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Discussion

Comments on the paper “Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain Region, USA: Paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses” by Stephen T. Hasiotis

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## 1. Introduction

Hasiotis (2004) has described and interpreted a relatively diverse and potentially very interesting ichnofauna from the Upper Jurassic Morrison Formation of the western United States. An effort was made by the author to bring the data to the reader, but, in our opinion, his analysis is seriously flawed and the resulting discussion and conclusions are not sufficiently supported by data. The unsupported ichnotaxonomic treatment and attributions of trace fossils to their supposed producers throughout Section 4 (*Ichnology*) undermines the 23 pages of discussions and conclusions. We believe that the contribution contains several problems that would deserve a critical and detailed analysis, which regrettably cannot be accomplished

herein because of editorial restrictions. Only salient points are addressed herein.

## 2. Approach and method

Hasiotis' paper (2004) devotes 50 pages in the description and interpretation of 75 morphotypes of trace fossils grouped into 51 major types. However, the descriptions and comparisons are unusually brief, and functional analyses are not provided. Accordingly, the scope of inferences largely exceeds the reliability of these taxonomic attributions. The single “disclaimer”, on page 184, stating “*These interpretations are supported by comparing...*” (Hasiotis, 2004) is unacceptable for a paper in which discussion and conclusions are mostly based on interpretations of important topics in continental ichnology. In addition, the classification outlined on page 182, as introduced by Hasiotis (2000), mimics an earlier one created for classifying soil

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organisms based on their water requirements (Varga, 1956; McKevan, 1962, p. 12), which currently is considered of limited usefulness.

### 3. Ichnotaxonomy and trace makers

The attribution of trace fossils to ichnotaxa and tracemakers as presented by Hasiotis (2004) is one of the weakest points of the paper. The problems occurring in this section comprise: (1) incomplete descriptions, (2) figures that do not support key features mentioned in the descriptions, (3) lack of formalized ichnotaxonomic treatment, and (4) unsupported inferences about tracemakers. Hasiotis failed to follow the established procedure of binomial nomenclature that is accepted by almost all practicing ichnologists. The resulting problems of this approach largely have been analyzed in basic ichnology textbooks (e.g. Bromley, 1996, pp. 164–165), and consequently such analyses will not be repeated here. In addition to these recurring problems found in all of the described types of trace fossils, there are other concerns for particular groups. Given their relevance, those concerning Types 3, 5, 10, and 38 will be specifically discussed below. Types 1, 2, 6, 8, 9, 11, 12, 50 and 51 (simple traces from terrestrial invertebrates) display very simple morphologies and can be attributed indistinctly to various groups of organisms. Indeed, these very simple traces can be indistinctly attributed to various terrestrial, freshwater and marine invertebrates (e.g. Alpert, 1974; Häntzschel, 1975; Frey et al., 1984; Keighley and Pickerill, 1994; Buatois and Mángano, 1995; Ratcliffe and Fagerstrom, 1980; Retallack, 1990; and see Genise et al., 2004 for a more detailed discussion). However, Hasiotis (2004) attributes many of these trace fossils to particular groups of insects without corresponding detailed analyses of their affinities. Types 23, 24, 25, 26, 28, 29, 30, 32 and 33 correspond to traces of freshwater or marine invertebrates. Most of the identifications are dubious at best, providing a cautionary note on speculations about the existence of tidal deposits. The problems found in the description and interpretation of footprints, trackways and vertebrate burrows (types 44, 45, 46, 47, 48, 49) are similar to those encountered in previous trace-fossil categories. Table 1 summarizes our specific concerns with Hasiotis' approach and identifications.

### 4. Fossil record of ecological keystone insects

Types 3, 5, 10, and 38 are particularly relevant because ecologically keystone insect taxa are suppos-

edly identified, namely termites, bees, ants, and dung-beetles. The fossil record of these taxa extends to the Cretaceous and Hasiotis' similar previous interpretations of Triassic and Jurassic trace fossils have been systematically rejected (Labandeira, 1998; Grimaldi, 1999; Thorne et al., 2000; Engel, 2001; Jarzembowski, 2003; Genise, 2004; Grimaldi and Engel, 2005). Unfortunately, Hasiotis makes no attempt to answer previous critics in this paper.

