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Hexapodichnus casamiquelai isp. nov.: an insect trackway from the La Matilde Formation (Middle Jurassic), Santa Cruz, Argentina

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Abstract. The Estancia Laguna Manantiales is a well-known ichnological locality from the continental Jurassic (La Matilde Formation, Callovian) of Argentina (Santa Cruz province). This locality, which has been studied during the last four decades, has produced abundant collections of trace fossils including important material of vertebrate footprints, such as the ichnogenus *Ameghinichnus*, one of the oldest evidence of mammals from South America. Since the first studies, various authors have mentioned the existence of abundant arthropod trackways from this locality, but without providing further details. In this contribution, the arthropod trackways are described, as part of an integral ichnological study of this locality. The trackways are attributed to a new ichnospecies of *Hexapodichnus* Hitchcock, *H. casamiquelai* isp. nov. The morphology of these trackways, composed of alternate series of three, non-aligned, tracks on each side of the mid-line, allows us to attribute them to pterygote insects. The ichnotaxobases used in the identification of these trackways are: (1) number of tracks within series, (2) trackway symmetry, (3) absence of medial groove, (4) arrangement of tracks within series (including alignment, angle between tracks and of individual tracks with the midline), and (5) morphology of individual tracks.

Resumen. *HEXAPODICHNUS CASAMIQUELAI* ISP. NOV.: HUELLAS DE INSECTOS DE LA FORMACIÓN LA MATILDE (JURÁSICO MEDIO), SANTA CRUZ, ARGENTINA. La Estancia Laguna Manantiales es una reconocida localidad icnofosilífera del Jurásico continental (Formación La Matilde, Calloviano) de la Argentina (provincia de Santa Cruz). Esta localidad ha aportado importante material de pisadas de vertebrados, entre los que se encuentra el icnogénero *Ameghinichnus*, que constituye una de las evidencias más antiguas de la presencia de mamíferos en América del Sur. Desde las primeras descripciones, distintos autores mencionaron la presencia de abundantes huellas de artrópodos, pero sin profundizar en el tema. En esta contribución se describen las huellas de artrópodos como parte de un estudio icnológico integral de esta localidad. Se las atribuye a una nueva icnospecie de *Hexapodichnus* Hitchcock, *H. casamiquelai* isp. nov. La morfología de estas huellas, compuestas por series alternadas de tres marcas no alineadas, a cada lado de la línea media, permite adjudicarlas a insectos pterigotos. Las icnotaxobases usadas en la identificación de estas huellas son las siguientes: (1) número de marcas dentro de las series, (2) simetría del rastro, (3) ausencia de surco medio, (4) disposición de las marcas dentro de las series (incluyendo alineamiento, ángulo entre las marcas y de las marcas individuales con la línea media), y (5) morfología de las marcas individuales.

Key words. Insect trackways. *Hexapodichnus*. La Matilde Formation. Middle Jurassic. Santa Cruz. Argentina.

Palabras clave. Huellas de insectos. *Hexapodichnus*. Formación La Matilde. Jurásico Medio. Santa Cruz. Argentina.

Introduction

The Jurassic vertebrate ichnofauna from the La Matilde Formation (Callovian) at Estancia Laguna Manantiales (Santa Cruz, Argentina) was extensively studied by Casamiquela four decades ago (Casamiquela, 1961a, 1961b, 1964). This author defined four new vertebrate ichnotaxa: *Ameghinichnus patagonicus*, attributable to Mammalia, *Wildeichnus navesi* and *Sarmientichnus scagliai*, attributable to Theropoda, and *Delatorrichnus goyenechei*, regarded as an Ornithopoda trackway. The Laguna Manantiales ichnofauna contains an exceptional assemblage of mammal trackways, occasionally with a hopping gait, and small-sized theropod dinosaurs, giving valuable information about the primitive locomotion of reptiles and mammals (Rainforth and Lockley, 1996). It also contains one of the oldest evidence of mammals from Argentina, along with Middle-Late Jurassic bone remains from the Cañadón Asfalto Formation (Rauhut *et al.*, 2002), and purported mammal tracks from the Late Triassic Los Menucos ichnofauna (Casamiquela, 1964). Along with this vertebrate ichnofauna, Casamiquela (1964)

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also mentioned the presence of insect trackway, probably produced by a coleopteran. Leonardi (1994) also mentioned the common association of *Ameghinichnus* with arthropod trackways on the same slabs. However, these abundant arthropod trackways have not been described in detail, in spite of being an important component of the Laguna Manantiales ichnofauna.

