

TETRAPOD ICHNOFACIES AND THEIR UTILITY IN THE PALEOZOIC

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ABSTRACT: Two distinct traditions exist in the study of ancient ichnofaunas, which may be termed the ethological (invertebrate ichnology) and the biotaxonomic (tetrapod ichnology). Consequently, there are two different kinds of ichnofacies, each peculiar to one tradition, and we term them ethoichnofacies (invertebrate ichnofacies) and biotaxonichnofacies (tetrapod ichnofacies). In the Paleozoic, the *Chelichnus* and *Batrachichnus* (named herein) biotaxonichnofacies encompass all Carboniferous-Permian tetrapod ichnofaunas. Nevertheless, the concept of tetrapod ethoichnofacies in the Paleozoic merits further development. Recognition of two tetrapod biotaxonichnofacies in the Paleozoic has important bearing on biochronologic and facies analysis.

INTRODUCTION

More than two centuries ago, tetrapod tracks were the first trace fossils recognized by scientists (Steinbock, 1989). However, for most of the next two centuries, the study of tetrapod trace fossils lagged behind that of invertebrate trace fossils in both volume and complexity. This situation changed in 1986 with the catalyzing "First International Symposium on Dinosaur Tracks and Traces," held in Albuquerque, New Mexico. Prior to this meeting, there had been little intellectual exchange between the tetrapod ichnologists scattered around the world. This meeting and the subsequent publication of its proceedings (Gillette and Lockley, 1989) sparked a renaissance of interest in tetrapod trace fossils.

Invertebrate ichnologists have long realized that recurrent assemblages of trace fossils can be discriminated. For example, Seilacher (1964a, 1964b, 1967) recognized recurring associations of trace fossils through much of the Phanerozoic, and these associations became the basis of the concept of ichnofacies. Invertebrate ichnologists now use the term ichnofacies in three different ways (Bromley, 1990, 1996): (1) large-scale "Seilacherian ichnofacies" that can be traced through the Phanerozoic; (2) medium-scale ichnofacies that have a widespread distribution in space and time and can be considered subsets of the "Seilacherian ichnofacies"; and (3) small-scale ichnofacies for individual units in a particular rock sequence. We concur with Bromley (1990, 1996) in his reservations about the third usage since it does not refer to any recurrence in space or time.

Lockley et al. (1994) first synthesized information on tetrapod ichnofacies. They recognized the concepts of an ichnocoenosis for a single assemblage of tracks preserved on a single horizon (Leonardi, 1987) and an ichnofacies for multiple ichnocoenoses that are similar in ichnotaxonomic composition and show recurrent association with particular (paleo)environments. This concept of the ichnofacies is equivalent to the medium scale ichnofacies of the invertebrate ichnologist. We employ this concept of tetrapod ichnofacies here.

The purpose of this paper is to discuss the importance and utility of tetrapod ichnofacies in the Paleo-

zoic tetrapod footprint record. However, this requires some discussion of the two different traditions of ichnology evident in invertebrate and tetrapod paleontology.

THE DIFFERENT TRADITIONS OF INVERTEBRATE AND TETRAPOD ICHNOLOGY

Two distinct traditions can be identified in the study of ancient ichnofaunas, and we term them the ethological and the biotaxonomic. Invertebrate paleontologists mostly use an ethological approach to ichnology by describing and naming behavioral interactions between an organism and the substrate. In contrast, vertebrate paleontologists have principally applied a biotaxonomic approach by attempting to relate tracks and traces to the taxonomy of the producer. In other words, vertebrate ichnologists treat vertebrate ichnotaxa as proxies of biotaxa. Thus, vertebrate ichnofaunas are dominantly used to reconstruct evidence about the biotaxonomic composition of track assemblages ("faunas") that is useful for paleoecology, biostratigraphy and biogeography, whereas invertebrate ichnofaunas are utilized more for environmental reconstruction and paleogeographic analysis.

Ichnofacies can be described as associations of ichnotaxa recurrent in time and space. Obviously, there must be two different kinds of ichnofacies, one peculiar to each ichnological tradition. They may be termed ethoichnofacies for invertebrate ichnology and biotaxonichnofacies for tetrapod ichnology.

