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A limulid trackway from the Late Jurassic (Tithonian) Lagerstätte of Canjuers (Var, France)

Une piste de limulidé dans le Lagerstätte du Jurassique supérieur (Tithonien) de Canjuers (Var, France)

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A B S T R A C T

The first record of an invertebrate trackway from the lithographic limestones of the Canjuers Lagerstätte is described here. The preserved part of the trackway is approximately 39 cm long and 17 cm wide; it consists of two successive sets of imprints and the beginning of a third one. Two kinds of imprints have been recorded: the first one, well-preserved, is tetradactyl and the second one is straight, narrow and in sets of two or three imprints. The tracks described in this paper are similar to the type specimen of the ichnogenus *Kouphichnium*. The trackway, corresponding to locomotion behavior and left by a 26 cm wide specimen, can be related to the ichnospecies *Kouphichnium lithographicum*. This is the first evidence of a limulid from the Canjuers Lagerstätte.

R É S U M É

Nous décrivons ici la première dalle à empreintes d'invertébré retrouvée dans les calcaires lithographiques du Lagerstätte de Canjuers. La piste visible à la surface de la dalle a une longueur de 39 cm, pour une largeur d'environ 17 cm. Elle est formée de deux paires de séries d'empreintes successives ainsi que du début d'une troisième. Les empreintes se présentent sous deux formes : les mieux préservées sont tétradactyles, alors que les traces intermédiaires, par groupes de deux ou trois lorsqu'elles sont visibles, sont fines et allongées. Les empreintes décrites dans cet article sont similaires à celles du spécimen type de l'ichnogenre *Kouphichnium*. La piste, assimilée au comportement locomoteur d'un spécimen d'environ 26 cm de large, peut être associée à l'ichnoespèce *Kouphichnium lithographicum*. Il s'agit de la première mention d'un limule dans le Lagerstätte de Canjuers.

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1. Introduction

Several Konservat-Lagerstätten are known from the Late Jurassic of Europe, including Canjuers (Var, France), Cerin (Ain, France), Crayssac (Lot, France), and Solnhofen (Bavaria, Germany). The last is probably the most famous because the Solnhofen lithographic limestones preserve a rich assemblage of fossilized organisms including the 11 specimens of the oldest known bird, *Archaeopteryx lithographica* (Wellnhofer, 2009). During the Late Jurassic, Europe was a vast archipelago and the Konservat-Lagerstätten listed above represent marine or estuarine environments (Fig. 1). The Tithonian limestones of Crayssac represent a large littoral mud-flat with sedimentation in the inter- to supratidal area, whereas most of the localities in the Solnhofen area, and the Cerin and Canjuers Lagerstätten preserve lagoonal environments (Atrops, 1994; Barthel et al., 1990; Bernier, 1984; Charbonnier et al., submitted for publication) (Fig. 1). Until now, each of them has yielded tracks and trackways of vertebrates and/or invertebrates. Turtle and limulid trackways have been found in Cerin (Gaillard, 2011; Gaillard et al., 2003), Solnhofen has preserved limulid and crustacean traces (e.g. Barthel, 1974; Lomax and Racay, 2012; Malz, 1964; Vallon and Röper, 2006), and crustacean and limulid traces have been discovered at Crayssac (Gaillard et al., 2005), as well as pterosaur, dinosaur, crocodylomorph and turtle tracks (Mazin et al., 1997). Rhynchocephalian trackways were briefly mentioned in the Canjuers lithographic limestones (Michard, 1989) (Fig. 1).

Here we describe and study the first trackway from the Late Jurassic lithographic limestones of Canjuers. This Lagerstätte is famous for the skeleton of the small coelurosaurian dinosaur *Compsognathus longipes* (Peyer, 2006) as well as many other vertebrates including turtles, pterosaurs, crocodilians, rhynchocephalians, actinopterygians and chondrichthyans (Fabre et al., 1982), marine invertebrates including echinoderms, brachiopods, crustaceans, ammonites and bivalves (Roman and Fabre, 1986; Roman et al., 1991), and plants (Roman et al., 1994).

