

NEW LOWER PERMIAN NONMARINE ARTHROPOD TRACE FOSSILS FROM NEW MEXICO AND SOUTH AFRICA

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ABSTRACT—The Lower Permian (Late Wolfcampian) marginal marine facies of the Robledo Mountains Member (Hueco Formation) of the Robledo Mountains, New Mexico, contains a diverse ichnofauna dominated by vertebrate trackways. Four new arthropod ichnotaxa are described. *Tonganoxichnus robledoensis* new ichnospecies, consists of repeated small traces comprising imprints of anteriorly directed legs, an elongate tapering abdomen, and a thin tail. *Hedriumichnus apacheensis* new ichnogenus and ichnospecies consists of isolated small traces comprising imprints of laterally-directed legs, a broad tapering abdomen, and a short tail. *Rotterodichnium major* new ichnospecies is a large trace with imprints of the head and thorax, a long thin abdomen and three pairs of legs, increasing in length posteriorly. *Quadrispinichna parvia* new ichnogenus and ichnospecies consists of four diverging or sub-parallel linear or curvilinear imprints of approximately equal length.

Tonganoxichnus, previously known from the Upper Carboniferous of eastern Kansas, is interpreted as produced by a jumping monuran (an extinct group of wingless insects). *Hedriumichnus*, known only from the Robledo Mountains, is interpreted as the resting trace of a nymph of a primitive Ephemeroptera or Plecoptera. *Rotterodichnium*, previously known from the Lower Permian of Germany, is interpreted as the resting trace of a large dragonfly-like form (Protodonata, Odonata, or Megasecoptera). *Quadrispinichna*, previously recorded but not named, from the Lower Permian Ecca succession of South Africa, is interpreted as a resting trace of a crustacean. These rare traces increase our understanding of the diversity and behavior of nonmarine arthropod communities in the Lower Permian.

INTRODUCTION

TRACE FOSSILS are important for revealing the diversity and paleoenvironmental distribution of arthropods in the fossil record. As they occur in situ they reliably record the presence of an animal in a particular environment, as opposed to body fossils, which may have been transported. Arthropod trackways and trails reveal important evidence of the locomotory capabilities of extinct arthropods, although only the imprints of the distal part of the legs are usually preserved, thus limiting interpretations of the producer. Resting traces may provide much more information on the morphology of the producer than trackways, as they often preserve an impression of the entire animal. They therefore contribute more information than trackways towards our understanding of the diversity of ancient arthropod communities.

Paleozoic nonmarine arthropod resting traces are rare but include forms produced by each of the major arthropod groups. Crustacean resting traces include *Kingella* and *Gluckstadtella* from the lacustrine Dwyka Series (Late Carboniferous to Lower Permian) of South Africa, interpreted as produced by syncarids or peracarids (Savage, 1971). Nonmarine occurrences of *Rusophycus*-like bilobed resting traces, widely recorded from Devonian to Permian subaqueous deposits, were probably produced by notostracan or phyllopod crustaceans (Pollard, 1985; Gand, 1994). Chelicerate (xiphosuran) resting traces include *Selenichnites*, known from the Ordovician to Jurassic (see Romano and Whyte, 1987; Trewin and McNamara, 1995, for review), and *Limulicubichnus*, from the Pennsylvanian of Tennessee (Miller, 1982). Insect resting traces include *Rotterodichnium*, *Avolaticinium* and *Orbiculichnus* from the Lower Permian of southeast Germany (Walter, 1983) and Czech Republic (Holub and Kozur, 1981). Additionally, Mángano et al. (1997) recently described the monuran resting trace *Tonganoxichnus* from the Upper Carboniferous of eastern Kansas, and Guerra Sommer et al. (1984) described, but did not name, a similar resting trace from the Lower Permian Itararé Group of Brazil.

In this paper we describe four new arthropod ichnotaxa and discuss their probable producers and the behavior represented, by comparing them with other arthropod resting traces and by considering the fossil record of potential trace makers. Three of these new ichnotaxa are interpreted as resting traces (cubichnia), while one (*Tonganoxichnus robledoensis*) is repeated body imprints,

produced by a jumping arthropod (repichnia). One of the forms, referred to the new ichnogenus *Hedriumichnus*, is unique to the Lower Permian Robledo Mountains ichnofauna of New Mexico. Two other forms, also from the Robledo Mountains ichnofauna, are assigned to new ichnospecies of *Tonganoxichnus* Mángano et al., 1997, first described from the Upper Carboniferous of eastern Kansas, and *Rotterodichnium* Walter, 1983, first described from the Lower Permian of Germany, respectively. The fourth, a new ichnogenus *Quadrispinichna*, from the Lower Permian post-glacial Ecca succession of South Africa, was first described by Anderson (1974), in her doctoral thesis. Although Anderson published several studies on the Paleozoic ichnology of South Africa (e.g., Anderson, 1981) this trace remained unpublished. Its importance was recognized by SJB when analyzing the type material in the South African Museum. Similar trace fossils had previously been noted from the Robledo Mountains ichnofauna (Brady, 1998), although their affinities at this time were unknown. *Quadrispinichna* is therefore a widely distributed component of Lower Permian nonmarine ichnofaunas. It is attributed to crustaceans. Anderson's original name (and choice of type material) is retained, not only to avoid potential confusion for subsequent workers but also to acknowledge her important contribution to South African ichnology.

Tonganoxichnus, *Hedriumichnus*, and *Rotterodichnium*, from the Robledo Mountains ichnofauna, are attributed to insects. The earliest hexapod is *Rhyniella praecursor*, from the Devonian Rhynie Chert in Aberdeenshire (Whalley and Jarzembowski, 1986). The lack of insects in the Upper Devonian may reflect a lack of suitable preservational environments rather than a true low diversity. A massive radiation of insects occurred during the Carboniferous (Kukalová-Peck, 1994; Labandeira and Sepkoski, 1993; Jarzembowski and Ross, 1996), accompanied by two primary evolutionary innovations: 1) the evolution of flight (in Pterygota) and; 2) the ability to fold the wings back over the abdomen (in neopteran Pterygota). All insect orders present during the Late Carboniferous persisted into the Lower Permian. Some groups (e.g., Palaeodictyoptera) apparently had a lower diversity than in the Carboniferous, although this may reflect an incomplete fossil record (Labandeira and Sepkoski, 1993). Other orders (e.g. Orthoptera; grasshoppers) became very abundant and some (e.g., Odonata; dragonflies) appeared for the first time in the Permian.

Paleozoic insect traces include insect-plant interaction traces (e.g., Scott and Taylor, 1983) and trackways (e.g., Holub and Kozur, 1981; Walter, 1983; Kozur and Lemone, 1995; Braddy, 1998). Insect resting traces are very rare (e.g., Walter, 1983; Mángano et al., 1997); therefore the material described here provides important evidence for the diversity, paleoecology and behavior of Lower Permian insects.

GEOLOGICAL SETTING AND ASSOCIATED ICHNOFAUNA

New Mexico.—The traces from the Robledo Mountains were collected from several localities (see Lucas et al., 1995, for locality details), from the Lower Permian (Late Wolfcampian) Robledo Mountains Member of the Hueco Formation, which represents a sequence of nonmarine red beds (fine grained, red-grey micaceous sandstones and mudstones) and intertidal deposits, which are “truncated by, or grade laterally into, rare channel sandstones, which represent tidal-creek or estuarine facies” (Mack and James, 1986, p. 635). Mud cracks and rain prints, sometimes preserved alongside the traces, indicate subaerial conditions, but ripple marks preserved on other surfaces, indicate that exposure was intermittent, perhaps as part of a tidal flat, inferred on sedimentary structures and the paleogeographic setting (Lucas et al., 1995). Plant fragments (*Walchia*) are very common at some localities, indicating that the paleocoastline was locally vegetated. Body fossils are generally absent, except for a single enrolled millipede (MacDonald, 1992, p. 38).

The Robledo Mountains ichnofauna, arguably the most abundant and diverse Permian marginal marine ichnoassemblage in the world (Hunt et al., 1993; MacDonald, 1994), is dominated by the trackways of vertebrates (e.g., Haubold et al., 1995), which have received considerable scientific study, and arthropods (e.g., Braddy, 1998). The producers of the vertebrate trackways include temnospondyl amphibians, araeoscelids, ?diadectids, and pelycosaurs (Haubold et al., 1995). Braddy (1998, 1999) also noted several examples of traces regarded as the work of limbless amphibians, probably lysorophians, which resemble those produced by modern side-winding snakes (Braddy et al., in review).