Ichnologic research on invertebrate continental trace fossils from Jurassic strata are scarce (*e.g.*, Pienkowski, 1985; Gierlowski-Kordesch, 1991; Metz, 1992; Genise and Hazeldine, 1995; Buatois *et al.*, 1996; Hasiotis, 1998; Hasiotis and Demko, 1996, 1998; Hasiotis *et al.*, 1998; Hu *et al.*, 1998 and other references cited in Buatois *et al.*, 1998). Contributions on Jurassic arthropod trackways are even fewer (*i.e.*, Hitchcock, 1858; Leonardi and Sarjeant, 1986; Metz, 1993, 1996; Olsen, 1995).

The aim of this contribution is to describe and to assign ichnotaxonomically the arthropod trackways from Laguna Manatiales, in order to complete the picture of the invertebrate ichnofauna associated with that of the vertebrates. This contribution is part of a complete ongoing revision of the Jurassic ichnofauna of Laguna Manantiales. The examined material was collected along with vertebrate footprints in different field trips since Casamiquela's first studies and is currently housed in four institutions from Argentina: the Museo de La Plata (MLP), Museo Paleontológico "Egidio Feruglio" at Trelew (MPEF), Instituto Miguel Lillo at Tucumán (PVL) and Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" at Buenos Aires (MACN). Regrettably, it was not possible to find the piece of the sandstone slab MLP 60-X-31-1 (paratype of *Ameghinichnus patagonicus*), which contains the arthropod trackway mentioned and illustrated by Casamiquela (1964). We follow the terminology of Trewin (1994) for the description of arthropod trackways. This author does not propose a convention for naming individual tracks within series, and there is no current agreement among ichnologists on the subject. Some of them do not name the individual tracks (*e.g.*, Briggs *et al.*, 1979; Trewin, 1994), others label the marks "A", "B", "C" from the outer to the inner marks in relation to the midline (e.g., Hanken and Størmer, 1975; Walter, 1984; Braddy and Anderson, 1996) and others designate them with Arabic numerals from front to back (*e.g.*, Brady, 1947; Anderson, 1981; Sadler, 1993). The last alternative, which stems from the conventional numbering of arthropod appendages, is followed here (Manton, 1977); it does not necessarily reflect the original order of foot emplacement (Sadler, 1993).

Figure 1. Map showing location of the trace fossil locality (black triangle) / *Mapa mostrando la ubicación de la localidad icnofosilífera (triángulo negro).*

Geologic setting

Arthropod and vertebrate trackways occur in greenish, laminated, fine-grained tuffaceous sandstone and siltstone from the La Matilde Formation, which crop out at Estancia Laguna Manantiales, Santa Cruz Province, Argentina (figure 1). The La Matilde Formation is composed mainly of tuffs, tuffaceous sandstone, mudstone, and conglomerate, and laterally and vertically interfingers with the Chon Aike Formation, which together comprise the Bahía Laura Group (Stipanicic and Reig, 1956; Lesta and Ferello, 1972). The La Matilde Formation has been interpreted as representing accumulation in a low-energy fluvial system, including associated shallow ponds. Sedimentation was accompanied by intense volcanic activity whose products were commonly reworked by diluted fluvial currents (de Barrio *et al.*, 1999). Based on the abundant plant and anuran remains found in this formation, Stipanicic and Reig (1956) assumed a wet and temperate climate during deposition of the La Matilde Formation. On the basis of fossil remains the unit was assigned either to the late Middle Jurassic to early Late Jurassic (Stipanicic and Reig, 1956) or early-middle Callovian (Stipanicic and Bonetti, 1970). There are a large number of radiometric ages for the partially correlative Chon Aike Formation (see review in de Barrio *et al.*, 1999) that help to constrain the age of the La Matilde Formation to the range 160 Ma-171 Ma (*i.e.* Bathonian-Callovian after the scale of Gradstein *et al.*, 1995).