TWO LATE PALEOZOIC BIOTAXONICHNOFACIES

Among Paleozoic tetrapod footprint assemblages (Fig. 1), recurrent associations of ichnotaxa allow the recognition of two medium-level biotaxonichnofacies (Fig. 2). Baird (1965) first emphasized that in the American West, the differences between the Permian ichnofaunas of the redbeds and those of eolianites might be the result of facies differences. Subsequently, Lockley

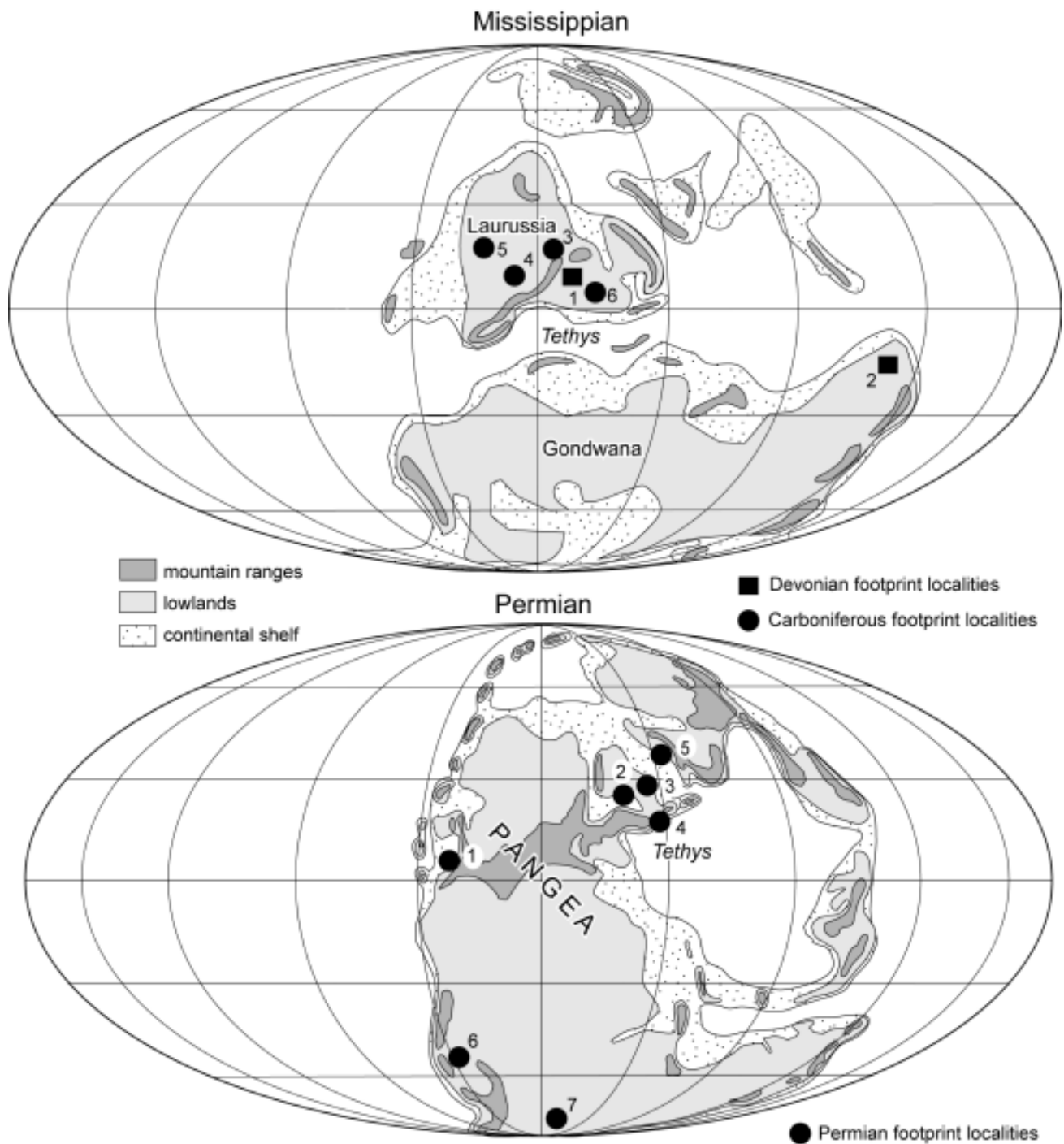


FIGURE 1. Global map of Paleozoic tetrapod ichnofaunas. Upper map shows distribution of principal Devonian-Carboniferous tetrapod tracksites. Devonian sites are: 1, Ireland and Scotland, 2, eastern Australia. Carboniferous sites are: 3, Nova Scotia, 4, eastern United States, 5, western United States, 6, western Europe. Lower map shows distribution of principal Permian tetrapod tracksites on Permian Pangea. Locations are: 1, western United States, 2, France, 3, Germany, 4, Italy, 5, Russia, 6, Argentina, 7, South Africa. Base maps after DiMichele and Hook (1992).