Our principal criticism with these attributions is twofold. First, and most important, is the lack of detailed descriptions, comparisons and functional analyses that would provide a basis minimally for further discussion and the acceptance or rejection of the interpretations and inferences that have been proposed. Specifically, no ant, termite, bee, or dung-beetle nest can be identified in the documentation presented by Hasiotis (2004) that would provide a basis for discussion. A second, more theoretical point is that these ecologically keystone insects, having well-known evolutionary histories (Grimaldi and Engel, 2005) have not been found in pre-existing nonangiosperm-dominated environments, although in principle earlier Mesozoic occurrences of some of these taxa seems plausible. Nevertheless, the earliest fossil occurrences of vespoid wasps, bees, ants, higher (apoditrysan) lepidopterans, and higher (cyclorrhaphan) dipterans parallel that of flowering plants, not before the mid Early Cretaceous (Thorne et al., 2000; Grimaldi and Engel, 2005). These taxa, with the exception of lepidopterans, have fair to good body-fossil records and lack taphonomic constraints on preservational quality. Much data currently support this scenario, including the body-fossil record of the relevant insect clades (Krell, 2000; Thorne et al., 2000; Engel, 2000; Nel et al., 2004; Grimaldi and Engel, 2005), presence of associated groups of organisms such as flowering plants, grasses, and fungi (Taylor and Taylor, 1993; Grimaldi, 1999; Retallack, 2004), and phylogenetic inferences based on molecular analysis (Nalepa and Bandi, 2000). A comparatively reliable trace fossil record (Genise, 2004, and references therein) also supports this scenario, as the oldest well-documented insect nests and pupation chambers in palaeosols are recorded from the Upper Cretaceous, and their record is sparse in comparison with that of the Cenozoic (Genise, 2004). Genise and Bown (1994, p. 114) were the first to discern why the nests of diverse insect taxa, such as bees, termites and dung-beetles, were the most common in palaeosols, attributing such abundance to the high potential for preservation of the constructed traces, in contrast with the merely excavated ones.

Table 1

Trace fossil type (Hasiotis, 2004)	Interpretation (Hasiotis, 2004)	Comments (this paper)
Type 1 (adhesive meniscate burrows)	Soil bug traces (Insecta: Heteroptera)	Two important points mitigate against this assignment. (1) In one contribution on soil bugs, which depicts chambers (Willis and Roth, 1962), quoted by Hasiotis (2004), it is stated that burrows are absent. (2) In addition, alternating zones of oxidized and unoxidized iron compounds are a pattern usually resulting of the original alternation of faecal material within sediment (e.g. Keighley and Pickerill, 1994). The presence of such alternating menisci in burrows produced by insects that do not ingest sediment, is unlikely (Frey et al., 1984).
Type 2 (cf. <i>Ancorichnus</i> isp.)	Beetle traces	Insects do not ingest sediment and do not use appendages to size-sort sediment backfills. <i>Ancorichnus</i> has been restricted by Keighley and Pickerill (1994) to meniscate trace fossils having a structured peripheral mantle (Bromley, 1996, Fig. 8.3). These authors considered that a hydrostatic anchor produces the mantle of <i>Ancorichnus</i> , which is unknown for insects and is the converse of Hasiotis' (2004, p. 187) statement "Because of the distinct burrow walls and menisci, the burrower must have had fairly well sclerotized (sic) exoskeleton and appendages."