The arthropod trackways and trails indicate a diverse aquatic and subaerial community including myriapods (*Diplichnites*, *Diplopodichnus*, and *Mirandaichnium*), scorpions (*Paleohelcura*), spiders (*Octopodichnus*), eurypterids (*Palmichnium*), xiphosurans (*Kouphichnium*), crustaceans (bilobed trails), and several different types of insects (*Permichnium*, *Eisenachichnus*, *Robledoichnus*, *Shalemichnus*, *Pterichnus*, and *Punctichnium*) (Braddy, 1995, 1998; Kozur and Lemone, 1995). Arthropod resting traces include the new ichnotaxa described here and large *Rusophycus*, associated with bilobed trails, probably produced by crustaceans. Several slabs are covered with hundreds of tiny isolated bilobed resting traces, 1–3 mm long, similar to *Isopodichnus minutus* Debriette and Gand, 1990, which were probably produced by very small crustaceans or ostracodes. Other rare invertebrate traces consist of paired triangular clusters of many fine scratches, similar to *Striatichnium* Walter, 1982, probably produced by a foraging arthropod, and infaunal burrows (*Taenidium*, *Treptichnus*, and *Cochlichnus*) (Braddy, 1998).

South Africa.—*Quadrispinichna* is known from three localities in the Lower Permian Ecca Series in the southwest region of the Great Karoo Basin of South Africa: Zak River, Laingsburg, and Askop (Anderson, 1981, fig. 1). The succession is interpreted as freshwater (shallow lacustrine), and overlies the Upper Dwyka (non-glacial) shales and the Dwyka Series (glacial deposits), which formed in freshwater periglacial lakes (Savage, 1971). Biostratigraphic correlations between these units are poor as fossils are rare, apart from plants.

The Zak River locality (31°1'24"S, 20°17'E), 58 km south of Brandvlei in mid-western Cape Province, lies in an argillaceous

clastic sequence of the “central Ecca facies.” The most common trace is the arthropod (crustacean) trackway *Umfolozia*, but *Cochlichnus*, fish trails, the star-like *Stelloglyphus*, infaunal burrows, and rare *Quadrispinichna* are also known. The environmental setting is shallow lacustrine; quiet but not necessarily deep water (Anderson, 1981).

The Laingsburg locality (33°11'30"S, 20°50'E), 2 km west of Laingsburg, lies in a thick sequence of Lower Ecca grey shales and intercalated (greywacke) sandstones of the “southern Ecca facies.” A vertical transition from distal to proximal turbidites was noted by Theron (1967). Burrows are common but other traces are rare; about one-half of these are *Umfolozia*, one-third are *Scolicia*-like trails, and the rest comprise fish trails, indeterminate ichnotaxa, and rare *Cochlichnus*, *Stelloglyphus*, and *Quadrispinichna*. The environmental setting is deeper water than Zak River (Anderson, 1981).

The Askop locality (33°8'24"S, 22°45'42"E), on the Farm Klipgat, about halfway between Prince Albert and Willowmore, lies in basal Ecca Series, also of the “southern Ecca facies.” Burrows are common and most of the arthropod trackways are *Umfolozia*, although *Maculichna* is also known. Fish trails and *Quadrispinichna* are rare. The environmental setting is similar to Laingsburg (Anderson, 1981).

TERMINOLOGY AND MATERIAL

Terminology.—The ethologic category “cubichnia” is widely applied to resting traces, although there is some confusion about the affinities of some complex cubichnia that have been regarded as body fossils (i.e., external molds of the ventral surface). *Protolimulus eriensis* Packard, 1886, for example, was originally described as a body fossil, but was reinterpreted by Anderson (1996) as the trace fossil belonging to *Selenichnites*. In such cases a simple criterion may be used to determine whether they are body or trace fossils. If the fossil shows any evidence for activity (e.g., features produced by movement) the animal must have been alive, and the structure is a trace fossil. Body fossils, on the other hand, would have remained in the impression until they were degraded. In very rare cases arthropods are even found within their resting traces (e.g., the trilobite *Flexicalymene* within *Rusophycus pudicum*; Osgood, 1970, pl. 58). This distinction is relevant here as some workers might regard *Hedriumichnus* as a body fossil but there are clear signs of activity (see below), which identify it as a trace fossil.

The terminology used is that of Mángano et al. (1997), who followed Trewin's (1994) nomenclature for trackways (although resting traces are not trackways, many terms can be applied to both). An “imprint” is a discrete isolated mark. An “impression” is a more continuous mark. The term “track” should be applied to walking traces; we therefore prefer the term “imprint” to describe the marks left by the legs in a resting trace. “Mid-line” refers to the medial axis of the trace. The terms “proximal” and “distal” (relative to the mid-line) may be applied to individual imprints or impressions.

A discussion on appropriate ichnotaxobases for the classification of arthropod resting traces has been lacking in the literature; the absence of a hierarchy of diagnostic elements has caused previous workers to apply different ichnotaxonomic procedures. Ichnotaxa are form taxa, and should be based on the morphology of well preserved material, not on assumptions regarding the producer, or the stratigraphic or environmental occurrence (Keighley and Pickerill, 1998). Fürsich (1974) proposed the use of “significant” (to define ichnogenera) and “secondary” (to define ichnospecies) diagnostic criteria in ichnotaxonomy. The use of “minor” diagnostic criteria is here suggested to define “forms” or “types” (i.e., extramorphological variation associated with topology, ontogeny, or minor behavioral changes).



FIGURE 1—*Tonganoxichnus robledoensis* n. isp. in negative epirelief. 1, Holotype (type 1), NMMNH&S P24020a, $\times 2$; 2, paratype (type 2), NMMNH&S P24020d, $\times 2$.

Repository.—The material is held by: 1) the New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, U.S.A. (NMMNH&S); 2) the South African Museum, Cape Town, South Africa (SAM); 3) the Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa (BPIPR); and 4) the Geological Survey of Pretoria, South Africa (GSP).

Where two or more traces occur on the same slab, and carry the same repository number, individual traces are distinguished by a lower case letter following the specimen number (e.g., NMMNH&S P24020 has six separate resting traces on one slab, i.e., P24020a–f). As in many resting traces occurring in groups, a single well-preserved individual trace is selected as the type specimen, following, for example, Mángano et al. (1997) and Gand (1994). This is because trace morphologies may vary slightly within a group, and an ichnotaxon must be based upon a single morphotype.

SYSTEMATIC ICHNOLOGY

Ichnogenus *TONGANOXICHNUS* Mángano, Buatois, Maples, and Lanier, 1997

Type ichnospecies.—*Tonganoxichnus buildexensis* Mángano, Buatois, Maples, and Lanier, 1997.

TONGANOXICHNUS ROBLEDSENSIS new ichnospecies
Figures 1, 2

Insect resting trace, HUNT ET AL., 1993, p. 29, fig. 10F.

Resting traces, MÁNGANO, BUATOIS, MAPLES, AND LANIER, 1997, p. 123.