et al. (1994), in the context of an overview of the utility of the ichnofacies concept for tetrapod tracks, recognized a *Laoporus* ichnofacies for Permian eolian ichnofaunas of the United States. This ichnofacies was later amended to the *Chelichnus* ichnofacies because of synonymy (*Chelichnus* = *Laoporus*), and it is also

present in Europe and South America (e.g., Lockley et al., 1995; Morales and Haubold, 1995; McKeever and Haubold, 1996; Hunt and Santucci, 1998; Hunt and Lucas, 1998a; Lockley and Meyer, 2000; Melchor, 2001). Since 1995, various articles have addressed Paleozoic tetrapod ichnofacies (e.g., Hunt et al., 1995c;

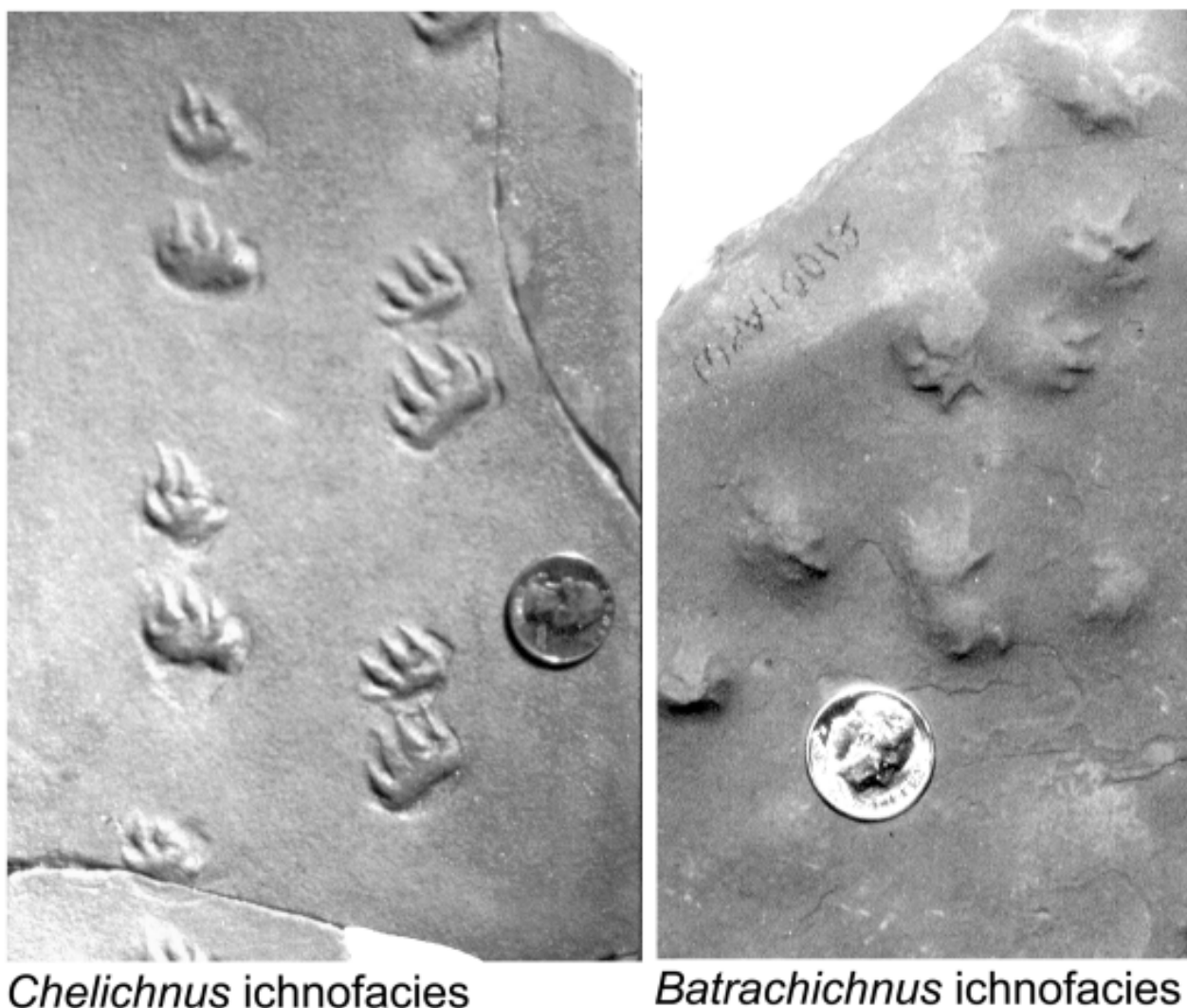


FIGURE 2. Representative tracks of the two Paleozoic tetrapod ichnofacies: left, the *Chelichnus* ichnofacies (eolian) represented by *Chelichnus duncani* (scale is coin with diameter of 24 mm); and right, the *Batrachichnus* ichnofacies (water-laid, including red beds) represented by *Batrachichnus delicatulus* (scale is coin with diameter of 18 mm).