Systematic ichnology

Ichnogenus ***Hexapodichnus*** Hitchcock 1858

Hexapodichnus Hitchcock, 1858, p. 158; Lull, 1915, p. 60; Lull, 1953, p. 44; Häntzschel, 1975, p. W 70; Walter, 1983, p. 152; Keighley and Pickerill, 1998, p. 92.

Type ichnospecies. *Hexapodichnus magnus* Hitchcock 1858, designated by Lull (1953).

Diagnosis. Tracks arranged in series of three, in rows on each side of the mid-line; the inner tracks running nearly parallel to the mid-line. Outer tracks parallel, or diverging outwards from the mid-line. Alternate on opposite sides of the mid-line (after Hitchcock, 1858).

Remarks. Key features of *Hexapodichnus* are the presence of series of three tracks, one of them parallel to mid-line, arranged with alternate geometry, and the absence of medial impression. Keighley and Pickerill (1998) suggested to exclude the alternate symmetry from the diagnosis of *Hexapodichnus* arguing that part of the type specimen (AC 36/11 from Amherst College, Pratt Museum of Natural History) displays other kind of symmetry. However, we prefer to retain this character because (as recognized by Keighley and Pickerill, 1998) most of the type material displays an alternate symmetry and it is considered herein as an important ichnotaxobase. Other ichnogenera showing series of three tracks and lacking a medial trail display different morphologies from the trace fossils described herein. In *Copeza* Hitchcock, 1858, the distribution of tracks is more irregular, the internal ones being perpendicular to the mid-line, whereas the outer ones are parallel to it. In *Lithographus* Hitchcock, 1858, the outer track is crooked. Walter (1983, 1985) described and redescribed ten ichnogenera under the informal group "Tripodichnia": *Secundumichnus*, *Heterotripodichnus*, *Tripodichnus*, *Tarsichnus*, *Punctichnium*, *Heftebergichnus*, *Glasbachichnium*, *Permichnium*, *Etterwindichnus*, and *Warvichnium*. However, most of these ichnogenera show an irregular pattern and only in some parts of the illustrated specimens the three tracks are clearly displayed. In *Secundumichnus*, *Heterotripodichnus*, *Tripodichnus* and *Etterwindichnus* the three tracks lay more or less in the same line. Only in *Permichnium ritualis* Walter, 1983 it is possible to clearly recognize series of three tracks that are not aligned. In this ichnospecies the inner and outer tracks display a "V" pattern, whereas the middle one is placed in the bisecting line of the "V", slightly displaced backwards, and lays parallel to the midline of the trackway.

Hexapodichnus casamiquelai isp. nov.
Figures 2, 3.A-B and 4

Etymology. Dedicated to Rodolfo Casamiquela for his significant contributions to the understanding of the Laguna Manantiales ichnofauna.

Diagnosis. Two rows of three, non-aligned, elongate, comma-shaped or tapered tracks in which the internal one is almost parallel to the mid-line, whereas the external ones diverge from it, composing a "V" open at its vertex, that forms an angle from 45° to 70°.

Remarks. *Hexapodichnus casamiquelai* differs from *H. magnus* Hitchcock, 1858 by showing the three tracks in most cases and also by the angle between the outer tracks, which in *H. magnus* are almost parallel. *Hexapodichnus horrens* Hitchcock, 1858 shows some degree of morphological variation, but considering the diagnosis, it differs in several important traits from *H. casamiquelai.* In the former, the outer tracks diverge up to 10°, being almost parallel, whereas in the latter the angle of the "V" ranges from 45° to 70°. The outermost track diverges up to 40° from the midline in *H. horrens*, whereas in *H. casamiquelai* it diverges from 58° to 78°. In addition, in *H. horrens* the outer tracks seem to be placed in advance of the inner one, whereas in *H. casamiquelai* the outer tracks are placed backwards.