Type 3 (interconnected polydomal chambers and galleries)	Ant nests	This assignment is supported by a single descriptive paragraph and six figures, in which the characters of the description cannot be seen clearly. The quotes of classical ant papers in the tracemaker section are misleading, since the previous authors quoted are not involved in such attribution. The unique statement in support of this attribution (p. 189) is: "The composite nature of these terraphilic ichnofossils indicates social behavior..." A composite trace fossil results from the interpenetration of the same or different ichnotaxa (Pickerill, 1994). As such, a network of burrows is not the result of possible cooperative behaviour, but of superposition of individual burrows. Networks do not necessarily indicate social behaviour; similarly, single burrows do not rule out such a possibility (e.g. Michener, 1974; Bromley, 1990). Moreover, every network found in subaerial facies should not be attributed to social insects when a better explanation can be found. Instead, positive termite or ant diagnostic characters are required.
Type 5 (a–c: cf. <i>Celliforma</i> isp.; d: <i>Rosellichnus</i> isp.)	Bee nests	The only set of traits to identify a bee cell unequivocally is the spiral closure cap in combination with a smooth lining (Genise, 2000). These essential characters, although mentioned in the description, are not documented in the figures (which display features unusual in bee nests). Hasiotis' description also contains characteristics, such as U-shaped tunnels and multiple-branched networks that would be unusual for bee nests.
Type 6 (spindle- to tablet-shaped cocoons)	Wasp cocoons	Characters other than shape are needed for the positive identification of wasp cocoons (e.g. Genise, 2004; Genise and Cladera, 2004), particularly when the body fossil record of aculeate wasps commences during the Lower Cretaceous (Rasnitsyn, 1975). The surficial thread-like pattern mentioned by Hasiotis (2004), which would suggest an insect cocoon, is not illustrated. The accompanying Fig. 8 is so poor that it is impossible to see the mentioned structures, which are indicated only by inscribed dashed lines.
Type 7 ( <i>Steinichnus</i> isp.)	Mole cricket burrows (nonbranching) and mud-loving beetle burrows (branching)	<i>Steinichnus</i> was defined to encompass only branched burrow systems (Bromley and Asgaard, 1979). This ichnogenus was subsequently synonymized with <i>Spongeliomorpha</i> (e.g. Ekdale et al., 1984). Mole crickets typically construct branched burrows as well.
Type 8 (cf. <i>Cylindrichum</i> isp.)	Tiger beetle burrows	According to the provided description, we assume that cf. <i>Cylindrichum</i> isp. is most likely a <i>lapsus calami</i> for <i>Cylindricum</i> Linck rather than for <i>Cylindrichnus</i> Toots. The form is attributed to tiger beetles without any explanation. Other invertebrates, such as spiders, ground beetles, cicadas, and hymenopterans, also construct simple vertical burrows (e.g. Ratcliffe and Fagerstrom, 1980). The ichnotaxonomic status of <i>Cylindricum</i> is uncertain; recently Schlirf et al. (2001) regarded <i>Cylindricum</i> as a potential junior synonym of <i>Skolithos</i> .
Type 9 (cf. <i>Scoyenia</i> isp.)	Coleopteran or dipteran traces	Insects are not considered as producers of this ichnotaxon (Frey et al., 1984). See Type 2.

