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Xiphosurid trackways in a Lower Cretaceous tidal flat in Patagonia: Palaeoecological implications and the involvement of microbial mats in trace-fossil preservation

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ABSTRACT

Lower Cretaceous trackways assignable to xiphosurids were recently found in tidally influenced marginal-marine deposits of the Agrio Formation (Patagonia, Argentina). The aim of this paper is to describe these trace fossils in detail, discuss their conditions of preservation, make palaeoecological and taphonomic inferences from them, and analyse the importance of their palaeogeographic location. These trace fossils are assigned to *Kouphichnium*, and five track morphotypes are established. Microbially induced sedimentary structures (MISS) are associated with the trackways. Scanning electron microscope (SEM) studies document the involvement of microbial mats in the preservation of the trackways by the presence of cyanobacteria-like filament sheaths. The microbial mats enabled preservation of the tracks by binding and biostabilisation of the sediment surface. The mostly likely producers of the trackways are from the subfamily Limulinae. The studied surface could represent a high-tide mating ground associated with a very shallow water deposit on a warm Cretaceous tidal flat. These records are the first convincingly documented trackways produced by xiphosurids in the Early Cretaceous worldwide and the second fossil record of this group from the Cretaceous in the Southern Hemisphere.

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1. Introduction

Tracemakers cannot always be inferred by the study of their trace fossils. There are, however, some exceptions. For instance, the morphology of some arthropod trackways is reflective of the producer's anatomy, together with the prevailing substrate conditions (Minter et al., 2007). An exceptional preservation of the trace fossils presented in this work allowed the observation and study of certain features that suggest xiphosurids as the tracemakers. The presence in the basin of ichnofossils attributable to these organisms had also been recently suggested by Pazos et al. (2012). The associated sedimentary structures, which indicated a possible involvement of microbial mats, and the remarkable quality of preservation of the trackways, led to explore substrate conditions and the role played by microbial mats, taking into account the co-occurrence in the same studied surface of trace fossils and wrinkle structures.

Xiphosurids are aquatic, chelicerate arthropods with a stratigraphic record ranging from the Palaeozoic (Cambrian) to the present day. Approximately 30 genera and 50 species of xiphosurids are known (including extinct lineages); of these, four species, belonging



to three genera, are extant (Babcock et al., 2000). Because xiphosurids are non-biomineralising arthropods, their body fossils are rarely preserved. Notable exceptions to this rule are the specimens found in the Solnhofen Limestone (Jurassic of Germany), the Mazon Creek Konservat-Lagerstätte (Carboniferous of the U.S.A.) and the Carboniferous Montceau-les-Mines Lagerstätte from France (Racheboeuf et al., 2002 and references therein). Given the scarcity of the body fossil record, particularly during the Mesozoic, xiphosurid trace fossils are extremely important in the reconstruction of the palaeontological record of these arthropods.

Several reports have attributed Palaeozoic trace fossils to xiphosurids (e.g., Caster, 1938; King, 1965; Bandel, 1967; Hardy, 1970; Goldring and Seilacher, 1971; Eagar et al., 1985; Miller and Knox, 1985; Tyler, 1988; Aceñolaza and Buatois, 1991, 1993; Babcock et al., 1995; Buatois et al., 1998; Babcock et al., 2000; Buta et al., 2005; Lucas and Lerner, 2005; Minkin, 2005). In contrast, Mesozoic occurrences (e.g., Opper, 1862; Nopcsa, 1923; Abel, 1935; Caster, 1939, 1944; Malz, 1964; Romano and Whyte, 2003; Lucas et al., 2006; Pieńkowski and Niedźwiedzki, 2008; Diedrich, 2011; Gaillard, 2011) are scarcer and are mostly restricted to a few Triassic and Jurassic examples (see a Cretaceous record in Section 9).

Over 60 trackways assignable to *Kouphichnium* Nopcsa, which is the archetypal trackway of xiphosurids, were recently found in the uppermost levels of the Lower Cretaceous Agrio Formation, Neuquén Basin, Argentina. The aim of this paper is to describe the morphological variation in these trackways in detail, assign them producers, discuss their

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conditions of preservation, present some palaeoecological and taphonomic inferences, and analyse the importance of their palaeogeographic location, taking into account that xiphosurids were never before reported in the basin and their trackways have not been found in deposits of Lower Cretaceous age around the world.

2. Geological setting

The Neuquén Basin (Fig. 1A) is located in west-central Argentina (northern Patagonia) between 34° and 41°S. The basin contains more than 7000 m of marine and continental deposits of Late Triassic to Palaeogene age (Vergani et al., 1995; Legarreta and Uliana, 1999). Most of the Jurassic and Early Cretaceous deposits are composed of diverse, highly fossiliferous marine facies associated with transgressions from the Pacific Ocean (Howell et al., 2005). The Agrio Formation (Weaver, 1931) is the last unit of a mainly marine interval within the Mendoza Group (Fig. 1B).

The Upper Member, or Agua de la Mula Member (Leanza et al., 2001), of the Agrio Formation is a Late Hauterivian–Early Barremian (Aguirre-Urreta et al., 2007, 2008a) mixed carbonate–siliciclastic marine (Spalletti et al., 2001) and marginal-marine (Pazos and Fernández, 2010; Fernández and Pazos, in press) succession that is exposed in the Neuquén province, Argentina. For the specific area studied here, Pazos et al. (2012) have recently reported marginal-marine facies and provided a thorough discussion of palaeoenvironmental conditions that confirm a tidal control rather storms as traditionally was proposed to explain the evolution of the sedimentary record of the upper unit of the Mendoza Group. This new record supports the interpretation of

the complete infilling of the interval in the eastern and southern parts of the basin, as was suggested by Pazos et al. (2012), rather than erosion, as was proposed by Leanza et al. (2001), with the involvement of the overlying Huitrín Formation.

3. Studied interval

The trackways analysed here are concentrated at the top of one of the uppermost levels of this unit (Fig. 1B), which are part of the upper stratigraphic sequence of Guler et al. (2013), very close to the overlying Huitrín Formation, in outcrops located at Cerro Rayoso (37° 44' 54" S, 69° 56' 9" W; Fig. 1A). Episodes of exposure, such as siliciclastic and carbonate desiccation cracks, represent the end of a previous depositional cycle, while the interval that contains the trackways (Fig. 2) documents a new transgressive cycle. The logged section starts with heterolithic intervals with rippled beds, pelitic levels containing plant debris, slightly bioturbated (*Arenicolites* Salter) fine-grained sandstones and one intensely monospecifically bioturbated sandstone with abundant cf. *Ilmenichnus devonicus* Hecker. Stratigraphically upwards, the sandstone that makes up the studied surface contains very well-preserved ripples (Fig. 3A–B). The ripples are asymmetrical and have mostly sinuous crests that are often unconnected, forming linguoid ripples. They average 2–3 cm in height and are never more than 4 cm high. Some ripples have flat tops that reflect subaerial exposure (Figs. 3A–B, 4D). The dominant eastward palaeocurrent reflects an onshore flow direction, which agrees with the generally accepted eastern border of the basin (see Fig. 1A). Occasionally, wrinkle structures are preserved in the ripple