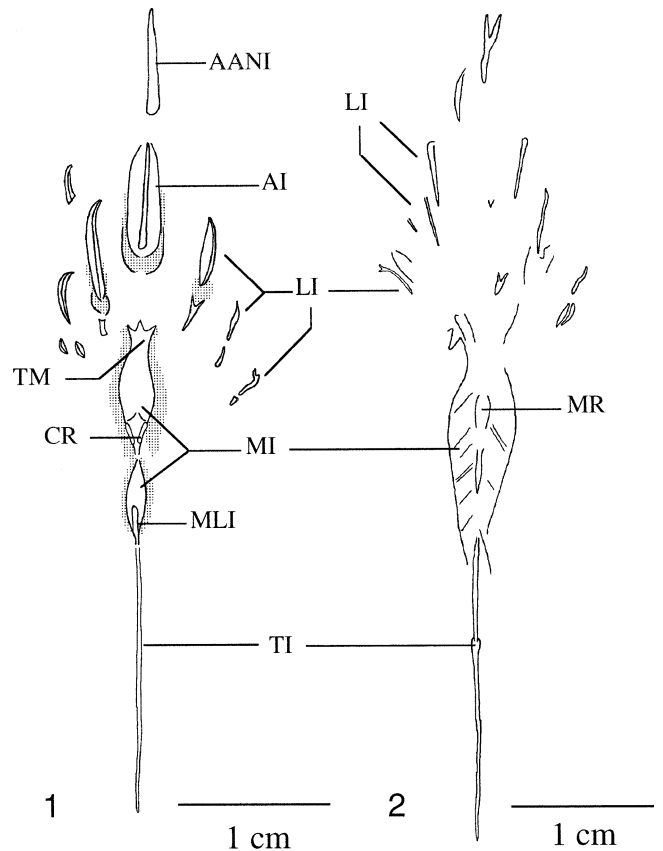


FIGURE 2—Interpretative drawing of *Tonganoxichnus robledoensis* n. isp. 1, Holotype (type 1), NMMNH&S P24020a; 2, paratype (type 2), NMMNH&S P24020d. Abbreviations: AANI, accessory anterior narrow imprint; AI, anterior imprint; CR, converging ridges; LI, lateral imprints; MI, middle hourglass-shaped imprint; MLI, medial linear imprint; MR, medial slender hourglass-shaped region; TI, terminal imprint; TM, trifurcate margin.

Resting traces B and C, BRADY, 1998, p. 96.

An undescribed, new resting trace, BRADY, 1999, p. 6, fig. 1b, c.

Diagnosis.—Regularly repeated, bilaterally symmetrical, epichnial trace consisting of three medial imprints; a deep anterior elongate imprint (sometimes absent), a tapering (sometimes segmented) or hourglass-shaped posterior imprint and a long thin, terminal imprint. Three pairs of short, anteriorly directed, curvilinear (sometimes straight) imprints occur laterally.

Description.—Preserved in negative epirelief. Two (behavioral) forms are recognized. Type 1 consists of three repeated traces that occur in a line, (P24020a–c), the most clearly preserved example (P24020a; holotype; Figs. 1.1, 2.1) occurring at the end, total length 54 mm. Each trace is bilaterally symmetrical with medial imprints divided into three sections: 1) an anterior broad, deep imprint (AI), bordered posteriorly by a mound of substrate (with an accessory anterior narrow imprint (AANI) in P24020a), followed by; 2) a middle hourglass-shaped imprint (MI), comprising an anterior elongate portion, the anterior margin trifurcate (TM), the posterior bordered by two converging ridges (CR), and a posterior oval-shaped portion, with a medial linear imprint (MLI) in the posterior part, and; 3) a long thin terminal imprint (TI). The anterior and middle medial imprints are flanked by three pairs of short curvilinear lateral imprints (LI), each slightly inclined away from the mid-line (equivalent to the “anterior bifid or single

scratch marks" of *T. ottawensis*). The anterior, inner lateral imprints are bordered posteriorly by sharp sediment mounds. No clear sediment mounds are associated with the middle or posterior lateral imprints.

Type 2 consists of three isolated traces (P24020d–f; Figs. 1.2, 2.2) on the same slab as the repeated trace. Each trace is the same length, and similar morphology to type 1, but the anterior medial imprint is lacking, the middle medial imprint is larger, with several faint oblique lineations, and an additional pair of frontal imprints occurs anteriorly to the lateral imprints, which are all generally straighter than in type 1. The medial imprints are divided into two sections: 1) a middle, posteriorly tapering imprint (MI), the anterior region constricted, the anterior margin not preserved (within this imprint, a medial region (MR) with a slender hourglass-shape is flanked by faint oblique lineations); and 2) a long thin terminal imprint (TI). There is an additional pair of frontal imprints at the anterior of the trace, the right one apparently bifid.

Etymology.—Named after the Robledo Mountains, from where this material was collected.

Types.—Holotype, NMMNH&S P24020a (Figures 1.1 and 2.1), paratypes, NMMNH&S P24020 b–f, five other traces on the same slab.

Occurrence.—Locality L846 (see Lucas et al., 1995) from the Lower Permian (Late Wolfcampian) Robledo Mountains Member of the Hueco Formation of the Robledo Mountains, New Mexico.

Discussion.—*Tonganoxichnus robledoensis* is similar to *T. ottawensis* Mángano, Buatois, Maples and Lanier, 1997, but differs in the presence of the anterior medial imprints (AI and AANI). The three pairs of lateral imprints (LI) are situated laterally, not anteriorly as in *T. ottawensis* (and they are also not bifid), and the medial imprint (MI) lacks pronounced appendage imprints (but these may be represented by the faint oblique lineations in type 2). The medial imprint also has a trifurcate anterior margin (TM). While this variation is considered sufficient to assign this material to a new ichnospecies, we note that *T. robledoensis* is preserved in negative epirelief and *T. ottawensis* is preserved in positive hyporelief; trace morphology (e.g., the lack of pronounced abdominal appendage imprints in *T. robledoensis*) may be influenced by undertrace fallout. The abdominal appendage imprints are variably expressed in *T. ottawensis*, and may be absent in poorly preserved forms (e.g., Mángano et al., 1995, Fig. 5B).

The differences between types 1 and 2 are considered insufficient for discrete ichnospecific status and are interpreted as representing minor behavioral variations (see below); in type 2 the abdomen was more inclined posteriorly or more force was applied to the substrate during the jump, possibly as an escape reaction (hence the anterior medial imprint is lacking and the middle medial imprint is deeper).

The trace maker.—The trace was clearly produced by an arthropod, as evidenced by the pattern of tagmosis (i.e., into head/thorax, abdomen and tail spine imprints). The oblique lineations in the middle medial imprint (in type 2) suggest abdominal appendages. Further, the three pairs of lateral (appendage) imprints suggest an insect producer (the additional frontal imprints in type 2 are attributed to the palps). Only three major groups amongst extinct (fossil) and extant insects, the Monura, Archaeognatha and Thysanura, possess three pairs of thoracic legs, an elongate abdomen bearing delicate appendages, and thin caudal filaments (Shear and Kukalová-Peck, 1990). The Archaeognatha (bristle-tails) and Thysanura (silverfish) possess a short tail filament with relatively long, lateral cerci, and long appendages which extend laterally from the underside of the abdomen, structures that are not represented in the trace. The Monura, an extinct group of wingless insects known from the Upper Carboniferous to Upper Permian, possessed a single long tail filament. They are favored

as producers as their size and ventral morphology are consistent with this trace. Mángano et al. (1997) suggested that a monuran was the likely producer of their ichnospecies of *Tonganoxichnus*: *T. buildexensis* was interpreted as a typical resting trace, most likely related to "water skimming" behavior. *T. ottawensis* was interpreted as a more complex jumping/feeding structure, the anterior scratches recording the scraping of algae from the substrate. An entomofauna from the Lower Permian Carrizo Arroya assemblage, north of the Robledo Mountains, includes Monura indet. (see Rowland, 1997, for review). Thus, the probable producers of this trace are known from contemporaneous deposits just to the north of this locality.

In order to interpret the origin of individual structures in this trace, we can compare them with various features of monuran morphology (e.g., *Dasyleptus*: see Kukalová-Peck, 1987; Mángano et al., 1997, fig. 6). The middle medial imprint represents an impression of the abdomen. The posterior converging ridges (CR) may represent paired slits (?tracheal openings) towards the posterior of the abdomen (although such structures are unknown from the body fossils), and the posterior projection (MLI) may represent the external ovipositor. The oblique lineations (in type 2) may represent an impression of the body segments, although their orientations suggest that they represent imprints of abdominal appendages. The long thin terminal imprint represents the terminal filament. The lateral imprints were produced by the thoracic appendages. The frontal imprints (in type 2) and the accessory anterior narrow imprint (in type 1; AANI) were probably produced by the maxillary or labial palps scraping the substrate (although they may be expected to be situated more laterally), or a ventral projection from the head (e.g., mandible).