Haubold, 1996; Hunt and Lucas, 1998a, b, 2003, 2004b; Lockley and Meyer, 2000; Lucas et al., 2004a,b; Melchor and Sarjeant, 2004).

Clearly, another widespread Paleozoic biotaxonichnofacies is present in water-laid non-marine strata, and it has generally been referred to as the red-bed ichnofacies (e.g., Hunt and Lucas, 1998a). Lockley and Meyer (2000) named this the *Anthichnium-Limnopus* assemblage, and we formalize this as the *Batrachichnus* ichnofacies for the cosmopolitan ichnogenus (trackmaker = small temnospondyls) that extends from the ?Early Mississippian to the Early Permian. The type ichnofaunas of this biotaxonichnofacies is from the Robledo Mountains Formation of the Hueco Group in southern New Mexico (Hunt et al., 1995a, b; Lucas et al., 1995, 2002, 2004b).

Among the ichnofaunas that can be assigned to this biotaxonichnofacies are: (1) in Europe, Permian tetra-

pod tracks from England, Pennsylvanian-Permian footprints from Germany (Haubold et al., 1995; the *Rotliegendes sensu lato*) and correlative strata in Germany, France and Italy, and in other countries such as Poland (e.g., Haubold, 1971); (2) tetrapod tracks of Mississippian-Permian age from the American Southwest (principally Arizona, Utah, Colorado, New Mexico and Texas), the southeastern and eastern United States (primarily West Virginia, Ohio and Alabama) and eastern Canada (Nova Scotia and Prince Edward Island) (e.g., Cotton et al., 1995; Hunt et al., 1995a); (3) in South America, redbed ichnofaunas from the Permian of Argentina (Melchor and Poiré 1992; Melchor, 1997; Melchor and Sarjeant, 2004); and (4) redbeds of the northern Caucasus, Russia (Lucas et al., 1999).

The *Batrachichnus* biotaxonichnofacies, thus, is widespread temporally and geographically (Hunt and Lucas, 1998a). The *Chelichnus* and *Batrachichnus*

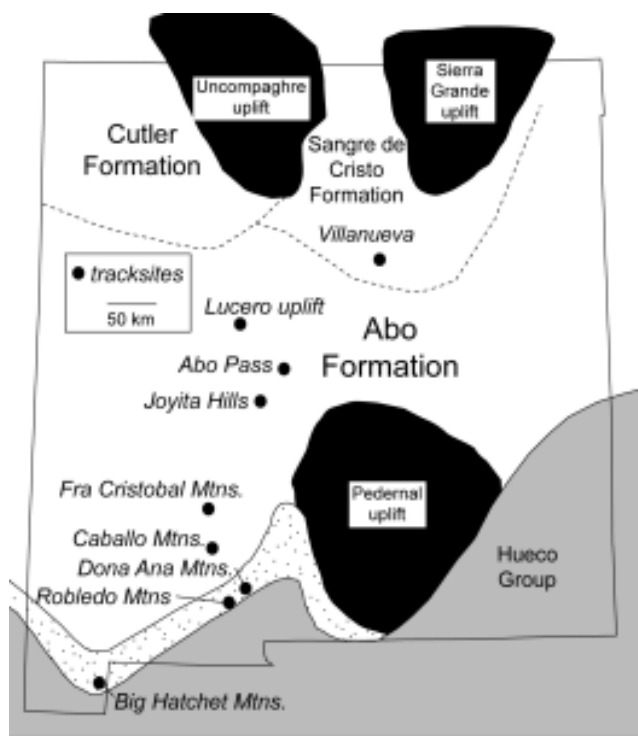


FIGURE 3. Paleogeographic map of New Mexico during the Early Permian.

ichnofacies encompass all Carboniferous-Permian tetrapod footprint ichnofaunas. Thus, tetrapods define only two non-marine ichnofacies in the late Paleozoic, in contrast to the more numerous invertebrate ichnofacies in coeval marine strata. Paleozoic tetrapods thus provide less precision than invertebrates in defining ichnofacies, but it is important to consider that tetrapods are vagrant organisms that are not substrate dependent, although they are environment dependent (Hunt et al., 1995c). Therefore, they should provide much less specificity in the identification of substrates. However, it is also important to realize that we are comparing unlike entities because invertebrate ichnofacies are ethoichnofacies and tetrapod ichnofacies are biotaxonichnofacies.

ECOLOGICAL GRADIENTS AND SUBDIVISIONS

Permian strata of the American Southwest represent a variety of non-marine environments. In New Mexico, it is possible to reconstruct an ecological transect from tidal flat through distal alluvial fan (Figs. 3-4). The ichnofaunas from these ecosystems contain the common Late Pennsylvanian-Early Permian ichnotaxa *Batrachichnus*, *Limnopus*, *Amphisauropus*, *Dromopus*, *Dimetropus* and *Gilmoreichnus* and represent the *Batrachichnus* biotaxonichnofacies.