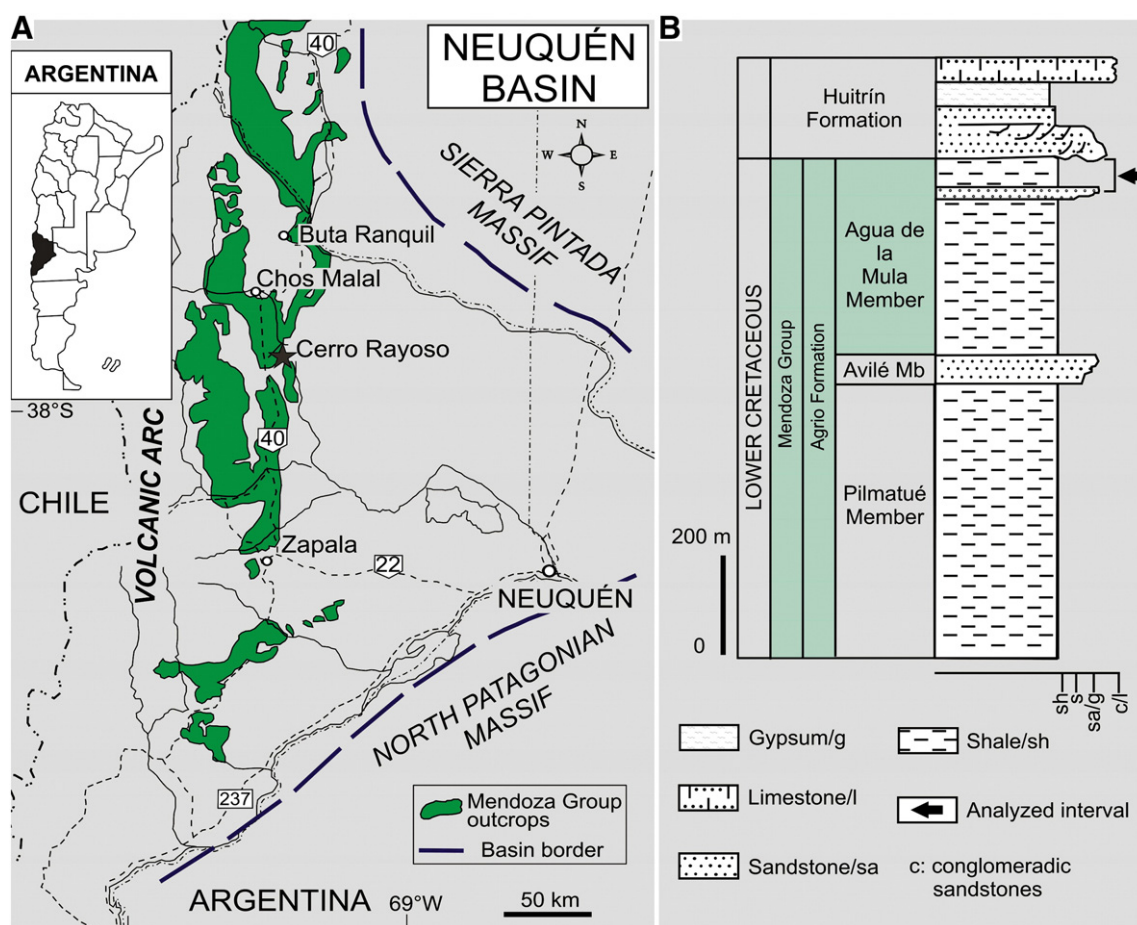


Fig. 1. Neuquén Basin and stratigraphic column of the Mendoza Group: (A) Map of the Neuquén Basin and its location in Argentina. The location of the study site (Cerro Rayoso) is marked with a star. (B) Stratigraphic column of the Mendoza Group. The arrow marks the location of the studied interval.

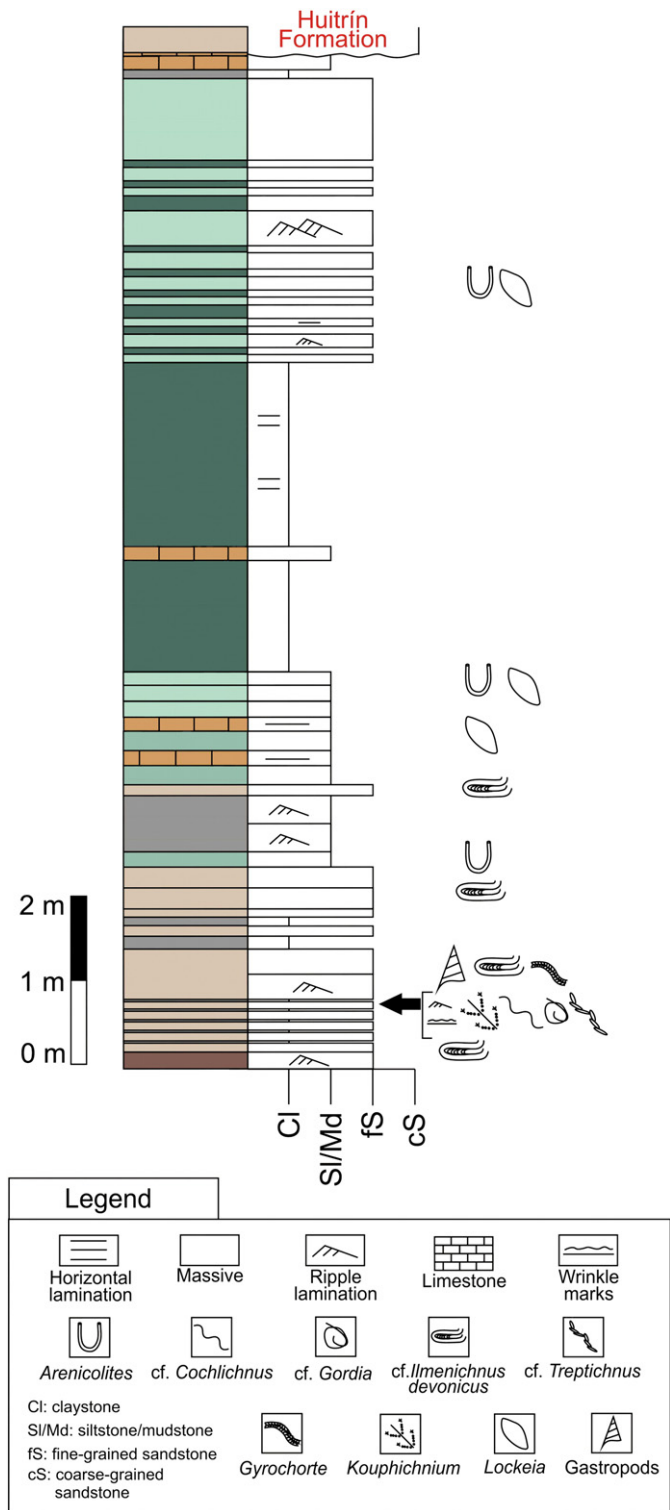


Fig. 2. Logged section of the upper part of the Agua de la Mula Member in the Cerro Rayoso locality. The studied surface is marked with a black arrow.

crests (Fig. 3C). Pelitic and moderately bioturbated (*Arenicolites*, *Gyrochorte* Heer, *I. devonicus*, *Lockeia* James) heterolithic beds overlie the studied bed. Scarce undetermined gastropods (different from the potamidids that were documented in the same locality by Pazos et al., 2012) are present in several levels.

The sedimentological and palaeontological datasets (e.g., fossils and ichnofossils) from the logged section (Fig. 2) indicate that this marine setting was tidally influenced (suggested by the presence of

bipolar structures and reactivation surfaces) and underwent variations in energy and exposure, as was recently documented in the area and in one of the sections studied by Pazos et al. (2012) or further south in the basin (Fernández and Pazos, in press). The surface analysed in this paper is interpreted to have been affected by very shallow depths or exposed in an inter- to supratidal flat depositional setting.

4. Material and methods

Due to the characteristics of the outcrop, only a few specimens (CPBA 20442.1-2; 20443) of the trace fossils were collected. The other examples included in this work are field photographs. The institutional abbreviation CPBA stands for Collection of the Área de Paleontología, Departamento de Ciencias Geológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina.

Morphological terms used for describing arthropod trackways follow the standardised terminology proposed by Minter et al. (2007). The term ‘undertrack’ is used *sensu* Goldring and Seilacher (1971). The xiphosurid trackways were described, interpreted and assigned to an ichnotaxon (see Section 6). Other associated trace fossils were only assigned at an ichnogeneric level because any further description of these ichnofossils was not within the aim of the study.

Vertical sections of the uppermost millimetres of samples CPBA 20442.1-2 were analysed under a scanning electron microscope (SEM; Zeiss Supra 40 with ultrahigh-resolution field-emission scanning) and photographed (see Section 6.3) at magnifications from 2000× to 12,000× using standard sample preparation (thin gold coat). Energy-Dispersive X-Ray Spectroscopy analyses, commonly known as EDS analyses, were also conducted on particular areas.

5. Biological characteristics of xiphosurids implicated in the trackway record

A short summary of some characteristics of xiphosurids is included here. The summary focuses on the interpretation of these trackways and the palaeoecological and palaeoenvironmental inferences that the trackways provide.

These arthropods have inhabited marine, marginal marine and possibly (see Section 8) freshwater environments. In particular, horseshoe crabs (Order Xiphosurida) have extant representatives (Suborder Limulina), and their oldest fossil record is of Early Ordovician age (Rudkin and Young, 2009). Currently, they mainly live in shallow marine waters. The xiphosurid Bauplan is highly conservative (Rudkin et al., 2008), consisting of a crescentic prosomal shield, fused opisthosomal tergites and a styliform telson (Fig. 4A). Extant horseshoe crabs reach 60 cm in length (Ruppert and Barnes, 1994), but documented ancient forms were usually smaller than this.