Production of the trace.—The regular repetition, spacing, and consistent morphology of the traces in a straight line (in type 1) implies that they were produced by the same individual jumping forward. The position of the substrate mounds associated with the anterior medial and lateral (appendage) imprints (in type 1) confirms that the insect was jumping forwards. Jumping in monurans is thought to have resembled that in modern archaeognaths (Kukalová-Peck, 1987; Shear and Kukalová-Peck, 1990), which employ an essentially random jump in escape reactions, most of the thrust derived from the abdomen (Evans, 1975). The palps and legs are essentially passive and do not contribute towards locomotion (a "legless jump"). The repeated nature of the type 1 trace indicates that short repeated jumps were part of this insects' primary locomotory mechanism (i.e., repichnia). In type 2 the imprints are isolated (i.e., do not occur in a line), and the deeper abdominal imprint suggest that more thrust was provided by the abdomen, possibly as an escape reaction.

Ichnogenus HEDRIUMICHNUS new ichnogenus

Type ichnospecies.—*Hedriumichnus apacheensis* new ichnospecies.

Diagnosis.—Isolated, bilaterally symmetrical, epichnial trace fossil consisting of a small anterior oval imprint, and a short, broad, tapering segmented posterior imprint composed of several oblique lobes. Three pairs of long, broad, "articulated" imprints occur laterally.

Etymology.—From Latin, *hedrium*, little seat, and *ichnus*, trace.

HEDRIUMICHNUS APACHEENSIS new ichnospecies

Figures 3, 4

Larval dragonfly resting trace, MACDONALD, 1992, p. 36.

Resting traces A and D, BRADY, 1998, p. 96.

Tonganoxichnus isp. nov., BRADY, 1999, p. 6, fig. 1a.

Diagnosis.—As for the ichnogenus.

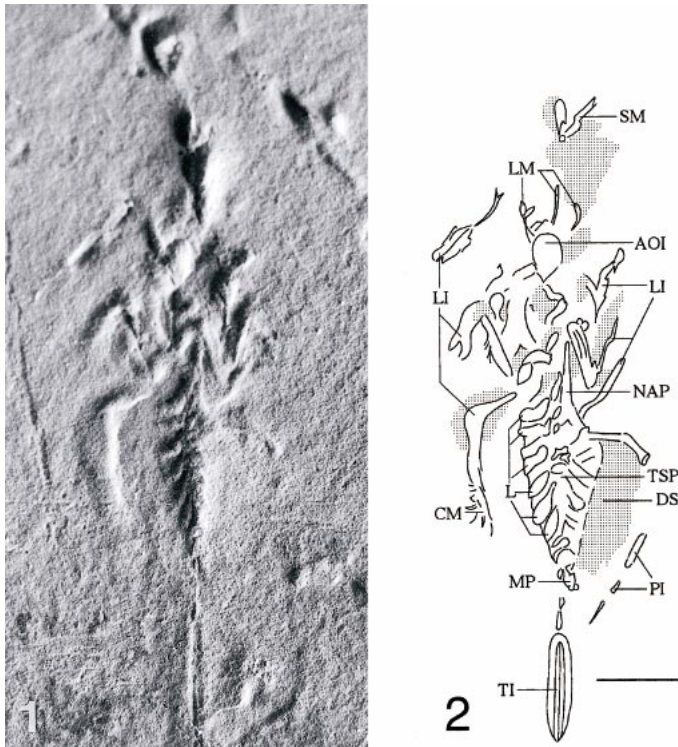


FIGURE 3—*Hedriumichnus apacheensis* n. igen. and isp. in negative epirelief. 1, Holotype (type 1), NMMNH&S P3902b, $\times 2.12$; 2, Interpretative drawing, NMMNH&S P3902b. Abbreviations: AOI, anterior oval imprint; CM, “claw” marks; DS, disturbed sediment; L, lobes; LI, lateral imprints; LM, short linear marks; MP, medial projection; NAP, narrow anterior portion of posterior imprint; PI, podomere imprints; SM, anterior small mark; TI, terminal imprint; TSP, tapering “segmented” portion of posterior imprint.

Description.—Preserved in negative epirelief. Two (preservational) forms are recognized. Type 1 is an isolated, bilaterally symmetrical, horizontal trace of remarkable detail (P3902b; Fig. 3). Length 31 mm, from front of anterior oval imprint to back of terminal imprint. Medial imprints divided into three sections: 1) a small anterior oval imprint (AOI), with three short linear marks in front (LM); 2) a large “segmented” posterior imprint, comprised of a narrow anterior portion (NAP), and a large tapering “segmented” portion (TSP), incorporating a series of several lobes (L), and; 3) a short terminal imprint (TI). The lobes of the posterior imprint are well preserved on the left side where they vary from oval-shaped, transverse lobes anteriorly to larger, pear-shaped, oblique lobes posteriorly. The final three lobes are shorter and more angular. Posterior to the lobes is a short medial projection (MP), ending in paired circular structures. The sediment to the right of the posterior medial imprint is disturbed (DS). Laterally there occur three pairs of long angular imprints (LI), most clearly preserved on the left side. The posterior lateral imprint flanks the posterior medial imprint; on the left side this terminates in a few short “claw” marks (CM), and on the right side the distal section apparently shows imprints of individual leg podomeres (PI). In front of the anterior medial imprint is a small mark (SM), with an area of disturbed sediment behind it, which may represent an accessory imprint produced by the animal repositioning its anterior right leg. An additional accessory imprint of the proximal part of the posterior right leg occurs in front of the posterior right lateral imprint (posteriormost of imprints labelled LI), also representing repositioning of this leg.

Type 2 consists of an isolated trace (P24351; Fig. 4), 46 mm long, comprising a poorly preserved anterior medial imprint (AMI), the left half of the posterior medial imprint (PMI), a faint trace of the terminal medial imprint, twisted slightly to the left (TI), and only the proximal portions of the lateral imprints (LI). The axis of the trace is curved slightly to the left. The posterior tapering imprint is only preserved on the left side, where around twelve narrow oblique lobes are apparent, giving a segmented appearance to this structure. Only the proximal portions of the lateral imprints are preserved, apart from the posterior left lateral imprint, which apparently consists of imprints of several podomeres (PI).

Etymology.—Named after the Apache Canyon in the Robledo Mountains, where the holotype was collected.

Types.—Holotype, NMMNH&S P3902b (Fig. 3.1, 3.2), paratype, P24351 (preservational variant), on a separate slab (Fig. 4.1, 4.2).

Occurrence.—Localities L3902 and L2817 (see Lucas et al., 1995; NMMNH&S 3902b and P24351, respectively) from the Lower Permian (Late Wolfcampian) Robledo Mountains Member of the Hueco Formation of the Robledo Mountains, New Mexico.

Discussion.—*Hedriumichnus apacheensis* is similar to *Tonganoxichnus buildexensis* Mángano, Buatois, Maples, and Lanier, 1997, but differs in the more detailed anterior medial imprint, the broader and shorter posterior (abdominal) medial imprint, the shorter terminal imprint and (most importantly) the longer, more complex lateral (appendage) imprints. The similarity to *Tonganoxichnus* initially suggested assignment to that ichnogenus (Braddy, 1999, fig. 3a), but these differences reveal a different morphological plan, and are here considered sufficient to warrant a new ichnogenus. The shorter length of the terminal imprint is not a reliable character to define this new ichnotaxon, as this material is not abundant enough to get a clear picture of this feature; it is poorly defined in the type 2 trace and may be susceptible to preservational or minor ethological variation. The differences between types 1 and 2 are considered insufficient for discrete ichnospecific status and are interpreted as representing preservational variations; in type 2 the trace was partially eroded (e.g., partial obliteration by wind in a dryer substrate).

The trace maker.—The producer of *Hedriumichnus*, while clearly an arthropod, is more uncertain than that of *Tonganoxichnus*. The distribution and morphology of medial imprints, reflecting the tagmosis of the producer, and the three pairs of lateral (appendage) imprints favor an insect. The paratype (NMMNH&S P24351; Fig. 4) was attributed to a larval dragonfly by MacDonal (1992). The lateral imprints of the thoracic legs appear too long to have been made by an apterygote, particularly a monuran (cf. Kukulová-Peck, 1987; Mángano et al., 1997, fig. 6) in contrast to *Tonganoxichnus* (see above; Mángano et al., 1997).