Hunt et al. (1995c) recognized three subdivisions of this biotaxonichnofacies, and further work has confirmed this trichotomy (Fig. 4): (1) inland/distal alluvial fan settings characterized by the presence of *Ichniotherium* and a paucity of *Dimetropus*; (2) allu-

vial plain settings characterized by the presence of *Amphisauropus*; and (3) coastal/tidal flat settings characterized by the relative abundance of *Batrachichnus* and *Dimetropus*. These subdivisions of the *Batrachichnus* biotaxonichnofacies provide a basis for discriminating environments in other areas in Upper Pennsylvanian-Lower Permian strata (e.g., Lucas et al., 2004a, b).

TETRAPOD ETHOICHNOFACIES?

Vertebrate paleontologists have published little on ethoichnofacies. However, certain preserved tetrapod behaviors (interactions between organism and substrate) may have implications for ethoichnofacies recognition using tetrapod trace fossils.

For example, oblique up-dune progression with downslope sand crescents is well documented in the Permian ichnogenus *Chelichnus*. This response to progression over an unstable substrate on a steep slope may be recognizable throughout the Phanerozoic in eolian sediments. Indeed, there are clear similarities in eolian tetrapod ichnofaunas throughout the Phanerozoic that bear more study. For example, Lockley et al. (1994) noted the similarity in foot structure of tracks from eolian environments of the Permian and Jurassic that suggest the continuity of the *Chelichnus* (or a *Chelichnus*-like) ichnofacies into the Jurassic.

Another example of the potential for tetrapod ethoichnofacies is provided by tidal flat environments such as the Permian Robledo Mountains Formation in New Mexico, which preserve more tail drags in tetrapod trackways than do other environments; this presumably reflects the slipperiness of the muddy substrate. Hunt and Lucas (2004a) demonstrated a similar abundance of tail drag marks in dinosaur trackways in a Cretaceous coastal plain setting.

Clearly, there are features of tetrapod tracks from the Paleozoic (e.g., oblique progression and associated sand crescents, tail drag marks) that are, thus far, not utilized in ichnofacies analysis. This is largely because of the philosophy of vertebrate paleontologists, but these features may have utility throughout the Phanerozoic for the recognition of paleoenvironments and in paleogeographic analysis. There is thus a need for much more study of the concept of tetrapod ethoichnofacies, particularly in the Paleozoic.

BIOCHRONOLOGICAL AND FACIES APPLICATIONS

The construction of biochronologies using trace fossils requires a clear understanding of ichnofacies. Several European workers have constructed complex biochronologies of the Permian based on tetrapod tracks (e.g., Haubold, 1971; Holub and Kozur, 1981; Boy and Fichter, 1988). These studies virtually ignored ichnofacies concerns. Thus, for example, the *Harpagnichnus* zone of Boy and Fichter (1988) is based on tracks from an eolian (Cornberg Sandstein) unit, whereas their other Permian footprint zones are based on tracks from redbeds.

