

The Insect Trace Fossil *Tonganoxichnus* from the Middle Pennsylvanian of Indiana: Paleobiologic and Paleoenvironmental Implications

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The ichnogenus *Tonganoxichnus*, produced by one or more monuran insect taxa, is now recorded from the Middle Pennsylvanian Mansfield Formation of Indiana. *Tonganoxichnus* is a resting trace that has three important implications. First, it represents a recurrent behavioral pattern in Upper Carboniferous to Lower Permian marginal marine environments of North America. Second, it provides finely resolved anatomical information for axial and appendicular body structures and behaviors that are difficult to determine from body-fossil material alone. Third, integrated sedimentologic and ichnologic observations indicate that the *Tonganoxichnus* assemblage, inclusive of other ichnotaxa, is common in tidal rhythmites that were developed under freshwater conditions, probably in the innermost part of estuarine systems, close to or at the fluvioestuarine transition.

Keywords Carboniferous, Ichnotaxa, Indiana, Insecta, Monura, Pennsylvanian, *Tonganoxichnus*

INTRODUCTION

The ichnogenus *Tonganoxichnus* was proposed by Mángano et al. (1997) to name superbly preserved insect sedimentary structures exhibiting unique anterior and posterior sets of mor-

phologic features, present in Upper Pennsylvanian (Virgilian) tidal rhythmites of Buildex Quarry in eastern Kansas. This trace fossil is one of the few from from the Late Carboniferous attributable to a specific insect clade, even though the ichnofossil record from the Paleozoic is exceedingly dominated by evidence of plant-arthropod associations (Labandeira, 1998a). Other Paleozoic insect traces are probably trackways (e.g., Holub and Kozur, 1981; Walker, 1985; Hunt et al., 1993). After the end-Permian mass extinction, much of the taxonomically distinctive Paleozoic Insect Fauna was succeeded by mostly the hemipteroid and holometabolous lineages of the early Mesozoic (Labandeira and Sepkoski, 1993; Jarzembowski and Ross, 1993). This diversification also is reflected by a significant increase in abundance and diversity of insect sedimentary structures. From the ichnofossil record, this rise is documented initially by soil-associated coleopteran nests and tracks of varied insects in eolian environments and culminated in the domiciles of social hymenopterans and isopterans in Cretaceous paleosols (calichnia *sensu* Genise and Bown, 1994; Ekdale and Picard, 1985; Buatois et al., 1998; Labandeira, 1998b). This increasingly better Mesozoic ichnologic record is attributable not only to the evolution of insect nesting behavior in sedimentary substrates, but also to an increased preservational potential from the constructional nature of the nesting structures that includes their intermixing with mucilaginous

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exudates, excrement, or ambient organic products (Genise and Bown, 1994).

Tonganoxichnus buildexensis, by contrast, is a rare Paleozoic sediment trace that combines significant anatomical information of the fabricator with a narrow circumscription of its habitat of occurrence. It is characterized by an anterior region with a frontal pair of right-and-left maxillary palp impressions, a median head impression, and three pairs of bilaterally positioned thoracic appendage impressions. The posterior abdominal region is commonly segmented and displays numerous delicate abdominal appendage impressions, including a typically separate, thin terminal extension. This ichnospecies, initially described from the Buildex Quarry in Kansas, was interpreted as the resting trace of a wingless insect, most likely a monuran (Mángano et al., 1997). A similar Early Permian (Wolfcampian) resting trace was illustrated by Hunt et al. (1993) from the Robledo Mountains of south-central New Mexico, who suggested that a member of the Insecta was the possible fabricator. This material was investigated by Braddy (1999) who assigned one of the forms to *Tonganoxichnus*, making the New Mexican material the second occurrence of this ichnogenus. More recently, specimens of the ichnospecies *T. buildexensis* have been found in the Middle Pennsylvanian Mansfield Formation of Indiana. As noted by Norman and Pickerill (1996), it is not uncommon that many ichnotaxa are only known from their type localities, and in those cases the recurrence of a behavioral pattern remains untested. Documentation of additional examples of *Tonganoxichnus*, therefore, is essential to provide evidence supporting the utility of this ichnotaxon. Specimens of *Tonganoxichnus buildexensis* from Indiana exhibit additional morphological features by comparison to their Kansas occurrences, thus allowing for further investigation of the paleobiology of the tracemaker and elucidation of the behavioral and environmental implications of this peculiar ichnotaxon. Given this context, the aim of this paper is (1) to document the second occurrence of *Tonganoxichnus buildexensis*, (2) to further explore the biology of the maker of *Tonganoxichnus* and to provide links with modern analogs, and (3) to compare specimens and associated facies and traces from Indiana with those of Kansas in order to reconstruct the particular environmental and taphonomic conditions that led to the preservation of these delicate biogenic structures.

GEOLOGIC AND DEPOSITIONAL SETTING

Tide-dominated, marginal marine systems were ubiquitous in the Midcontinental Illinois Basin during the Pennsylvanian. Tidally influenced environments commonly developed within inland estuarine paleovalleys as well as more coastal settings, such as the inner epicontinental shelf (Kvale and Barnhill, 1994; Kvale and Mastalerz, 1998). Recent geochemical studies have shown that at least some of these tidal deposits formed in brackish to freshwater settings (Mastalerz et al., 1997, 1999; Kvale and Mastalerz, 1998). The insect traces described herein