From the Lower Permian Carrizo Arroyo entomofauna of central New Mexico (Rowland, 1997), contemporaneous with the Robledo Mountains ichnofauna, the orthopteroids (Orthoptera or Protorthoptera) often have well-developed spines on their legs, which would correlate with the “claw marks,” and are the only known group that exhibit a prominent external ovipositor able to produce the terminal imprint (which would imply a female orthopteroid). However, orthopteroids can be discounted as they lack abdominal appendages, which would have produced the lobes of the posterior medial imprint. *Hedriumichnus* may therefore have been produced by a nymph of a primitive Ephemeroptera (Mayflies; the lobes representing abdominal leglets), or Plecoptera (Stoneflies; the lobes representing globular gills). The families Prottereismatidae (Ephemeroptera), and Phenopteridae, Liomopteridae, and Idelliidae (Plecoptera) are known from the nearby Carrizo Arroyo entomofauna (Rowland, 1997).

The remarkable detail (in type 1) allows various parts of this

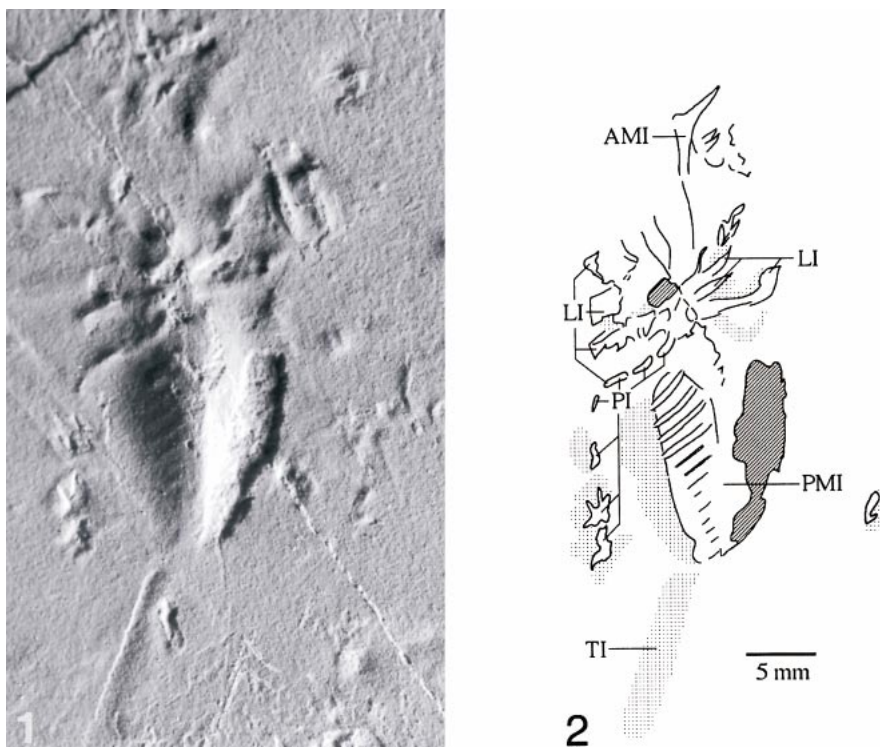


FIGURE 4—*Hedriumichnus apacheensis* n. igen. and isp. in negative epirelief. 1, Paratype (type 2), NMMNH&S P24351, $\times 2$; 2, Interpretative drawing, NMMNH&S P24351. Diagonal shading denotes broken surface. Abbreviations: AMI, anterior medial imprint; LI, lateral imprints; PI, podomere imprints; PMI, posterior medial imprint; TI, terminal imprint.

trace to be attributed to aspects of the producer's morphology. The anterior oval imprint was produced by the head, the three short linear marks situated in front of it, probably produced by the mouthparts. The posterior medial imprint represents an impression of the abdomen, the lobes imprints of abdominal appendages (the orientation and shape of these lobes is unlike abdominal segmentation). An ovipositor may have produced the short posterior medial projection (MP), or terminal imprint (TI) if it were long, but given that an orthopteroid producer is unlikely, the terminal imprint was probably produced by a tail spine. Given the limited material and poor preservation of the terminal imprint in the type 2 trace, this feature may not be completely preserved in the type 1 trace, so it is unclear whether the producer possessed a short or long tail spine. The lateral imprints represent the thoracic appendages; toward the posterior of the trace, imprints of individual podomeres and terminal claws are apparent. The additional lateral imprints on the right side reflect repositioning of the legs.

Production of the trace.—The level of detail in this trace may be explained by the preservational circumstances and the producer's behavior. It is likely that the animal actively nestled down into a moist substrate, perhaps for concealment or to avoid being blown away by the wind. The area of disturbed substrate to the right of the type 1 trace may be explained by sideways movement of the abdomen as the animal nestled down into the substrate. This would correlate with the repositioning of the legs.

Ichnogenus ROTTERODICHNIUM Walter, 1983

Type ichnospecies.—*Rotterodichnium longinum* Walter, 1983.

Emended diagnosis.—Isolated bilaterally symmetrical epichnial trace. On each side of the mid-line are three to four singular imprints, showing a tendency to increase in length posteriorly.

Anterior imprints inclined outwards. Elongate posterior medial imprint may be present.

Discussion.—This ichnogenus was named after the Rotterode locality, an outcrop of the Rotliegendes Supergroup at the north-east base of the Hefteberges Mountain, in the Thüringer Forest of south-east Germany, from where the type specimen, *R. longinum* was collected (Walter, 1983). Additional specimens from the same locality can only questionably be referred to *Rotterodichnium*.

Rotterodichnium longinum, 46 mm long, consists of small proximal anterior imprints, that lie (if present) almost medially, followed by imprints that are inclined slightly outwards. These are followed by a second pair of angular imprints lying perpendicular to the mid-line and the last pair of imprints which are very long and curved, and almost parallel to mid-line.

Walter (1983) distinguished *R. longinum* from *Avolatichnium dipedum* Walter, 1983, on the basis of the presence of imprint pairs that can be referred to particular legs; their angular development and lack of backpush mounds, in contrast to *A. dipedum*, represents only the morphology of the legs, not the behavior of the producer launching itself into the air. The pair of occasional anterior short median imprints may have been produced by the mouthparts. *Orbiculichnus vulgaris* Holub and Kozur, 1981 was regarded by Walter (1983) as a similar volichnia (landing trace) to *Rotterodichnium* with higher variability. The new material described herein, from the Robledo Mountains ichnofauna, is referred to *Rotterodichnium* with some expansion of Walter's (1983) original diagnosis.

ROTTERODICHNIUM MAJOR new ichnospecies

Figure 5

Resting trace E, BRADY, 1998, p. 96.

Rotterodichnium isp. nov., BRADY, 1999, p. 6, fig. 1d.