2. Material and brief introduction to the Canjuers Lagerstätte

2.1. Origin of the studied slab

The original slab was discovered during the 1970s among a batch of large slabs (Dalles de Provence) sold by quarry-workers for paving. Later, it was sold by the first owner to Mr Guy, who graciously loaned the slab to the Muséum national d'histoire naturelle (MNHN) in Paris, in order to cast and study it. The original slab is at the moment in a small French museum, the Préhistorama de Rousson, in the Department of Gard (catalogue number: MPR1). Unfortunately, some 40 years after its discovery, it is impossible to find out where the slab comes from with certainty. Nevertheless, the main quarry of Canjuers was exploited during the 1970s for the Dalles de Provence and the former owners of the slab stated to Mr Guy that it came from this site. There is no reason to doubt this testimony. Moreover, the sedimentological features of the slab fit perfectly with other slabs stored at the MNHN.

The original slab preserved the negative imprint of a trackway composed of 18 individual tracks (Figs. 2 and 3). It was cast at the MNHN in order to obtain the counterpart of the slab and study the positive imprint of the trackway (Fig. 4).

The trackmaker had been first considered a pterosaur based on the main imprints. But, given the presence of intermediate tracks, the second hypothesis establishing

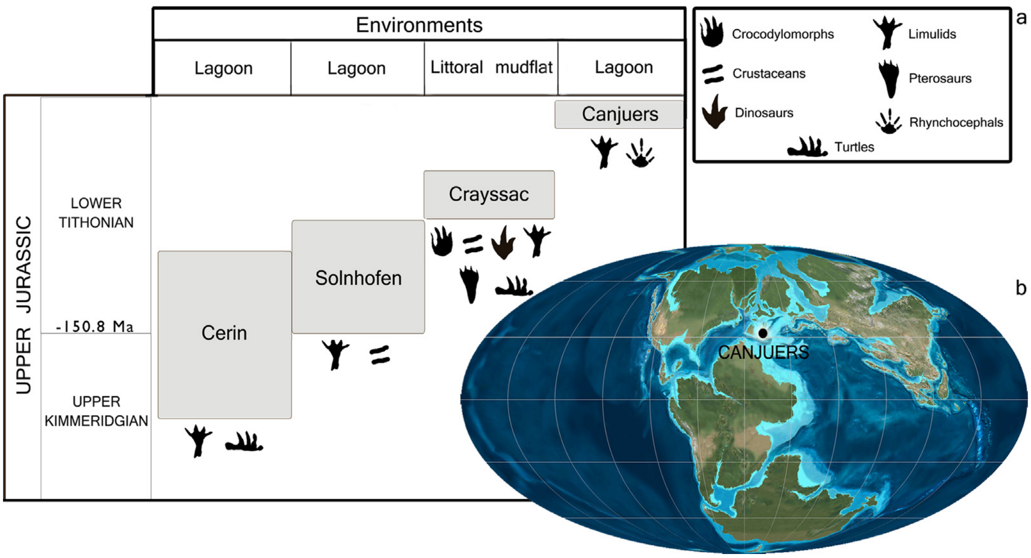

Fig. 1. a: main Late Jurassic Lagerstätten from western Europe with tracks found in each one and their environment functions of time (modified from Mazin et al., 1997); b: location of Canjuers in Late Jurassic paleogeography (150 Ma) (modified from http://cpgeosystems.com).

Fig. 1. a : principaux Lagerstätten du Jurassique supérieur d'Europe occidentale, avec les empreintes trouvées dans chacun d'eux et leur environnement en fonction du temps (modifié d'après Mazin et al., 1997) ; b : localisation de Canjuers dans la paléogéographie du Jurassique supérieur (150 Ma), (modifié d'après http://cpgeosystems.com).

Fig. 2. Original trackway of *Kouphichnium lithographicum* from the Late Jurassic of Canjuers. Scale bar = 10 cm.
Fig. 2. Piste originale de *Kouphichnium lithographicum* du Jurassique supérieur de Canjuers. Barre d'échelle = 10 cm.

a limulid as the trackmaker was more congruent with our observations. In the past, limulid tracks have already been mistaken for bird or pterosaur tracks (Lockley et al., 2008; Wellnhofer, 1991). Moreover, the trackway from Canjuers is very similar to one recently described from Cerin (Gaillard, 2011).