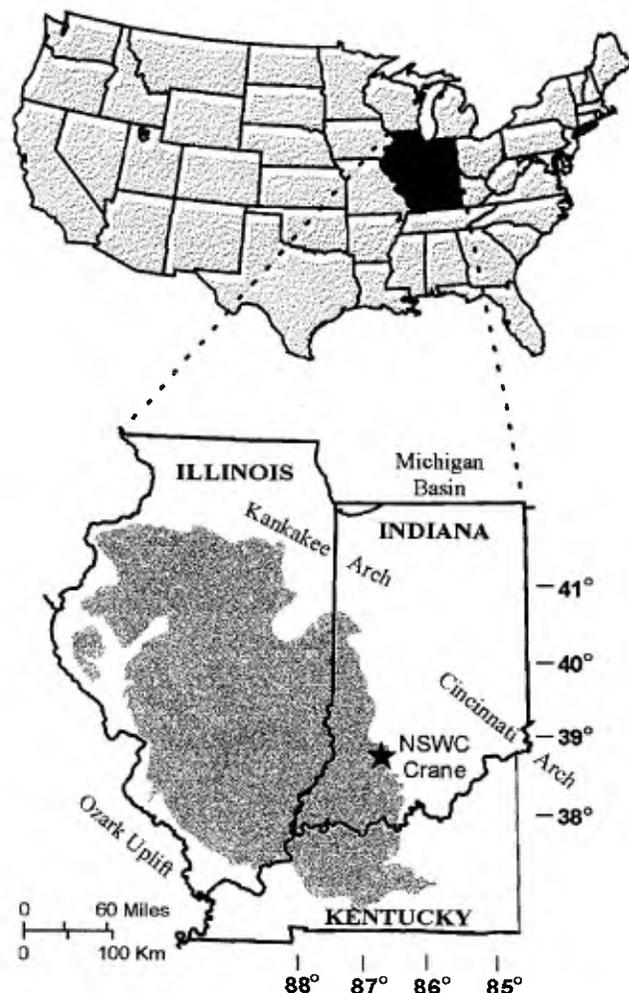


FIG. 1. Location map showing the Illinois Basin and the Crane trace-fossil locality.

were found within a tidal succession of the upper part of the Mansfield Formation, of Middle Pennsylvanian age (Morrowan to Atokan), at the Naval Surface Warfare Center (NSWC) near Crane, Martin County, Indiana (Figure 1). At this locality the Mansfield Formation, by correlation to palynologically dated outcrops to the south, is probably Atokan in age. It consists predominantly of sandstones, shales, interbedded sandstones and mudstones, thin coal beds, and well-developed paleosols that are informally subdivided into three successions: lower, middle, and upper (Figure 2).

The trace fossils occur toward the base of the outcrop in a well-sorted, laminated siltstone that coarsens upwards to very fine-grained sandstone with small cut-and-fill rill-like structures, forming the lower part of the Crane section. The siltstones are vertically stacked in layers, with each layer generally less than 1 cm thick. These layers are separated by very thin clay drapes, typically in the order of a fraction of a millimeter. The laminae appear to thicken and thin vertically just above the underlying coal, indicating a tidal influence similar to that de-

NE NW NW 20-5N-4W

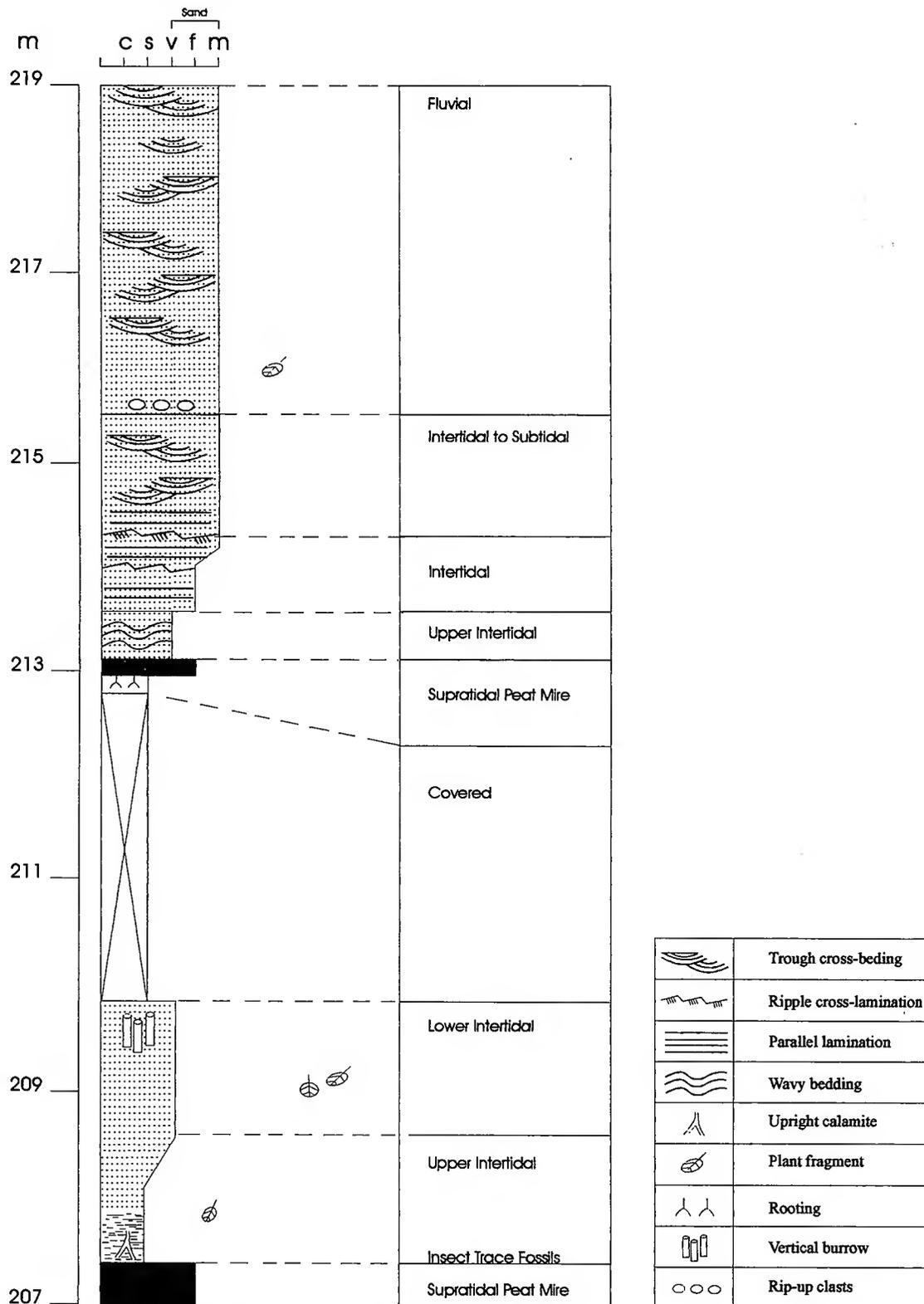


FIG. 2. Stratigraphic section at Crane. Insect trace fossils are present in the lower part of the section.

scribed for the slightly older Pennsylvanian Hindostan Whetstone beds (Morrowan), also of the Mansfield Formation (Kvale et al., 1989; Kvale and Archer, 1991). Well-preserved plant fragments are present in this unit; an example is an upright calamite trunk that is rooted in the upper part of the underlying coal. This calamite, basically vertical in orientation, extends approximately 40 cm into the overlying siltstone, at which point it becomes almost horizontal. Other plant fragments include articulated fern leaves and stems and *Lepidodendron* twigs and bark fragments.