(continued on next page)



Table 1 (continued)

Trace fossil type (Hasiotis, 2004)	Interpretation (Hasiotis, 2004)	Comments (this paper)
Type 10 ( <i>Coprinisphaera</i> isp.)	Dung-beetle nests (balls)	The diagnostic characters of the ichnogenus are mentioned but not illustrated. On the contrary, the structures are shown from some distance.
Type 11 (J-shaped burrows)	Rove beetle burrows	Hasiotis (2004, p. 202) stated that J-shaped burrow morphologies are similar to modern burrows constructed by rove beetles and other insects such as dung beetles and crickets. However, the author concluded that type 11 trace fossils are rove beetle burrows based on the grain size, sedimentary structures, and overall composition of the deposit. What are the background references, if any, for such a statement?
Type 12 (vertical tubes)	Sphecoid wasp burrows	This ichnofossil is scarcely distinguishable from Type 8, other than having a larger diameter, and lacking scratches in the walls. However, Type 12 is attributed to sphecoid wasps, despite the fact that sphecoid wasps always make at least one cell at the end of the tunnel (e.g. Iwata, 1976), and that the oldest spheciform taxa date from the Early Cretaceous (Engel, 2001).
Type 25 ( <i>Arenicolites</i> isp.)	Polychaete worm burrows	All illustrated specimens are preserved on the bedding plane, thus their full morphology is not appreciated and the assignment is uncertain. These trace fossils are regarded by Hasiotis as most likely constructed by polychaete worms and are interpreted to have occurred in tidal environments. However, <i>Arenicolites</i> occurs in continental environments (e.g. Bromley and Asgaard, 1979; Schlirf et al., 2001; Buatois and Mángano, 2004).
Type 28 ( <i>Scolicia</i> isp.)	Invertebrate traces similar to a gastropod, amphipod-like crustacean, or irregular echinoid	The name <i>Scolicia</i> should be used for complex endichnial structures, characterized by a meniscate backfill, and a double ventral cord or drain (e.g. Bromley and Asgaard, 1975; Smith and Crimes, 1983; Uchman, 1995). In post-Triassic marine deposits, where unquestionable <i>Scolicia</i> is found, these backfilled structures are produced by spatangoid echinoids. These simple epirelief furrows lack all the diagnostic elements of <i>Scolicia</i> and may occur in both continental and marine environments, and are neither indicative of tidal environments, nor of marine deposits.
Type 30 (patterned surface trails)	Gastropod or shoreline-dwelling crab grazing traces	The corrugated morphology of this ichnofossil is strongly suggestive of the presence of a microbial mat, rather than an intrinsic trace-fossil feature. The same corrugations can be locally observed outside the area delineated by dashed lines in Fig. 15F.
Type 32 ( <i>Tektonargus kollaspilas</i> )	Trichopteran traces	Fossil caddisfly cases have an extensive and old ichnotaxonomy (e.g. Bosc, 1805; Sukacheva, 1982, and references therein). These trace fossils should be included in the ichnogenus <i>Terrindusia</i> , created to include cases constructed with sand grains. Hasiotis (2004, p. 215) states that “ <i>Caddisfly larval cases in Jurassic deposits suggest that: (1) trichopterans were present in the Jurassic although no body fossils have been found in the Morrison or elsewhere in time-equivalent Jurassic rocks</i> ”. This statement is incorrect because the oldest trichopteran fossils originate from the Lower Permian (e.g. Novokshonov, 1992; van Dijk, 1997), several families are represented throughout the Triassic (Gall, 1996; Martins-Neto et al., 2003; Fraser and Grimaldi, 2003), and both body and trace fossils are abundant by the Jurassic (Sukacheva, 1999).
Type 33 (bivalve traces)	Bivalve dwelling/resting (a) locomotion (b) and escape (c) traces	Hasiotis claims that the Morrison trace fossils likely require their own ichnogenera because they do not fit the description of <i>Lockeia</i> . However, transitions among these behaviours are very common with bivalve trace fossils and have been extensively reported in the literature (Bandel, 1967; Seilacher and Seilacher, 1994; Mángano et al., 1998; Ekdale and Bromley, 2001; Mángano et al., 2002). Most of these structures can fit within previously erected ichnotaxa. Large elliptical to almond-shape structures comprising behavioural pattern <i>b</i> (Fig. 18E and F) resemble the ichnogenus <i>Lockeia</i> . Behavioural type <i>c</i> (Fig. 18D), clearly records transitions from locomotion to resting, and are well known compound ichnotaxa ( <i>sensu</i> Pickerill, 1994) and do not require the erection of a new name. Typical chevronate locomotion structures preserved as positive hyporelief are included in the ichnogenus <i>Protovirgularia</i> (e.g. Seilacher and Seilacher, 1994; Mángano et al., 1998; Ekdale and Bromley, 2001; Mángano et al., 2002). Exceptionally, <i>Protovirgularia</i> can be preserved as a negative epirelief ( <i>Chevronichnus</i> preservation) (Mángano et al., 2002, Fig. 51A). Hasiotis regards these trace fossils as produced by unionid bivalves in the text and specifically by the taxon

Table 1 (continued)