The ventral surface of their prosoma (anterior tagma) is concave and bears six pairs of appendages (Owen, 1873), the anteriormost of which are the chelicerae (characteristic of chelicerate arthropods; Fig. 4A). These appendages are relatively small and end with a chela or pincer; each is composed of three articles, and the distal two form the chela. The distalmost article is a movable finger, and the penultimate article is an immovable finger; they oppose each other, forming a grasping organ. The next four appendages are chelate walking legs that are similar to each other (Fig. 4A), although the first is sometimes referred to as a pedipalp. These pedipalps are followed by three pairs of unspecialised walking legs. Both pedipalps and the walking legs are similar in morphology. The sixth cephalothoracic appendages are “pushers” (Fig. 4A) that differ from the more anterior limbs. They are used to push the body over the soft surface of the substrate, acting as a ‘snowshoe’ (Caster, 1938). The movable portion of the pusher consists of two main parts: the trochanter–femur and the patella–tibia (Fig. 4A). This last article of the pusher bears a blade with four petal-like spines that flare apart when pushed against the sand and a tarsus with a chelate pretarsus. When modern horseshoe crabs are manipulated and lifted

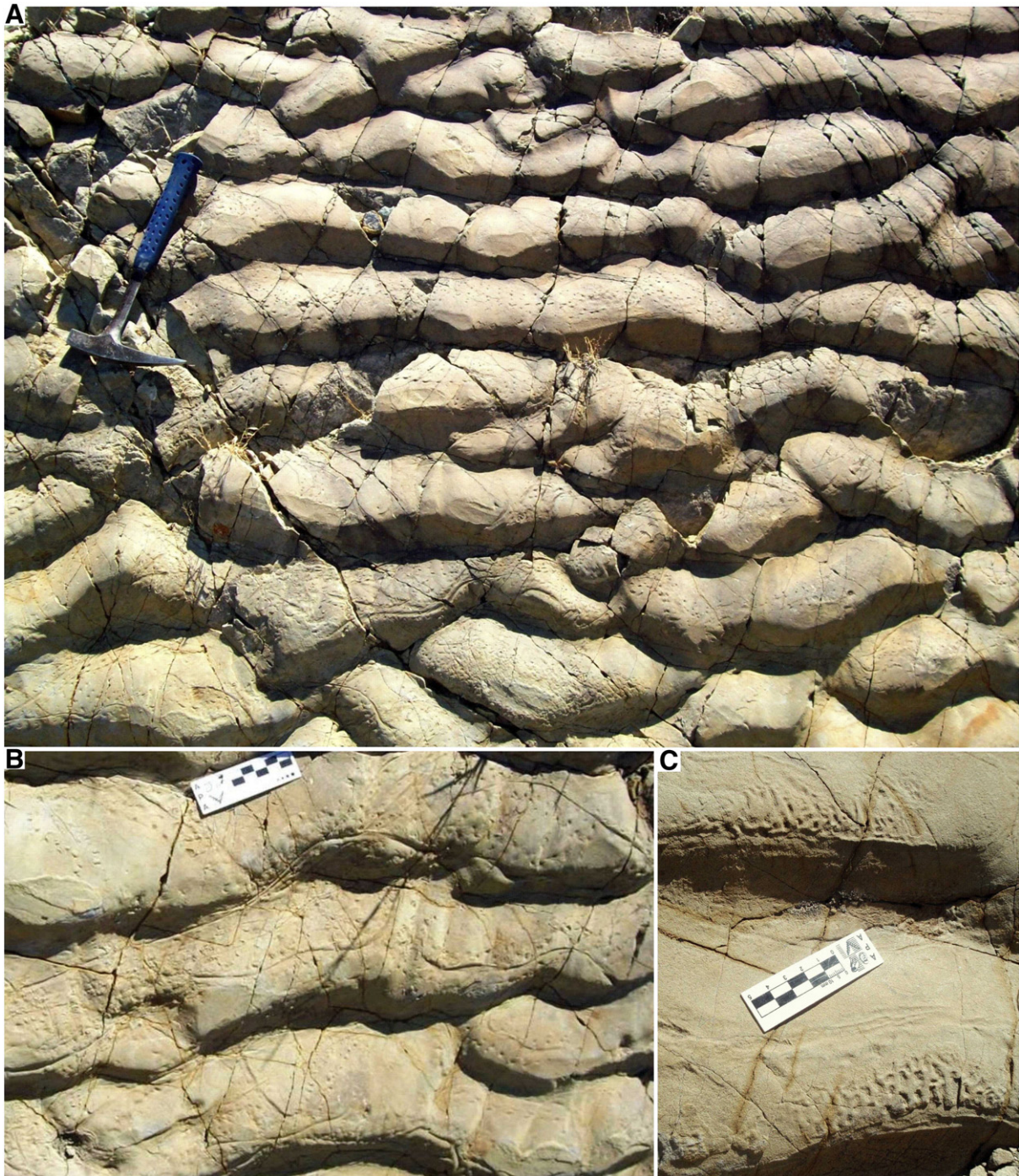


Fig. 3. Photographs of the studied surface. The rock pick is 33 cm long, and the ruler is in cm increments. (A) General view of a portion of the bed. Note the trackways (associated tracks with or without medium drag marks) and the flat tops of some ripples. (B) A close-up of another portion of the studied surface. Note the trackways and the sinuous/linguoid ripples, some of which are flat-topped. (C) Wrinkle structures are visible in some areas of the bed.

from the ground, the pusher leg is also able to stretch out away from the body, first forward and then laterally and posteriorly, to describe a semicircle (see, for example, the footage available at [David Hodgson's web page: http://www.horseshoe-crabs.com/](http://www.horseshoe-crabs.com/)).

Throughout the evolutionary history of the group, these appendages have been subject to only a small amount of differentiation (Owen, 1873; Størmer et al., 1955); the differences are minimal even between the extant species. They are morphologically distinctive and therefore are able to leave very characteristic tracks. The first four pairs of legs can leave V-shaped, bifid or more simple linear to semicircular tracks, while the pusher legs may leave any of these morphologies as well as trifold or birdfoot-like tracks.

The opisthosoma (posterior tagma) bears a telson, which is a long pointed structure that, while rigid throughout its length, is highly mobile (Ruppert and Barnes, 1994).

6. Trace fossils

6.1. Description and interpretation

The trackways are preserved as negative epirelief rows of symmetrically arranged tracks (Figs. 3, 4B–D, 5–7). The external width averages 25 mm and is very uniform, and the maximum preserved length is 60 cm. They are abundant and display a number of variations in

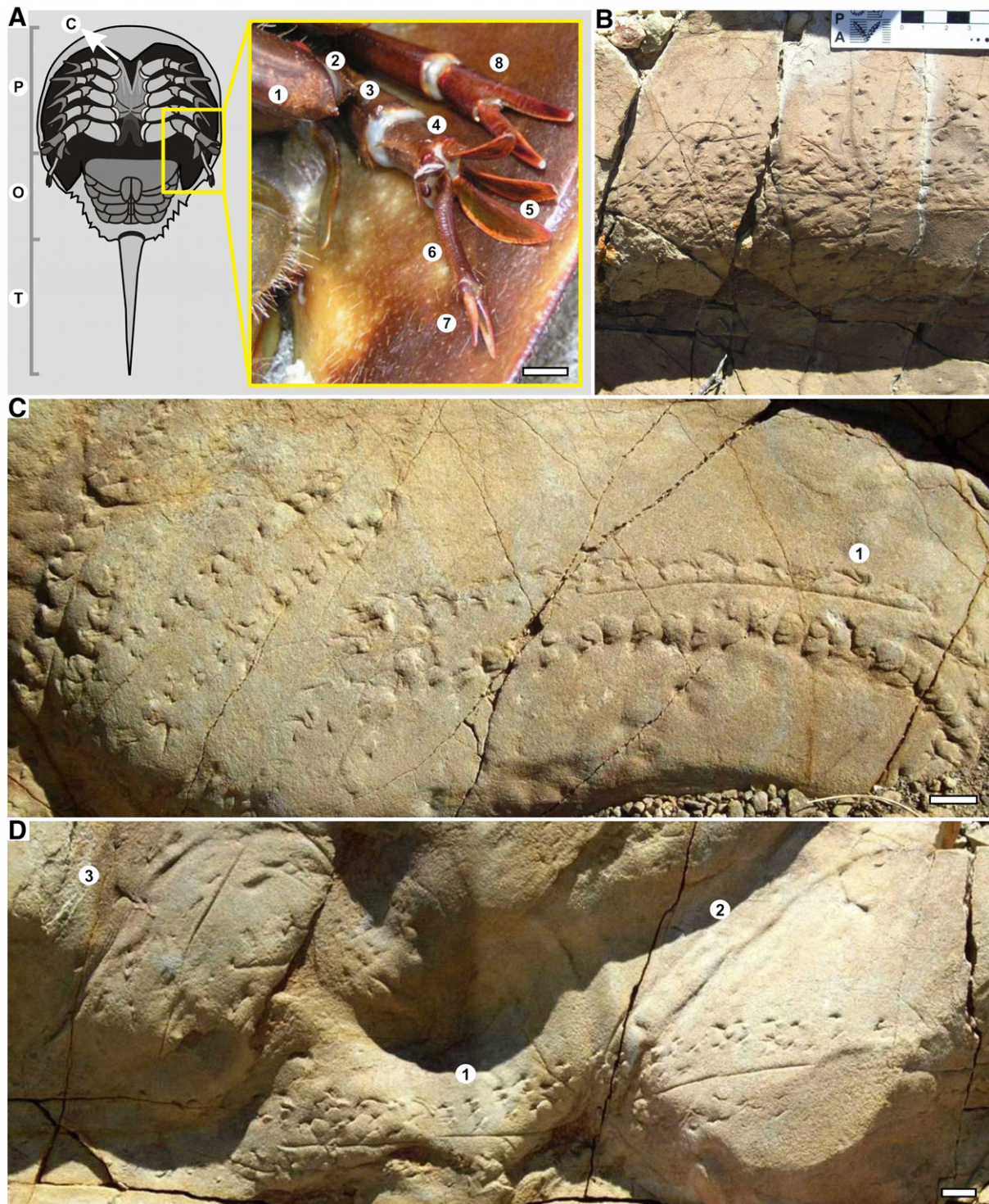


Fig. 4. Pusher leg of a limulid and field photographs of the xiphosurid trackways. Rulers are in cm increments. Scale bars = 1 cm. (A) Line drawing of the ventral side of a Recent horseshoe crab (*Limulus polyphemus*) and close-up photo of the pusher leg and the fifth appendage. Photo courtesy of David Hodgson. (P) prosoma, (O) opisthosoma, (T) telson, (C) chelicerae, (1) trochanter, (2) femur, (3) patella, (4) tibia, (5) blades, (6) tarsus, (7) pretarsus, (8) fifth appendage. (B) An area of the studied surface with a high density of tracks. Series, sets, rows, stride, etc. cannot be determined. (C) Three trackways where the typical push-back pile and anterior drag piles are present. (1) is an example of a very shallow undertrack left by the pusher leg (track morphotype C), which shows that the animal was moving from left to right. (D) Three trackways, one with single (track morphotype A), bifid (track morphotype B) and trifid (track morphotype C) markings and medium drag marks (1), one with straight marks (2) and one with winding marks (3); all have only a few appendage markings and a medium drag mark.