Tonganoxichnus buildexensis at Crane is associated with other invertebrate traces, such as *Treptichnus bifurcus*, *Gordia indianaensis*, and amphibian trackways. Raindrop impressions also are present. Strata containing the multitude of amphibian trackways found in this part of the section are informally known as the "Crane Tetrapod Quarry." The top of the very fine-grained sandstone unit overlying the siltstone package is bioturbated, exhibiting small (1–2 mm diameter) vertical burrows with laminated infill. The succession from the top of the underlying coal to the top of the sandstone with vertical burrows is interpreted as a transgressive lithofacies succession similar to that recognized for the tidal flat deposits in the tide-dominated German Bight (Reineck, 1972; Davis and Clifton, 1987). In this model, an initial relative rise in the sea level causes drowning of the coal-forming mire and landward migration of the upper intertidal mudflat and lower intertidal sandflat. The presence of the rill-like structures, which are best explained as drainage features, and the trace fossil assemblage indicates that the lower part of the Crane succession remained within an intertidal environment. A three-meter-thick covered interval separates the lower and middle parts of the Crane section. Recurring thickness variations suggest deposition under tidal influence.

The base of the middle section is represented by a thin paleosol and a superposed thin coal bed, interpreted as a supratidal peat mire deposit. This coal is overlain by another coarsening upward succession. The base of this succession consists of a thin, wavy-bedded sandstone and shale interval that is erosively overlain by a fine-grained, flat-bedded, and flaggy sandstone with ripple- and parallel-laminated cosets having clay drapes. This fine-grained sandstone interval coarsens upward to a trough cross-stratified, medium-grained sandstone. Paleoflow within this unit is bipolar in this exposure, with clay layers several millimeters thick draping many of the bedforms. This part of the sequence is clearly transgressive and records deposition from upper intertidal to subtidal environments.

The tidally influenced sandstone of the middle part of the Crane section is overlain erosively by a large-scale, trough cross-stratified, fine- to medium-grained sandstone. Goethite-cemented rip-up clasts occur along the erosive scour at the base of the unit. Large, poorly preserved plant fragments are also found within this unit. Paleoflow is unidirectional and to the west. This upper part of the succession probably records deposition in fluvial channels.

SYSTEMATIC ICHNOLOGY

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

Tonganoxichnus buildexensis Mángano, Buatois, Maples and Lanier 1997

Figure 3A,B; Figure 4A–D; Figure 5

Emended diagnosis. *Tonganoxichnus* with anterior area characterized by the anterior-most pair of imprints oriented subparallel to the median axis, anteromedian impression and three pairs of conspicuous ellipsoidal imprints perpendicular or at a high angle to the median axis. A second set of circular to slightly elongate lateral distal imprints may be present. The posterior area is composed either of numerous, delicate, oblique appendage markings or a wedge-like inflated structure. Thin, straight terminal extension commonly present (modified after Mángano et al., 1997).

Material. Four slabs containing 19 specimens housed at the Department of Geological Sciences, Indiana University, Bloomington (IU 21246, IU 21247) and at the Indiana State Museum, Indianapolis (INS M71.3.136, INSM 71.3.137), Indiana, USA.

Description. Bilaterally symmetrical traces typically consisting of an anteromedian mark, three pairs of conspicuous anterior appendage impressions and numerous, delicate V-shaped markings or more commonly, a wedge-like inflated structure at the posterior part (Figures 3A,B; 4A–D). Some specimens display apparent transverse annulations at the posterior part of the trace (Figure 4B,D). In addition, two elongate frontal impressions parallel to subparallel to the median axis are present in most specimens (Figures 3A; 4A,B). The frontal anteromedian impression, crescentic or subtriangular in shape, is a prominent feature in some specimens (Figures 3A; 4A,B), but it may be poorly preserved or absent in others (Figure 4D). The three pairs of ellipsoidal lateral impressions are oriented perpendicular to oblique to the median axis (Figure 3A,B). In addition, a second set of circular or elongate lateral markings, more or less equidistant to the median axis, is present in several specimens (Figures 3A, 4B). The posterior part of the trace is quite variable in morphology. In the Mansfield material, wedge-like, high relief posterior elements represent the dominant morphology (Figures 3A, 4C). However, more shallow preservational variants composed of three to six nested V-shaped markings and/or transverse segment-like annulations also are present (Figures 3B; 4B,D). Upon close examination, each V-shaped mark can be seen to be composed of two discrete elongate impressions, obliquely inclined to the median axis. In well-preserved specimens, each segment-like impression is coupled with a pair of oblique impressions (Figure 4A,B). The angle subtended by each V-shaped mark typically decreases posteriorly and varies from 87° to 20°. Two distinctive "half body" preservational variants are present in the Mansfield material. In a few specimens, the anterior area of the trace is virtually absent, and the last pair of prominent anterior impressions is succeeded by the posterior part of the trace (Figure 4A, lower left).

