do they resemble the third ichnogenus *Crocodylopus*. Thirdly, we must ask if any differences warrant differentiation at the level of ichnofamily, as the present classification implies. In order to better understand the descriptions of these ichnotaxa, we have reproduced them in the section that follows with appropriate amendments that standardize terminology in English.

SYSTEMATIC DISCUSSION

Owing to the existence of both the ichnofamily Batrachopodidae (Lull, 1904) and the recently proposed ichnofamily Crocodylopodidae Fuentes Vidarte and Mejjide Calvo (1999), it is helpful to compare their diagnoses (*in italics*) and provide amendments (**in bold**). For Batrachopodidae, based on the *B. deweyi* type specimen (Hitchcock catalog number 26/5 in the Pratt Museum collection) we quote the following.

Original Diagnosis for Batrachopodidae (Lull, 1904, p. 482)

“Family Characters. The same as those given for the order. Digits of the pes with acuminate claws.”

The “ordinal characters” are given as follows: *Quadrupedal in gait; manus generally much smaller than the pes and five fingered though all may not impress. Pes with four digits, generally dinosauroid in form though plantigrade. Limbs generally long.*

These forms seem to represent survivors of the ancient stem from which the dinosaurs arose; they may, however, represent primitive quadrupedal dinosaurs which had not yet acquired the erect gait.”

Here Lull (1904, p. 482) uses “order” to refer to his category “Order? Proterosauria.” It is not clear whether the final sentence is meant as part of the diagnosis or as a subsequent comment. We suggest it be taken as an interpretative afterthought and that the familial diagnosis be amended as follows.

Revised Diagnosis for Batrachopodidae (Lull, 1904)

Nominal Ichnogenus *Batrachopus* (Diagnosis as for Ichnofamily)

Trackway of a quadruped with pronounced heteropody; manus pentadactyl, digitigrade and much smaller than the pes. Pes tetradactyl, plantigrade with four digits, sometimes terminating in acuminate claw impressions. Pes digits II and IV subequal in length and slightly shorter than digit III: digit I shortest.

Trackway narrow, about twice pes width. Inner margin of pes tracks falls on or near trackway axis: outward rotation 24–33° based on alignment of digit III (foot axis) in relation to trackway axis. Placement of manus also close to trackway axis and typically immediately in front of the pes. Step about 2–3 times pes length; pes pace angulation about 150–160°.

Referred Ichnotaxa

Initially, Lull (1904) only included the ichnogenus *Cheirotheroides* (Hitchcock, 1858) in the Batrachopodidae. As noted previously, some workers consider *Antipus* a junior synonym of *Batrachopus* (Olsen and Padian, 1986). Although Coombs (1996) does not support this conclusion he makes no inference that *Antipus* is different at a suprageneric (i.e., ichnofamily level). Olsen and Padian (1986) go so far as to include 13 other “Hitchcockian” ichnogenera, besides *Cheirotheroides*

and *Antipus*, as synonyms of *Batrachopus*. We should also note that their “emended diagnosis” of the type species (*B. deweyi*) includes reference to traces of digit V and the segmentation of digits into pads. We suggest that at least one other “Hitchcockian” ichnogenus (*Selenichnus*) may represent an extramorphological (preservational) variant of *Batrachopus* (see Lockley et al., this volume). For these reasons Batrachopodidae can not be treated as a mono-ichnogenetic ichnofamily as is the case with the ichnofamily Crocodylopodidae.

Original Diagnosis for Crocodylopodidae Fuentes Vidarte and Mejjide Calvo (1999)

Not distinguished from that given for *Crocodylopodus* and the type ichnospecies (*C. mejjidei*) translated from the original Spanish (Fuentes Vidarte and Mejjide Calvo, 1999, p. 332–333) with square brackets and quotation marks added for clarification of translation.

“Ichnites of a tetrapod with different autopodia. The front autopodium is pentadactyl, digitigrade with slender, sinuous digits, separated from the base and terminating in claws; digits I and V are opposed and oriented towards to the trackway axis; digits II, III and IV oriented outwards. The hind autopodium is tetradactyl, plantigrade, with long slender digits which originate at the same level, ending in claws oriented towards the animal’s direction of progression.; the heel is oval, almost symmetrical with respect to the central axis [of the foot] and has a “little heel.”