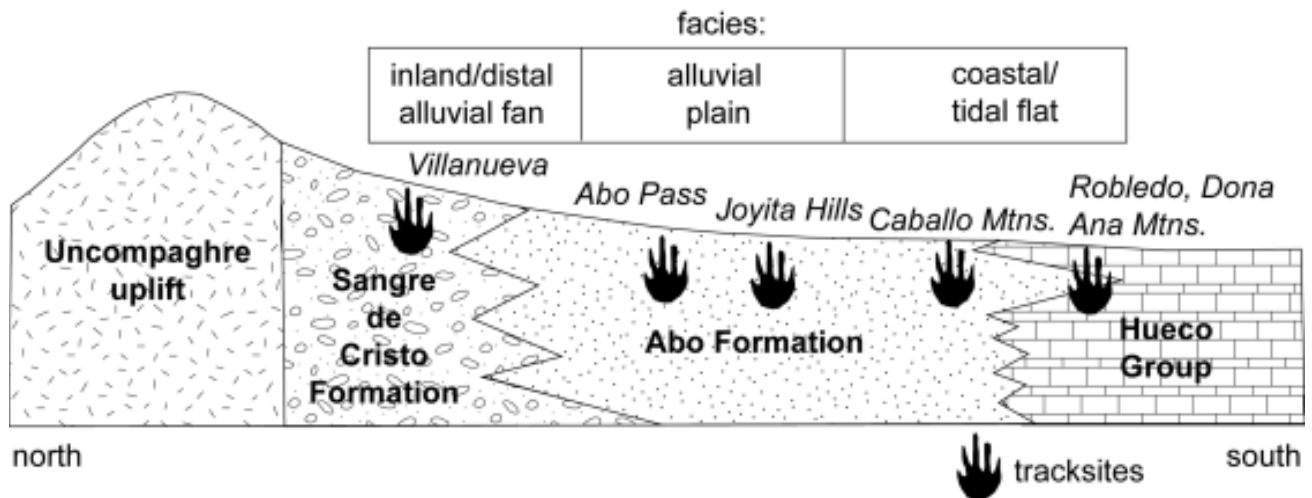


FIGURE 4. North-south transect of Early Permian redbeds in New Mexico showing distribution of ichnofaunas of the *Batrachichnus* biotaxonichnofacies.

Gilmore (1927) first noted the close similarity between Permian ichnofaunas from the eolian Coconino Sandstone of Arizona and from the Corncockle, Lochabriggs and Hopeman Sandstone formations of Scotland. Lockley et al. (1994) and McKeever and Haubold (1996) subsequently recognized a widespread eolian ichnofacies that characterizes these units as well as the Permian DeChelly Sandstone of Arizona, Lyons Sandstone of Colorado and the Cornberg Sandstein of Germany. This ichnofacies is also present in the Permian Yacimiento Los Reyunos Formation of Argentina (Melchor, 1997) and is characterized by low diversity ichnofaunas consisting almost exclusively of species of *Chelichnus* with rare occurrences of *Dromopus* and *Dimetropus*. It is distinctive, widespread and reflects a persistent facies rather than a biostratigraphic datum. Clearly, any biochronology utilizing the ichnofaunas of the *Chelichnus* biotaxonichnofacies is, at least in part, reflecting temporal changes in environment as much as evolutionary patterns.

Recognition of tetrapod biotaxonichnofacies in the Paleozoic also elucidates some apparent problems of facies analysis. For example, the distinctive Early Permian tetrapod ichnotaxon *Ichniotherium* has an unusual distribution. It is well known from some European ichnofaunas (e. g., Tambach Sandstein), but until relatively recently it was unknown in contemporaneous ichnofaunas in the American Southwest. Haubold (1971) first identified this ichnogenus from the Hermit Shale of Arizona, and Hunt et al. (1995c) documented it in the Sangre de Cristo Formation of New Mexico.

One significant aspect of the tetrapod ichnofaunas from the Permian of New Mexico, with respect to ichnofacies, is that they occur along an environmental transect from alluvial fans in the north to coastal plains in the south (Figs. 3-4). Hunt et al. (1995c) presented an initial hypothesis that the northern ichnofaunas would be more similar to those from the intermontane deposits of the Rotliegendes of Europe than to the ichnofaunas

from the coastal plains of southern New Mexico. *Ichniotherium* in New Mexico is restricted to the northern Sangre de Cristo Formation, which was deposited near the base of the mountain front (Fig. 3). Thus, the rarity of *Ichniotherium* in North America may be facies controlled. Only in northern New Mexico and possibly in northern Arizona (Hermit Shale) are ichnofaunas preserved in depositional environments broadly similar to those of Europe. Thus, the distribution of *Ichniotherium* can be explained if it is a facies fossil restricted to more "intermontane" or "inland" environments

This hypothesis is bolstered by the distribution of the amphibian track *Limnopus*. *Limnopus* is relatively uncommon in North America, but is known from abundant specimens from Europe (Gand, 1985; Haubold et al., 1995). In the Lower Permian of New Mexico, *Limnopus* becomes increasingly common in ichnofaunas to the north, away from the coastal plain. It thus appears that *Limnopus* is relatively common in more "inland" ichnofaunas, and this could explain the gross differences between its frequency in Europe and North America.

CONCLUSIONS

1. There are two distinct traditions in the study of ancient ichnofaunas, which may be termed the ethological and the biotaxonomic.

2. There are, thus, two different kinds of ichnofacies, each peculiar to each tradition, and we term them ethoichnofacies (invertebrate ichnology) and biotaxonichnofacies (tetrapod ichnology).

3. The *Chelichnus* and *Batrachichnus* ichnofacies encompass all Carboniferous-Permian tetrapod ichnofaunas.

4. There is need for much more study of the concept of tetrapod ethoichnofacies, particularly in the Paleozoic.

5. Recognition of Paleozoic tetrapod

biotaxonichnofacies has potentially important applications to problems of biochronology and facies analysis.