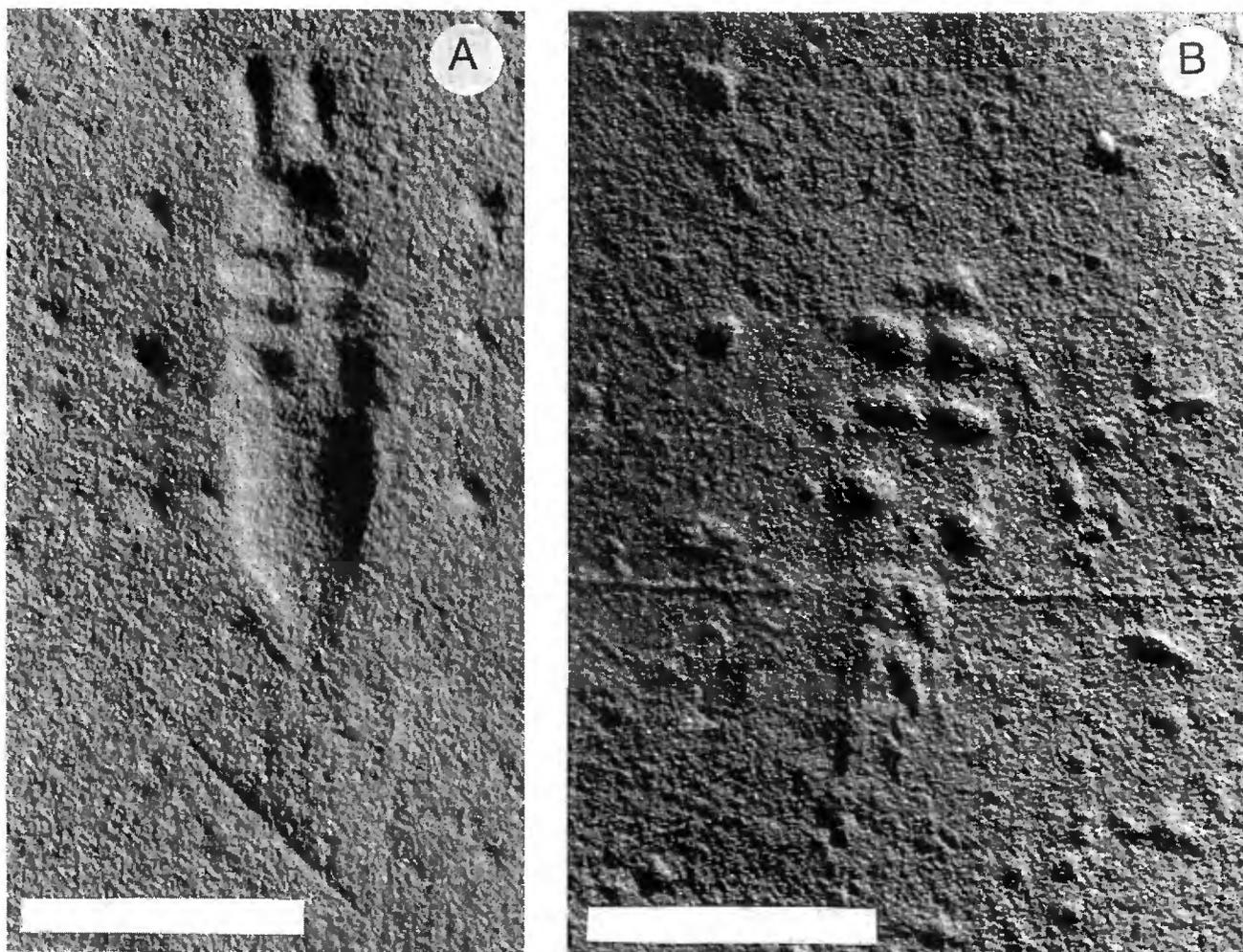


FIG. 3. Typical morphology of *Tonganoxichnus buildexensis*. Scale bars = 0.5 cm. (A) Negative epirelief of the anterior-most paired palp impressions, prominent head, three pairs of thoracic appendage impressions at the anterior part of the trace, and inflated wedge-like posterior part. Note the second set of circular anterior impressions representing the digitigrade tarsus of each thoracic appendage. The straight marks (lower part) are interpreted as terminal filament drag marks produced by the *Tonganoxichnus* tracemaker. (B) Positive hyporelief of a poorly preserved subtriangular head impression, three pairs of better preserved and conspicuous thoracic appendage impressions at the anterior part, and V-shaped shallow impressions at the posterior part. Note the presence of circular to elongate impressions at a distance of approximately 0.75 that of the body width, which most likely represent the walking trackway of the digitigrade tracemaker responsible for the resting structure. Other indistinct circular imprints (lower right) may be undertracks of previously produced trackways. The straight mark in the central portion of the photograph represents a drag mark of a terminal filament produced prior to the resting trace.

In other specimens, the frontal mark and two or three pairs of lateral impressions are preserved, and the posterior part of the trace is absent (Figure 4B, lower right). A thin, short, cylindrical axial projection has rarely been observed. Tracks of disorganized circular imprints (Figures 3B, 4B), and slightly curved or straight marks (Figure 3A,B) are commonly associated with distinct resting traces. Irregular traces formed of multiple segment-like impressions are common within this trace fossil assemblage (Figure 4B). The traces are predominantly preserved as positive hyporeliefs on soles of very fine-grained silty sandstones or more rarely as negative epireliefs.

Remarks. The ichnogenus *Tonganoxichnus* was proposed by Mángano et al. (1997) for monuran traces preserved in Upper Pennsylvanian tidal rhythmites of eastern Kansas. Two ich-

nosppecies, *T. buildexensis* for resting traces and *T. ottawensis* for feeding traces, were proposed. Mángano et al. (1997) also commented on two resting traces from the Early Permian of the Robledo Mountains in New Mexico, illustrated by Hunt et al. (1993), suggesting similarity to *T. buildexensis*. Recent research by Braddy (1998, 1999) on the ichnofauna of the Robledo Mountains provided additional information on these and other resting traces. Braddy (1999, figure 1) illustrated four resting traces. He regarded two of these as new resting traces and described the other two informally as new ichnospecies of *Tonganoxichnus* and *Rotteroidichnium*. Superficially, the nested V-shaped markings of *Tonganoxichnus* may be confused with some preservational variants of chevronate locomotion traces of bivalves included in *Protovirgularia* M'Coy 1850 and its junior