Except for the use of the term “autopodium,” which is not often used in English descriptions, and the term “taloncillo” suggesting a “little heel” projection on the end of the heel, this is a straightforward, and clearly illustrated description of well-preserved material, as provided by Fuentes Vidarte and Mejjide Calvo (1999). However, the monospecific ichnofamily, ichnogenus and ichnospecies descriptions are all rolled into a single diagnosis.

Given this all purpose, tri-level description and our conclusion that a new ichnofamily is not necessary we suggest the following revised diagnosis for the ichnogenus that reflects details of trackway configuration such as step, stride and manus pes rotation. We also note that the original description designates three holotypes, labeled “Rastro A, Rastro B and Rastro C”. This is not permissible by International Code of Zoological Nomenclature (IZCN) rules so we select only Rastro A, the most complete trackway (Fig. 6) as the holotype and designate the other two (B and C) as paratypes (also topotypes).

Revised Diagnosis for Ichnogenus *Crocodylopodus* (Type species *C. mejjidei*)

Ichnites of a tetrapod with pronounced heteropody. The manus track is pentadactyl, digitigrade with slender, sinuous digits, separated from the proximal base and terminating in claws; digits I and V are opposed and are oriented antero-medially and postero-laterally, respectively with respect to the trackway axis; manus digit II is therefore oriented almost

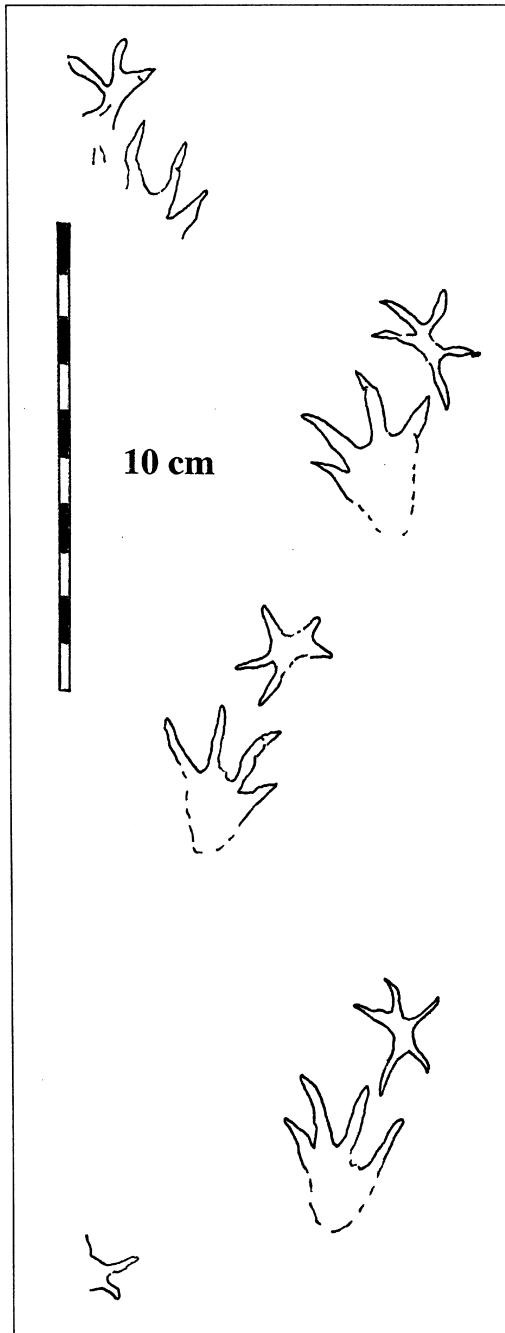


FIG. 6. Type material of *Crocodylopodus* (*C. meijidei*) from Spain (after Fuentes Vidarte and Meijide Calvo, 1999).

parallel to the trackway axis, with digits III and IV oriented laterally. The pes impression is tetradactyl, plantigrade, with long slender digits which originate at the same level, ending in claws oriented towards the animal's direction of progression. Pes digit divarication, between I and IV high, up to about 70° in the holotype. Pes digits II and IV subequal in length and slightly shorter than digit III; digit I shortest. The heel is oval, almost symmetri-

cal with respect to the central axis [of the foot] and has a "little heel."

Trackway narrow, about twice pes width. Inner margin of pes tracks falls on or near trackway axis: pes rotation slight or even inward, with digit III (foot axis) typically more or less parallel to trackway axis. Placement and rotation of manus more variable but generally placed lateral to trackway and pes axes, with opposed digits I and V typically aligned at about 40° to the trackway axis. Step 2–3 times pes length, pes pace angulation about 150° .