preservation that mostly depend on their orientation with respect to the ripple crests, although undertrack fallout cannot be disregarded (see Section 6.3). They are mostly preserved on the crests and are parallel to them. In some cases, they climb up and down the ripple crests and troughs. Individual series are difficult to determine because they

overlap but more than 60 trackways can be estimated on the studied surface.

Individual tracks are also highly variable, but some morphotypes can be identified. The tracks are mainly cuneiform, linear (simple) or V-shaped (bifid); most were most likely left by the first five pairs

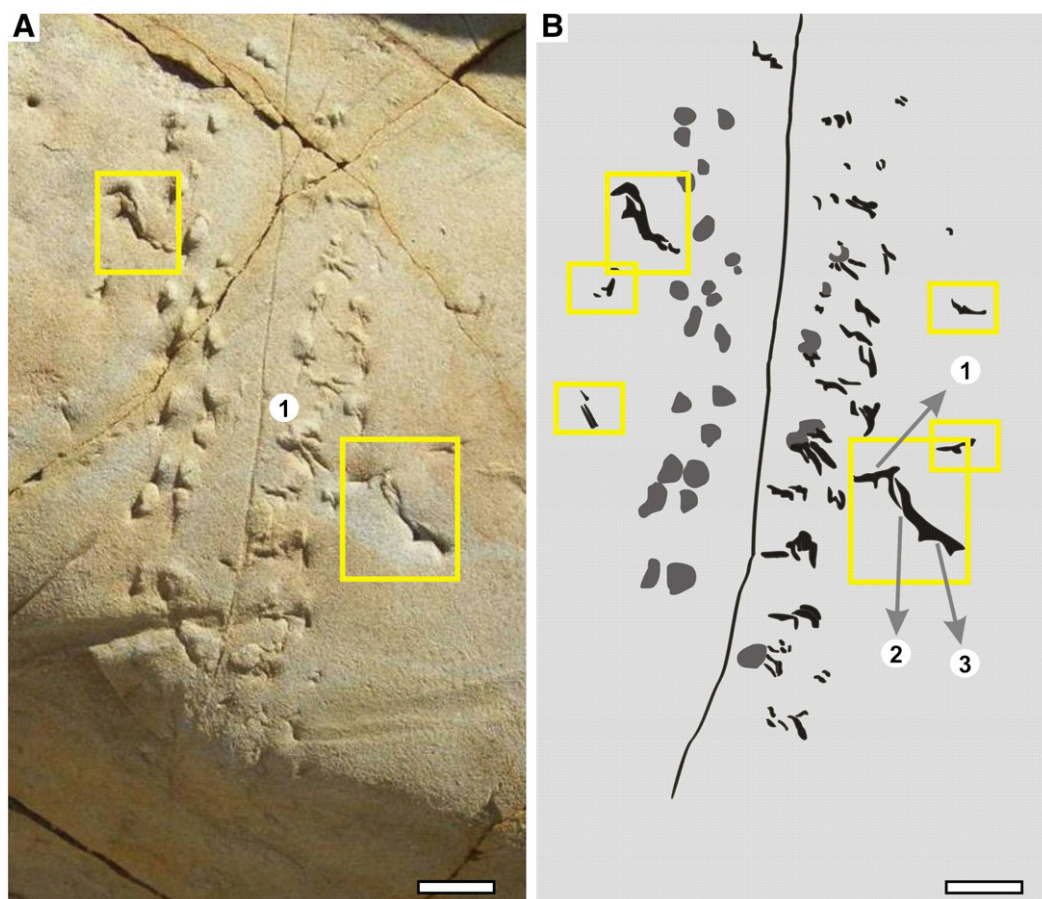


Fig. 5. Trackway running perpendicular to a ripple crest. Scale bars = 1 cm. (A) Field photograph. Note the shallow pusher-leg undertracks with anterior drag piles (1). The animal was climbing the ripple (bottom to top in the picture). Note the bifid, trifold and other more irregular marks, the particular markings of the pusher leg (track morphotype D) left when it stretched out forward and posteriorly (marked with rectangles), the telson marking (medium drag mark) and drag piles. An example of track morphotype C is marked as (1). (B) Line drawing of the trackway shown in (A) detailing positive (grey) and negative (black) structures. Note that the positive aspects have been drawn on the left side of the drawing, particularly the anterior drag piles, because their shadows did not allow the definition of the associated negative structures (markings). The particular markings that the pusher leg left when stretched out forward and posteriorly shown in (A) are also marked with rectangles, and a few similarly generated markings are included. (1) represents the marking made by the trochanter–femur, (2) the marking made by the patella–tibia, and (3) the marking of the blade with its petal-like spines closed.

of appendages, in particular by the third to fifth sets of walking legs. The simple markings (track morphotype A; Fig. 4D) were made with closed pincers, while the bifid markings (track morphotype B; Fig. 6A–B) were produced when the pincers opened and then closed while making the track (Bandel, 1967).

The other type of track is the typical pusher-leg track. These are less abundant than the single or bifid tracks; this difference in relative abundance was also noted by Caster (1938) and Bandel (1967), and it is expected because the pusher legs make up only one of the six pairs of appendages. Although the pusher leg was able to leave bifid imprints (Caster, 1938), which form our track morphotype B, other track morphotypes (C–F) could also have only been produced by the pusher leg and not by the other appendages. Track morphotype C includes imprints that are mostly trifold (e.g., Fig. 6A–B) but can sometimes show a fourth extension (e.g., Figs. 4C, 5A); they are variable and irregular.

One example of these tracks (track morphotype D; Fig. 5) reflects a typical pusher-leg movement that has not been reported in fossil trackways: the stretching out of the pusher legs anterior- and posteriorly. The direction of movement was perpendicular to the ripple crest. The unusual height of the ripples is likely the reason why no other fossil examples of this movement have been reported; in the present case, the ripple was so high that it must have been difficult for the animal to climb it. The backward movement of the pushers is the same motion that present-day limulids use to burrow into the sediment (Wang,

1993), although it is not related to burrowing in this case. The imprints made by the trochanter–femur, the patella–tibia and the closed blades are marked as 1, 2 and 3, respectively, in Fig. 5B.

Another example of a well-preserved pusher-leg track is track morphotype E (e.g., Fig. 6C–D), which resembles those shown by Caster (1938); Figs. 1C and 3) and Gaillard (2011); Figs. 4–5). In our case, the imprints are attributed to the blades (Fig. 6D) and to the tarsus–pretarsus (Fig. 6D).

The medial impressions are relatively shallow, continuous and conspicuous grooves but are not always present; they are interpreted as telson impressions. Most of the telson impressions are along the mid-line, but some are slightly displaced to the side, most likely due to the motility of the telson (Tyler, 1988). Although the pusher tracks alone are diagnostic of the producers (Goldring and Seilacher, 1971), the telson dragging impressions and the variety of preserved tracks made by different appendages suggest that xiphosurids made the tracks. Push-back piles and anterior drag piles (Goldring and Seilacher, 1971) are also present (Figs. 4C and 5).