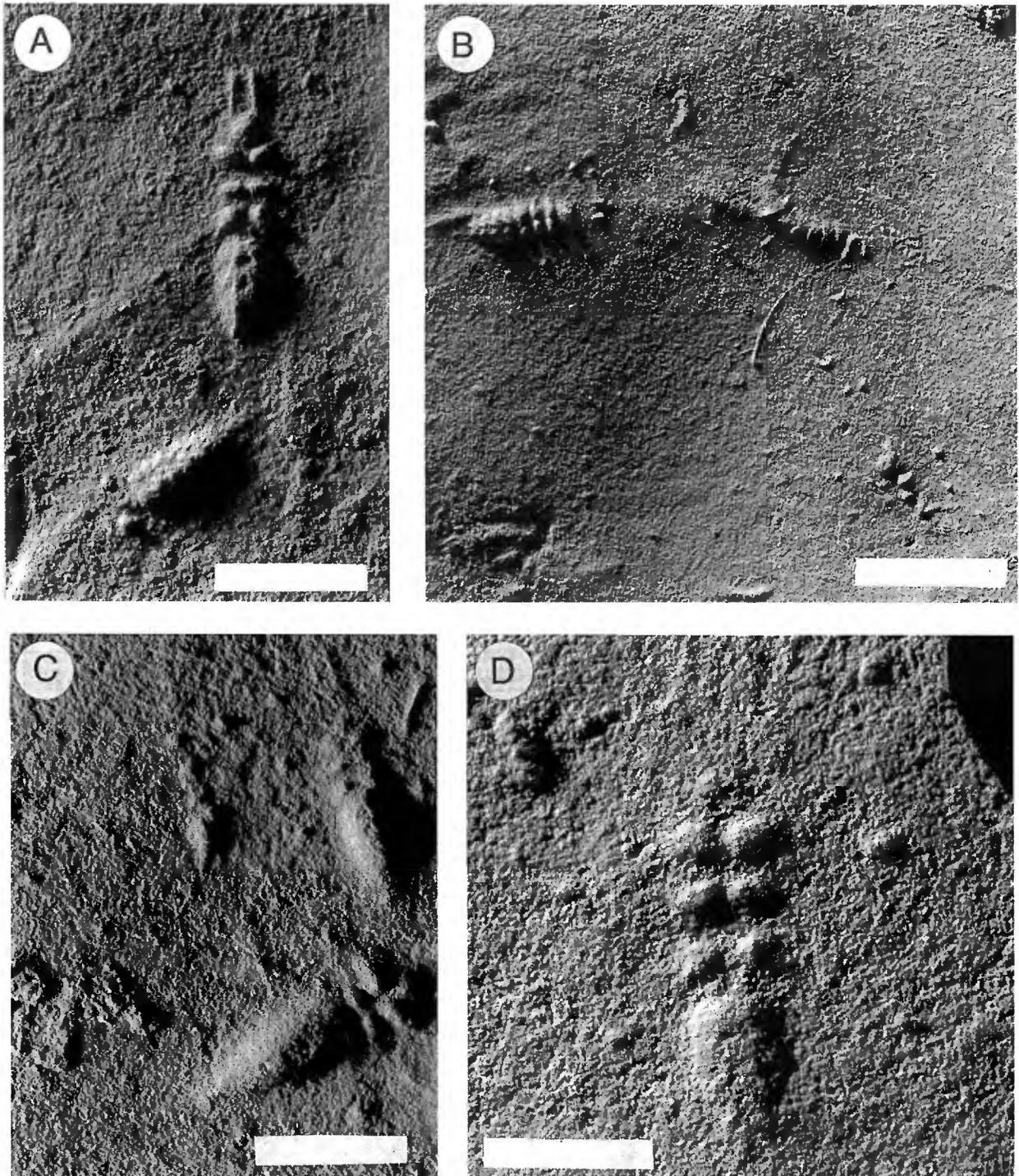


FIG. 4. Preservational variants of *Tonganoxichnus buildexensis* in positive hyporelief. Scale bars = 0.5 cm. (A) Upper specimen exhibits typical anterior and posterior features of *T. buildexensis*; at lower left a specimen displays a “half body” position that shows the posterior, or abdominal, aspect of the original trace-maker. (B) A cluster of three specimens. An exquisitely preserved specimen (upper left) with five nested, delicate, V-shaped marks at the posterior part and a second set of three pairs of associated circular impressions revealing tarsal contact points. A specimen displaying annulated morphology (upper center) interpreted as three partly superimposed “half body” imprints, each representing seven evident abdominal segments without associated tarsal impressions. A specimen showing the half body anterior-part preservation (lower right). Note the presence of circular imprints (lower) most likely representing partially preserved undertracks. (C) A cluster of two specimens showing an inflated posterior part with poorly preserved, posterior morphological features. (D) Closeup of a specimen showing very shallow, almost indistinct, head impressions; three pairs of thoracic appendage impressions; an annulated, segment-like posterior part; and probable circular tarsal marks at left.

synonym *Biformites* Linck 1949 (see, for example, figure 2H of Miller and Knox, 1985). However, overall morphology and distinct anatomical details of *Tonganoxichnus* clearly distinguish this ichnogenus from chevronate bivalve trails.