Trace fossil type (Hasiotis, 2004)	Interpretation (Hasiotis, 2004)	Comments (this paper)
Type 33 (bivalve traces)		<i>Unio</i> sp. in the figure caption. However, no morphological comparison between the trace fossils and the supposed trace maker is provided to support this interpretation.
Type 36 ( <i>Kouphichnium</i> isp.)	Horseshoe crab resting (a) and locomotion (b) traces	The ichnogenus <i>Kouphichnium</i> is only available for trackways. Resting traces should be assigned either to <i>Limulicubichnus</i> or <i>Selenichnites</i> .
Type 38 (multiarchitectural, coterminous chambers and galleries)	Termite nests	This attribution has the following (repetitive) problems: (1) brief, weakly informative descriptions, (2) poor documentation in figures, (3) lack of comparative work with modern nests and ichnotaxonomic treatment, (4) lack of concern for the oldest body fossils of the supposed producers, which are from the Early Cretaceous (Thorne et al., 2000), and (5) support of a hypothesis based on past speculative ideas that are no longer supported (Thorne et al., 2000) and self referencing of similarly interpreted traces from Triassic deposits, subsequently rejected by other workers (e.g., Zherikhin, 2002).
Type 44 ( <i>Pteraichnus</i> isp.)	Pterosaur tracks (a) and feeding traces (b)	The track shown in Fig. 25F matches the morphology of a <i>Pteraichnus manus</i> , not <i>Pteraichnus pes</i> as indicated in the figure caption (compare Lockley et al., 1995). Type 44b ( <i>Pteraichnus</i> feeding traces) is not adequately documented in Fig. 26C and no pes track can be seen in connection with the elongated furrows, a feature that is essential to support the interpretation. In addition, the morphology of type 44b traces does not fit under the diagnosis of <i>Pteraichnus</i> or the ichnofamily Pteraichnidae (Lockley et al., 1995) and should be considered under a separate ichnotaxon.
Type 45	Small reptile swimming tracks	This poorly preserved material does not meet the essential criteria needed to identify tetrapod swimming traces, namely incomplete and elongated digit imprints or spurs, preferential impressions of distal digits, and the palaeoenvironmental context interpreted from sedimentary structures (e.g. McAllister, 1989).
Type 46 (large circular depressions)	Sauropod tracks	Under this type are included structures that are not reliable as footprints (Fig. 27A, D, E) and also fossil tracks that cannot be assigned with confidence to any vertebrate group as they are seen in cross-section (Fig. 27C). The presence of trampled intervals (like those in Fig. 27C of Hasiotis, 2004) is used to infer the presence of “large herds of sauropods and other herbivores” (p. 229) without presenting any evidence for the simultaneous formation of the tracks.
Type 47	Ornithopod (a) and theropod (b) tracks	Type 47a (purported ornithopod track) is very similar to supposed sauropod tracks (type 46). Theropod tracks (type 47b traces) are not illustrated.
Type 48 (simple large diameter, inclined burrows)	Reptilian? burrows	The reptilian affinity is considered tentative in the heading. However, it is constrained in the text to include only crocodiles or sphenodontids based on their size-range and attribute the work of Voorhies (1975). Yet, Voorhies (1975) did not specify any size-range as characteristic of burrows of these vertebrate groups. The identification of the trace maker is “refined” on page 234 to include only sphenodontid reptiles, with no further discussion.
Type 49 (complex, large-diameter burrows)	Mammal? burrows	The key features of the description of these structures, namely spiral tunnels, surficial scratches and chambers are not illustrated. By contrast, the figured structures strongly resemble concretionary bodies found in some paleosols.
Type 51 (quasivertical striated burrow)	Burrows of insects similar to extant cicada nymphs (Insecta: Homoptera)	There is arbitrary attribution without any comparative analysis or reference to any neoichnological study.

Accordingly, constructed nests and pupation chambers are produced by the insect taxa whose first appearances presently are known from the Early Cretaceous.

##### 5. Palaeoenvironmental, palaeoecological, palaeohydrological, and palaeoclimatic inferences

Our criticisms with respect to trace fossil identifications are not just mere technicalities; environmental,

ecological, climatological and evolutionary interpretations based on unsound trace fossil classifications become problematic. Many of the family-rank taxa that supposedly are the tracemakers are not present in any Jurassic rocks worldwide. More importantly, taxa that have keystone ecological roles and are not documented for the Jurassic are those most used to extract the most exceptional palaeoecological inferences in this contribution.

Hasiotis (2004, pp. 238, 243–246) presents inferences that greatly exceed the data. Such inferences are scattered throughout the discussion and conclusions. Sedimentological and ichnological evidence indicating a marine transgression within the Morrison Formation is controversial. It should be noted that our point here is methodological. It may well be that subsequent research will document the presence of marine deposits in the contested section, but the evidence provided here is insufficient and in many cases irrelevant. As discussed above, the identification of marine ichnotaxa in the Tidwell Member is questionable. This issue is further complicated because no attempt is made to discuss the ichnology of these deposits within the framework of the present knowledge of brackish-water, estuarine ichnofaunas (e.g. Wightman et al., 1987; Pemberton and Wightman, 1992; MacEachern and Pemberton, 1994; Mángano and Buatois, 2004).