No clear prosoma impressions (e.g., genal spine marks) were found with the trackways. Some markings in Fig. 7C resemble the structures that Caster (1938) attributed to the dragging of peripheral spines, but in this case they are most likely another preserved variant of pusher-leg tracks (track morphotype F). In addition, a small area of the studied surface bears what could be a very poorly preserved xiphosurid burrow

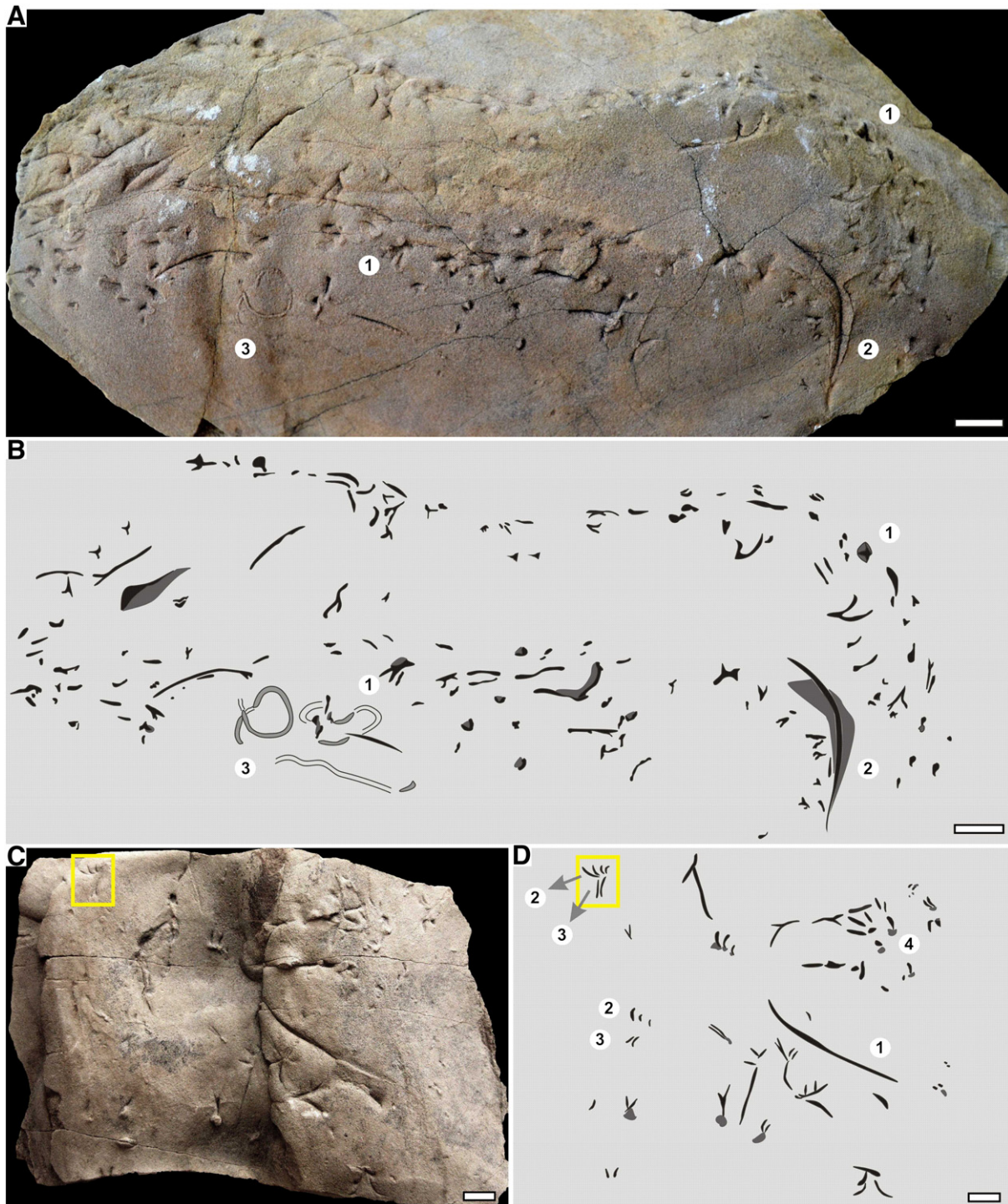


Fig. 6. Samples of xiphosurid trackways on ripples. Scale bars = 1 cm. CPBA 20442.1–2; 20443. (A) Trackway running along the axis of a flat-topped ripple. Track morphotypes C (1), B and A and a medium drag mark (2) are identifiable. Given their orientation and number, it is possible that the tracks belong to more than one individual trackway. A specimen of cf. *Gordia* (3) is present on the lower left side of the picture. (B) Line drawing of B detailing positive (dark grey) and negative (black) structures; cf. *Gordia* in light grey (when positive) and only shown when nothing but the outline of the trail is preserved. (C) Trifid and bifid tracks along with other more complex tracks. A well-preserved pusher-leg track (track morphotype E) is marked with a rectangle. (D) Line drawing of C detailing positive (grey) and negative (black) structures and one possible medium drag mark (1). Morphotype E imprints attributed to the blades (2) and to the tarsus–pretarsus (3) are present in the track. Track morphotype C is also present (4).

(Fig. 3B, lower left side), but because no well-preserved example of a similar structure was found, this possibility is provisionally disregarded.

Two of the trackways in Fig. 4D appear to meet. Given their differences in preservation, however, they were likely not produced at the same time. Fig. 4B illustrates the high density of these tracks in some

areas. In Fig. 7A, two trackways intersect each other in a V-shaped pattern, while in Fig. 7B, two associated trackways have a circular to spiral pattern. A possible ethological interpretation is included in Section 8.

Other ichnotaxa found in the studied surface are preliminarily assigned as cf. *Treptichnus* (Fig. 7D), cf. *Gordia* (Figs. 6A–B, 7E) and

cf. *Cochlichnus* (Fig. 7F). As mentioned earlier, further descriptions of these ichnofossils are not within the aim of this study.

6.2. Ichnotaxonomic assignment of the trackways

Given their diagnostic features (pusher tracks, telson dragging impressions, push-back piles and anterior drag piles), morphology and overall arrangement (see Section 6.1), these trackways are assigned to *Kouphichnium* Nopcsa, 1923. Trace fossils assigned to this ichnogenus are notoriously variable (Häntzschel, 1975), ranging from simple, straight-coursed trackways with distinct tracks to complex, sinuous trackways with superimposed tracks (Romano and Whyte, 2003). These locomotion traces are clearly distinguishable from resting and burrowing/feeding ichnofossils that have also been attributed to xiphosurids (*Limulicubichnus* Miller, 1982; *Selenichnites* Romano and Whyte, 1990).

Numerous ichnospecies are included in *Kouphichnium*, several of which are considered valid (see Häntzschel, 1975; Buatois et al., 1998; Diedrich, 2011; Gaillard, 2011). In this study, the trackways have been classified only at the ichnogenus level. The fossils are not assignable to any existing valid ichnospecies because the telson impressions are only present in some cases and because the trackways have different configurations (straight, winding, circling) and morphotypes. The ichnospecies were introduced with ichnotaxobases that represent minor variants in locomotion. Buatois et al. (1998), Romano and Whyte (2003) and Lucas et al. (2006) noted that a taxonomic review of the ichnospecies is needed.

K. lithographicum (Oppel, 1862) is a straight locomotion trace, while *K. walchi* Malz, 1964 is more curved (and is also usually classified as *mortichnia*). Both holotypes come from the Solnhofen lithographic limestone. Gaillard (2011) noted that trackways with intermediate characteristics between these two ichnospecies have been found in the Solnhofen area and therefore questioned the use of two distinct ichnotaxa. *K. arizonae* Caster, 1944 does not show bifid tracks (track morphotype B), and the series do not overlap. *K. variabilis* (Linck, 1949) does not include the pusher imprints found in track morphotype C. *K. gracilis* (Linck, 1949) lacks a median impression. In *K. didactylus* (Willard, 1935), the individual imprints that comprise one track are longer and thinner than in the material described in this study; only some of the tracks (Willard, 1935, plate 10, Fig. 3) resemble track morphotype E. No existing ichnospecies includes structures such as those of track morphotype D. The material studied here shares characteristics with different ichnospecies without necessarily implying a change in behaviour.

Casamiquela (1965) attributed *Orchesteropus atavus* Frenguelli, 1950 from the Carboniferous of Argentina (Aceñolaza and Buatois, 1993; Pazos, 2000, 2002) to xiphosurids. In track density and relative abundance, the surface presented here resembles the monospecific ichnocoenosis containing high densities of single imprints assigned to *Orchesteropus* that was described by Pazos (2002). *Orchesteropus* resembles *Kouphichnium* but presents two “medial impressions” and widely separated sets, none of which are observed in our material. Seilacher (2007) tentatively refers *O. atavus* to ‘galloping’ xiphosurans.

As stated by Goldring and Seilacher (1971), the variations in preservation and undertrack fallout complicate the ichnotaxonomy of these trackways. Lucas and Lerner (2005) also mentioned this as a problem that obscures any further ichnotaxonomic assignment within *Kouphichnium*. The undertrack fallout of these trackways is discussed further in Section 6.3.

After working with this material and reviewing the literature, we agree that a revision of the ichnogenus is needed. Because of their variety, preservation and association with microbial mats, we believe that these trackways will be of interest to future revisions of *Kouphichnium*.