2.2. Location and brief historical introduction to the Canjuers Lagerstätte

The Canjuers Lagerstätte is located in the military camp of Canjuers, in southeastern France, in the Haute-Provence region, more precisely in the Department of Var, near the village of Comps-sur-Artuby. The Canjuers lithographic limestones were first exploited in the late 1960s by several families of quarry-workers to produce ornamental stones called "Dalles de Provence" (see above). The commercial exploitation continued until the early 1970s when Canjuers was declared a military camp. Fortunately, access to the site by the scientific community was still granted. The first scientific studies of the locality date back to the 1970s (Ginsburg and Mennessier, 1970). Until the early 1980s, J. Fabre led the excavations at Canjuers (Fabre et al., 1982). During the 1980s, the Ghirardi family sold their collection of fossils, including the small dinosaur *Compsognathus*, to the MNHN. From 1983 to 1993, paleontologists from the Paris Museum excavated the site exclusively during the summer; these excavations resulted in the discovery of new fossils (de Broin, 1994; Poyato-Ariza and Wenz, 1994). From the mid-nineties to 2004, paleontologists cancelled field trips to the Canjuers Lagerstätte. In 2010 and 2011, two geological field seasons permitted a fuller understanding of the geology, sedimentology, and paleoenvironmental history of the site (Charbonnier et al., unpublished data).

2.3. Local geological context

The ten quarries of Canjuers that have yielded fossils are located in a single area called "Les Bessons", which covers a surface of more than 15 ha. The outcrop is composed of three distinct lithological units. There are, from the base to the top, lithographic limestones, bioclastic limestones and sublithographic limestones. Only the basal unit, characterized by alternations of thin lithographic limestone beds, corresponds to the Canjuers Konservat-Lagerstätte (Charbonnier et al., unpublished data). The composition of the lithographic beds indicates that the different units were deposited during different hydrodynamic cycles within the lagoon. Indeed, the lagoon's water was evaporating or refilling depending on the connection with the open sea. This connection was based on environmental conditions. Sometimes a complete rupture of this link caused the drying of the lagoon. Hence, the exceptional preservation of the fossilized organisms was favored, above all if microbial

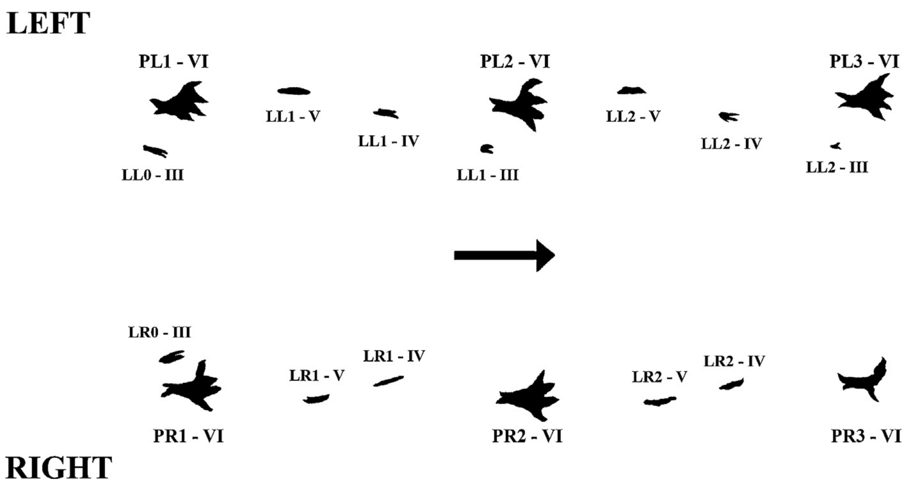

Fig. 3. Drawing of the whole trackway showing the sets of imprints and their designation. The arrow indicates the direction of movement. Not at scale. PL: left pusher, PR: right pusher, LL: left leg, LR: right leg.
Fig. 3. Dessin de la piste entière, montrant tous les ensembles d'empreintes et leur dénomination. La flèche indique le sens du déplacement. Non à l'échelle. PL : empreinte principale gauche, PR : empreinte principale droite, LL : appendice gauche, LR : appendice droit.