Holotype. MPEF-IC 194. A curved trackway from a sandstone slab deposited in the Museo Paleontológico "Egidio Feruglio" (Trelew, Chubut, Argentina) (figures 2, 3). In the same slab there is also a trackway of the vertebrate ichnogenus *Ameghinichnus.*

Paratypes. Two trackways occurring in a sandstone slab from the collection of fossil vertebrates of the Instituto Miguel Lillo (Tucumán, Argentina) labeled PVL 3696 (figure 4).

Examined material. MPEF-IC 195 to 197 (three trackways). PVL 3696 (one trackway); PVL 3699 (four trackways). All material preserved as concave epirelief.

Description and interpretation. The trackways are noticeable because of their large width (up to 41 mm) and also that of individual tracks (up to 2 mm). Two parallel, compound, track rows 210 mm in length, producing a gently curved trackway compose the holotype (MPEF-IC 194). The external width of the trackway ranges from 38 mm to 41 mm, the internal one from 13 mm to 16 mm, whereas each track row is 12 mm to 13 mm wide and consists of three imprint series. The series show alternate symmetry in relation to the mid- line of the trackway. Each track series displays different arrangements of the three marks, identified as 1, 2, and 3 in figure 3.B. Some tracks show a raised rim at one side produced by the leg pushing against the substrate that, in turn, would in-

Figure 2. Holotype of *Hexapodichnus casamiquelai*, MPEF-IC 194. Scale bar: 1 cm / *Holotipo de* Hexapodichnus casamiquelai, *MPEF-IC 194. Escala: 1 cm.*

dicate that the producer moved from *b* to *a* (figure 3.B). Towards the extreme *a*, the series of the left track row shows a well-defined, internal track almost parallel to the mid-line and two divergent external tracks, displaying a "V" having an open vertex. The "V" is oriented with its vertex towards the internal track and its bisecting line almost perpendicular to it. Towards the extreme *b*, the "V" is displaced backwards and the track 3 is rotated about 20º backwards in relation to the mark 1 compared with those in the other extreme. The angle of the "V" ranges from 45° to 70°. The angle between tracks 1 and 2 ranges from 58º in the most curved sections of the trackway to 78º in the straightest ones. The right row shows a more disorganized pattern, the track 3 even lacking in some series, and displaying series that resemble those at extreme *b*.

The track 1 may be elongate, tapered or comma-shaped, in that case the wider side is oriented backwards. The track 2 is externally tapered (rounded base) to triangular (angular base), and the track 3 is elongate to externally tapered. The marks are preserved as negative epirelief, ranging from 1 mm to 1.5 mm in depth, and having a maximum length of 7 mm and a maximum width of 2 mm, regardless their morphology. There is no overlap between two successive series of tracks.

The repeat distance, which represents the stride of the producer, is measured on both sides as the distance between the external point of the track 2. In the left track row, it differs from 19 mm to 25 mm because of the curved trackway path. The right track row shows shorter strides, from 15 mm to 21 mm. Differences in morphology and measures between left and right track rows are common in curved arthropod trackways because of the different interaction of the legs on each side of the body with the substrate (*e.g.* Briggs *et al.*, 1984).

The paratypes (two trackways in PVL 3696) show no significant morphological differences with the holotype (figure 4.A). Both trackways are longer than the holotype, one displays a sigmoidal path, whereas the other shows a slight curvature as in the holotype. The other examined material consists of poorly preserved undertracks, which do not yield any additional distinguishing feature, with the exception of three undertracks of PVL 3699, which are almost half the size of the remaining specimens.