6.3. Preservation and taphonomy

In laminated beds, each track can be preserved superimposed on successive laminae, changing its pattern with depth (undertrack fallout, *sensu* Goldring and Seilacher (1971). Based on this concept and their work on limulid undertracks (Goldring and Seilacher, 1971), and given the preservation of simple and pusher-leg tracks and telson drag impressions but the lack of any genal grooves, we might assume that most of the tracks are not superficial tracks. However, this is unlikely given the preservation potential (Goldring and Seilacher, 1971). It is more plausible that the tracks are the record of very shallow undertracks (similar to the case reported by Romano and Whyte, 2003). According to Goldring and Seilacher (1971), undertracks are always the sharpest and most complete tracks. It is also possible that tracks from different undertrack levels are preserved on the same horizon (Goldring and Seilacher, 1971) if they were produced at different times, by different pressures or suffered differential erosion because of their positions in the crests and troughs. The markings included in morphotype E (Fig. 7C) that are interpreted as another preservational variant of pusher-leg tracks may correspond to the lowest (or a lower) undertrack level (Goldring and Seilacher, 1971: Fig. 2A).

The preservational characteristics are similar amongst the trackways shown in Fig. 7A–B. In Fig. 7A, the medial impression in the trackway at the lower part of the picture is slightly deeper than that located in the upper portion, but that is expected because the lower impression was made on the ripple's crest.

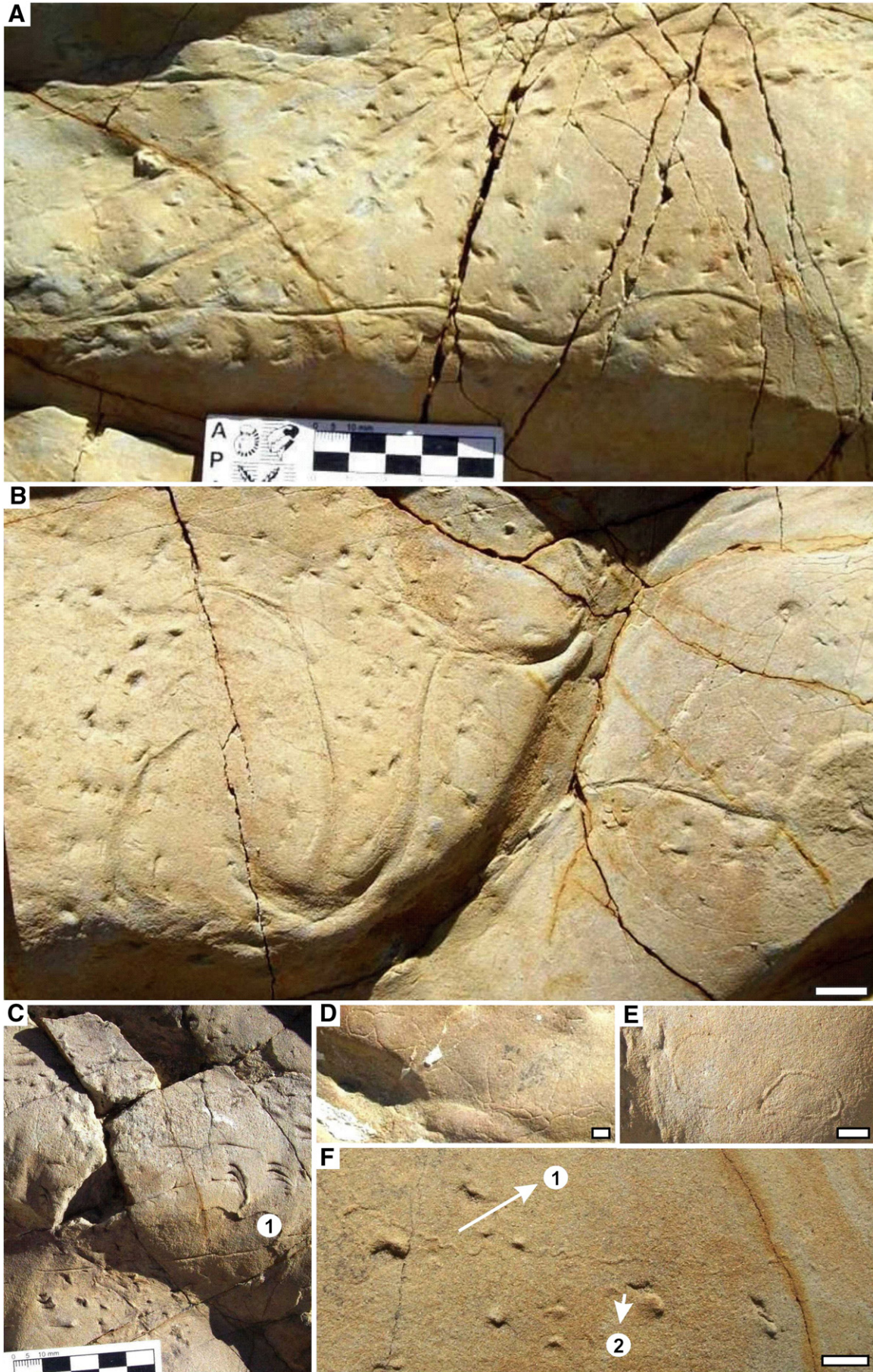
Based on the distinct relief of the ripples, particularly on the lee sides, and the varied orientations of the trackways, it is plausible to assume that the penetration of the walking appendages into the sediment must have been heterogeneous over the analysed surface. Therefore, the differences in preservation must not be attributed entirely to undertrack fallout *sensu* Goldring and Seilacher (1971). Considering that no clear prosoma impressions were found in association with the trackways, it is possible that the body weight was partially supported by water (buoyancy); given the size of the possible producer (see Section 7), the water could have been only a few cm deep, or even emergent, taking into account the flat-topped ripples.

The preservation of the trackways, particularly on the lee sides of the ripples, indicates the substrate was stable at the time the trackways were produced (see below). The tops of the ripples were flattened after the production of the trackways, which implies a decrease in water depth. Some imprints are visible on these flat tops (e.g., Fig. 4C, lower right), but they are very thin and shallow; they represent a lower undertrack level that is only visible due to erosion.

Given the cross-cutting relationships, the associated trace fossils (cf. *Treptichnus*, cf. *Gordia* and cf. *Cochlichnus*) were most likely produced underwater after the xiphosurid trackways.

Many *Kouphichnium* examples and traces that resemble them are found in marginal-marine settings (e.g., Caster, 1938; Bandel, 1967; Miller and Knox, 1985; Babcock et al., 1995; Buatois et al., 1998; Babcock et al., 2000; Buta et al., 2005; Lucas and Lerner, 2005; Minkin, 2005; Diedrich, 2011; Gaillard, 2011) such as estuaries, deltas and tidal flats. According to Babcock et al. (1995), marginal-marine settings are “the environments where potentially preservable horse-shoe crab tracks are being formed during modern times”; the sediment must be cohesive at the time the animal passes through it, and the environment “must inhibit the existence of other creatures” that could destroy the trace. However, conditions that commonly occur in marginal-marine settings are not sufficient to explain the excellent preservation of these trackways on the high, sandstone ripples of the studied surface.

Substrate cohesion might be involved with microbial mats. Microbially induced sedimentary structures (MISS), and therefore the presence of microbial mats, have been found in deposits of