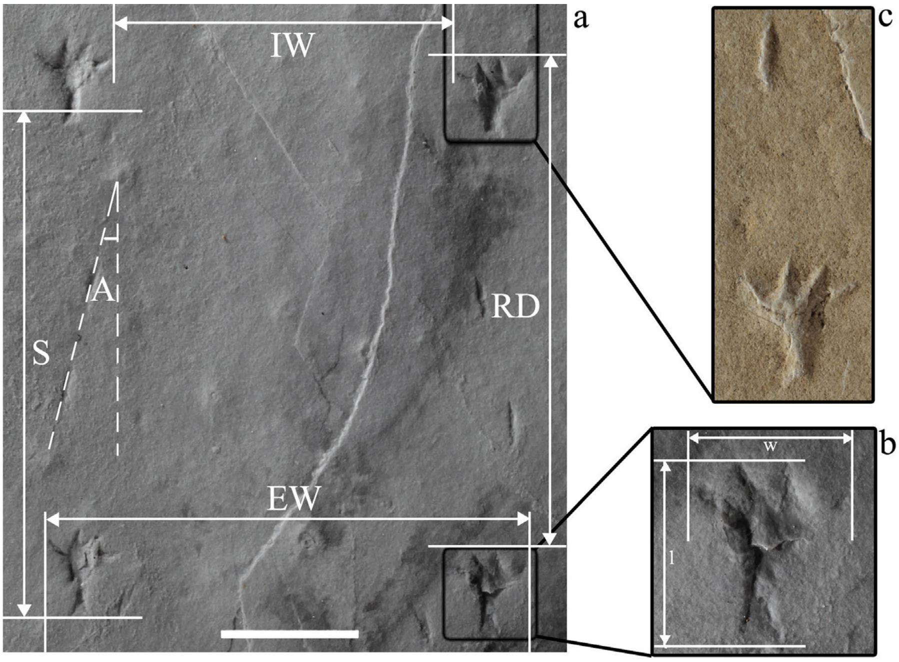

Fig. 4. Main measurements made on the slab: a: a part of the trackway (positive imprints) and measurements associated; b: detail of a main "pusher" imprint (positive) and measurements associated; c: detail of a main and an intermediate imprints (negative) on the original slab. EW: external width, IW: internal width, S: series, RD: repeat distance, w: width, l: length, A: angle. Scale bar = 5 cm.

Fig. 4. a : principales mesures réalisées sur la piste (empreintes) ; b : détail d'une empreinte principale (empreinte) ; c : détail d'une empreinte principale et d'une intermédiaire sur la dalle originale (contre-empreintes). EW : largeur externe, IW : largeur interne, S : série, RD : enjambée, w : largeur, l : longueur, A : angle. Barre d'échelle = 5 cm.

mats were laid down (Atrops, 1994). The organisms found in the lithographic limestones are either from marine or continental environments.

3. Methods

3.1. Measurements

The first observations were done by the naked eye in order to observe the main characteristics of the trackway such as the alignment and the disposition of the tracks. Then we used the methodologies proposed for locomotion traces of arthropods (Gaillard, 2011; Trewin, 1994) in order to carry out precise measurements on the whole trackway. We first evaluated the external (EW) and internal (IW) widths of the trackway, which were measured between each pair of main tracks and correspond to the maximum and minimum width of the trackway. We estimated the length of each series (S) of imprints. One series is composed of a main imprint and the three following intermediate imprints found on the same side of the trackway. The stride was also measured; it corresponds to the repeat distance (RD), it means the length between two sets of imprints. The width (w) and length (l) of each main imprint were evaluated. Concerning the intermediate tracks, we only estimated the length. Finally, the value of the angle (A) to mid-line was measured (Fig. 4). All the measurements were made twice using a ruler graduated in millimeters. In order to check some of them, we used the software Mesurim (Madre, 1998–2011) on digital pictures of the slab.

4. Systematic Paleontology

Ichnogenus *Kouphichnium* Nopsca, 1923

Diagnosis (following Häntzschel, 1975, p. W75). Heteropodous tracks of great variability; complex track consisting of two kinds of imprints: (1) two chevron-like series each of four oval or round holes or bifid V-shaped impressions or scratches, forwardly directed (made by anterior four pairs of feet); and (2) one pair of digitate or flabellar, toe-shaped or otherwise variable imprints (made by bird-foot like 'pushers' of fifth pair of feet, with their four or five leaf-like movable blades); track with or without median drag mark.

Ichnospecies *Kouphichnium lithographicum* Oppel, 1862

Diagnosis. This ichnospecies was first proposed for simple straight locomotion traces found in the Solnhofen area. The slab from the Canjuers lithographic limestones exhibits a simple, straight trackway and was thus assigned to *K. lithographicum*.