## 6. Status of the ichnofacies model and ichnology of palaeosols

Hasiotis' (2004) recent analysis seems to suggest the impossibility of recognizing archetypal continental ichnofacies and questions the validity of the ichnofacies concept itself. We agree that the ichnofacies model has several limitations and this problem has been known for some time. Nevertheless, ichnofacies are utilitarian and widely applied (e.g. Pemberton et al., 2001). Unfortunately, Hasiotis' analysis confuses ichnocoenoses with Seilacherian ichnofacies, which are quite different concepts, applicable to different scales of analysis (see Bromley, 1990, 1996; Genise et al., 2000; Pemberton et al., 2001). Seilacherian ichnofacies may appear as “*broad and ambiguous*” (p. 238) if the analyzed scale is that of ichnocoenoses. Comparisons between ichnofacies and ichnocoenoses are not properly addressed, switching from one scale of analysis to the other while ignoring the different hierarchies and empirical content and theoretical context involved in these concepts. Also of relevance, Hasiotis (2004) seems to have missed the point that the ichnofacies model is based upon recurring ichnocoenoses and trace fossil associations. To make things more complicated, the supposed ichnocoenoses are not defined in his paper because of the lack of documentation of cross-cutting relationships or evidence supporting observations that trace fossils in the assemblages were coeval. When ichnotaxonomy is ignored and attributions to ichnotaxa or to possible tracemakers are flawed, it is very difficult or almost impossible to recognize ichnofacies. This is the first

fundamental problem for applying the ichnofacies model to the Morrison Formation.

Hasiotis (2004, p. 246) suggested that other ichnologists have confused palaeosols with deposits. This is not the case. To quote just one example, Genise et al. (2000, p. 59), when proposing the *Coprinisphaera* ichnofacies, pointed out clearly: “*In brief, the Coprinisphaera ichnofacies is an archetypal association having enough temporal and spatial recurrence to be used reliably as a paleoecological indicator of terrestrial herbaceous communities occurring in paleosols developed in alluvial plains, desiccated floodplains, crevasse splays, levees, abandoned point bars, and vegetated eolian deposits. These herbaceous communities range from dry and cold to humid and warm climates and it is possible to obtain additional paleoclimatologic precision by considering the relative abundance of the different traces within each particular assemblage*”. In the same section and page Genise et al. stated that “*Soils have little time to mature, and thus have biologic and pedogenic characteristics typical of entisols or inceptisols (relatively immature soils)*”. However, biological activity within soils, as expressed among ichnofabrics in palaeosols, is independent of the degree of maturation; in fact, some palaeoentisols and palaeoinceptisols exhibit a high bioturbation index (Genise et al., 2004).

On page 247, it is stated: “*Currently, only the Scoyenia ichnofacies (Seilacher, 1967) is accepted as a valid archetypal assemblage of continental environments; yet, it is broadly defined and poorly constrained*”. Such a statement would have been appropriate in a paper written in the early eighties. Although the *Scoyenia* ichnofacies is occasionally misused in sedimentological papers in such a broad sense, this is not the current consensus view among ichnologists. Since the seminal work by Frey et al. (1984), ichnologists have a more precise definition of the *Scoyenia* ichnofacies that restricts its use to within the continental environment, and specifically to low-energy environments periodically exposed to air or periodically inundated and intermediate between aquatic and nonaquatic settings (see also Frey and Pemberton, 1984, 1987). Curiously, the doctoral dissertation of Hasiotis (1997), quoted by him several times in the paper, is titled “*Redefining continental ichnology and the Scoyenia ichnofacies*”.

In contrast to Hasiotis' (2004) view, the more recently proposed *Mermia*, *Coprinisphaera* and *Termitichnus* ichnofacies are rapidly gaining acceptance and have been recognized in various ichnological studies of continental successions (Metz, 1996, 2000; Uchman and Álvaro, 2000; De, 2002; Melchor et al., 2003; Mikuláš,

2003; Melchor, 2004; Ebnother and Elliott, 2004). In addition, these facies have been incorporated in palaeoecology textbooks (Brenchley and Harper, 1998), palaeopedology textbooks (Retallack, 2001) and major trace fossil contributions (Pemberton et al., 2001). The reader is referred to the recent review by McIlroy (2004) for a balanced treatment of the topic.