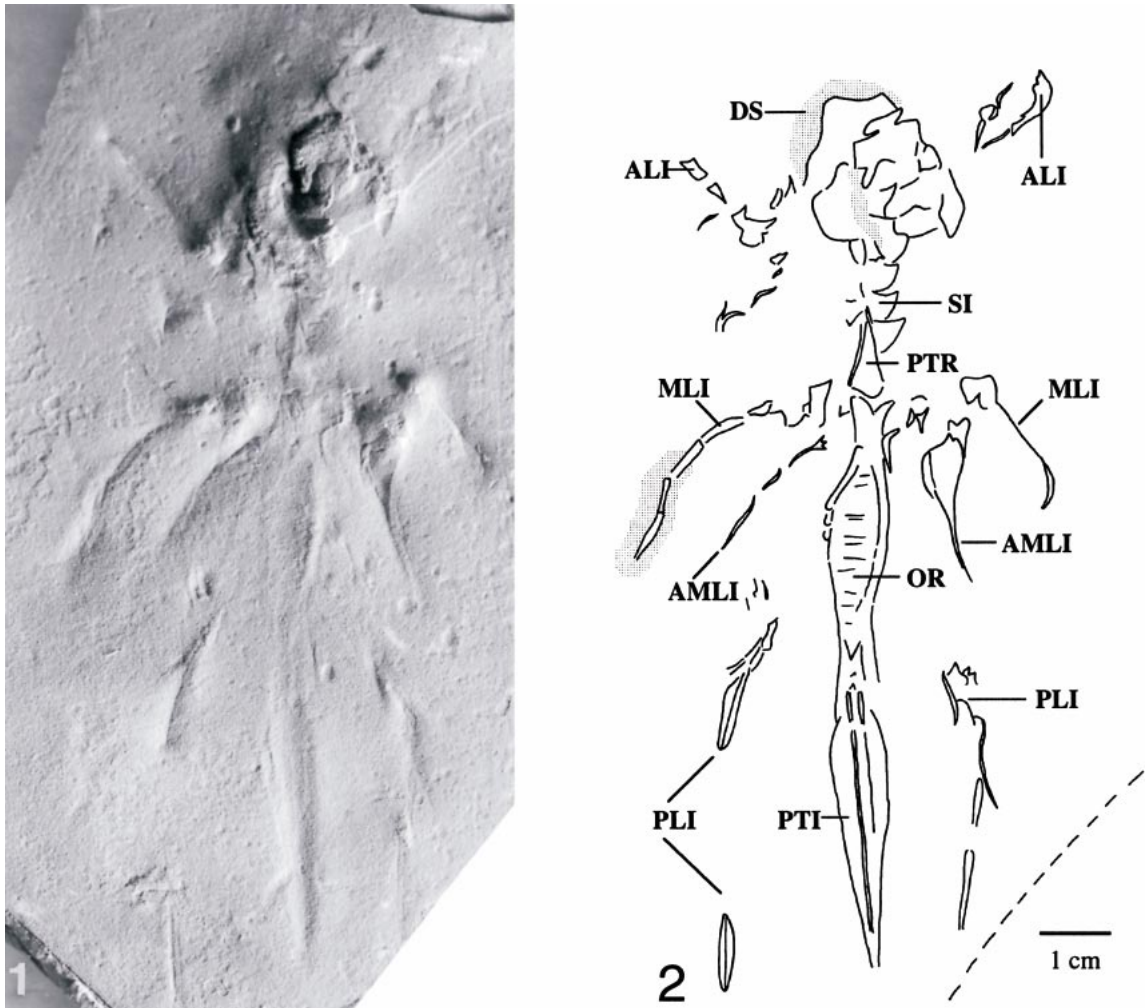


FIGURE 5—*Rotterodichnium major* n. isp. in negative epirelief. 1, Holotype, NMMNH&S P3903. $\times 1.1$; 2, Interpretative drawing, NMMNH&S P3903. Abbreviations: ALI, anterior lateral imprint; AMLI, accessory middle lateral imprints; DS, disturbed sediment; MLI, middle lateral imprints; OR, oval anterior region of posterior imprint; PLI, posterior lateral imprints; PTI, posterior tapering imprint; PTR, posteriorly expanding triangular region; SI, "segmented" medial imprint.

Diagnosis.—A large *Rotterodichnium* with two medial imprints, an irregular anterior region and a long thin posterior imprint. Three pairs of lateral imprints; small anterior imprints, inclined slightly outwards, middle pair of curved imprints and a posterior pair of long imprints, situated parallel to the mid-line.

Description.—Preserved in negative epirelief. This trace consists of an isolated, bilaterally symmetrical, epifaunal trace (NMMNH&S P3903; Fig. 5), total length 124 mm. Medial imprints divided into two sections: 1) an anterior irregular imprint, bordered anteriorly by a region of disturbed sediment (DS); the posterior portion displays three or four imprints preserved on the right side apparently corresponding to segments (SI), the posterior margin composed of a posteriorly expanding triangular region (PTR); and 2) a long, thin posterior imprint, divided into two sections; an elongate oval anterior region with several transverse lineations (OR), and a posterior tapering imprint (PTI), with a pair of medial longitudinal linear structures. The medial imprints are flanked by three pairs of lateral imprints. The short anterior imprints (ALI) are inclined outwards; on the left side they are linear and on the right side they are slightly curved. The middle pair of lateral imprints (MLI) are curved; on the left side around four podomere imprints are apparent and on the right side this

imprint is much fainter. Faint accessory middle lateral imprints are preserved slightly proximally (AMLI). The posterior lateral imprints (PLI) flank the rear of the posterior tapering imprint, aligned almost parallel to the trace axis; on the left side this imprint is composed of two short marks, and on the right side it is more continuous.

Etymology.—Named after the large size of the trace, which is over three times larger than *R. longinum*.

Types.—Holotype, NMMNH&S P3903 (Fig. 5), one slab with one specimen.

Occurrence.—Locality L3902 (Lucas et al., 1995) from the Lower Permian (Late Wolfcampian) Robledo Mountains Member of the Hueco Formation of the Robledo Mountains, New Mexico.

Discussion.—This trace can be assigned to *Rotterodichnium* Walter, 1983, but it differs from *R. longinum* in its much larger size, and the presence of medial imprints.

The trace maker.—The producer of this trace is interpreted as a large insect. Some of the primitive Carboniferous Pterygota were very large; the wingspan of Palaeodictyopteroidea was up to 40 cm and that of Ephemeroptera and Protodonata up to 70 cm. The large size, and length of the posterior medial imprint, suggests a dragonfly-like producer (e.g., Protodonata or Odonata).

The diversity of the Protodonata in the Lower Permian remained around the same as in the Upper Carboniferous (Labandeira and Sepkoski, 1993). The Odonata (dragonflies) appeared for the first time in the Permian. Rowland (1997) noted large dragonfly-like forms (i.e., Megasecoptera) from the early Permian Carrizo Arroya entomofauna of central New Mexico, indicating that such forms are present in the region at this time.

The anterior medial imprint was produced by the head, the "segmented" posterior portion by the thorax. The posterior medial imprint was produced by the abdomen; the transverse lineations attributed to abdominal segments. The paired medial linear structure in the posterior tapering medial imprints infer the ventral abdominal morphology (?ovipositor) of the producer. The lateral imprints are attributed to the legs, the faint accessory pair of middle imprints representing repositioning of the middle pair of legs.

Production of the trace.—This trace is attributed to a large dragonfly-like insect resting on the substrate. The medial imprints indicate that the abdomen was actively placed down; the producer rested more heavily on the substrate than in *R. longinum*, where only the legs imprinted upon the substrate. The disturbed area of substrate in front of the trace indicates that the head also made contact with the substrate, perhaps indicating that the producer was searching for prey.

Ichnogenus QUADRISPINICHNA new ichnogenus

Type ichnospecies.—*Quadrspinichna parvia* new ichnospecies.

Diagnosis.—Small, isolated, bilaterally symmetrical trace composed of four parallel or slightly diverging linear or slightly curved imprints. Inner imprints parallel or diverging slightly, close-set at anterior. Outer imprints situated anteriorly, diverging at greater angle than inner imprints. Outer and inner imprints may be joined. A faint triangular, medially divided mark or a pair of pear-shaped marks occasionally occur at anterior.

Etymology.—From Latin, *quattuor*, four and *spina*, thorn.

Discussion.—*Quadrspinichna parvia* was named by Anderson (1974) in her doctoral thesis, but has remained unpublished. To avoid potential confusion, we have retained her name herein, although the diagnosis is modified to accommodate the Robledo material. Anderson (1974) compared *Quadrspinichna* with *Incisifex*, *Ichnispica*, and *Stelloglyphus*, all known from South Africa. However, *Quadrspinichna* is most unlike these ichnotaxa; the first two are arthropod trackways, and the last is a star-like trace composed of around 25 radial lines.

QUADRISPINICHNA PARVIA new ichnospecies

Figures 6–8

- undesigned tetrapod tracks, HAUGHTON, 1919, p. 11.
- undesigned tetrapod tracks, HAUGHTON, 1925, p. 28.
- undesigned tetrapod tracks, ABEL, 1935, figure 85.
- undesigned tetrapod tracks, THERON, 1967, figure 12.
- Quadrspinichna parvia*, ANDERSON, 1974, p. 80, pl. 61, figure 5; pl. 73, figure 5, 6.
- impressions, loosely termed tetrapod tracks, ANDERSON, 1981, p. 92.
- invertebrate resting traces, BRADY, 1998, p. 96.

Diagnosis.—As for the ichnogenus.

Description.—Preserved as epi- or hyporeliefs. Two (preservational) forms are recognized; type 1 (South African material), are preserved in finer grained rocks than type 2 (Robledo material), which have broader imprints, and faint accessory features (see below). The similar size and morphology of these traces, however, are considered sufficient to identify them as the same ichnotaxon.