Morphologic elements of *T. buildexensis* are illustrated in Figure 5. Based on the anterior-most elongate pair of impressions (interpreted as maxillary palp resting sites), the frontal anteromedian impression (representing the head), the three pairs of conspicuous anterior markings (that undoubtedly are thoracic appendage marks), and delicate abdominal structures, we conclude that the Crane material warrants inclusion within *Tonganoxichnus buildexensis* (cf. Mángano et al., 1997). In addition, the size range is similar to that of *T. buildexensis*. The second set of distal circular lateral impressions commonly associated with the thoracic area most likely represent digitigrade

tarsal impressions; the more proximal, ellipsoidal thoracic markings adjacent to the axis are interpreted as impressions of the coxae. Interestingly, although not described in the original material, these impressions seem to be partially preserved in the *Tonganoxichnus buildexensis* holotype (cf. Mángano et al., 1997; figure 3A) and other specimens of the Tonganoxie Sandstone Member. The fact that some morphologic features are lacking in some specimens favors an undertrace origin for many of the preservational variants of *Tonganoxichnus buildexensis*. As opposed to a surface trace, the undertrace represents the duplicate imprint on lower surfaces (see Goldring and Seilacher, 1971). The digitigrade tarsal impressions, palp segment, and last-segment abdominal impressions are more shallow than other impressions, such as the coxae, and may not be preserved on relatively deep subsuperficial laminae. Although the terminal filament mark is not in physical continuity with the abdominal impressions, isolated linear marks and anterior palp impressions coupled with posterior linear marks indicate that a tail-like feature was present in the tracemaker. A similar mode of occurrence was documented by Mángano et al. (1997; see figure 3B), and interpreted as a result of sliding-on-the-water behavior with the sensorial maxillary palps probing the sediment surface and the tail-like projection passively touching the substrate. Interestingly, the preservational variant characterized by the third pair of thoracic appendages and abdominal impressions (Figure 4A, lower left) is similar to the insect trace illustrated by Hunt et al. (1993, figure 10, left). This "half body" undertrace, with the anterior features virtually absent, suggests the center of gravity was located on the third thoracic appendage and may represent a prejumping position (cf. Evans, 1975). Undertracks of circular or elongate imprints are too incomplete to deserve formal description, but they most likely represent a fast-walking gait performed by thoracic appendages (see next section). Irregular, multiple, segment-like impressions are difficult to interpret in terms of ethology; they are variable in morphology and record the impressions of different parts of the body. Some may well represent landing structures of bodies that are upside down or on their side (Figure 4B, center; see next section).

Mángano et al. (1997) interpreted differences in ichnofossil morphology, principally in the relative proportions of the head, thorax, and abdomen that occur between large and small specimens. These differences reflect different developmental, or instar, stages. The size range and morphological characters of the specimens from the Mansfield Formation are compatible with those documented for adult monurans (cf. Sharov, 1961; Durden, 1978; Kukulová-Peck, 1987, 1991).

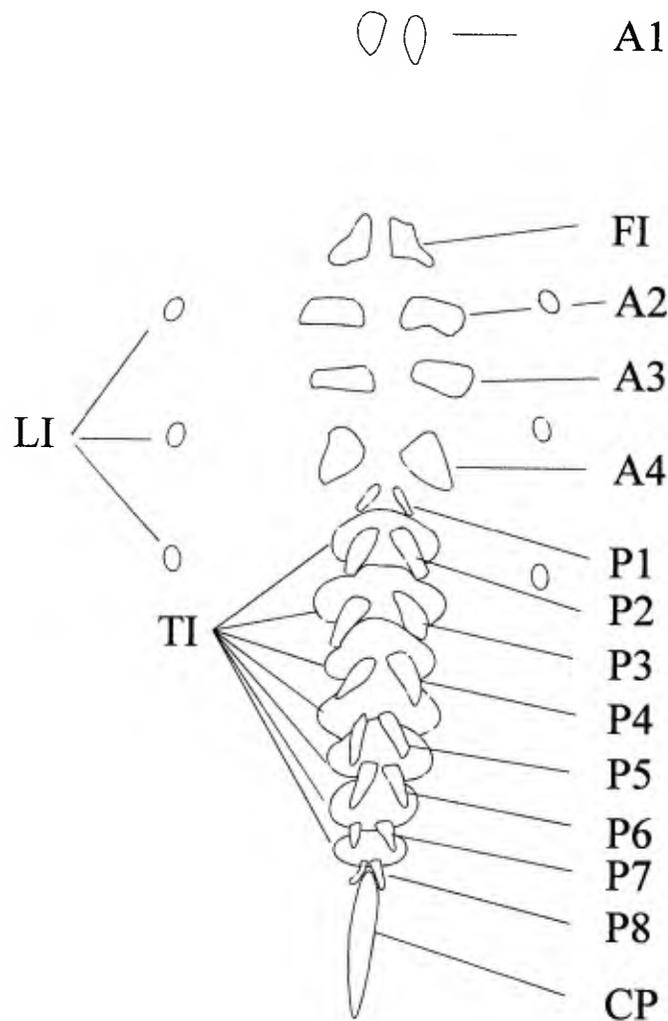


FIG. 5. Morphologic components of *Tonganoxichnus* (modified from Mángano et al., 1997). A1 = Anterior-most pair of appendage imprints, A2–A4 = Second to fourth pairs of anterior appendage imprints, FI = Frontal impressions, P1–P8 = First to eight pairs of posterior appendage imprints, CP = Cylindrical projections, TI = Transverse segment-like body impressions, LI = Lateral impressions.

THE PALEOBIOLOGY OF TONGANOXICHNUS

The Lower Pennsylvanian Mansfield Formation of Indiana is the third locality in North America to reveal *Tonganoxichnus* traces and, together with the Kansas material, preserves delicate hyporelief and rare epirelief impressions consistent with fossil monuran and modern archaeognathan ventral anatomy.

The morphological similarities between Pennsylvanian to Permian Monura and modern Archaeognatha are striking, as both groups have been considered to be closely related clades (Lauterbach, 1972; Kukulová-Peck, 1991) or subgroups of the same clade (Carpenter, 1992; Rasnitsyn, 1999; Goldbach, 2000), even though these two lineages are probably derived from an earlier ectognathous, monocondylic lineage present during the Early and Middle Devonian (Shear et al., 1984; Labandeira et al., 1988). Archaeognathans are some of the earliest known detritivores in terrestrial ecosystems (Shear and Kukulová-Peck, 1990; see also Watson, 1989) and have a sporadic and sparse record extending from the Early Devonian to the present (Kukulová-Peck, 1987; Sturm and Bach de Roca, 1993; Bitsch and Nel, 1999). The Monura, however, are only known from the Middle Pennsylvanian to early Late Permian (Sharov, 1957, 1966; Durden, 1978; Kukulová-Peck, 1987; Rowland, 1997). Machilid Archaeognatha are not only morphologically similar to Monura (Kukulová-Peck, 1991; Rasnitsyn, 1999), but also they occur in coastal, humid environments (Delany, 1954; Benedetti, 1973; Sturm and Bach de Roca, 1993), thus allowing useful comparisons regarding the morphology of the possible tracemakers and the overall behavior and feeding habits represented by *Tonganoxichnus*.