5. Description

5.1. Trackway morphology

The preserved part of the trackway is symmetrical, straight and 39 cm long. It represents two complete sets of imprints and the beginning of a third one. The two first sets show two well-preserved main imprints and two or

Table 1
Measurements on the trackway. External (EW) and internal (IW) width of the trackway, series (S) length, repeat distance (RD) and angles (A) with the median axis of the trackway. PL: pusher left, PR: pusher right, SL: series left, SR: series right.
Tableau 1
Mesures réalisées sur la piste. Largeurs externe (EW) et interne (IW), longueurs des séries (S), enjambées (RD) et angles (A) par rapport à l'axe médian de la piste. PL : empreinte principale gauche, PR : empreinte principale droite, SL : série gauche, SR : série droite.

	EW (mm)	IW (mm)
PL1 – PR1	172	119
PL2 – PR2	178	123
PL3 – PR3	?	122
Mean	175	121
S (mm)		
Left		
SL1	181	
SL2	182	
Right		
SR1	178	
SR2	?	
Mean	180.3	
RD (mm)		
Left		
PL1 – PL2	177	
PL2 – PL3	181	
Right		
PR1 – PR2	175	
PR2 – PR3	?	
Mean	177.7	
A (degrees)		
Left		
SL1 – SL2	14	
SL2 – SL3	16	
Right		
SR1 – SR2	12	
SR2 – SR3	13	
Mean	13.75	

three intermediate imprints. The third set is located at the end of the slab and only preserves main imprints (intermediate are not visible); the one on the right is damaged at the extremity. No median imprint was observed on the trackway, which means that the limulid's telson was not in contact with the substrate during its motion (Fig. 3). The mean of the external width of the trackway is 175 mm and the mean of the internal width is 121 mm. The average series length is 180 mm (SL1 corresponds to the distance between PL1 and LL1-III, SL2 is from PL2 to LL2-III, the same for the right side). The mean stride is 178 mm. The angle to the mid-line was measured in the four cases; its mean is 13.75° (Table 1).

5.2. Main imprints

The main imprints of the trackway are the most external ones. In each set, two of them are symmetrically opposed: they correspond to the imprint left by the sixth pair of legs. These tracks are triangular-shaped: their anterior part is tetradactyl whereas the posterior part is narrower and bifid. They are the result of the contact between the substrate and the extremity of the sixth pair of legs, which leads to the flattening of their five individual pieces: four pieces spreading on the anterior part of the extremity and the fifth, which is bifid at the end, restoring the balance on the posterior part. The six imprints show equivalent proportions. On average, imprints made by the left leg VI (PL) are 28 mm long and 25.7 mm wide. Those of the right leg VI (PR) are 31 mm long and their width is 25.5 mm (Table 2).

Table 2
Measurements on the imprints. Length (l) and width (w) of the pusher imprints (legs VI) and length (L) of the intermediate imprints (legs III, IV and V), left and right. PL: left pusher, PR: right pusher, LL: left leg, LR: right leg.
Tableau 2
Mesures réalisées sur les empreintes. Longueur (l) et largeur (w) des empreintes principales (appendices VI) et longueur (L) des empreintes intermédiaires (appendices III, IV et V), gauches et droites. PL : empreinte principale gauche, PR : empreinte principale droite, LL : appendice gauche, LR : appendice droit.

Pushers	l (mm)	w (mm)	Legs	L (mm)
Left				
PL1	28	25	LL0 – III	18
PL2	27	26	LL1 – V	19
PL3	29	26	LL1 – IV	17
			LL1 – III	9
			LL2 – V	15
			LL2 – IV	15
			LL2 – III	12
Mean	28.0	25.7	Mean	15
Right				
PR1	31	25	LR0 – III	14
PR2	31	26	LR1 – V	15
PR3	?	?	LR1 – IV	16
			LR1 – III	?
			LR2 – V	18
			LR2 – IV	10
			LR2 – III	?
Mean	31.0	25.5	Mean	G

5.3. Intermediate imprints

These vary in number: two or three are in each set. Among them, two are fine, elongate and single: they are the imprints of appendages IV and V. The other type is slightly thicker and double: it is the mark of the third appendages, the first walking legs. The marks of appendages IV and V are inserted between two main imprints, and more internal than the latter. They are straight and slightly oblique because their anterior part points to the median axis of the trackway. Tracks of appendages III are located next to the main imprints, on their inner side. Two imprints do not appear on the trackway: LR1 – III and LR2 – III. Appendage III does not always contact the substrate, probably because of their small size or because we are dealing with undertracks (Goldring and Seilacher, 1971). The latter hypothesis is nevertheless unlikely because the preservation of imprints of the other appendages is good. On average, intermediate imprints are 15 mm long on the left and 14.6 mm long on the right of the trackway (Table 2).