We note some variation in the parameters noted above in paratype specimens. For example, in comparison with the holotype (Rastro A), Rastro B and Rastro C appear to be slightly wider gauge. As noted below there is some variation in heteropody, which becomes less pronounced in larger specimens.

THE STATUS OF BATRACHOPODIDAE, LULL 1904, AND CROCODYLOPODIDAE, FUENTES VIDARTE AND CALVO, 1999

According to the ICZN (Article 35.1), "The family group encompasses all nominal taxa at the ranks of superfamily, family, subfamily, tribe, subtribe and any other rank below superfamily and above genus that may be desired (see also Article 10.3 for collective groups and ichnotaxa)." Article 10.3 states that "A name proposed for a collective group is treated as a genus-group name [Article 42.2.1]." This article holds that "names established expressly for certain assemblages of taxonomic convenience known as "collective groups" and names for trace fossils (ichnotaxa) established at the genus group level are to be treated as genus group names."

Both Batrachopodidae and Crocodylopodidae (the latter here considered invalid) are nominal family group taxa based on their respective nominal genera (see revised diagnoses above). Lull (1904) provided separate "generic characters" for *Batrachopus*, and Olsen and Padian (1986) revised the description of the type species. These "generic characters" may be important given that Batrachopodidae is not a monogeneric ichnofamily: i.e., the need arises to distinguish ichnotaxa within the ichnofamily.

Comparison between Batrachopodidae (*Batrachopus*) and Crocodylopodidae (*Crocodylopodus*)

The diagnoses given above indicate that these two ichnofamilies are quite similar. Each is based on a type with a narrow trackway. The most notable differences seem to be in the slenderness of both the manus and pes digits. Fuentes Vidarte and Meijide Calvo (1999) tabulated various morphological differences, also noting the difference in digit thickness and significant differences in digit divarication and pace angulation. We agree with the divarication differences but, because they are variable, consider the pace angulation differences of less significance than stated by Fuentes Vidarte and Meijide Calvo (1999). We also note that the pes of *Crocodylopodus* is much less outwardly rotated than *Batrachopus*. However the reverse is true for the

manus which is much more strongly rotated in *Crocodylopdus*. In fact *Crocodylopdus* reminds us of *Chirotheroides pilulatus* (Hitchcock, 1858) which Olsen and Padian (1986) consider a synonym of *Batrachopus*. If this is the case, then manus rotation is quite variable in *Batrachopus*.

Lull (1953, p. 235) observed that *Batrachopus* manus digits are "broad" and "apparently clawless," and Olsen and Padian (1986) make no reference to claw impressions in their emended diagnosis of the ichnogenus. However, Lull (1904) noted that acuminate pes claws are associated with digits I-III, and these seem to be evident in a number of his illustrations (Lull, 1953). By contrast reference to claws is explicit in the diagnosis of *Crocodylopdus* (Fuentes Vidarte and Meijide Calvo, 1999). Thus claw impressions appear to be characteristics of both *Batrachopus* and *Crocodylopdus*, though they may not always be preserved in all digit impression in the former ichnogenus.

We also note that the outward rotation of the pes (averaging 35°: range 14–33°: N = 7) in type *Batrachopus* is significantly greater than in *Crocodylopdus* where the average rotation is 1° inwards (range 15° out to 10° in: N = 3). For these reasons it appears reasonable to distinguish between the two ichnogenera. However, the question arises as to whether the ichnogenera are different enough to be separated into different ichnofamilies, as done by Fuentes Vidarte and Meijide Calvo (1999). These authors appear to have been inconsistent in referring to Batrachopodidae as both a family and a superfamily containing five ichnogenera (though they list none other than *Batrachopus* and do not cite the synonymy lists of Olsen and Padian, 1986). There is no precedent for the superfamily concept in ichnology so we consider it best abandoned. Lull (1904) referred too generally to ordinal characters (Order? Proterosauria), and Haubold (1971) subsumed ichnofamily Batrachopodidae (or morphofamily in his terminology) under Order Crocodylia. It would be convenient and helpful to the non-specialist if Crocodylopdidae were to be a valid label to accommodate fossil crocodylian tracks. Unfortunately, ichnotaxonomic history makes this impossible.