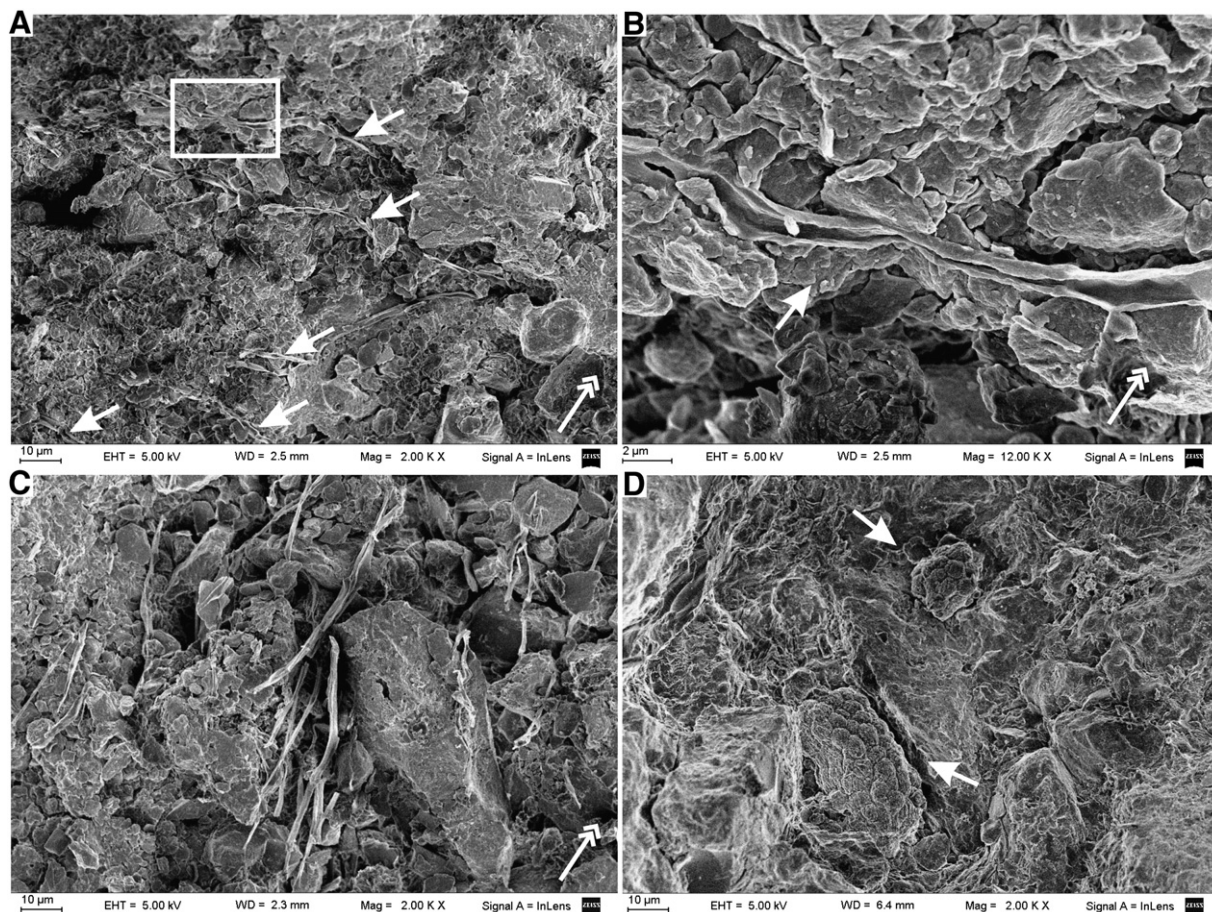


Fig. 8. SEM photographs of fragments of the uppermost part of the studied surface. The double-headed arrow points to and is perpendicular to the bedding plane. (A) Filament-like forms (marked with arrows) parallel to the bedding plane. 2000 \times . (B) Detail of the rectangle in A showing a filament sheath. 12,000 \times . (C) Filament-like microstructures perpendicular to the bedding plane. 2000 \times . (D) Clusters of coccoidal forms. 2000 \times .

different ages (Noffke et al., 2008 and references therein). This notion, together with the presence of wrinkle structures (a type of MISS) on the same level, indicates the involvement of microbial mats in this bed (Hagadorn and Bottjer, 1997). Fragments of the surface of the material (CPBA 20442.1-2) were photographed under a scanning electron microscope (SEM). Filament-like microstructures are present between the sand particles of the uppermost few millimetres of the surface. Most are oriented parallel to the surface and are laterally continuous (Fig. 8A–B), but some are perpendicular to the bedding plane (Fig. 8C). They resemble filaments of bacteria or cyanobacteria such as those from ancient tidal flats described in the literature (Noffke, 2010). The structures preserved here appear to be the sheaths (Fig. 8B) and not the filaments themselves, so they were most likely ensheathed forms, one of the most common morphotypes of benthic cyanobacteria involved in mat and biofilm formation (Gerdes et al., 2000). Small clusters of possible coccoidal forms are also associated with the structures (Fig. 8D). Contrasting areas rich in sheaths with those who lacked them completely, and were instead rich in clay minerals or quartz, the results of the EDS analyses show that the filament sheaths are basically composed of carbon (C = 50.51%). Further studies will deal with purely sedimentological and chemical analyses of this surface.

This endobenthic mat had been formed by the time the trackways were produced. The presence of these filamentous mats explains the

exceptional preservation of the trace fossils through the binding and biostabilisation of the layer, which counteracts erosion (Noffke, 2010) and induces early cementation (Carmona et al., 2012 and references therein). These microbial mats are a necessary condition for the preservation of this small-scale Lagerstätte.

7. Mesozoic record of xiphosurids and possible tracemakers

The Superfamily Limuloidea von Zittel, 1885 comprises all post-Palaeozoic xiphosurids (Selden and Siveter, 1987). Extant xiphosurids are represented by the Family Limulidae von Zittel, 1885, which includes horseshoe crabs. The Limulidae is divided into two subfamilies: the Limulinae von Zittel (including the extant genus *Limulus* Müller) and the Trachypleinae Pocock. The Limulinae, which ranges from the Jurassic to Recent, contains several extinct genera, but none are present within the second subfamily (Feldmann et al., 2011). Only five Cretaceous body fossils have been assigned to Limulidae, several of which are known from single specimens (Feldmann et al., 2011). Three are from North America, one is from Lebanon and one is from Australia. They are all included within the Subfamily Limulinae. Based on the phylogeny and fossil record of the xiphosurids (Størmer, 1952; Rudkin and Young, 2009; Feldmann et al., 2011) and the Early Cretaceous age of these

Fig. 7. Other field photographs of the xiphosurid trackways and associated trace fossils on the studied surface. The ruler is in cm increments. Scale bars = 1 cm in (B) and 5 mm in (D–F). (A–B) Possible mating-related trackways. (A) Two trackways meeting in a V-shaped pattern. (B) Two trackways following a circular to spiral pattern. (C) More examples of the trackways. Track morphotype F is marked as (1). (D) cf. *Treptichnus*. (E) cf. *Gordia*. (F) cf. *Cochlichnus*.

deposits, the mostly likely producers of these trackways are within the Subfamily Limulinae.

The size of horseshoe crabs has, on average, increased over their palaeontological history (Diedrich, 2011). During the Triassic, the width of the prosoma (at least in European examples) ranged from 1 to 15 cm, while in modern specimens it ranges from 15 to 30 cm. Mesozoic and Cenozoic horseshoe crabs are similar to Recent forms, but the increase in size is significant (Størmer, 1952). In xiphosurids, the distance between the extremes of the walking legs is similar to the width of the prosoma (see discussion in Romano and Whyte, 2003). In the present case, the prosoma of the producers was at least 2.5 cm wide. Information on the possible life stage and sex of the producers is included in Section 8.

8. Palaeoecological implications of the trace fossils and modern and ancient analogues

Modern horseshoe crabs live in waters on the continental shelf. They migrate to shallow waters (beaches, intertidal areas) and “walk” extensively only during the limited mating season in the spring (Caster, 1938). They are able to withstand brackish conditions even when they are mainly marine (Caster, 1944). They have been considered by some authors (Sekiguchi and Shuster, 2009 and references therein) to be ecological and environmental generalists; some are essentially estuarine dwellers. They are able to cope with wide-ranging environmental conditions, including hypersalinity. The modern species *Limulus polyphemus* (Linnaeus), for instance, has been observed swimming in shallow nearshore waters or estuaries or crawling along beaches or tidal flats (Babcock et al., 1995), but they only come ashore to tidal flats and beaches of the eastern U.S.A. at the new and full moon high tides during spring and summer (Brockmann, 1990).

When extant horseshoe crabs come to shore to mate, they perform particular and short-lived mating rituals. Males walk in circles then follow a V-shaped pattern until they meet and lock onto the female. The male then climbs onto the female and grasps onto her margins. She continues walking and drags him ashore (intertidal or supratidal setting). On sandy beaches, this sequence of movements leaves characteristic tracks: two sets of tracks following a circular to spiral pattern until they meet, after which only one “combined trackway” can be observed. Some fossil trackways have been attributed to xiphosurid mating rituals. Bandel (1967) notes that when two sets of pusher prints and two sets of median grooves appear together, the “combined trackway” could have been left by two animals attached to each other during mating. Diedrich (2011) recently provided an extraordinary example of xiphosurid trackways related to mating behaviour from Middle Triassic intertidal flats in Germany. In that case, the circular and V-shaped patterns are present in several paired trackways (Diedrich, 2011; Fig. 12). Another interesting example of this behaviour in the fossil record was presented by Colette et al. (2012), who suggested that the mating activities of euthycarcinoid-like arthropods could have resulted in some particular trace fossils they studied from tidal facies of the Elk Mound Group (Cambrian of North America). These authors used Recent limulids as analogues.

The surface studied here may include some examples of this behaviour. Some of the trackways (Fig. 7A–B) follow similar patterns, including the V-shaped pattern (Fig. 7A) and the circles (Fig. 7B) that resemble the “mating dance”.

Females of Recent *L. polyphemus* are larger than males (males may be only two-thirds the size of females). Sexual dimorphism is not documented in this location; the external width of the trackways does not show a bimodal distribution. The maximum difference from the average width is approximately 3 mm, but it could mostly be related to the height differences of the rippled substrate. Diedrich (2011) found a much higher maximum relative difference from the average width (between 6 and 10 cm wide, with an average of 8 cm) and concluded that all the trackways were produced by fully

grown or nearly grown limulids of reproductive age. Because that material presents evidence of mating trackways, males and females were inferred to have produced the tracks. Observations of modern horseshoe crabs by Brockmann and Penn (1992), in particular the fact that sexual dimorphism in modern horseshoe crabs is expressed by a difference in the first pair of walking legs, led Diedrich (2011) to consider why no sexual dimorphism was found in the Triassic material and concluded that it is most likely “the result of the state of preservation and problems in mapping trackways, together with the small size and rare preservation of running leg footprints”. In this study, the small size of the trackways most likely prevents the clear differentiation of sizes. On the other hand, the modern horseshoe crab population has equal numbers of males and females, but given their reproduction cycles, the sex ratio of reproductively active individuals is strongly male biased (Penn and Brockmann, 1995; Johnson and Brockmann, 2010). This fact may obscure sexual dimorphism in the fossil record. In the present case, if the trackways shown in Fig. 7 were in fact related to mating, the male-biased sex ratio possibility seems more likely.