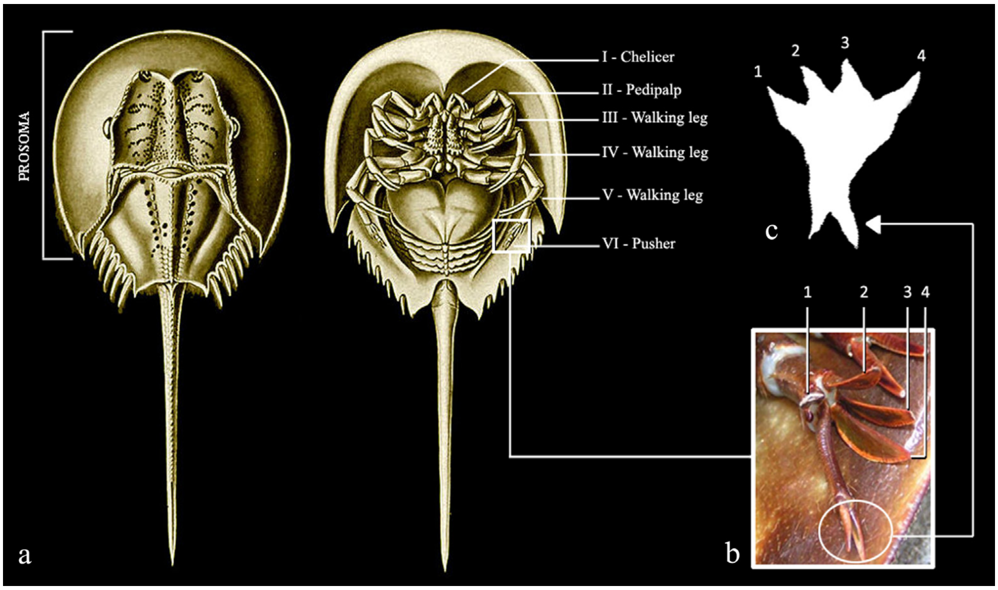

Fig. 5. a: dorsal (left) and ventral (right) view of an extant limulid. On the ventral view, the different appendages on the prosoma are visible (modified after Dunlop, 2012); b: detail of the main "pusher" appendage; c: main "pusher" imprint from the studied trackway.

Fig. 5. a : faces dorsale (à gauche) et ventrale (à droite) d'une limule actuelle. La face ventrale montre les différents appendices portés par le prosome (modifié d'après Dunlop, 2012) ; b : détail de l'appendice principal ; c : empreinte principale de la piste étudiée.

6. Discussion

6.1. Limulid morphology

Limulidae belong to Xiphosura, a taxon that includes both extinct and extant families (Dunlop, 2012). Recent forms are marine and their body plan consists of two parts: the cephalothorax or prosoma and the abdomen or opisthosoma (Fig. 5a). The latter ends in a long, peaked, tail called the telson. The upper surface of the cephalothorax is covered by a solid, horseshoe-shaped carapace and its underside bears six pairs of uniramous appendages (Dunlop, 2012). At the front of the animal, the first pair of appendages (I), the chelicers, is the smallest. They are used to grasp food and are followed by a pair of pedipalps (II) and four pairs of walking appendages, or legs (III to VI). Within Chelicerata, pedipalps are often transformed, yet within the limulids they are morphologically identical to the legs although smaller. The three first pairs of legs (III to V) are real locomotory appendages, bifid at their ends (Fig. 5a). The last pair (VI) is also used in locomotion but is transformed into more complex and longer legs, adapted to push the animal forward and is often called the pushers. The last segment of the pusher is not bifid anymore but is formed of five individual pieces (Fig. 5b).

Pusher appendages are only known within Xiphosura (Davis et al., 2007; Eiseman and Charney, 2010). Thus, within Chelicerata, Limulidae is the only group able to leave a trackway such as the one we are studying. Pycnogonida and Arachnida also leave numerous tracks but none of them looks like the main imprints here (Davis et al., 2007).