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REFERENCES

- Baird, D., 1965, Footprints from the Cutler Formation: U. S. Geological Survey Professional Paper 503C, p. C47-C50.
- Boy, J. A. and Fichter, J., 1988, Zur Stratigraphie des höheren Rotliegenden im Saar-Nahe-Becken (Unter Perm: SW Deutschland) und seiner Korrelation mit anderen Gebieten: Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, v. 176, p. 331-394.
- Bromley, R. G., 1990, Trace fossils: biology and taphonomy: London, Unwin Hyman, 250 p.
- Bromley, R. G., 1996, Trace fossils: biology and taphonomy (second edition): London, Unwin Hyman, 361 p.
- Cotton, W. D., Hunt, A. P. and Cotton, J. E., 1995, Paleozoic vertebrate tracksites in eastern North America: New Mexico Museum of Natural History and Science Bulletin, no. 6, p. 189-211.
- DiMichele, W. A. and Hook, R. W., 1992, Paleozoic terrestrial ecosystems; in Behrensmeyer, A. K., Damuth, J. D., DiMichele, W. A., Potts, R., Sues, H-D. and Wing, S. L., (eds.), Terrestrial ecosystems through time: Chicago, University of Chicago Press, p. 205-325.
- Gand, G., 1985, Significations paléobiologique et stratigraphique de *Limnopus zelleri* dans le partie nord du bassin Permien de Saint-Affrique (Aveyron, France): Geobios, v. 18, p. 215-227.
- Gillette, D. D. and Lockley, M. G., 1989, eds, Dinosaur Tracks and Traces: Cambridge, Cambridge University Press, 454 pp.
- Gilmore, C. W., 1927, Fossil footprints from the Grand Canyon: second contribution: Smithsonian Miscellaneous Collections, v. 80(3), 78 p.
- Haubold, H., 1971, Ichnia amphibiorum et reptiliorum fossilium: Handbuch der Paläoherpologie, Teil 18: Stuttgart, Gustav Fischer Verlag, 124 p.
- Haubold, H., 1996, Ichnotaxonomie und Klassifikation von Tetrapodenfährten aus dem Perm: Hallesches Jahrbuch für Geowissenschaften, ser. B., v. 18, p. 23-88.
- Haubold, H., Hunt, A. P., Lucas, S. G. and Lockley, M. G., 1995, Wolfcampian (Early Permian) vertebrate tracks from Arizona and New Mexico. Bulletin of New Mexico Museum of Natural History and Science, v. 6, p. 135-165.
- Holub, V. and Kozur, H., 1981, Revision einiger Tetrapodenfährten des Rotliegenden und biostratigraphische Auswertung der Tetrapodfährten des obersten Karbon und Perm: Geologische Paläontologische Mitteilungen Innsbruck, v. 11, p. 149-193.
- Hunt, A. P. and Lucas, S. G., 1998a, Implications of the cosmopolitanism of Permian tetrapod ichnofaunas: New Mexico Museum of Natural History and Science Bulletin, no. 12, p. 55-57.
- Hunt, A. P. and Lucas, S. G., 1998b, Vertebrate ichnofaunas of New Mexico and their bearing on Lower Permian vertebrate ichnofacies: New Mexico Museum of Natural History and Science Bulletin, no. 12, p. 63-65.
- Hunt, A. P. and Lucas, S. G., 2003, Tetrapod ichnofacies in the Paleozoic; in Martin, A. J., ed., Workshop on Permo-Carboniferous Ichnology, Program and Abstracts, Alabama Museum of Natural History, Geological Survey of Alabama, p. 8-11.
- Hunt, A. P. and Lucas, S. G., 2004a, Multiple, parallel, dinosaur tail drags from the Early Cretaceous of New Mexico. Journal of Vertebrate Paleontology, v. 24 (supplement to no. 3), p. 73A.
- Hunt, A. P. and Lucas, S. G., 2004b, Tetrapod ichnofacies in the Paleozoic: 32nd International Geological Congress Italia 2004 Abstracts Part 1. International Union of Geological Sciences, p. 600.
- Hunt, A. P. and Santucci, V. L., 1998, Taxonomy and ichnofacies of Permian tetrapod tracks from Grand Canyon National Park, Arizona; in Santucci, V. L. and McClelland, L., eds., National Park Service Paleontological Research. National Park Service Geological Resources Division Technical Report NPS/NRGRD/GRDTR-98/01, p. 94-96.
- Hunt, A. P., Lucas, S. G. and Lockley, M. G., 1995a, Paleozoic tracksites of the western United States: New Mexico Museum of Natural History and Science Bulletin, no. 6, p. 213-217.
- Hunt, A. P., Lucas, S. G., Haubold, H. and Lockley, M. G., 1995b, Early Permian (late Wolfcampian) tetrapod tracks from the Robledo Mountains, south-central New Mexico: New Mexico Museum of Natural History and Science, Bulletin no. 6, p. 167-180.
- Hunt, A. P., Lucas, S. G., Lockley, M. G., Haubold, H. and Braddy, S., 1995c, Tetrapod ichnofacies in Early Permian red beds of the American Southwest: New Mexico Museum of Natural History and Science Bulletin, no. 6, p. 295-301.
- Leonardi, G., ed., 1987, Glossary and manual of tetrapod footprint palaeoichnology: Departamento Nacional da Produção Mineral, Brasilia, 75 p.
- Lockley, M. G. and Meyer, C., 2000, Dinosaur tracks and other fossil footprints of Europe: New York, Columbia University Press, 323 p.
- Lockley, M. G., Hunt, A. P. and Meyer, C., 1994, Vertebrate tracks and the ichnofacies concept: implications for paleoecology and palichnostratigraphy; in Donovan, S., ed., The palaeobiology of trace fossils: London, John Wiley, p. 241-268.
- Lockley, M. G., Hunt, A. P., Haubold, H. and Lucas, S. G., 1995, Fossil footprints in the DeChelly Sandstone of Arizona: with paleoecological observations on the ichnology of dune facies. Bulletin of New Mexico Museum of Natural History and Science, v. 6, p. 225-233.
- Lucas, S. G., Krainer, K. and Kues, B. S., 2002, Stratigraphy and correlation of the Lower Permian Hueco Group in the southern San Andres Mountains, Doña Ana County, New Mexico: New Mexico Geological Society Guidebook, no. 53, p. 223-240.
- Lucas, S. G., Lerner, A. J. and Hunt, A. P., 2004, Permian tetrapod footprints from the Lucero uplift, central New Mexico, and Permian footprint biostratigraphy: New Mexico Museum of Natural History and Science Bulletin, no. 25, p. 291-300.
- Lucas, S. G., Lozovsky, V. R. and Shishkin, M. A., 1999, Tetrapod footprints from the Early Permian redbeds of the northern Caucasus, Russia: Ichnos, v. 6, p. 277-281.
- Lucas, S. G., Anderson, O. J., Heckert, A. B. and Hunt, A. P., 1995, Geology of Early Permian track sites, Robledo Mountains, south-central New Mexico: New Mexico Museum of Natural History and Science Bulletin, no. 6, p. 13-32.
- Lucas, S. G., Lerner, A. J., Bruner, M. and Shipman, P., 2004a, Middle Pennsylvanian ichnofauna from eastern Oklahoma, USA: Ichnos, v. 11, p. 45-55.
- McKeever, P. J. and Haubold, H., 1996, Reclassification of vertebrate trackways from the Permian of Scotland and related forms from Arizona and Germany: Journal of Paleontology, v. 70, p. 1011-1022.
- Melchor, R. N., 1997, Permian tetrapod ichnofaunas from Argentina: further evidence of redbed shallow lacustrine and aeolian vertebrate ichnofacies: Abstracts and papers of Workshop on