Ethologically, these trackways can be classified as locomotion traces (repichnia) or described as walking/crawling traces following the classification proposed by Gaillard (2011). Other than reproduction-related structures designed for breeding activity (calichnia), no formal ethological category restricted to mating activities has been erected. In our case, the alleged mating behaviour would be linked to locomotion.

Tyler (1988) reported the existence of five instars (juveniles) based on xiphosurid trackways from the Upper Carboniferous Bude Formation (England). In that case, the track set width (‘external width’ in terms of Minter et al., 2007) was measured. Five groups (width intervals) were recognised, the largest of which had a mean external width of 22.9 mm. The smallest Recent horseshoe crab instars bury themselves during high tide and feed constantly when they emerge (Walls et al., 2002, and references therein). In this study, the size of the producers is rather small when compared to most (not all) of the other fossil examples, but no clear burrowing or feeding trace fossil is present, supporting the possibility that this was a reproduction area (Diedrich, 2011). Therefore, unlike the example presented by Tyler (1988), inferences about ontogenetic aspects cannot be made, and an early instar stage is disregarded. More importantly, traces made by juvenile limulids are distinguishable from those made by adult organisms and do not resemble *Kouphichnium* (Martin and Rindsberg, 2007).

According to Størmer et al. (1955), the environment in which xiphosurids lived has changed throughout their fossil record. For example, during the Devonian, xiphosurids lived in marine environments, whereas some Carboniferous and Permian examples have been regarded as fresh water forms. However, Goldring and Seilacher (1971) show that the large number of occurrences of xiphosurid fossil trackways in non-marine settings is a fossilisation bias. They propose that their main habitats have always been shallow marine seas, but the preservation potential (as body- and ichnofossils) is higher in marginal and partially non-marine environments. The Cretaceous record examined here is one of many (see Section 6.3) found in marginal-marine environments throughout geological history. In non-marine sequences, limulinid trace fossils may be useful indicators of very distal marine connexions (see Romano and Whyte, 2003). Miller (1982) affirms that, given their trace fossil record, limulids may have always been capable of withstanding salinity variations in marine and marginal marine environments. The material presented here appears to confirm that idea because salinity fluctuations have been reported for the Agrio Formation (Lazo et al., 2008; Fernández and Pazos, in press).

Few invertebrate trace fossils clearly indicate their producers. *Kouphichnium*, which is one of those ichnofossils, is of great palaeoecological importance in a setting where body fossils of xiphosurids have not been found. Given the resistance of their exoskeletons to breakage and disarticulation (Babcock, 1994), the

presence of horseshoe crab body fossils would not be sufficient evidence of them inhabiting a particular area. Their trace fossils, however, show that they occupied this marginal-marine setting (Babcock et al., 1995), at least during a particular time of the year (perhaps late spring–early summer).

In summary, an actualistic approach would indicate that these trackways are evidence of a high-tide mating ground associated with very shallow water deposits in a Cretaceous tidally influenced environment (as was recently documented by Pazos et al., 2012). Given the preservation characteristics mentioned above, by the time the trackways were produced, the xiphosurids (more likely grown and of reproductive age) remained underwater. A male biased sex-ratio may explain the absence of evidence of sexual dimorphism in the trackways.

9. Cretaceous trackways, body fossils and palaeobiogeographical discussion

Trackways attributed to xiphosurids have been found in Devonian to Jurassic deposits from England (e.g., King, 1965; Goldring and Seilacher, 1971; Tyler, 1988; Romano and Whyte, 2003), Germany (e.g., Nopcsa, 1923; Abel, 1935; Diedrich, 2011), Poland (e.g., Pieńkowski and Niedźwiedzki, 2008), France (Gaillard, 2011), the U.S.A. (e.g., Caster, 1938, 1939, 1944; Bandel, 1967; Miller and Knox, 1985; Babcock et al., 1995; Buatois et al., 1998; Buta et al., 2005; Lucas and Lerner, 2005; Minkin, 2005; Lucas et al., 2006), Canada (e.g., Goldring and Seilacher, 1971) and Argentina (Aceñolaza and Buatois, 1991, 1993; Pazos, 2000). Some have only been described and have not been named. Younger records have been described in an extended abstract presented at the 3rd Annual Meeting of the European Association of Vertebrate Palaeontologists, where Meyer et al. (2005) described dinosaur tracks from Late Cretaceous deposits in Mexico; they also mentioned “faint scratches” that were assigned to *Kouphichnium*.

As mentioned earlier in this paper, only five Cretaceous limulid body fossils have been recorded, and only two are of Early Cretaceous age: *Victalimulus mcqueeni* Riek and Gill, 1971 from Victoria (Australia) and *Crenatolimulus paluxyensis* Feldmann et al., 2011 from Texas (U.S.A.). Therefore, the studied surface represents the second Cretaceous fossil record of xiphosurids in the Southern Hemisphere and the first record of xiphosurid trackways from the Lower Cretaceous worldwide.

The main large-scale limitations on the distribution of Recent horseshoe crabs are the extent of continental shelves (which define space availability), certain tidal regimes, and low temperatures (Sekiguchi and Shuster, 2009). Although extant xiphosurids have planktonic larvae, their long-range dispersal is limited (Botton and Loveland, 2003).

During the Early Cretaceous, the Neuquén Basin was connected to the Pacific Ocean through an island arc chain to west (Fig. 1A); the arrival of nektonic (and planktonic in larval stage) North Pacific and Tethyan faunas along the western South American margin has already been documented (Aguirre-Urreta et al., 2008b). The palaeogeographic location of the basin produced warm temperatures and shallow waters. The palaeogeographic reconstruction of the Early Cretaceous (Hauterivian–Barremian) by Smith et al. (1994) and the marine connexions of the Neuquén basin supported by Lazo (2007) and Aguirre-Urreta et al. (2008b), Fig. 7) suggest a marine connexion between this locality and the Australian and North American sites. Nevertheless, given the large-scale limitations on the distribution of Recent horseshoe crabs, a direct passage between the three localities would most likely imply a continuous palaeocoastline with relatively shallow waters, which has not been documented.

Today, horseshoe crabs are found in two regions of the world. Three species occupy coastal waters from India to Japan (including the Dutch East Indies and Philippine Islands), and one (*L. polyphemus*) is found along the North American Atlantic coastline from Maine to

the Yucatan (Walls et al., 2002). Shishikura et al. (1982) indicates that the divergence of the American species from the Indo-Pacific species took place approximately 135 million years ago. Shuster (1982) proposed that the ancestor of the present species originated in the Mesozoic in Europe and migrated east and west. These studies were based on genetic analyses and the distribution of extant species. No palaeobiogeographic, migration or distribution studies on xiphosurids have been carried out using the fossil record. Because the Cretaceous records are scarce, the presence of xiphosurids in the Lower Cretaceous of Patagonia is relevant for further reconstructions of the distribution of the American and Asian groups.

10. Conclusions

- Abundant xiphosurid trackways with a number of variations in preservation are found in the uppermost levels of the Agrio Formation. The inferred palaeoenvironment is a tidally influenced marginal-marine setting with signs of subaerial exposure. The trackways are found on ripples that indicate an onshore flow direction.
- The trackways are shown and described in this paper. Five track morphotypes are established; three are only attributable to the pusher leg, while one reflects a typical pusher-leg movement that has not been reported previously in fossil trackways.
- The trackways are assigned to *Kouphichnium*. The heterogeneity of the material prevents the trackways from being assigned to any ichnospecies. This example also supports the idea that a taxonomic review of the ichnospecies is needed. Given their variety and great preservation, these trackways may be useful in solving the ichnotaxonomic problem of the *Kouphichnium* ichnospecies.
- The involvement of microbial mats in the preservation of the trackways is documented by the presence of filament sheaths between the sand particles in the uppermost few millimetres of the studied surface. The presence of these filamentous mats explains the exceptional preservation of the trace fossils through the binding and biostabilisation of the layer, which is a necessary condition for the preservation of this small-scale Lagerstätte.
- Based on the phylogeny and fossil record of the xiphosurids and the Early Cretaceous age of these deposits, these trackways were mostly likely produced by members of the Subfamily Limulinae.
- The studied surface could represent a high-tide mating ground associated with a very shallow water deposit on a warm Cretaceous tidal flat. The xiphosurids remained underwater while the tracks were produced. A male biased sex-ratio may explain the absence of evidence of sexual dimorphism.
- These trackways represent the first record of xiphosurid trackways from the Early Cretaceous (worldwide) and the second fossil record of this group for the Cretaceous in the Southern Hemisphere.
- Given the Early Cretaceous age and the palaeogeographic location (Patagonia), this finding is relevant for future palaeobiogeographic, migration and/or distribution studies on fossil limulids.

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