6.2. Locomotion behavior

The morphology of a complete limulid trackway is now well established based on observations of fossil and recent taxa (Caster, 1944; Gaillard, 2011). It is composed of two main lateral imprints, corresponding to legs VI (Fig. 5c). There are also eight intermediate imprints, four on each side of the trackway (legs II to V). Chelicers are too short to leave a trace on the substrate. The telson can leave, in some cases, an axial median imprint. The prosoma only leaves a trace if the animal is ploughing. The studied trackway does not exhibit any telson or prosoma imprint. It is only composed of the imprints of legs III to VI. We observed that the legs VI left relatively well-preserved imprints compared to others: it confirms that the pushers play an important role in the locomotion of limulids. Conversely, the tracks of the other appendages are shorter and more superficial, some legs III imprints are even missing; this is the proof they have a minor role in the limulid locomotion. However, the visible imprints left by legs III show a bifid part (Figs. 2–4); it probably means that when these appendages did contact the substrate, their entire extremity was used. All the tracks we have described as "oblique" show a low angle (on average 13.75°, Table 1) toward the central axis of the trackway. The regularity of the position of the tracks is consistent with a regular gait of the limulid. The principal stride (177.7 mm on average, Table 1) combined with the linearity of the trackway reveal a high speed. We used the characterization of limulid trackways defined by Gaillard (2011) to reconstruct the locomotory behavior of the Canjuers specimen. All the characteristics we have pointed out above, from the tracks to the set size, including the angle of the tracks regarding the median axis, demonstrate that the limulid was walking.

6.3. Size of the trackmaker

To infer the size of the limulid that made the tracks, we used a model peculiar to limulids (Malz, 1964) based on the following formula: $I = W \times 1.5$, where I is the width of the prosoma of the trackmaker and W the external width of the trackway. In the Canjuers specimen, W equals 175 mm (Table 1), giving a width of the prosoma of 262 mm. In extant limulid species, the total length is 2 to 2.2 times the width of the prosoma (Sekiguri, 1988). It suggests a length ranging from 525 to 577 mm for the Canjuers specimen.

The limulid from Canjuers is slightly larger than the largest extant species, *Tachypleus gigas* Müller 1785, which has a 250 mm wide prosoma (Vijayakumar et al., 2000). Among extinct species, only the limulids from Solnhofen and Cerin seem to be larger (Frickhinger, 1994; Gaillard, 2011). Indeed, most of the fossil limulids are small, many only a few centimeters long (Babcock et al., 2000; Lomax and Racay, 2012; Pickett, 1984). The most imposing limulid trackway known is from Solnhofen and was described by Frickhinger (1994): it is 330 mm wide but remains an exception, because few invertebrate ichnofossils reach such a spectacular size.

6.4. Taxonomy

The use of locomotor behavior is a recurrent problem in invertebrate ichnotaxonomy. Bromley (2004) stressed that, within fossil traces, "the same individual or species can produce different structures corresponding to different behavior patterns". On the one hand, some authors hold that the only valuable ichnotaxonomic basis is morphological criteria (Bertling, 2007) and reject using variations in the behavior of the producer to synonymize ichnotaxa. On the other hand, other authors acknowledge that limulid trackways are among the most variable, depending on how they behave (Gaillard, 2011; Seilacher, 2007). Thus, several limulid ichnospecies have been described based on this criterion (for instance the different ichnospecies attributed to *Kouphichnium* such as *Kouphichnium variabilis* Linck, 1949 and *Kouphichnium rossendalensis* Hardy, 1970). Here we describe traces rather close to those studied by Gaillard (2011) and we decided to consider behavior as valuable for taxonomic assessment.

The limulid ichnogenus *Kouphichnium* is quite common during the Late Jurassic. It was described by Nopsca (1923) and is based on the type ichnospecies *Ichnites lithographicus* Oppel, 1862 from Solnhofen. In 1964, Malz coined the specific name *Kouphichnium walchi* to the tracks of a dying limulid (mortichnia), also from Solnhofen. Later, Hasiotis (2004) introduced resting and locomotion traces from the Morrison Formation, which he referred to *Kouphichnium isp*. Finally, *K. lithographicum* tracks were found in the Nusplingen lithographic limestone (Schweigert and Dietl, 2002) and, more recently, Gaillard (2011) assigned this ichnospecies to a straight trackway from Cerin.

The Canjuers trackway cannot be referred to *K. walchi* (Malz, 1964) because the latter is a mortichnia, which really differs from the tracks described above. However, our trackway is quite similar to the one described in Cerin (Gaillard, 2011) and can be referred to the ichnospecies *K. lithographicum.* The only difference between both trackways is the size of the imprints and the width of the trackway, which could be the result of a different ontogenetic stage of the animal.