Evidence regarding the habitat of the *Tonganoxichnus* fabricator indicates that it inhabited coarse silty substrates on tidal flats that were periodically inundated with water and influxes of sediment. Placement of these trace fossils along a seaward-to-landward gradient suggests typically freshwater conditions that extended marginally into shore sediments that were deposited by marine tidal currents (Buatois et al., 1997; Mángano et al., 1997). The size of the *Tonganoxichnus buildexensis* culprits fits comfortably into the adult range of modern machilid Archaeognatha, which ranges from 8 to 14 mm for adult females and males from several measured taxa (Reilly, 1915; Wygodzinsky, 1944; Sturm, 1952, 1955; Delany, 1957, 1959, 1960). Many modern machilid archaeognathan species are restricted to coastal localities, including *Dilta littoralis* Womersley occurring along coastal regions of western Europe but sometimes extending somewhat inland (Delany, 1954), and *Petrobius brevistylis* Carpenter and *P. maritimus* Leach inhabiting the rocky coasts of northern North America and northwestern Europe, respectively (Delany, 1959; Wygodzinsky and Schmidt, 1980). Whereas modern archaeognathans are fundamentally detritivores (Adis and Sturm, 1987; Sturm and Bach de Roca, 1993), their dietary strategy in these coastal habitats is better described as opportunistic and includes bacteria, surface-film algae, lichens, decaying fruit, dead leaves, fungi, and unidentified solid organic debris (Willem, 1924; Wygodzinsky, 1944; Delany, 1954, 1959; Smith, 1970; Sturm, 1984). Some species consume spores and pollen (Kaplin, 1978; Benedetti, 1973), and mineral matter also has been recovered from gut contents (Wygodzinsky, 1944). During feeding, machilid archaeognathans employ long, leglike, seven-segmented maxillary palps to probe and scratch the substrate and also to assist

in food handling (Willem, 1924; Sturm, 1955); a similar activity occurs during copulation, in which there is "drumming" by the maxillary palps (Goldbach, 2000). These palps are typically held in a curved, sigmoidal position at rest with the dorsal surface of the distal segments positioned on the substrate surface and aligned in a subparallel fashion, a behavior also inferred from *Tonganoxichnus buildexensis* (Figures 3A, 4A,B). These maxillary-palp impressions range from relatively short ellipsoids representing one segment each to slightly asymmetrical structures indicating a more oblique position (Figure 3A,B).

Modern archaeognathans use sensillae-rich abdominal styli for tactile communication with the substrate and to prop their abdomen when slowly walking or at rest (Willem, 1924; Smith, 1970). Only under rapid locomotion do abdominal styli not contact the ground. Styli apparently are not internally muscled and thus are minimally movable structures that leave an en echelon series of a few to several V-shaped impressions on soft substrates (Sturm, 1955; Smith, 1970). Such chevron-shaped impressions are deployed segmentally and imbricately in extant machilid Archaeognatha (Delany, 1959; Machida, 1981; Sturm and Messner, 1992), a feature that is clearly recorded in several *Tonganoxichnus buildexensis* specimens from Indiana (Figures 3B, 4A, and especially Figure 4B) where there are up to five well-preserved sets of styli indentations. Unlike acuminate styli, thoracic legs bear a double claw that contacts the substrate in a digitigrade stance and produce footprint tracks that are placed from the lateral body margin at a distance of approximately 0.75 times that of the body width (Willem, 1924, Figure 2), corresponding closely to the body-margin to circular distal footprint distances in *Tonganoxichnus buildexensis* (Figures 3A; 4B). By contrast, the terminal filament, typically elevated above or barely in contact with the substrate surface (Smith, 1970; Kukulová-Peck, 1987), is used as a jumping device that can launch the insect up to 20 cm in the air (Evans, 1975; Sturm and Bach de Roca, 1993). This is done in conjunction with dorsoventral abdominal flexion and movement of paired maxillary palps. Subsequent landing is somewhat haphazard and can occur in various orientations, including touchdowns on all or some of the tarsi, on lateral body exposures, or other positions (Sturm, 1955). Linear impressions of the terminal filament, which can approximate or exceed the body length in modern bristletails (Bär, 1912), are commonly associated with some specimens of *Tonganoxichnus buildexensis* (Figure 3A,B), although these are interpreted as shallow drag marks. Also, there is no evidence of conjugate jumping and landing structures, such as those documented in *Tonganoxichnus ottawensis* from eastern Kansas (Mángano et al., 1997). Although speculative, some irregular multiple segment impressions (Figure 4B, center) may record random landing structures. A considerably wider, postero-medial structure extending from the posterior-most abdomen may be a female ovipositor (Figure 4A,B), representing a stouter, thicker structure when compared to a gently-tapering median filament (Agrell, 1945; Sturm and Bach de Roca, 1992).