Ichnogenera assigned directly to the ichnofamily Batrachopodidae or considered closely related to *Batrachopus* include *Chirotheroides* (Lull, 1904), *Antipus* (Coombs, 1996) from the Lower Jurassic of New England and possibly *Datotherium* from France (Lapparent and Montenat, 1967). We also consider *Selenichnus* an extramorphological (perservational) variant of *Batrachopus* (Lockley et al., this volume) with similarities to *Palamopus* (Hitchcock, 1845; Lull, 1953). We agree that most of the synonyms proposed by Olsen and Padian (1986) should, at least provisionally, be considered under the umbrella of Batrachopodidae pending further investigation. Many appear to be extramorphological variants of *Batrachopus* or *Batrachopus*-like tracks. Haubold (1971, 1984, 1986) supports this position for some of the proposed synonyms: e.g., *Shepardia*.

Many *Batrachopus*-like tracks (e.g., *Palmopus* and *Selenichnus*, Lockley et al., this volume) are preserved as relatively deep impressions in fine-grained mudstones that sometimes preserve rain drop impressions. Thus, in many cases the evidence sug-

gests very soft sediments. Although the types specimens of *Antipus*, *Batrachopus* and *Crocodylopdus* all preserve fairly clear digit outlines, in many specimens from the Hitchcock collection and some from Europe, digit impressions are reduced to a single line marking the base of a V-shaped groove. These may be interpreted as underprints of digit traces that correspond to wider impressions on surfaces a few millimeters higher in the sedimentary sequence. Track bearing layers may split along the actual surface where the foot made contact with the substrate, or along under layers, (or over layers), but, it is rare to find several successive surfaces split open within a thin succession so as to allow the type of direct comparisons permitted in the case of Hitchcock's famous fossil book (Hitchcock, 1858; Lockley, 1991).

Antipus (like *Sustenodactylus*) differs from *Batrachopus* in having slender and curved digits and a wider separation between manus and pes. Coombs (1996) attributed this separation to the inferred length of the trackmaker's legs. While such an inference is of interest, other factors such as speed, type of gait and/or type of overlap (primary, secondary or tertiary) may be equally if not more parsimonious as explanations. However, step length is only of ichnotaxonomic significance if it can be shown that the relative placement of the hind and front feet is consistently different (among different ichnofaunas) in a substantial sample. If this is the case then an argument may be made that distinct ichnotaxa can be named on the basis of such diagnostic differences in trackway parameters. As noted above the small size of available samples hampers comparative studies, leaving open the question of the affinity of *Antipus*.

Fuentes Vidarte and Meijide Calvo (1999) argued that it was not advisable to include the Spanish crocodylian ichnogenus *Crocodylopdus* and another unnamed form (Moratalla et al., 1995) in Batrachopodidae because this ichnofamily appears to be limited to the Middle Triassic through Early Jurassic. We dispute this point for two reasons. First *Batrachopus* (Batrachopodidae) is evidently mostly restricted to the Lower Jurassic. Second, and more importantly, *the age of tracks should not be a factor in assigning them names*: morphology provides the only diagnostic criteria. In this case, however, Fuentes Vidarte and Meijide Calvo (1999) did provide evidence that *Crocodylopdus* is morphological different from *Batrachopus*, if only in relatively minor details, as indicated above. For example, in our opinion the greater outward rotation of the *Batrachopus* pes in relation the *Crocodylopdus*, indicates a significant difference that may be attributable to the latter form having a more advanced ankle structure.

MORPHODYNAMIC OBSERVATIONS

Peabody (1948) noted that *Chirotherium* trackmakers could be divided into two broad groups with large and small manus, respectively. Lockley (1999, 2001) has shown that this same distinction applies to sauropods and is associated with an anterior shift in the center of gravity of the whole body. The same anterior, whole body shift was inferred by Soergel (1925) in his study of

chirothere trackmakers. Since chirothere trackmakers, such as sauropods and crocodylians, were all archosaurs, we may be able to resolve patterns of archosaur footprint and trackway variation into recognizable heteropody trends. For example, small-manus chirothere tracks are typically narrower (more elongate) than the large-manus varieties (Tresise, 1996; Avanzini and Lockley, 2002).