- the Ichnofacies and Ichnotaxonomy of the Terrestrial Permian, Halle, p. 59-60.
- Melchor, R. N., 2001, Permian tetrapod footprints from Argentina. *Hallesches Jahrbuch für Geowissenschaften*, ser. B, v. 23, p. 35-43.
- Melchor, R. N. and Poiré, D., 1992, Sedimentological and paleoecological implications of invertebrate and tetrapod ichnocoenosis from a Permian fluvial/lacustrine sequence: Carapacha Formation, La Pampa Province, Argentina: *Cuarta Reunión Argentina de Sedimentología*, Actas III, p. 247-257.
- Melchor, R. N. and Sarjeant, W. A. S., 2004, Small amphibian and reptile footprints from the Permian Carapacha Basin, Argentina: *Ichnos*, v. 11, p. 57-78.
- Morales, M. and Haubold, H., 1995, Tetrapod tracks from the Lower Permian DeChelly Sandstone of Arizona: systematic description: *New Mexico Museum of Natural History and Science Bulletin*, no. 6, p. 251-261.
- Seilacher, A., 1964a, Biogenic sedimentary structures; in Imbrie, J. and Newell, N., eds., *Approaches to Paleoecology*: New York, Wiley, p. 296-316.
- Seilacher, A., 1964b, Sedimentary classification and nomenclature of trace fossils: *Sedimentology*, v. 3, p. 253-256.
- Seilacher, A., 1967, Bathymetry of trace fossils: *Marine Geology*, v. 5, p. 413-428.
- Steinbock, R. T., 1989, Ichnology of the Connecticut Valley: a vignette of American science in the early nineteenth century; in Gillette, D. D. and Lockley, M. G., eds., *Dinosaur Tracks and Traces*: Cambridge, Cambridge University Press, p. 27-36.

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