Discussion and conclusions

The presence of arthropod trackways in the Laguna Manantiales vertebrate footprint locality has been mentioned in the first report (Casamiquela, 1964) and also repeated in subsequent ones (*e.g.* Leonardi, 1994). However, the ichnotaxonomy and biological affinities of this material were not clarified until now. Casamiquela (1964) attributed these trackways tentatively to a coleopteran, without further comments on the reasons that led to

Figure 3. A, Interpretative drawing of the holoptype MPEF-IC 194 / *Dibujo interpretativo del holotipo MPEF-IC 194*. **B,** detail of a set of imprints showing marks 1, 2 and 3. Scale bars: 1 cm / *Detalle de una serie de huellas mostrando las marcas 1, 2 y 3. Escalas: 1 cm*.

this conclusion. On the other hand, Hitchcock (1858) claimed that *Hexapodichnus horrens*, a similar trackway, was "one of the most perfect and delicate of all the insect tracks yet discovered (sic)" by that time, having no doubts with respect to its insect origin.

The alternate symmetry of the series of tracks with respect to the mid-line indicates that at least three appendages were at the ground simultaneously. This feature restricts the possible producer to certain groups of arthropods, such as spiders, scorpions and insects, ruling out other groups such as millipedes (Trewin, 1994). Series of three tracks are characteristic of insects (Manton, 1977, fig. 7.12). However, scorpions and spiders can produce series of three or even two tracks, as well, depending on substrate conditions (Sadler, 1993), in the same way that insects can produce series of two (figure 3, right track row). In these cases, the series showing more tracks are considered to be diagnostic because they would show the minimum number of legs of the producer. The morphological variation from series of four to three tracks in trackways of spiders and scorpions can be observed even in the same trackway (Sadler, 1993), contrasting with *H. casamiquelai*, in which no specimen shows series of four tracks. In addition, the absence of the tail trace rules out scorpions as its producer.

Manton (1977) distinguished two different types of track series in hexapods. In those of most aptery-

Figure 4. *Hexapodichnus casamiquelai* in slabs that also contain footprints assigned to *Ameghinichnus patagonicus* / Hexapodichnus casamiquelai *en lajas que también contienen huellas asignadas a* Ameghinichnus patagonicus. **A,** paratype in the slab PVL 3696 / *paratipo en la laja PVL 3696*. **B,** slab PVL 3699 / *laja PVL 3699.* **C,** specimen MPEF-IC 195. Scale bars: 5 cm / *especimen MPEF-IC 195. Escalas: 5 cm.*

gote insects the three tracks fall in a same line, whereas in those of pterygote insects and jumping Machilidae, the third track is not aligned with the other two (Manton, 1977) as in *Hexapodichnus casamiquelai*. However, machilids can be ruled out as possible trace makers by two reasons: a) in the jumping gaits of Machilidae the arrangement of the three tracks is quite irregular (Manton, 1977, fig. 7.13g); b) they are produced only when the insect moves slowly, whereas at a higher speed the three tracks lay in the same line as in the remaining apterygote insects (Manton, 1977, fig. 7.13h). If the producers of the trace fossils were machilids, we would expect to find the two morphologies in the specimens examined.

The diagnostic criteria used for assignation of the La Matilde Formation arthropod trackways and which may be of use as ichnotaxobases for similar trace fossils are: (1) number of tracks within series, (2) trackway symmetry, (3) presence or absence of medial groove, (4) arrangement of tracks within series (including alignment, angle between tracks and of individual tracks with the midline), and (5) morphology of individual tracks. Criteria 1 to 3 are envisaged as valid for identification of ichnogenera, while the remaining may be used as specific ichnotaxobases.

Hexapodichnus casamiquelai is moderately abundant in the collected slabs, suggesting that the producer was a conspicuous component of the environment inhabited by the vertebrates. The insects were of aquatic or riparian habits or they fell to water or waterlogged sediments by accident (*i.e.* Metz, 1987a, 1987b; Poiré *et al.*, 1998). Experimental and field research will produce data to interpret further aspects of this trace fossil. The known stratigraphic record of *Hexapodichnus* is Carboniferous-Jurassic (Keighley and Pickerill, 1998; Hitchcock, 1858; this paper), although it is reasonable to suppose that modern insects can also produce traces of similar morphology.

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