In an attempt to try and discriminate such differences, in the small *Antipus-Batrachopus-Crocodylopdus* sample available, we measured manus and pes length (l) and width (w) and

l/w ratios, manus and pes area (a) and the manus/pes area ratio (Fig. 7, Table 1) as a measure of heteropody. The results suggest that *Batrachopus* has a relatively narrow pes, and in two of the French examples, a significantly smaller manus (greater heteropody). The length of the *Batrachopus* pes is much longer in some tracks than others due to a faintly impressed heel trace. For example in Fig. 1A, the type specimen, also illustrated by Olsen and Padian (1986, fig. 20.1) the pes may be twice as long as wide. However in some cases the heel is not impressed, suggesting an alternation between plantigrade and semi-digitigrade stance.

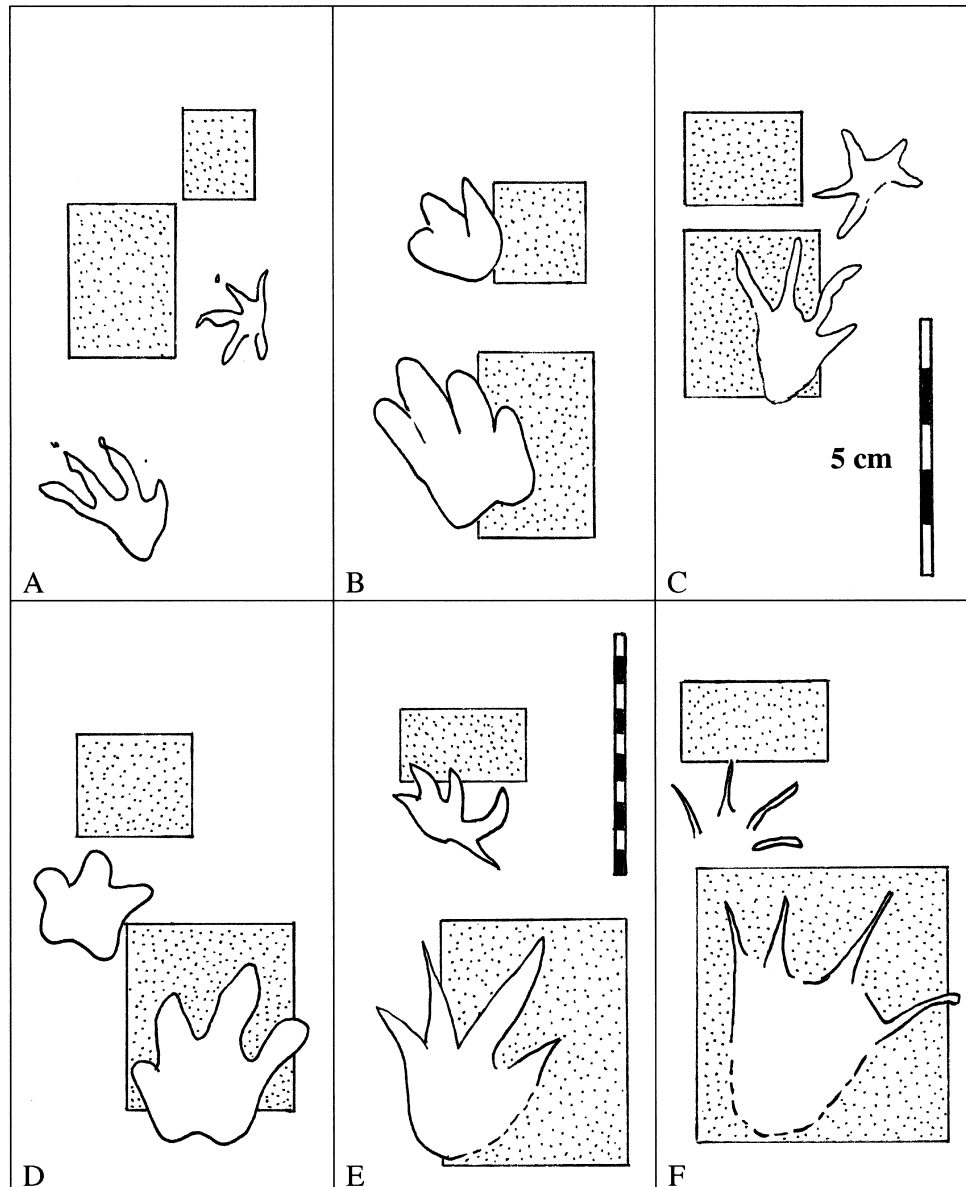


FIG. 7. Comparison of manus-pes size in Batrachopodidae trackways. A: *Antipus*, after Coombs (1996); B: type *Batrachopus* (Hitchcock, 1845), redrawn from tracing made by the authors, C: *Crocodylopdus*, (Fuentes Vidarte and Calvo, 1999), D: *Batrachopus* from the la Veillon collection (traced by authors), E: *Batrachopus* after Dematieu and Sciau (1995) and F: *Batrachopus* (traced by authors) in the Basel Museum collections. Compare with data from all drawn to same scale (5 cm) except for E (10 cm scale bar). Stippled boxes schematize length-width or heteropody ratios for manus and pes sets (with pes length axes reoriented to axis of page).