Because a single taxon can produce different kinds of trackways, the identification of a trackmaker is never obvious. However, two species are known from the Upper Jurassic fossil record. The first one, *Crenatolimulus* sp. n., is from Owadów-Brzezinki in Poland (Kin et al., 2013). The second one, *Mesolimulus walchii* (Desmarest, 1817), was found at the end of a mortichnia in Solnhofen and was also reported in Cerin (Gall et al., 1996). Both *Kouphichnium* and *M. walchii* are recorded in Solnhofen and Cerin. If *M. walchii* is responsible for the mortichnia *K. walchi*, we can assume that the same species is very likely the trackmaker of a part or the entire ichnogenus *Kouphichnium*, at least in the Upper Jurassic of western Europe. We tentatively refer the trackmaker of Canjuers to *M. walchii*, although we are aware that *K. walchi*, being part of a parataxonomy, is related to body fossils as well as tracks. We also acknowledge that the trackmaker could also be another species, not described yet. Indeed, extant limulid species are geographically isolated but have the same ecology, morphology (Shuster, 1982) and serology (Shuster, 1962). This implies that they could have coexisted during the Late Jurassic. The discovery of limulid specimens in Canjuers would reset our hypothesis.

6.5. Paleoecological and paleoenvironmental considerations

Extant limulids are mostly marine, live close to the shore (Dunlop, 2012) and are euryhaline (Barthel, 1974). However, some fossil limulids from the Paleozoic and Triassic are considered freshwater because they were found in continental freshwater deposits (Babcock et al., 2000; Häntzschel, 1975; Pickett, 1984). It was established that during the Late Jurassic Canjuers was a lagoon sometimes connected to the open sea via channels cutting across reef barriers and reef patches (Atrops, 1994; Charbonnier et al., submitted for publication). This connection was not stable, so the site had to withstand temperature and salinity variations. Hence, limulids living in the Canjuers lagoonal environment were marine, just like the extant ones. The size of the trackmaker is consistent with this conclusion: the Canjuers limulid is indeed very large while freshwater species are said to be smaller than marine ones (Babcock et al., 2000).

Extant limulids mainly feed on bivalves and polychaete worms (Botton et al., 2003), two organisms found in the lithographic limestones of Canjuers (Charbonnier et al., unpublished data), worms being the tracemakers of *Tubularina lithographica* (Gaillard et al., 1994). Considering this point of view, Late Jurassic limulids could have fed in the lagoon. Nowadays, marine turtles (like *Caretta caretta* Linnaeus, 1758) are one of the principal predators of limulids (Keinath, 2003). Plesiochelydae have been found in the Canjuers deposit (de Broin, 1994). Their presence could have exerted a pressure on limulids, turning the lagoon into a hostile environment for the latter. The discovery of organisms from various habitats in Canjuers (Charbonnier et al., submitted for publication; Fabre et al., 1982) allows us to hypothesize that limulids were maybe transient in the lagoon. Storms could be at the origin of an accidental, probably temporary, introduction of many animals in the lagoon (Bourseau et al., 1991; Roman, 1994; Wellnhofer, 2009). Another possibility is that limulids came into the Canjuers lagoon in order to lay their eggs on nearby beaches as extant species do. Those two hypotheses would explain why we study here the only one trackway known from Canjuers and why no body fossils of this group have yet been found there.

7. Conclusion

The Canjuers trackway was made by a limulid about 26 cm wide and 55 cm long, which is quite an imposing size compared to extant species, but not so far from the slightly older “giant” limulid of Cerin (Gaillard, 2011). The trackway is straight and exhibits well-marked imprints of walking legs VI, intermediate and more superficial imprints of legs III to V and the absence of prosoma or telson imprints. The rather high repeat distance and the shape of the tracks characterize a walking behavior. This differentiates the trackway from other behaviors known: a crawling behavior where the telson leaves a trail (Kolb, 1963), dying where telson and prosoma tracks are observed (Barthel et al., 1990) and ploughing behavior where the prosoma leaves deep prints (Hardy, 1970). The Canjuers trackway was eventually associated with the ichnogenus *K. lithographicum* already reported from Nusplingen (Schweigert and Dietl, 2002) and Cerin (Gaillard, 2011). So far, it is likely that the species *M. walchii* was the trackmaker. The tracks could illustrate an important connection between the Canjuers lagoon and the Tethys, or a spawning behavior, leading to a temporary introduction of typical marine animals in the lagoon.

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