Quadrspinichna parvia (type 1) may be isolated but tends to occur in sub-parallel groups (Fig. 6). One entire individual trace is typically 15 mm long, and composed of four diverging imprints

(Fig. 8). Inner imprints (II) slightly curvilinear, convex sides opposing, diverging posteriorly (15–18 degrees to mid-line), close-set at anterior, although occasionally in contact (e.g., S.A.M. 11604; Fig. 6.5). Outer imprints (OI), situated slightly anteriorly, generally straighter, diverging at a greater angle (c. 36–46 degrees to mid-line) than the inner imprints, typically perpendicular to each other. Proximal ends of outer imprints may be joined (e.g., Anderson, 1974, pl. 61, fig. 5; Fig. 8.1). Four imprints usually discrete, but the distal end of outer imprints may connect to proximal end of inner imprints (e.g., Anderson, 1974, pl. 73, fig. 6; Fig. 8.2).

Type 2 (Robledo material) slightly larger. The best-preserved example (i.e., bottom of Figs. 7, 8.3), total length 22 mm (including faint triangular anterior region), has close-set linear inner imprints (II), parallel to mid-line. Outer imprints (OI), situated anteriorly, also linear, diverge at a slight angle (c. 5–14 degrees to mid-line). Anterior of outer and inner imprints joined by faint curved mark. Faint triangular, medially divided, imprint occurs at anterior (MI). Another trace of this type (i.e., Figs. 7 (top two traces), 8.4), total length 18 mm, has no anterior triangular imprint, but has instead a pair of faint pear-shaped imprints (PI) situated between the inner and outer imprints. The anterior edge of the outer imprints are joined by a faint curved imprint, surrounding these pear-shaped imprints. The Robledo material includes a range of morphologies and sizes (e.g., NMMNH&S P23465 shows smaller traces, less than 10 mm long, with more pronounced curved marks joining the inner and outer imprints, resembling *Rusophycus*-like bilobed resting traces. Larger examples on the same slab, greater than 10 mm long, have the more typical *Quadrspinichna* morphology, composed of four imprints).

Etymology.—From Latin, *par*, alike and *via*, way or direction, to denote the similar orientation of grouped traces.

Types.—Holotype, SAM 3547 (Fig. 6.1), paratypes, SAM 3546, 11604 (Fig. 6.5), 11605 (Fig. 6.3), 11606, 11607 (Fig. 6.4), 11608 (Fig. 6.6), 11684 and 11688 (Fig. 6.7).

Other material examined.—SAM 3535–3545, 3548–3551, 3584–3591, 11598–11603, 11609 (Fig. 6.8), 11610–11617, 11680–11683, and 11685–11687. BPIPR Lb. K. E. 1–45, BPIPR Z. R. K. E. 1–29, GSP I 1–64, NMMNH&S P24212, 23165, 23295–6, 23465, and 23875.

Occurrence.—Only six specimens known from the Robledo Mountains: NMMNH&S P24212 (locality 2819), 23165 (locality 2851), 23295–6 (locality 2841), 23465 (locality 2821), and 23875 (locality 2851), but it is much more common in South Africa, where it is known from three localities (see above): SAM 3535–3551, 3584–3591, 11598–11617, 11680–1168 and BPIPR Z. R. K. E. 1–29 are from Zak River. BPIPR Lb. K. E. 1–45 are from Laingsburg. GSP I 1–64 are from Askop.

Discussion.—*Quadrspinichna parvia* is similar to *Isopodichnus furcosus* Gand, 1994, from the Permian of central France, but differs in the absence of the pronounced anterior paired oval imprints (i.e., *Isopodichnus*-like region), and different orientation of the linear imprints (i.e., in *I. furcosus* the imprints converge posteriorly, whereas in *Q. parvia* they diverge posteriorly). *Q. parvia* is also similar to the "anterior" region of *Gluckstadella cooperi* (Savage, 1971, fig. 15a).

The trace maker.—*Quadrspinichna parvia* was formerly interpreted as a tetrapod track (e.g., Haughton, 1925; Abel, 1935, fig. 85); the four sub-parallel linear marks, arranged in groups, are reminiscent of tetrapod tracks. However, *Quadrspinichna* is unlike tetrapod tracks as the four imprints that compose the trace are too close to each other, or are occasionally joined. Tetrapod tracks are usually composed of toe imprints of different lengths, unlike *Quadrspinichna*, in which the inner and outer imprints are the same length. This trace is therefore too bilaterally symmetrical, with no distinction between medial and lateral toes, to

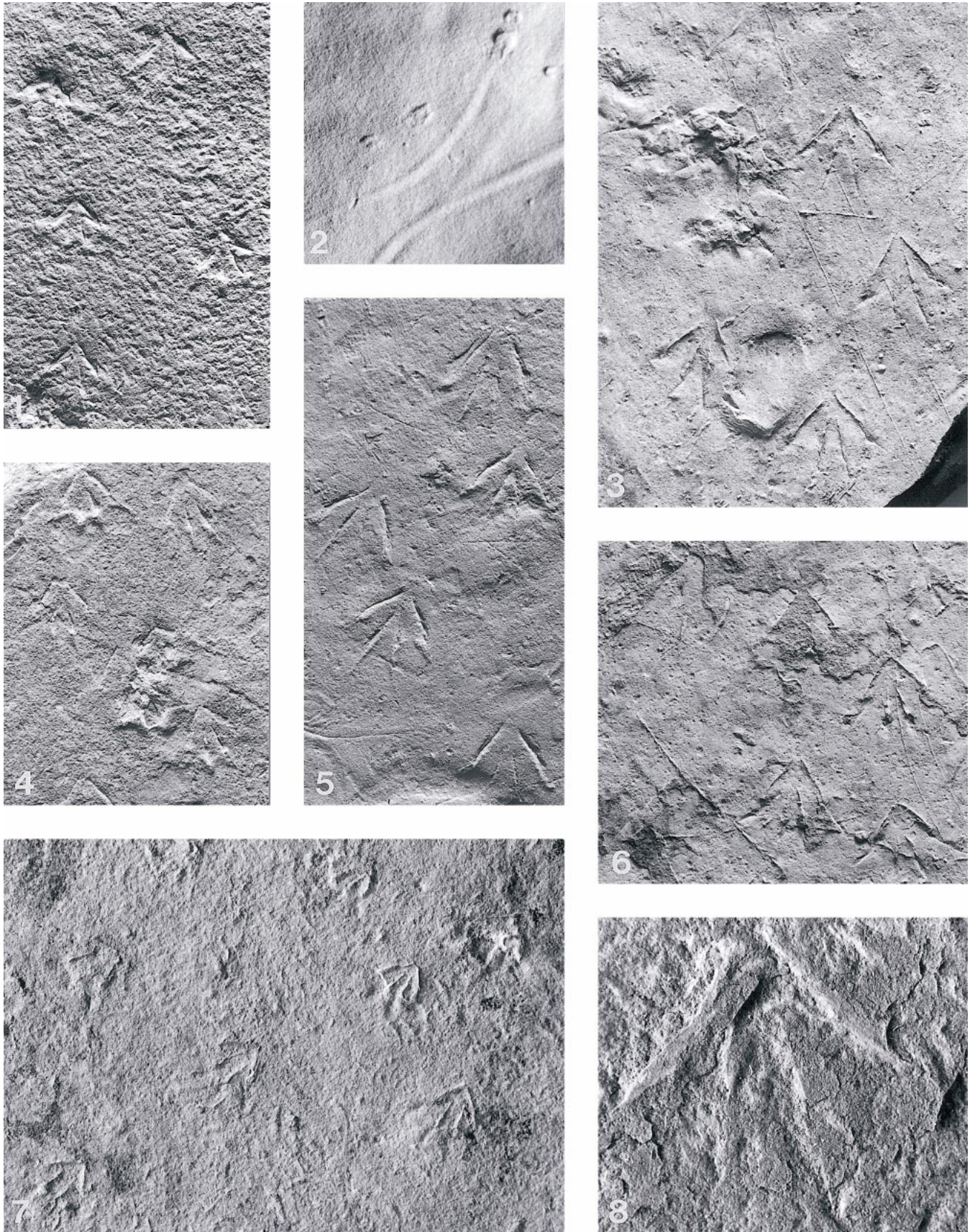


FIGURE 6—*Quadrispinichna parvia* n. igen. and isp., (type 1). 1, Holotype, SAM 3547, $\times 0.70$; 2, SAM 6494, poorly preserved *Q. parvia* associated with trail and isolated *Isopodichnus* isp., $\times 0.60$; 3, paratype, SAM 11605, $\times 0.65$; 4, paratype, SAM 11607, $\times 0.65$; 5, paratype, SAM 11604, $\times 0.43$; 6, SAM 11608a, $\times 0.67$; 7, paratype 11688, $\times 0.90$; 8, SAM 11609, magnification of one trace, $\times 3.8$.