TABLE 1

Measurements for pes and manus length (pl and ml), and pes and manus width (pw and mw) and pl/pw and ml/mw ratios for *Antipus*, *Batrachopus* and *Crocodylopodus*. Also, manus area (ma) and pes area (pa) and ma/pa ratios. F1-3 refers to three French *Batrachopus* sites corresponding to Figs. 7D, E and F. L refers to a large *Crocodylopodus* specimen. See text for details.

Specimen	pl	pw	pl/pw	ml	mw	ml/mw	ma/pa	ma/pa
<i>Antipus</i> type	3.1	2.2	1.41	1.4	1.8	0.78	2.5/6.8	0.37
<i>Batrachopus</i> type	4.8	2.5	1.92	2.0	1.8	1.11	3.6/12.0	0.30
<i>Crocodylopodus</i>	3.6	2.8	1.28	1.8	2.3	0.78	4.1/9.0	0.46
<i>Crocodylopodus</i> L	7.2	6.2	1.61	2.5	4.3	0.58	10.8/44.6	0.24
<i>Batrachopus</i> F1	4.0	3.1	1.29	2.2	2.2	1.00	4.8/12.4	0.39
<i>Batrachopus</i> F2	9.8	7.8	1.25	2.8	5.6	0.50	15.7/76.4	0.21
<i>Batrachopus</i> F3	(5.3)	4.5	(1.23)	1.6	2.7	0.59	4.3/22.8	0.27

To determine heteropody in *Crocodylopodus* we measured the ma/pa ratio in all manus-pes sets in Rastro A and in one well-preserved set in Rastro B. We obtained consistent ratios between 0.42 and 0.47 (mean 0.45). Notably, however, the manus/pes ratio for the largest *Crocodylopodus* specimen (Fuentes Vidarte and Calvo, Fig. 4) is only 0.24. This suggests an allometric increase in the relative size of the pes during growth, and is consistent with the higher heteropody ratios obtained for large *Batrachopus* from France (F2 and F3 in Table 1). The pes of the *Crocodylopodus* type specimen is also wider than the type of *Batrachopus*, but has essentially the same l/w ratio as the European *Batrachopus* specimens.

We tentatively suggest that differentiation of Mesozoic crocodylomorph trackways requires and understanding of manus-pes size differentials (heteropody) and shape (elongation v. width). If patterns seen in other archosaurs are reflected to any degree in crocodylian tracks, degree of manus and pes rotation may also be diagnostic. We are intrigued by the degree of apparent fleshiness or "robustness" of type *Batrachopus* and the specimen from Le Veillon, France (Fig. 7D and F1 of Table 1) in comparison with the slenderness (gracile) appearance of *Antipus* and *Crocodylopodus* and the F2 and F3 *Batrachopus* specimens. Although such differences may be in part to preservation (i.e., narrow digits may be due to sediment collapse or the underprinting phenomenon), it should be noted that the concept of robust and slender tracks has recently been a topic of debate in chirothere ichnology, where sexual dimorphism may be an explanation, (Tresise, 1996; Lockley, 1999; Avanzini and Lockley, 2002). Likewise with respect to sauropod tracks, there is a clear distinction between primitive small manus, narrow-gauge and derived large manus, wide-gauge forms. Thus, it seems clear that manus size co-varies with trackway gauge, which in sauropods is a diagnostic feature at the ichnogenus level (Lockley et al., 1994; Lockley, 1999, 2001).

Given that robust (large manus) and gracile (small manus) chirothere tracks, like wide-gauge, large manus and narrow-gauge, small manus sauropod tracks are assigned to different ichnogenera, *not to different ichnofamilies* (Haubold, 1984; Lockley et al., 1994), it would be consistent to avoid prolifer-

ation of ichnofamily names in the case of crocodylian tracks, especially given the small size of the available sample, which make the large-small manus and robust-gracile distinction difficult to resolve. Finally it should be noted that the morphodynamic trends noted here for large archosaurs (chirotheres and sauropod) are likely to be less well-defined in small archosaurs. As a general rule morphological disparity is more pronounced in larger animals.