On page 242, Hasiotis notes that: “*Morrison trace fossils in supralittoral and sublittoral lacustrine settings do not fit the definition of the Mermia ichnofacies.... Many of the Morrison traces reflect relatively firm substrates and shallow water with intermittent subaerial exposure*”. If this quote describes the associated depositional conditions, it is hardly surprising that the *Mermia* ichnofacies is not present because this ichnofacies characterizes permanent subaqueous conditions. Nevertheless, Hasiotis also notes that deeper water environments similarly lack the diversity expected and that only *Planolites* and simple U-shaped burrows are present. However, Buatois and Mángano (1998) noted that several factors may inhibit development of the *Mermia* ichnofacies. One of these factors is oxygen-depleted conditions. Interestingly, earlier in his paper (p. 225), Hasiotis attributes the presence of low-diversity *Planolites*-dominated assemblages in lacustrine deposits to poor oxygenation. Using this evidence to argue against the *Mermia* ichnofacies is akin to finding a totally bioturbated marine pelagic deposit and claiming that the *Nereites* ichnofacies is not a valid concept. Hasiotis finishes his analysis by stating that: “*Other lacustrine units examined in Mesozoic and Cenozoic outcrops in the Rocky Mountain region (e.g., Moussa, 1970; Hasiotis et al., in review; Hasiotis, unpublished data) do not show the ichnodiversity and behavioral variability described in purported lacustrine deposits in Carboniferous and Permian strata where the Mermia ichnofacies was defined (Buatois and Mángano, 1995; Buatois et al., 1998)*”. Definition of the *Mermia* ichnofacies was not based only on Carboniferous and Permian strata. Buatois and Mángano (1995) summarized occurrences of the *Mermia* ichnofacies from the Carboniferous to the Pleistocene and Buatois et al. (1998) discussed the temporal and spatial distribution of continental ichnofaunas and addressed the problem of how the *Mermia* ichnofacies evolved with geological time. Interestingly, after its original definition, the *Mermia* ichnofacies has been identified in a significant number of Mesozoic (Metz, 1996, 2000; Melchor, 2004) and Cenozoic (Uchman and Álvaro, 2000; Uchman et al., 2004; Ebnother and Elliott, 2004) units. The incorrect notion that the *Mermia* ichnofacies is exclusively Palaeozoic already

has been suggested by Hasiotis (2002). Incidentally, one of the supposed examples of Palaeozoic occurrences of the *Mermia* ichnofacies quoted by Hasiotis (2002, p. 30) is a paper by Buatois et al. (1996) that documented a *Jurassic* lacustrine ichnofauna from China.

Genise et al. (2000) have already cautioned about the incompleteness of the ichnofacies model for continental environments because of the lack of information about recurrent associations, and also pointing out that the Morrison was the only known *Jurassic* terrestrial trace fossil assemblage. The fact that these ichnofacies are based on ichnotaxa attributed to insect nests probably will restrict its presence to Cretaceous and younger rocks, which will not be a problem if the model proves to be useful for post-Cretaceous rocks and because similar palaeoenvironments would be probably recognized by other sets of trace fossils in older rocks. In marine ichnofacies, dominant ichnogenera are also replaced through geological time, with the appearance of new taxa of producers (Buatois et al., 2002).

Regarding vertebrate trace fossils and vertebrate ichnofacies, Hasiotis (2004) disputes in different passages of the paper (pp. 182, 229, 231) the utility of vertebrates in general and vertebrate traces in particular as palaeoecological and palaeoenvironmental indicators. The only argument presented in the paper is the apparent lack of preferred palaeoenvironmental occurrence of the vertebrate tracks and trackways described by Hasiotis (2004), which are poorly preserved, of uncertain assignment and, in many cases, even dubious as vertebrate trace fossils. In contrast, no mention is made by Hasiotis (2004) of the rich Morrison vertebrate ichnofauna reported previously (e.g. Lockley et al., 1986; Barnes and Lockley, 1994; Lockley and Hunt, 1995; Foster and Lockley, 1995).

## 7. Concluding remarks

Analyses and discussions that attribute trace fossils to insects or other arthropods should be carried out very carefully if the nascent field of continental palaeoichnology is to gain credibility and receive acceptance and recognition as a complementary discipline to invertebrate palaeontology and palaeoentomology. This is particularly relevant when attributions to putative tracemakers attempt to challenge previous empirical knowledge of their evolutionary history and that of their interacting organisms. In an open forum, one may or may not agree with the interpretation of the evidence provided. However, each contribution should contain



fundamental data and interpretations that can be objectively evaluated and discussed by colleagues.

Without sound ichnotaxonomy and analyses of affinities of trace fossils, it is not possible to arrive at sound climatic, biological, hydrological, ecological or palaeoenvironmental conclusions of the fossil record. We suggest in this discussion that critical scrutiny of the ichnofossils is essential, and when done, a different view of continental ichnology emerges and that the available evidence does not support Hasiotis' methodology and conclusions.

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