In a recent paper by Rasnitsyn (1999), a new monuran species was described, *Dasyleptus noli*, from the Late Pennsylvanian Commentary Basin in France. Also, three additional congeneric species were redescribed: *D. lucasi* Brongniart (1885), *D. brongniarti* Sharov (1957), and *D. sharovi* Durden (1978). Also mentioned was an interpretation of *Tonganoxichnus buildexensis* and *T. ottawensis* from Kansas (Mángano et al., 1997), in which it was claimed that this trace fossil was unlikely to be attributable to the Monura. The principal reason given was that *Tonganoxichnus* did not preserve a relatively deep, postabdominal furrow that would be produced by a terminal filament (median cercus) as it was suddenly depressed into the sediment for an aerial jump (Smith, 1970; Evans, 1975). However, an essential factor that was not discussed was that most of the *Tonganoxichnus* traces illustrated by Mángano et al. (1997) are landing or resting traces, with the terminal filament interpreted as either erect in the air or more rarely lying on the substratum. This anatomical position of the terminal filament was illustrated by Evans (1975), demonstrating that the posterior-most abdominal segments and terminal filament were kept in an upward position, clear of the sediment surface (Mángano et al., 1997; figure 7). Thus, with the possible exception of Figure 5A,B of Mángano et al. (1997), the Kansas *Tonganoxichnus* specimens were not take-off traces and thus are not characterized by much deeper postabdominal troughs that would have been consistent with the sudden depression of the terminal filament into the sediment for springing a jump. The *Tonganoxichnus* traces from Indiana apparently exhibit evidence only for landing or resting. In addition, although cited by Rasnitsyn (1999) as an unexplained absence, the distal tarsi of all thoracic legs do contact the sediment in the Indiana material, now indicated by three pairs of lateral point-indentations into the sediment located alongside the main body axis (Figures 3; 4B, D), which perhaps remained unnoticed in the Kansas material (Mángano et al., 1997; but see figure 4B). Interestingly, the lower-most Permian New Mexico locality from which Rowland (1998) described *Dasyleptus* sp., confirmed by Rasnitsyn (1999), is somewhat older than the Lower Permian site containing *Tonganoxichnus* mentioned by Braddy (1998, 1999) approximately 180 km to the south.

DISCUSSION AND CONCLUSIONS

A comparison among all three occurrences of *Tonganoxichnus buildexensis* reveals remarkable similarities. The age of the youngest occurrence of *Tonganoxichnus* is Early Permian, whereas the ages of the older trace fossil-bearing units is Middle to Late Pennsylvanian, with the *Tonganoxichnus*-bearing Mansfield Formation at Crane being slightly older (Atokan) than the Tonganoxie Sandstone Member at Buildex (Virgilian). These occurrences are consistent with the Middle Pennsylvanian to early Upper Permian stratigraphic range of the Monura. Although the trace fossil context of the Indiana Mansfield Formation deserves further investigation, the insect trace fossil as-

semblage is similar to that of the Tonganoxie Sandstone Member of Kansas. In both units, *T. buildexensis* is associated with probable insect feeding [*Treptichnus bifurcus* (Miller)] and grazing [*Gordia indianaensis* (Miller)] traces, as well as amphibian tracks and plant traces. The Buildex ichnofauna was analyzed systematically, and other forms, particularly arthropod trackways, were also documented (Buatois et al., 1998), although comprehensive trace-fossil sampling and study of the Crane rhythmites has not been undertaken. Bioturbation, namely vertical disturbance of primary structures, is negligible in both the *Tonganoxichnus*-bearing portions of the Buildex and the Crane deposits.

The presence on some bedding planes of crenulated curvilinear disruptions of laminae indicates the possible feeding on an algal surface mat. Although other surface-dwelling arthropods may be responsible for these distinctive microlaminar irregularities, it is highly likely that they are the result of palpal probes and mandible manipulation of a thin algal mat by monurans. Primary sedimentary fabric and surface traces are exquisitely preserved at the Indiana site. Interestingly, in both localities *T. buildexensis* is preserved in similar lithofacies, namely rhythmically bedded laminated siltstones with clay drapes, and structures indicative of subaerial exposure, such as rill marks and raindrop impressions, are present on bedding planes. Well-preserved plant fragments and *in situ* upright trunks are common in both units. Strata are stacked, forming thickening and thinning packages, suggesting tidal deposition. Delicate preservation of surface traces indicates absence of erosion. Estimations at Buildex, based on an analysis of tidal rhythmite cyclicity, suggest an elevated sedimentation rate of 3.8 m/yr (Lanier et al., 1993). Comparable calculations for the Crane site are not available, but field observations indicate similar depositional rates.

Marine indicators, either as trace fossils or as body fossils, are absent in both Buildex and Crane. Buatois et al. (1997) interpreted the Buildex ichnofauna as recording the activity of a typical freshwater to terrestrial benthos. These authors suggested that the existence of this mixed freshwater to terrestrial ichnofauna in tidal rhythmites was indicative of tidal flats in the most proximal area of the inner estuary under freshwater conditions, in a zone between the maximum limit of landward tidal currents and the salinity limit further towards the sea. The dominance of insect traces and the absence of a marine burrowing infauna in Crane also suggest freshwater conditions. Rapid burial, absence of significant erosive events, and absence of infaunal brackish water organisms were most likely the factors involved in the preservation of these delicate, superficial insect traces. Modern studies in tidal flats reveal a complex interplay between sedimentation and microbial growth (Noffke et al., 1996). High sedimentation rate and intense physical reworking commonly prevent significant biomass accumulation and development of microbially induced sedimentary structures. At Buildex and Crane, however, high sedimentation rates are interpreted as related to short-term depositional events, most likely seasonal flooding of fluvial systems (cf. Lanier et al.,

1993). At Buildex some sedimentary structures, such as wrinkle marks and pinch-out lamination, may be related to incipient tissue-like mats (cf. Noffke et al., 1996). The sharpness of morphologically delicate features of *Tonganoxichnus* also is suggestive of a relatively firm substrate that acted as a plastic casting medium. Cohesive behavior has been interpreted as a useful indicator of microbial mat colonization in siliciclastic sediments (Schieber, 1999).

The recording of the ichnogenus *Tonganoxichnus* in the Mansfield Formation of Indiana has three important implications. First, it confirms that this ichnotaxon documents a recurrent behavioral pattern in Upper Carboniferous coastal ecosystems. Second, it provides detailed ichnologic documentation for some body structures and behaviors that are difficult to infer from body-fossil material alone. Third, sedimentologic and ichnologic observations indicate that the *Tonganoxichnus* assemblage seems to be common in tidal flat rhythmites developed under freshwater conditions, probably in the innermost part of estuarine systems, adjacent to the fluvio-estuarine transition. We predict that further occurrences of *Tonganoxichnus* in late Paleozoic, fine-grained tidal rhythmites will be recorded in the near future.

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