CONCLUSIONS

The status of *Batrachopus* and several dozen related ichnotaxa remains uncertain and ambiguous. The suggestion that most or all Lower Jurassic crocodylomorph ichnotaxa be synonymized under *Batrachopus* (Olsen and Padian, 1986) has some merit and, if valid, would probably facilitate global correlation (Olsen and Galton, 1984; Haubold, 1986; Lockley and Meyer, 2000). However, caution should be exercised before the excessive splitting inferred in the work of Hitchcock (1858) and Lull (1953) is reversed by excessive lumping. The most general argument in favor of lumping is that, in reality, Lower Jurassic ichnofaunas are not highly diverse, despite the historically liberal tradition of naming tracks instituted by Hitchcock (1858) and continued by Lull (1904, 1953). Given the presence of only four (possibly five) highly distinctive dinosaur track types (*Anomoepus*, *Otozoum*, *Grallator*, *Eubrontes* and possibly *Anchisauripus*) it is unlikely, as recent literature suggests, that there are more than a few distinctive crocodylomorph ichnogenera other than *Batrachopus*. However, if all the ichnotaxa synonymized under *Batrachopus* belong in that ichnogenus (e.g., Olsen and Padian, 1986; Lockley et al., this volume), then the proportion of *Batrachopus* trackways in the Lower Jurassic trackway assemblages from New England may be higher than previously supposed. By contrast, only one ichnogenus (*Batrachopus*) has so far been reported from the Lower Jurassic of Europe.

However, crocodylomorph tracks (*Crocodylopodus*) similar to *Batrachopus* are also known from the Cretaceous. These differ from type *Batrachopus* in having a larger manus, wider foot, more slender and divergent digits, less outward rotation

of the pes and more outward rotation of the manus. However, they are quite similar in appearance to other Lower Jurassic tracks assigned to *Batrachopus* from two localities in France. Thus, we conclude that it is unnecessary to name the new ichnofamily Crocodylopodidae and propose that the large manus and differences in pes and manus rotation are adequately accommodated by placing *Crocodylopodus* in the ichnofamily Batrachopodidae.

Coombs (1996) suggestion that *Antipus* remain separate from *Batrachopus* based on his study of the type material is tentatively accepted, also on the basis of differences in trackway width and the slenderness and rotation of digits, *not* on the basis of inferences about the trackmaker proposed by Coombs (1996). Careful study of all the taxa attributed to *Batrachopus* by Olsen and Padian (1986) is probably necessary to determine if there are consistent patterns of morphological difference that are attributable to the animals foot morphology and not to preservational (extra-morphological) factors. As shown by Lockley et al. (this volume), at least one additional Hitchcock ichnogenus (i.e., *Selenichnus*) is probably an extramorphological variant of *Batrachopus*.

In the spirit of the ten paleoichnological commandments proposed by Sarjeant (1989), we advocate caution in any formal ichnotaxonomic revisions and suggest they only be undertaken in conjunction with careful study of the type material. In this study we have only attempted to highlight three aspects of this complex problem:

First, within the ichnofamily Batrachopodidae there are significant differences between robust, type *Batrachopus* morphotypes and the slender-toed varieties such as are found in France and illustrated herein.

Second, the ichnogenus *Antipus*, applied to a slender-toed, wide gauge (= short stepping) form from the Lower Jurassic, is only one of about a dozen ichnotaxa considered synonymous with, or very similar to *Batrachopus*. Many of these are also slender-toed and may be the result of preservation in wet sediments. Thus, they may appear more similar to *Antipus*, or Cretaceous *Crocodylopodus*, than to type *Batrachopus*.

Third, similarities between *Batrachopus* and *Crocodylopodus* extend the ichnotaxonomic discussion of the range of Batrachopodidae into the Cretaceous. Although the concept of ichnofamily Crocodylopodidae suggests a convenient resonance with the skeletal concept Crocodilia, as presently defined, ichnofamily Crocodylopodidae is not sufficiently different from Batrachopodidae to stand alone. Pending further study we suggest that it be regarded as synonymous with Batrachopodidae.

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