FIGURE 7—*Quadrispinichna parvia* n. igen. and isp., (type 2), NMMNH&S P24212, three traces, $\times 1.38$.

support a tetrapod producer. More importantly, the traces do not form an organized trackway and the traces are all alike with no distinction between fore and hind feet. Thus, the belief that *Mesosaurus* was responsible for this trace is unsupported; the feet of *Mesosaurus* had toes of differing lengths and the fore feet had five toes, so would not have produced the four marks characteristic of this trace (Anderson, 1974).

A tetrapod producer was not supported by Anderson (1974), who argued that the sporadic distribution of these traces was evidence that they were produced by a school of swimming animals making contact with the substrate. She suggested that this trace might have been produced by a small fish: the outer imprints produced by the pectoral fins and the inner imprints by the pelvic fins. Anderson (1974) also discussed the possibility that the swimming animals were invertebrates, possibly larvae of some sort, although noting that this trace was quite unlike other invertebrate resting traces, she concluded that the producer remained enigmatic.

The Robledo material (type 2) provides additional evidence for an invertebrate interpretation. The triangular anterior mark in P24212 suggests the imprint of an arthropod carapace. Small examples preserved alongside larger, more typical traces (e.g., NMMNH&S P23465) have a bilobed, *Isopodichnus*-like morphology (see above). Indeed, *Quadrispinichna* is somewhat similar to the posterior portion of *Isopodichnus furcosus* Gand, 1994, from the Permian of central France, although the orientation of the imprints differs (see above). *Isopodichnus furcosus* was attributed to a crustacean, probably a notostracan, by Gand (1994). Thus, the presence of an arthropod carapace imprint, the *Isopodichnus*-like morphology of small examples, and the similarity to *I. furcosus*, supports a crustacean producer for *Quadrispinichna*. Additionally, where *Quadrispinichna* occurs, it is always associated with other crustacean-produced ichnotaxa (Anderson, 1974,

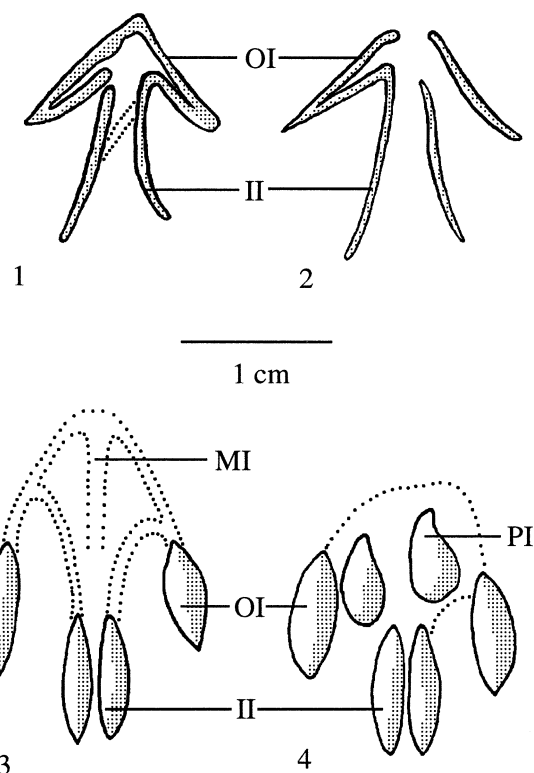


FIGURE 8—Interpretative drawing of *Quadrispinichna parvia* n. igen. and isp. 1, South African material (type 1), SAM 11604 (paratype), showing joined outer and inner imprints; 2, type 1, SAM 11604 (paratype), showing isolated outer and inner imprints; 3, Robledo Mountains material (type 2), NMMNH&S P24212, showing anterior triangular medial imprint; 4, type 2, NMMNH&S P24212, showing pear-shaped imprints. Abbreviations: II, inner imprint; MI, medial imprint; OI, outer imprint; PI, pear-shaped imprint.

1981). The crustacean trackway *Umfolozia longula* always occurs at the same South African localities as *Quadrispinichna*. *Quadrispinichna* is somewhat similar to the “anterior” imprints of *Gluckstadella cooperi* (Savage, 1971, fig. 15a), which was interpreted as a syncarid or peracarid crustacean resting trace. The four diverging imprints in *Quadrispinichna* are attributed to the thoracic appendages.

The following Robledo material, catalogued as “insect hopping traces” in the NMMNH&S collection, is regarded as vertebrate undertracks, probably of *Gilmoreichnus* (Braddy, 1998). Most (e.g., NMMNH&S P23185, 23206–7, 23415, 23418, 23422, 23597–8, P23638, 23640, 23692, 23701, 23880–1, 23901, and 24038) consist of short (c. 6 mm long) paired, slightly diverging, linear marks, some with a third (e.g., P23224) or additional pair of marks (e.g., P24485; Braddy, 1995, fig. 1C), outside and slightly behind the inner two. Many specimens (e.g., P23165–6, 23268, 23472, 23493, 23558, 23626, 23628, 23635, 23698, 23906, 23972, 24238, 24242, 24279, 24349–50, 24523, 24538, and 24539) evidence their vertebrate affinities more clearly; some display heel marks (e.g., P23187), toe marks (e.g., P23469, 23581, and 23699) or claw scratch marks (e.g., P23416, 24061, 24062, and 24174). Others (e.g., P23036, 23467, 23589, 23866, and 24331–7) are more complete, although poorly preserved, small vertebrate trackways.

Production of the trace.—This trace is interpreted as produced by a swimming crustacean lightly resting on the substrate (i.e.,

cubichnia). While the tracemakers were able to swim, they probably had a near-bottom existence, possibly as filter-feeding benthic epifauna. The animals occasionally nestled down deeper in the substrate, producing more *Isopodichnus*-like morphologies (Fig. 6.2). The grouping of traces may indicate a school of animals; their sub-parallel orientation possibly indicating alignment to the prevailing current direction, as in *Isopodichnus furcosus* (Gand, 1994), for hydrodynamic stability during resting periods, or to benefit their filter-feeding. Devera (1989) recorded over fifty examples of resting traces, composed of a broad head imprint followed by multiple, paired appendage imprints, and a bifurcated tail imprint, attributed to eumalacostracan crustaceans, that display a sub-parallel orientation (suggestive of quasi-social behavior), from the Early Pennsylvanian of Illinois.

CONCLUSION

Trace fossils provide important data on the paleoenvironmental distribution and behavior of extinct animals. Paleozoic nonmarine arthropod resting traces are rare, especially of insects, but reveal important morphological information on the diversity of ancient nonmarine arthropod communities, particularly where body fossils are lacking. The four new arthropod ichnotaxa described herein (including two new ichnogenera), from marginal marine facies (Robledo Mountains ichnofauna) of New Mexico, and shallow lacustrine facies (Ecca succession) of South Africa, are therefore significant as they increase our understanding of the distribution, diversity and behavior of Lower Permian nonmarine arthropod communities.

Tonganoxichnus robledoensis is interpreted as the locomotory trace (repichnia) of a jumping monuran (an extinct group of wingless insects). *Hedriumichnus apacheensis* is interpreted as the resting trace (cubichnia) of a nymph of a primitive Ephemeroptera or Plecoptera, actively nestling down in the substrate for protection or concealment. *Rotterodichnium major* is interpreted as the resting trace (cubichnia) of a large dragonfly-like form (Protodonata, Odonata, or Megasecoptera). *Quadrispinichna parvia*, from the Robledo Mountains ichnofauna (New Mexico) and Ecca succession of South Africa, is interpreted as a resting trace (cubichnia) of a swimming crustacean.

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